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A Review of the Properties of Sustained and Transient Retinal Ganglion Cells

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Introduction

During the past several years considerable evidence has been presented that on-center and off-center retinal ganglion cells ot cats can each be subdivided into two types. Although various names have been applied to these two types of units, we shall refer to them as the *sustained* and *transient* types[1] because of their response character. The present paper represents a review of single cell research which argues for these two classes of retinal ganglion cells. Speculations concerning receptive field organization, anatomical basis and functional significance of sustained and transient cells are also presented.

In the first study of the response properties of cat retinal ganglion cells, KUFFLER[2] showed that the receptive field (RF) is spatially organized into two concentrically-arranged, antagonistic regions. The units were classified into two groups according to the response to illumination of the center of the receptive field. Those units which responded with an increase in neural activity were called on-center cells, and those which responded with a decrease in firing were called off-center cells.

Quantitative studies of retinal ganglion cell receptive field organization by RODIECK and STONE[3] gave a more detailed description of the time course of the responses to stimuli at various locations in the receptive field. A spot flashed in the center of the receptive field of an on-center cell causes a discharge at light on and a silent period at light off before the cell returns to its spontaneous level of firing. The on portion of the response was found to have two components: an early, high frequency 'transient' component, which lasts about 75 msec, followed by a lower frequency 'steady state' component. Flashing a spot in the periphery of the receptive field of an on-center cell causes a decrease in neural activity at light on. The latency of this inhibitory response is (on the average) about 50 msec longer than the latency of the on response. At light off, there is a high frequency discharge but, again the latency is long.

According to RODIECK and STONE[3], the activity of retinal ganglion cells is controlled by two spatially overlapping processes. The term 'center mechanism' was used to refer to the process which predominates in the center of the receptive field. For an on-center cell this process causes the cell to increase its firing rate when the light is on and decrease its firing rate when the light is terminated. The 'surround mechanism' is the process which predominates in the receptive field surround. This process causes an on-center cell to decrease its firing rate when the stimulus is turned on and increase it when the stimulus is terminated. The effects of the center and surround mechanism are reversed for off-center cells. Both the center and surround mechanisms were described by Gaussian curves with peaks in the receptive field center; the Gaussian curve for the center mechanism had a higher mean and lower standard deviation than the Gaussian curve for the surround mechanism. Experimental evidence indicated that the surround mechanism extended through the receptive field center, but the center mechanism did not extend very far into the periphery of the receptive field. The latency of the response of the surround mechanism was described as being about 50 msec longer than the latency of the center mechanism.

It is of interest to this paper that KUFFLER[2] examined in some detail the sustained (or maintained) and transient nature (no steady state component) of the response of the ganglion cells. He reported that a unit which responded in a sustained manner when the center of the receptive field was stimulated, would respond in a transient way if the stimulus was displaced into the surround or made large enoungh to overlap the surround region of the receptive field. From these observations KUFFLER suggested that a unit which has a strong contribution from the center mechanism and a weak contribution from the surround mechanism

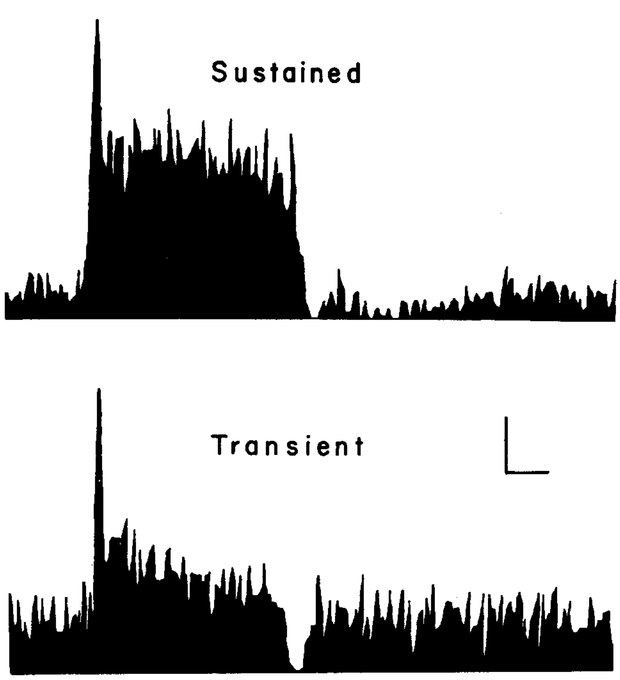
[1] B. G. CLELAND, M. W. DUBIN and W. R. LEVICK, J. Physiol., Lond. *217*, 473 (1971).
[2] S. W. KUFFLER, Cold Spring Harbor Symp. *21*, 281 (1952).
[3] R. W. RODIECK and J. STONE, J. Neurophysiol. *28*, 833 (1965).

will give a sustained response. As the strength of the surround contribution is increased, the sustained part of the response will diminish.

It is thus clear that the sustained and transient nature of the response of cat retinal ganglion cells has been known for a long time. However, it is only relatively recently that different functional roles have been attributed to each type because of their contrasting physiological properties. In this paper we wish to bring together observations made in several laboratories to determine whether these observations are consistent with the proposed functions.

Separation of units into sustained and transient types

Two relatively simple tests can be used to segregate ganglion cells into sustained and transient types. The first test is the response to a standing contrast. The stimulus for this test is a small spot of light (0.3–0.5°), stimulus intensity 1.0 to 1.5 log units above threshold, and centered on the most sensitive portion of the receptive field of an on center cell (a dark spot would be used for an off center cell). A comparison of the mean firing rate with just the background illumination, i.e., the spontaneous firing rate, with the mean firing rate after the spot of light has been turned on for about 30 sec, will separate the two types of units. The results from 45 on center units are shown in Table I. In those units which are classified as sustained (by this



Average response histogram of a sustained unit and a transient unit. Recordings from single optic tract fibres of the cat. Stimulus = 0.3 degrees, 24.0 cd/m^2. Background = 0.3 cd/m^2. 15 responses were averaged with a bin width of 10 msec. Calibration = 50 spikes/sec, 0.2 sec.

and other tests), the mean firing rate is approximately 100% higher with the stimulus. For the transient units, there is no significant difference between the spontaneous firing rate and the firing rate with the stimulus.

A second test is an extension of the first and consists of the response to a step input of light (Figure). The stimulus is identical to the above. When the spot of light is turned on, the sustained unit responds with a high frequency burst of spikes which decays to a maintained firing level which is significantly higher than maintained firing level which is significantly higher than the spontaneous level (approximately 100% higher). The firing level remains at this elevated level for the duration of the stimulus. The transient units respond to the same stimulus with a high frequency burst of spikes but the firing level decays rapidly to the spontaneous level. Because the time constant of decay is variable, the duration of the stimulus should be at least 1.0 sec in order to differentiate the two types of units.

At light off, the response of the sustained and transient units also differ. Both types of units respond to light off with strong inhibition but the duration of inhibition is longer in the sustained (200–500 msec) than for the transient (10–50 msec).

Other response properties of sustained and transient units

Units classified into sustained and transient types by the two tests will show the following differential response properties. It should be noted that some investigators suggest that more of the following tests should be conducted in order to segregate the units.

1. *Spatial summation in receptive field.* ENROTH-CUGELL and ROBSON[4] reported that if a dark edge is placed so that the edge runs through the center of the receptive field and the pattern is turned on and off, or if the contrast is reversed, two types of units will be found. In the units designated as the X-type, no net change in the firing rate occurs, but with the Y-type, changes in the firing rate occur whenever the pattern is changed. The X-type was shown subsequently by CLELAND, DUBIN and LEVICK[1] to be the sustained type while the Y-type corresponded to the transient units. Because the sustained units showed no net change in firing rate, ENROTH-CUGELL and ROBSON concluded that there was linear summation of signals arriving at the ganglion cells. For the transient units, the summation of signals was non-linear.

CLELAND, LEVICK and SANDERSON[5] demonstrated that both the sustained and transient units obey

[4] C. ENROTH-CUGELL and J. G. ROBSON, J. Physiol., Lond. *187*, 517 (1966).

[5] B. G. CLELAND, W. R. LEVICK and K. J. SANDERSON, J. Physiol., Lond. *228*, 649, (1973).

Ricco's Law with small targets. As the target diameter is increased, the threshold for sustained units shows a region where the threshold does not change but with larger targets the threshold rises significantly. For the transient units, the horizontal segment of the curve is longer and the rise in threshold is slight. This area-threshold method has been used to determine the 'equivalent size' of the receptive field center.

2. *Response to moving target. Sinusoidal grating.* If a grating of low spatial frequency (1 cycle/deg or less) is moved slowly (2 to 3 deg/sec) across the receptive field of retinal ganglion cells, both types of units will respond to each change in contrast with the appropriate modulation of the firing rate[4]. The mean pulse density histograms of the transient cells tend to be more distorted than those of the sustained cells. As the spatial frequency of the gratings is increased (with appropriate reduction in the velocity of the target to nullify temporal effects), the differences between the two types of units become more apparent. For the sustained units, the firing rate is modulated around a mean level which is maintained even at spatial frequencies too high to be resolved by the unit. This mean firing level is significantly higher than the spontaneous level and corresponds to the firing rate which would be elicited by the mean luminance of the target. For transient units, on the other hand, the firing level is modulated about a mean level which is dependent upon the spatial frequency of the target grating. With spatial frequencies too high to be resolved, the transient unit responds only to the initial movement of the target and the firing rate drops to the spontaneous level.

Moving edges. Sustained and transient units respond differently to edges moved through the receptive field[6]. For the sustained type, movement of a vertical slit of light, through the receptive field elicits first a decrease in the firing rate which is then followed by a high frequency burst of spikes. The decrease in firing, 'entry-inhibition', results from the inhibitory surround while the increase in firing results from the excitation from the center of the RF. When the target leaves the receptive field center the firing rate drops to zero and recovers slowly to the spontaneous level. For the transient units, there is no evidence of entry-inhibition with the same target, and the inhibition when the target leaves the receptive field center is of shorter duration. If the velocity of the target is increased, the transient units will respond to higher velocities.

CLELAND, DUBIN and LEVICK[1] also find differences in responses to variations in the size and speed of moving edges. Transient cells are more sensitive to large, rapidly-moving targets while sustained cells prefer small slowly-moving targets.

3. *Responses to stimuli restricted to the receptive field center.* In addition to the differences in the responses to a maintained stimulus, transient and sustained cells can be distinguished in several other ways by their responses to stimuli restricted to the receptive field center.

The sensitivity gradient (distance from receptive field center plotted against log sensitivity) of sustained cells is 10 times steeper than those for transient cells[7]. Also the response latency of sustained cells to a small spot in the receptive center is shorter than the latency of transient cells[7].

Transient and sustained cells also differ in their responses to brief central stimuli; sustained cells give longer impulse trains than transient cells. The spontaneous firing level of sustained cells is, on the average, higher than transient cells[5] (see also Table I).

Table I. Standing contrast

	Spontaneous activity	Stimulus on	n
Sustained	37 ± 3	66 ± 3	28
Transient	30 ± 2	32 ± 3	17

Stimulus, 0.5°, 34.3 cd/m². Background = 0.3 cd/m².

Just as the sustained and transient units respond differently to targets modulated in the spatial domain, they also respond differently to temporally modulated targets. For sustained units, increasing the flash rate of a target centered on the receptive field does not alter the mean firing rate[8]. For the transient units, the mean firing rate is increased. In addition to this difference, sustained units are able to follow higher flash rate than the transient cells[8].

4. *Differences in the inhibitory surround.* Further differences between the sustained and transient units are found if the inhibitory surround is examined[9,10]. If annuli with large inside diameters are used to stimulate the periphery of the receptive field, two types of response patterns are elicited. The sustained units repond to the annulus with a response which is characteristic of the surround mechanism, i.e., inhibition at light on and excitation at light off. The transient units respond to a large annulus with a response which is characteristic of both the center and surround, i.e., excitation followed by inhibition at

[6] D. I. HAMASAKI, J. ZENGEL and R. CAMPBELL, Experientia *29*, 808 (1973).
[7] H. IKEDA and M. J. WRIGHT, J. Physiol., Lond. *227*, 769 (1972).
[8] Y. FUKADA and N. SAITO, Vision Res. *11*, 227 (1971).
[9] R. W. WINTERS, T. L. HICKEY and J. G. POLLACK, Vision Res. *13*, 1487 (1973).
[10] T. L. HICKEY, R. W. WINTERS and J. G. POLLACK, Vision Res. *13*, 1511 (1973).

light on and inhibition followed by excitation at light off[9]. Although this mixed type of response can be elicited from the sustained units with small annuli, the mixed response is elicited from the transient units no matter how large the inside diameter of the annulus is made. These observations might suggest that the spatial arrangement of the center and surround mechanisms is different in the sustained and transient units[10]. This will be discussed below.

Studies with variable size annuli demonstrated that the center mechanism was relatively weak in the periphery of sustained units but relatively strong in the transient units[11]. It is possible to demonstrate linear summation of signals from the receptive field center and receptive field surround in sustained cells but not in transient cells[10,12].

Sustained and transient units also respond differently to local adaptation[5]. Adaptation of a small region of the periphery of transient units has very little effect on neighboring areas. For the sustained units the results are more variable; in some cells local adaptation affects all areas of the receptive field while other units behave as do the transient units with local changes.

ENROTH-CUGELL and PINTO[12] showed that on-center retinal ganglion cells can be divided into two groups on the basis of responses to peripheral stimuli. Pure surround responses can be obtained in about 50% of the cells even though a centrally located steady spot, which was used to desensitize the center mechanism, was presented in conjunction with a flashing peripheral annulus. ENROTH-CUGEL and PINTO[12] referred to cells that gave pure surround responses as 'surround revealing' cells. They probably correspond to the sustained cells described by other investigators. The surround response elicited by their units remained invariant in shape over a range as great as 1.38 log units above threshold intensity. Surround revealing cells showed linear summation of responses elicited by central and peripheral stimuli. The peripheral responses of the remaining 50% of the units, their 'surround concealing' cells, always showed contamination from the central response mechanism and it was not possible to demonstrate linear summation of central and peripheral signals for these units. These units probably correspond to transient cells.

IKEDA and WRIGHT[13,14] find that the classical inhibitory surround is encircled by a disinhibitory zone. Stimulation of this zone with a light spot produces an increase in firing during the on period for on-center cells and at the termination of the stimulus for off-center cells. The dynamic interactions between the disinhibitory zone and receptive field center were studied by two spot experiments. A spot presented in the disinhibitory zone caused response enhancement when presented in phase with a central spot and caused inhibition of the central reponse when presented 180° out of phase with the central spot. IKEDA and WRIGHT[14] find that the disinhibitory surround is strong and narrow in sustained cells but weak and broad for transient cells.

5. *Differential responses during eye movement.* When recordings are made from the optic tract fibres of unanesthetized cats with normal eye movements, three types of response patterns were found by NODA and ADEY (personal communication). The S-type which corresponds to the sustained units does not respond with a burst of spikes during a saccadic eye movement or a rapid movement of a grating across the receptive field. The T-units or transient units give a burst of spikes during the rapid movement (up to 1000°/sec) of the image over the retina. The M-type had properties of both the sustained and transient types. NODA and ADEY conclude that the T-type transmitted information about image movement while the sustained type signaled local differences in illumination.

6. *Size of receptive field center and surround.* Transient and sustained cells also differ in the size of their receptive field center and surrounds. Transient cells have larger receptive field centers[15,16] and larger receptive field surrounds[5] than sustained cells. MCILWAIN[17] showed that the central response of some retinal ganglion cells can be modulated by targets as far as 90° from the receptive field center. This phenomenon is referred to as the 'peripheral effect'. Both CLELAND, DUBIN and LEVICK[1] and IKEDA and WRIGHT[18] has shown that transient cells show the peripheral effect while sustained cells do not.

Higher centers. Units in the lgn (lateral geniculate nucleus) can be classified into sustained and transient types by the same tests[1,19]. By simultaneous recordings from the retina and lgn, CLELAND, DUBIN and LEVICK[1] were able to show that sustained lgn cells received input from sustained retinal ganglion cells, and similarly for transient lgn units. The conduction velocity of the sustained lgn units is slower than that for the transient lgn units. HOFFMANN and STONE[20] reported that the simple and hypercomplex cells receive input from axons with low conduction velocity (sustained cells) while the complex cells receive input from axons with fast conduction velocity (transient cells). HOFFMANN and STONE thus concluded that the sustained/transient character is carried through to the cortical level.

[11] R. W. WINTERS, T. L. HICKEY and D. H. SKAER, Vision Res. *13*, 1499 (1973).
[12] C. ENROTH-CUGELL and L. H. PINTO, J. Physiol., Lond. *220*, 403 (1972).
[13] H. IKEDA and M. J. WRIGHT, J. Physiol., Lond. *224*, 26 (1972).
[14] H. IKEDA and M. J. WRIGHT, J. Physiol., Lond. *226*, 511 (1972).
[15] H. IKEDA and M. J. WRIGHT, Vision Res. *12*, 1465 (1972).
[16] Y. FUKADA, Vision Res. *11*, 209 (1971).
[17] J. T. MCILWAIN, J. Neurophysiol. *27*, 1154 (1964).
[18] H. IKEDA and M. J. WRIGHT, Vision Res. *12*, 1857 (1972).
[19] P. HAMMOND, J. Physiol., Lond. *225*, 391 (1972).
[20] K. P. HOFFMANN and J. STONE, Brain Res. *32*, 460 (1971).

From data obtained by electrical stimulation of the superior colliculus, HAYASHI, SUMITOMO and IWANA[21] concluded that the faster conducting fibres in the cat optic tract tend to project to the superior colliculus. It is assumed that these faster conducting axons are transient units, and because movement is an important stimulus parameter for collicular units, it is argued that the transient units may form the initial stages for movement detection.

Other animals. Sustained/transient classification have been reported in monkeys[22], ground squirrels[23], *Necturus*[24] and rats[25]. In monkeys, GOURAS[22] reported that the transient units (his phasic units) receive input from the green and red sensitive cone mechanisms in both the receptive field center and surround. The sustained cells (his tonic unit) received input from one type of cone mechanism in the receptive field center (either blue, green or red) and a different cone mechanism in the periphery of the receptive field.

Anatomical basis for sustained/transient classification. The question arises whether the sustained/transient classification has an anatomical correlate. Because of the differences in the size of the receptive fields, in the conduction velocities and the distribution in the retina, it is generally agreed that the sustained units correspond to the smaller retinal ganglion cells concentrated in the area centralis. However, further correlation between anatomy and physiology cannot be made at this time because of the discrepancies in the anatomical data[5].

Some evidence has been presented regarding the inputs to the sustained and transient ganglion cells. From intracellular recordings WERBLIN and DOWLING[24] have shown that sustained and transient responding ganglion cells are present in *Necturus*. Because the bipolar cells respond in a sustained manner (the depolarization or hyperpolarization is maintained for the duration of the stimulus) and the amacrine cells respond in a transient way, WERBLIN and DOWLING suggest that the sustained units receive input mainly from bipolar cells while the transient cells receive input from amacrine cells.

Along this same line, WEST and DOWLING[26] have recently shown that the ganglion cells of the ground squirrel can be segregated into two types according to their synaptic input. In one group, the input was almost exclusively from the amacrine cells while in the other group, the input was from both bipolar and amacrine cells. Because MICHAEL[23] had reported earlier that sustained and transient types of ganglion cells were present in the ground squirrel, WEST and DOWLING suggested that the sustained cells correspond with the cells which received mixed inputs while the transient cells corresponded to the cells which receive mainly amacrine input.

Receptive field organization of sustained and transient units. Can RODIECK and STONE's model[3] of the receptive field account for the differences in the spatial and temporal properties of the sustained and transient units? In their model, the strength of the center and surround mechanisms is expressed by two Gaussian curves with the center mechanism having a higher mean and a smaller standard deviation. There exists, in this model, a region in the peripheral portion of the receptive field where the surround mechanism predominates. This spatial arrangement of the center and surround mechanisms can account for the presence of entry-inhibition in the sustained units and also accounts for the 'pure' response elicited by a large annulus. However, this spatial arrangement cannot account for the response of transient units to the same stimuli.

For transient cells HICKEY, WINTERS and POLLACK[10] proposed that the fields of the center and surround mechanisms were coextensive. Thus a large annulus placed in the periphery will always stimulate both mechanisms and elicit a mixed response. This spatial arrangement can also account for the absence of entry inhibition in transient units when a moving stimulus is used.

These differences in the spatial arrangement of the center and surround mechanism, however, are not sufficient to account for other observations. For example, ENROTH-CUGELL and ROBSON's[4] observations with alternating contrast patterns symmetrically placed on the receptive field cannot be explained by this spatial arrangement of the RF. In order to explain the on-off responses elicited by stimulating the intermediate regions of the receptive fields, RODIECK and STONE had earlier suggested that the surround mechanism had a longer latency than the center mechanism. This difference in latency can then explain the changes in the firing rate when a contrast pattern is alternated, as noted for the transient units. However, the question then arises why sustained units show no net change. Is it necessary to remove this latency difference for the sustained units? In support of this, HICKEY, WINTERS and POLLACK[10] have shown that with the sustained units, it is possible for a large annulus to suppress even the initial high frequency burst of spikes for sustained cells. This observation indicates that the latency of the peripheral response is as short as the central response.

[21] Y. HAYASHI, I. SUMITOMO and K. IWAMA, Jap. J. Physiol. *17*, 638 (1967).
[22] P. GOURAS, J. Physiol., Lond. *199*, 533 (1968).
[23] C. R. MICHAEL, J. Neurophysiol. *31*, 249 (1968).
[24] F. S. WERBLIN and J. E. DOWLING, J. Neurophysiol. *32*, 339 (1969).
[25] B. G. CLELAND and W. R. LEVICK, Invest. Ophthal. *11*, 285 (comments) (1972).
[26] R. W. WEST and J. E. DOWLING, Science *178*, 510 (1972).

Functional significance of transient and sustained cells. Both CLELAND, DUBIN and LEVICK[1] and FUKADA and SAITO[8,16] speculate that transient and sustained cells play different roles in the processing of visual information. Sustained cells, it is argued, are most sensitive to local differences in luminance and thus are best suited for coding spatial characteristics of the stimulus. Transient cells, on the other hand, are thought to be concerned with the analysis of temporal characteristics of the stimulus. Transient cells show greater responsiveness to either large objects moving at some distance from the receptive field center (i.e., the peripheral effect) or to any object which moves suddenly within their receptive fields. CLELAND, DUBIN and LEVICK[1] also point out that a substantial portion of the fast conducting axons (transient cells) project to the superior colliculus[21] and may provide the basis for direction selective units located here. IKEDA and WRIGHT[14] suggest that information from transient cells is used to organize the fixation reflex, i.e., centering an object of attention at the area centralis.

Two populations or one? It will be noticed that most of the studies dealing with transient and sustained cells were published after 1970. A question that naturally arises is why most of the studies prior to 1970 did not mention the existence of these two subtypes, much less delineate response difference. Table II shows 14 response differences between transient and sustained cells which have been reported from 6 different laboratories. It seems likely that earlier investigators would have encountered cells which differed on some of these dimensions.

The omission of these investigators may not represent an oversight but instead a legitimate difference in the way they may interpret variability in the data. They would argue that transient and sustained cells are the extremes of a normal distribution of cells in which a large portion of the cells show responses characteristic of both types of units. Those espousing that three are two types of cells would argue that they have sampled from two, perhaps overlapping, populations which are normally distributed. Units which show characteristics of both types of units would be cells sampled from the region in which the two populations overlap and thus these cells would be expected to be in the minority. It seems that what we have is a question for inferential statistics. If a microelectrode can be considered as a random sampler the question could be resolved with relative ease and with some statement about the probability of the decision being in error. However, since the microelectrode is not a random sampler the question must be answered by other means.

It might be argued that the differences between transient and sustained cells are the result of random variations in the relative strength and, or, the spatial distribution of the surround mechanism. Since the characteristics of the surround mechanism are modified by changes in adaptation level it might be expected that the differences between transient and sustained cells would only hold within a very narrow range of adaptation levels. A similar argument would apply if the response differences were the result of random variations in the relative amount of input from cones and rods. CLELAND, LEVICK and SANDERSON[5] contend that adaptation level is not crucial and give evidence that, at least with some of their tests, the distinctions between transient and sustained cells hold over a wide

Table II.

1. Stationary spot in the receptive field center	Transient cells give phasic response and sustained cells give tonic response[1,5,8,9,10,11,13–16,19]
2. Moving fine grating	Sustained cells give modulated response to moving grating pattern. High spatial frequencies produce unmodulated increase in mean discharge rate for transient cells[1]
3. Size and speed of moving targets	Transient cells prefer large rapidly moving targets while sustained cells prefer small, slowly moving targets[1]
4. Conduction velocity	Transient cells have higher conduction velocity than sustained cells[1,16]
5. Receptive field center size	Transient cells have larger receptive field centers than sustained cells[15,16]
6. Organization of receptive field disinhibitory surround	Disinhibitory surround is strong and narrow in sustained cells and weak and broad in transient cells[14]
7. Retinal location of receptive fields	Receptive fields of sustained cells tend to be more common near the area centralis while transient cell receptive fields are more common in the periphery of the retina[5,15,16]
8. Defocusing retinal image	Has greater effect on the response of sustained cells than transient cells[15]
9. Responses to distant peripheral stimuli i.e., stimuli outside of the apparent receptive field surround	Transient cells show the 'peripheral effect' but sustained cells do not[1,18]
10. Responses to stimuli in the receptive field periphery	Sustained cells show 'pure' surround responses but transient cells do not[11,12]
11. Center-surround interaction	Sustained cells show linear summation of central and peripheral signals but transient cells do not[11,12]
12. Intermittent photic stimuli	Sustained cells show horizontal frequency-response curve and transient cells show inverted U function[16]
13. Sensitivity gradients	Steeper for sustained cells than for transient cells[7]
14. Latency to small central spot	Shorter for sustained cells than for transient cells[7]

range of backgrounds ($3.4 \times 10-5$ cd/m^2 to 440 cd/m^2). Other results suggest that the range of backgrounds may be more limited. For example, when WINTERS, POLLACK and HICKLEY[27] examined the responses of transient and sustained cells to a standing contrast they found response differences to be minimal at a low -1.76 log cd/m^2 and high (1.23 log cd/m^2) adaptation level. Response differences were clearer at a medium (0.23 cd/m^2) adaptation level.

The most convincing argument for two types of cells would come from experiments which unequivocally demonstrate that the neural pathways through the retina are different for transient and sustained cells. This would require experiments in which the microscopic anatomy of the retina is correlated with intracellular recordings from the various types of cells in the retina, as described earlier for the *Necturus*.

Résumé

De récentes recherches sur les cellules ganglionnaires du chat ont montré deux types d'unités se distinguant par leur réponse à l'éclairement. Le type X répond d'une façon soutenue, le type Y d'une façon transitoire. Ces unités sont décrites et mises en correlation avec leurs particularités anatomiques et les propriétés fonctionnelles qu'on leur attribue. Les implications de cette classification à l'égard de l'arrangement spatial et temporelle des champs récepteurs sont discutés.

[27] R. W. WINTERS, J. G. POLLACK and T. L. HICKEY, Brain Res. *47*, 501 (1972).

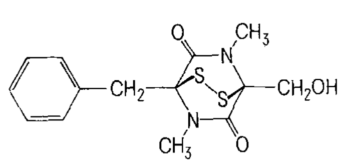
SPECIALIA

Total Synthesis of (±) Hyalodendrin

A recent addition to the group of biologically active epidithiodioxopiperazine fungal metabolites[1] is hyalodendrin (I) produced by a *Hyalodendron* sp.[2,3]. Hyalodendrin showed in vitro antimicrobial activity against a broad spectrum of fungi associated with disease in plants and trees, and decay in wood products[2]. Several microorganisms pathogenic to humans were also tested, and found to be sensitive to the antibiotic[2].

In a series of papers published recently, KISHI et al.[4–6] have developed an elegant and versatile strategy for the synthesis of members of this group of compounds, from a piperazine-dione precursor containing an ingeniously protected potential disulfide bridge. The utility of this approach has been amply demonstrated by its application in the synthesis of dehydrogliotoxin[5] and sporidesmin A[6].

We report here the synthesis of racemic hyalodendrin by a short route utilizing the KISHI approach[4].



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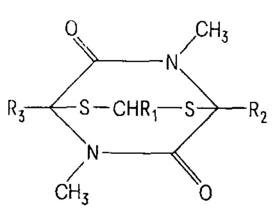

II $R_1 = p-CH_3OC_6H_4$
$R_2 = R_3 = H$

III $R_1 = p-CH_3OC_6H_4$
$R_2 = CH_2OCH_3$
$R_3 = H$

IV $R_1 = p-CH_3OC_6H_4$
$R_2 = CH_2OCH_3$
$R_3 = CH_2C_6H_5$

The monocarbanion, generated from thioacetal II in tetrahydrofuran at $-78°$ by treatment with *n*-butyl lithium (~ 1 equiv.), reacted as described with chloromethyl methyl ether to give the crystalline alkylated product III[4] in 51% yield (76% based on consumed II). A sample, recrystallized from benzene, had mp 168–170°; mass spectrum: *m/e* 368 (M^+), 184 (base peak) ($M - CH_3O.C_6H_4.CHS_2)^+$.

Alkylation of III with benzyl bromide was effected in a similar manner, giving IV as a colorless oil in 40% yield (54% based on consumed III); mass spectrum: *m/e* 274 ($M - CH_3O.C_6H_4.CHS_2)^+$. (The mass spectrum was very similar to that of IV, prepared as a diastereomeric mixture from hyalodendrin). Racemic IV was oxidized with *m*-chloroperbenzoic acid in methylene chloride at 0° to give a sulfoxide[4] (72% crystalline product, m.p. 135–139°, after preparative layer chromatography). Transformation of the latter to hyalodendrin was best effected in two steps. Thus, the sulfoxide in methylene chloride was treated with a 0.1 *N* solution of perchloric acid in tetrahydrofuran (2 equiv.) at ca. 22° for 24 h. Preparative layer chromatography of the product afforded

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