
REVIEW ARTICLE

Variability in the firing of retinal ganglion cells of goldfish: A review

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Abstract

The isolated retina of the goldfish has proven a valuable resource for studying the variability of firing of retinal ganglion cells. Three major areas of study are considered here: the variability of maintained discharges, the correlated firing of neighboring ganglion cells, and the variability of responses to light. The sources of variability, its relationship to retinal processing, and its possible functional role in perception are examined through these three aspects of variability. The results are related to similar studies in mammals (mainly cats). This retrospective is biased toward my studies over 30 years.

Keywords: Variability, Goldfish, Ganglion cell, Correlation

Introduction

The goldfish has a long and venerable history in the study of retinal physiology. In its gross organization and properties, the goldfish retina is a typical vertebrate retina. It sports the same basic cell types in the same layered organization as is found in the mammalian retina. Its ganglion cell receptive fields show clear spatial antagonism, comparable to that observed in cat (Kuffler, 1953). Goldfish ganglion cells are found in at least three varieties (each with ON-center and OFF-center sub-types), comparable to the X-, Y-, and W-cells of cat (Enroth-Cugell & Robson, 1966; Stone & Hoffmann, 1972; Levine & Shefner, 1979; Bilotta & Abramov, 1989). Features first described in goldfish, such as interplexiform cells (Dowling, 1979) and sublamination of the inner plexiform layer (Famiglietti & Kolb, 1976), have subsequently been found in mammals. Despite some differences, including a more complex inner plexiform layer than in primates (Dubin, 1970), the goldfish retina has proven a successful model system.

Goldfish retina was one of the first to be studied extensively because of several advantages it offered electrophysiologists in the days before advanced electronics and other technical improvements. In particular, the goldfish ganglion cell layer is relatively sparse, allowing one to record from the vicinity of a single cell without excessive intrusion by neighboring spiking cells. Because the fish is poikilothermic, it is easy to maintain the retina *in vitro* in a controlled stimulation chamber (MacNichol & Svaetichin, 1958). This “isolated retina” preparation allows direct imaging of

stimuli upon the receptor array, easily aligned with a recording microelectrode.

The isolated retina has a number of advantages for the study of variability of retinal outputs. Being isolated from the rest of the fish, there is no centrifugal feedback from central structures. There also is no variability due to physiological factors such as circulating hormones or modulators, respiratory state, or blood pressure. The preparation is slowly dying, but this is a slow non-stationarity.

In this paper, I review several aspects of the variability of discharges of ganglion cells, with a strong emphasis on the contributions from studies of goldfish.

The variability of maintained discharge

Like those of other vertebrates, goldfish ganglion cells display a robust but variable rate of discharge in the absence of time-varying photic stimulation. Where within the retinal processing hierarchy is that variability introduced? What can variability tell us about retinal processing?

The first question was considered by Schellart and Spekreijse (1973), who measured the amplitude spectrum of ganglion cell impulse trains. They compared maintained discharges against responses to lights that had their radiance modulated in time as a random process with a Gaussian amplitude distribution. Because the maintained discharges did not show the same frequency characteristics as the responses, they concluded the variability must be injected late in the retinal processing hierarchy. From various arguments involving the lack of effect of steady adaptation on the amplitude characteristics, they concluded that the variability is likely a feature of the spike generating mechanism itself.

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The statistics of the maintained discharge under similar experimental manipulations provided results consistent with those of Schellart and Spekrijse. Steady adapting lights had minimal or inconsistent effects on the normalized autocovariance (an approximation to the autocorrelation based on discrete events). Changes associated with alterations of mean rate could be attributed to the altered shape of the interval distribution. Similarly, the serial correlogram (an autocorrelation based on the order of the intervals between impulses rather than a uniform time grid) showed weak negative correlation between adjacent intervals, but was unaffected by adaptation (Levine, 1982).

A more sensitive way to reveal the long-term structure of the firing is to compare the standard deviation of rate (impulses/unit time in a sampling bin of a specific duration) with the duration of that sampling bin (Levine, 1980). Long trains of impulses in the absence of varying stimulation were subdivided into sampling bins of various lengths. Thus, a 30 s epoch would provide 30 1-s samples, 60 0.5-s samples, etc. Standard deviation of rate was plotted *versus* sample duration on double logarithmic coordinates.

In the absence of temporal structure, a line with a slope of -0.5 is expected; specifically

$$\sigma_{rate} = T^{-1/2} \sigma_{isi} \mu_{isi}^{-3/2} \quad (1)$$

where T is the sample duration, the σ represent standard deviations (of rate or intervals), and μ_{isi} is the mean interval. High-pass filtering of a random process would produce a steeper, more negative, slope. Low-pass filtering would place an upper limit on the minimum variance attainable for longer duration samples.

The observed slopes were steeper than -0.5 , at least to durations of about 2 s (at longer durations, non-stationarity led to a horizontal asymptote). This demonstrated high-pass filtering, and that pattern was essentially unchanged by adapting backgrounds. An example is shown in Fig. 1; note that the analyses of impulse trains obtained from randomly shuffling the order of the intervals in the original data are a reasonable approximation to the prediction of equation (1), shown by a solid line. Gaussian temporal modulation of the adapting light had virtually no effect upon the

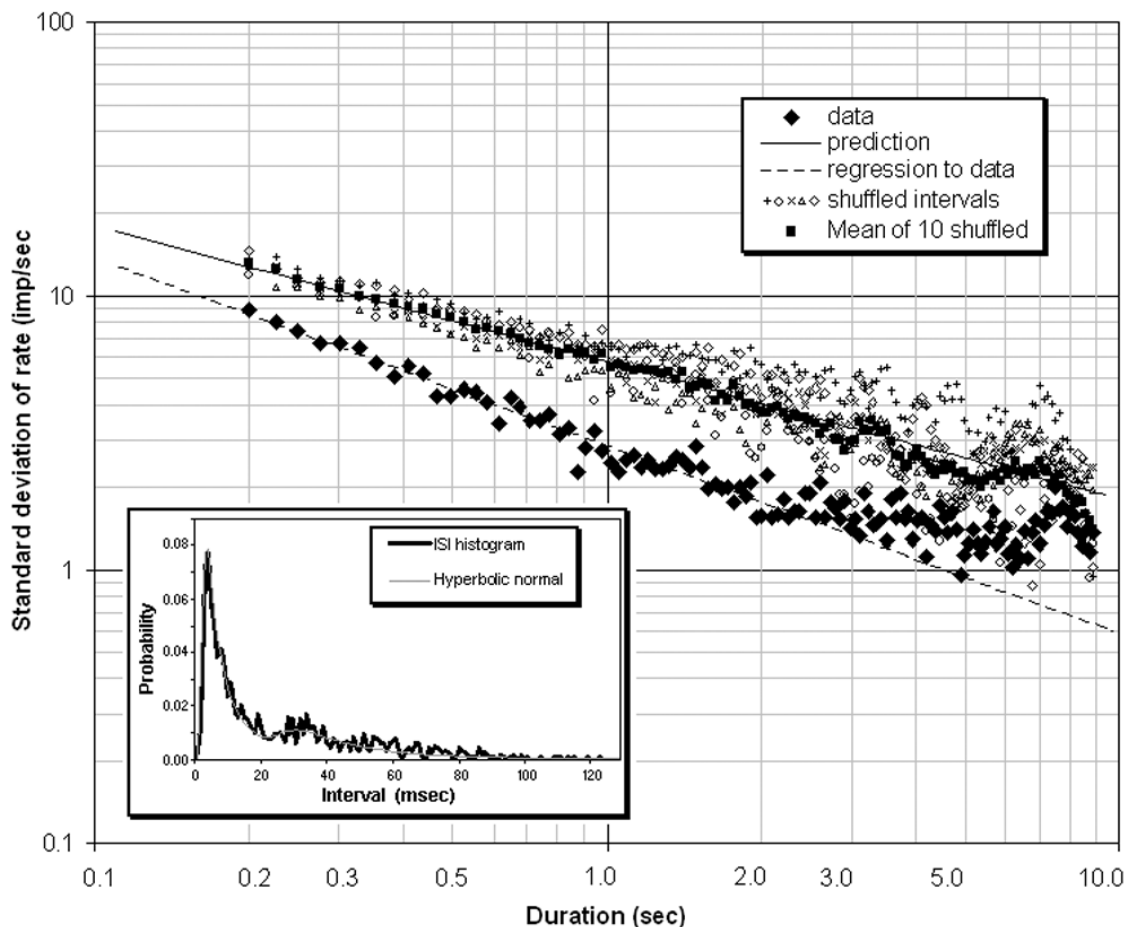


Fig. 1. Standard deviation of firing rate as a function of duration of the samples into which the impulse train is subdivided. Large solid diamonds represent 30 s of firing from a goldfish retinal ganglion cell; 1147 impulses, mean interspike interval = 26.05 ms. Logarithmic axes. The dashed line is a regression fit to durations from 200 ms to 2 s (slope = -0.686 , intercept = 2.51). The solid line is the predicted relationship assuming no autocorrelation (Eq. 1). The small open symbols and crosses represent five analyses of an impulse train generated by random shuffling of the order of intervals in the original impulse train; the small solid squares represent the average of 10 such random shuffled impulse trains. *Inset:* Interval distribution of the same impulse train (heavy line). The light gray curve is a fit with a bimodal hyperbolic normal distribution (Levine & Shefner, 1977a). The two modes are at 3.5 ms and 33 ms, with 90% of the area in the shorter mode. Red-off-center cell.

plots of standard deviation of rate. This was consistent with Schellart and Spekreijse's conclusions that the variability is injected at a late stage of the processing. The high-pass characteristic that acts upon both it and the visual signal could even be a property of the spike generating mechanism itself.

The same paradigm was applied to cat retinal ganglion cells to confirm these conclusions (Frishman & Levine, 1983). Although the results were similar, a striking difference emerged when comparing the statistics of maintained discharges to those of Gaussian modulated lights. As in fish, the responses to modulation showed a steep decline of standard deviation of rate with sampling duration. However, the maintained discharge showed only a slightly steeper than -0.5 slope on double logarithmic coordinates, and much less displacement from the line predicted for a purely random process. Frishman and Levine concluded that either the variability must be injected between stages of high-pass filtering, or that there are at least 2 sources of variability: a distal source that is high-pass filtered by essentially the same filters as the photic signals and a proximal source that is essentially unfiltered. (Note that the mean levels were high enough that Poisson photon noise was not a significant contributor to the overall variability.) By comparing serial correlograms obtained during Gaussian modulation to those from maintained discharges, they concluded that any variability must be introduced after the early transformations in the receptor outer segment. Because of the differences in the standard deviation of rate plots, they rejected the spike-generating mechanism as the sole source of high-pass filtering. That the variability in the goldfish retina seems to share most of the high-pass filtering of the visual signal could be attributable to the greater complexity of the fish inner plexiform layer, or to the relative amplitudes of the proximal and distal sources of variability.

Another goldfish study sought to reconcile these speculations. Rather than maintaining the isolated retina in a flow of moist oxygen, the retina was bathed in a flow of Ringer's solution; this allowed for the application and wash-out of chemical agents (Levine et al., 1988a). An initial observation was that superfusion lowered mean firing rates while increasing relative variability (compared to the moist oxygen retina), but attenuated the difference between the observed standard deviation of rate and that predicted by Eq. (1). This in itself seems to indicate the presence of two sources of variability, as suggested by Frishman and Levine.

The key findings of the superfusion study were obtained by altering the superfusate. Cobalt chloride (1–5 mM) was used to block calcium-dependent vesicular synaptic transmission (Weakly, 1973). This reduced the maintained discharge dramatically, almost always eliminating it. Thus, the maintained discharge is supported by a tonic synaptic input to the ganglion cells and is not an intrinsic bias of those cells, an insight that had been noted earlier (Negishi et al., 1978; Kato et al., 1983).

Firing was restored in most cells that were silenced by cobalt by the addition of carbachol (a cholinergic agonist that stimulates acetylcholine receptors and inhibits the associated cholinesterase at nicotinic synapses). Acetylcholine increases the maintained discharges of rabbit ganglion cells (Ariel & Daw, 1982). The restored firing had low variability, demonstrating that only a portion of the variability of firing is intrinsic to the ganglion cell itself. Moreover, the plots of standard deviation of rate *versus* rate were similar to those derived from the same cells in normal Ringer's solution, indicating that a portion of the high-pass characteristic is a property of the ganglion cell itself.

It was also noted that whereas the firing rate restored by carbachol was generally lower than that in normal Ringer's solu-

tion, the coefficient of variation (standard deviation of the intervals divided by the mean interval) was essentially the same. This supports a model for the generation of firing in which the variability effectively multiplies the steady bias responsible for maintained discharges (and responses), as suggested by Levine and Shefner (1977a).

To summarize the conclusions of these studies of the maintained discharges of ganglion cells, it appears that maintained discharges are driven by a tonic, synaptic input. Ganglion cell firing is apparently influenced by at least two sources of variability at different points in the processing hierarchy; at least one of these sources multiplies the tonic influence, and variability from one source passes through a high-pass filter that is possibly within the ganglion cell.

Correlations between the firing of neighboring ganglion cells

Neighboring ganglion cells often fire their action potentials in loose synchrony (or anti-synchrony). This was noted in passing for goldfish ganglion cells in the early 1970s (Schellart & Spekreijse, 1973), and later explored in detail (Arnett, 1978; Johnsen & Levine, 1983; Ginsburg et al., 1984). Similar effects were found in mammals, most notably documented in a careful series of studies of cat ganglion cells by Mastronarde, who determined the nature of the cross-correlation according to the response types of the two ganglion cells and explored the sources of cross-correlation (Mastronarde, 1983a, 1983b, 1983c).

The variability of maintained discharge was approached in the previous section with the goal of discerning the nature of variability and its relationship to retinal processing. Correlated firing of neighboring cells can also address these questions; in addition, there is the question of what role correlation might play in the encoding of visual stimuli.

Common variability shared by ganglion cells

The timing of impulses in two neighboring ganglion cells in fish is imperfectly correlated. That is, there is a tendency for one cell to produce more impulses within some relatively brief time (5 to 30 ms) of each impulse produced by the other cell than at other times. For cells of opposite response type (on- *versus* off-center cells), there is a paucity of impulses within that window. Because the synchrony or antisynchrony of firing is a probabilistic tendency, it accounts for only some of the variability of each cell's firing, implying two sources of variability must influence the firing of each cell: a "common" variability that affects both cells, and a "private" variability that each cell enjoys that has no influence on the other cell (Ginsburg et al., 1984). Of course, the private variability might conceivably be shared with other cells besides the other member of the pair being recorded. Nevertheless, studies of these sources of variability provide another window into the variability of firing that was the topic of the previous section.

The related firing of two ganglion cells is represented by a cross-correlogram: a plot similar to a peri-stimulus time histogram in which the firing of one cell is plotted as a function of time before and after each impulse in the other cell. Normalization by the mean rates produces the cross-covariance, an estimate of the expected value of the cross-product of the two variations (Ginsburg et al., 1984).

The cross-covariance revealed several features of the variability that reinforced other observations. First, the cross-covariance

represented only a fraction of the total variance of firing (a relatively constant proportion), again implying at least two independent sources of variability. Second, the cross-covariance during responses generally differed in amplitude from that observed during maintained discharge or OFF responses, supporting the suggestion that ON responses are generated by a different mechanism than firing in the absence of light (see "ON and OFF systems," below).

Finally, the relatively constant proportion of variance contributed by the common variability implies non-linear combination of signal and variability, as suggested by Levine and Shefner (1977a). Ginsburg et al. (1984) proposed that the common and private sources of variability enter within a feedback loop, with the photic stimulation affecting the feedback gain; this is consistent with the contrast gain model proposed for cat (Shapley & Victor, 1981).

The peak of the cross-covariance functions is generally not at zero time difference; that is, there is a lag between the firing of the one cell and the maximum increased or decreased probability of firing of the other. This lag is correlated with the relative latencies (time from stimulus onset or offset to the initiation of a change in firing rate) of the two cells. Interestingly, the difference in latencies is approximately twice the cross-covariance lag (Johnsen & Levine, 1983). This suggested that the common variability is introduced part-way down a chain of delays between reception and ganglion cell response; but why should the delays preceding the injection of common variability be temporally congruent with those of the pathways after its introduction?

A further analysis of the intervals between successive impulses preceding and following those impulses that correlated with impulses in the other ganglion cell of a pair led to a more complex model that reconciles these observations (Levine, 1997). This model includes a non-linearity: the common variability multiplies the leakage time constant of a leaky integrate-and-fire mechanism that is assumed to represent the ganglion cell spike generating mechanism, in addition to possibly adding to the integrator itself. This satisfies the constraint that cross-covariance be a relatively constant proportion of total variance, which was the motivation for the non-linearity proposed by Ginsburg et al. (1984). Moreover, it predicts that both response latency and cross-covariance lag would depend on the bias of the ganglion cell potential (which determines the mean rate) in a way that explains the relationship between latency and lag observed by Johnsen and Levine (1983).

Correlated firing as a potential source of multiplexed information

The preceding section addressed ways in which the cross-covariance could reveal the sources of variability and the processing network that it affects. But what, if anything, might correlated firing contribute to the information-handling capabilities of the retina?

One fairly obvious answer is that if two cells that synapse upon the same higher-order neuron fire in near synchrony, there is a better chance of activating that neuron. This would certainly be a mechanism by which specific patterns of activation would be most effective for particular cells, imbuing them with more selective properties than the lower-order neurons. A stimulus activating cells in synchrony might be enhanced by the implicit cross-covariance of retinal neurons (Stevens & Zador, 1998; Samonds & Bonds, 2004). In addition, the cross-correlation of ganglion cell firing during a response may be instrumental in triggering synchronous firing at higher levels (Samonds & Bonds, 2004). Synchrony in cortical firing apparently serves a role in tuning the specificity of these neurons (Gray & Singer, 1989; Samonds et al., 2004).

An intriguing possible alternative function for correlated firing in pairs of ganglion cells is that the coincident impulses might comprise an independent stream of information in addition to the 2 individual cells' firing (Meister et al., 1995; Meister, 1996). A coincidence detector at the next level could respond only to roughly coincident impulses, while other neurons relayed the separate firing of each cell. This would effectively multiply the information channels in the optic nerve to many more than the axon count, a valuable economy in view of the physical constraints on the size of the optic nerve.

This theory was tested with pairs of goldfish ganglion cells stimulated along various stimulus parameter dimensions (Levine et al., 2002). The two separate ganglion cell impulse trains were parsed into three: the firing of each cell, and the coincident firing. In no case was there better stimulus discrimination using the coincident firing; in fact, the better-suited individual cell far outstripped the coincident train in discriminating among stimuli along any dimension tested. Coincident firing apparently does not provide an independent "multiplexed" information channel of use to higher-order neurons. A similar conclusion was reached by Nirenberg and coworkers who applied an information-processing model to data from multiply recorded mammalian ganglion cells (Nirenberg et al., 2001).

A related idea is that the coincident train might not carry independent information about the stimulus, but could serve as a "key" for canceling the variability of the firing of the individual cells. That is, the firing might suffer intrinsic variability, and that variability might be of use for some functions (see "Variance of responses" later), but variability might be undesirable for other functions that require precision. The coincident firing might then serve as a decoder that allows the later removal of variability. This was also examined in the firing of pairs of goldfish ganglion cells; however, it was found that the raw ganglion cell firing trains were less variable than those with coincidences deleted (Levine, 2004). Correlation between the firing of neighboring ganglion cells in fish may not be a useful contributor to visual encoding at the retinal level.

Variability of responses to light

Whereas the source and form of the variability of maintained discharges is of interest, one is generally more concerned with responses to visual stimuli. When the identical stimulus is applied to the retina multiple times, the responses to that stimulus are not identical. Studies of variability of responses have shed light on the processing of visual signals, and sparked speculation about the possible role of variability in visual perception.

ON and OFF systems

When a light is presented to the retina, the largest changes in firing occur at the onset and offset of the light. It had often been assumed that the firing changes at offset represent a rebound from the excitation or inhibition during the illumination (a suggestion made by Kuffler, 1953) and implicit in many subsequent studies).

The statistics of responses in goldfish ganglion cells implied that responses at offset are not simply rebounds from the responses at onset (Levine & Shefner, 1975, 1977b). The evocative data consisted of lists of firing rates in a regimen in which a flash of light was presented for one second, and repeated every 30 s for at least 30 repetitions. A correlation matrix of the lists generated by this paradigm showed high positive correlations among the periods representing firing in the dark, and a lower correlation between any

period and the period corresponding to the ON response. Whereas those correlations were lower, they were not negative, as might be expected from the inverted direction of ON and OFF responses. This indicated the responses to onset incorporated a source of variability not patent in the dark.

There remained a danger that ON and OFF were indeed mirror responses, but superimposed on an additional variability that induced a high correlation against which the reverse influence at onset simply reduced correlation. This was refuted by autocorrelations of each of the lists. Autocorrelation is a measure of the relatedness of consecutive samples, alternative samples, 3-apart samples, etc. (In this analysis, samples are of the corresponding periods of each cycle, so consecutive samples for each autocorrelation function are actually separated by 30 s.) This examines structure across several minutes.

In many autocorrelations, the function corresponding to the ON response followed a distinctly different time-course than that from the other lists, which all tended to be similar. The implication was clear: responses to the onset of light and responses to its offset (or maintained firing in darkness) were independent; a different process was responsible for the variability of the ON response.

Responses to onset and to offset of lights in the center of the receptive field were independent, but the same processes applied to lights at separate spatial locations within the center of the receptive field (Shefner & Levine, 1979). However, responses to the onset and offset of annular lights effective for the surround were affected by another set of sources of variability (Levine & Shefner, 1977b).

A principal components analysis of these data reached similar conclusions: there are two main processes in the receptive field center, one associated with ON responses and the other controlling OFF responses and dominating maintained discharges. There is only one set of these processes in the entire receptive field center, but another set is evident in the surround (Chapman et al., 1981).

Levine and Shefner (1977b) proposed that depolarizing bipolars provided the ON responses to both ON-center and OFF-center cells, whereas hyperpolarizing bipolars determined the OFF responses and dominated the maintained discharges. The bipolar cells thereby provided a push-pull input to the ganglion cells, with one type responsible for increases in firing and the other responsible for decreases. This model was challenged by anatomical work showing separation of invaginating and flat bipolar cell terminals into the distinct sublaminae of the inner plexiform layer within which the dendrites of ON-center and OFF-center ganglion cells branched (Famiglietti & Kolb, 1976). This seemed to preclude a scheme in which both types of bipolar cell act upon each ganglion cell. However, later anatomical reconstructions of cat retina showed that beta ganglion cells receive apparently antagonistic input from two types of cone bipolar cells (Sterling, 1983; Wässle & Boycott, 1991). Subsequent recordings of ganglion and amacrine cells in carp retina also demonstrated a push-pull arrangement in which different types of amacrine cells provided the ON and OFF components (Toyoda et al., 1992).

Variance of responses

The preceding section discussed the variability of the responses to an identical stimulus presented multiple times. An interesting observation was made of mammalian cortical neurons when a series of stimuli of different effectiveness were each presented multiple times (Dean, 1981; Tolhurst et al., 1981, 1983). Regardless of the nature of the stimulus, the variance of the responses was in direct proportion to the mean firing rate of that response.

This striking result seemed inconsistent with the variability of the maintained discharges of ganglion cells. The coefficient of variation of cat ganglion cells is negatively correlated with the mean firing rate (Frishman & Levine, 1983). In a more detailed analysis, it was found that the coefficient of variation generally decreases approximately as the square root of rate, both for cat and goldfish (Levine, 1987). This predicts that the variance of rate should be independent of the mean rate, not directly proportional to it.

Is this a difference between responses to flashed stimuli *versus* maintained discharges, or a difference between retinal *versus* cortical firing? To answer this question, the variance of responses of goldfish retinal ganglion cells was compared to their mean responses. In these experiments, four stimuli of different strengths were interleaved in a pattern repeated for at least 20 cycles (Levine et al., 1988b). Variance of rate was found to increase with mean rate, but not in direct proportion; the function (on double logarithmic coordinates) was negatively accelerated. Levine and Zimmerman (1991) analyzed the retinal maintained discharges and responses to stimulation and found that if the variability of maintained discharges (the logarithm of the coefficient of variation) is nonlinearly related to the logarithm of the mean rate, the variance of responses is exactly as expected from the relationship between the coefficient of variation and mean maintained firing. The difference seemed not to be between maintained discharges and photically driven responses, but between retina and cortex.

However, a possible confound remained: the retinal responses were obtained from goldfish, whereas the cortical responses were from cat and monkey. Might there be species differences? The same paradigm was applied to cat ganglion cells, with results quite similar to those in goldfish (Levine et al., 1992). (These cat data were also included in the modeling by Levine and Zimmerman (1991).)

Fortuitously, the examination of cat retinal ganglion cells had been "piggy-backed" onto another series of investigations in which each ganglion cell was recorded simultaneously with a dorsal lateral geniculate neuron that received its only direct retinal input from that very ganglion cell. Thus, the same analyses could be performed for cells at the next processing level. Whereas all ganglion cells produced a curved double logarithmic function of variance *versus* rate (or a line with a slope less than unity, indicating a function with a fractional exponent), the X-type lateral geniculate cells displayed nearly perfect direct proportionality between variance of rate and mean rate. Y-type geniculate cells reproduced the curvilinear proportionality of their retinal inputs (Levine et al., 1996; the data collected for this analysis were supplemented with data from S-potentials recorded in the geniculate in another laboratory). It thus appears that the X-cell system, which is considered the principal system for the analysis of patterns, increases the variability transmitted from the retina and "tailors" it so that variance is directly proportional to mean response amplitude. This probably is of some use in the analyses of patterns. Tailoring is apparently not a property of the Y-system, which presumably has roles more related to motion detection and general alerting. Whether this increase in variability is instrumental in the process of pattern detection is an hypothesis worthy of further study.

A model for retinal variability

A schematic incorporating the features of the various models discussed here is shown in Fig. 2. The pathways to two ganglion cells, *a* and *b*, are shown. Each has its signal separated into ON and

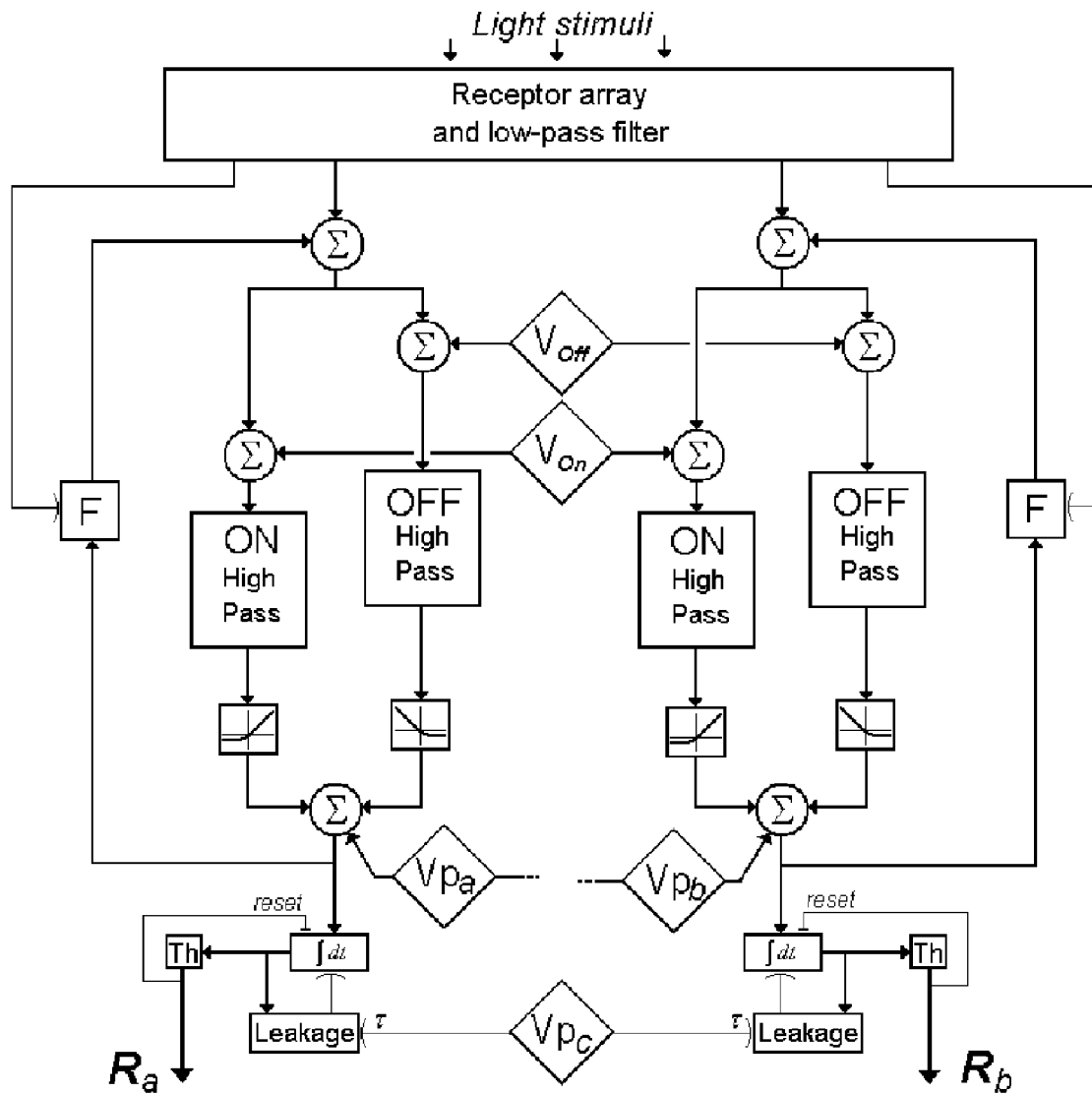


Fig. 2. Model for variability in goldfish retina. Light is processed by the outer retina (top of figure), before combining with variability. Distal sources of variability, the diamonds V_{on} and V_{off} are common to the two separate cell pathways but affect only the ON or OFF system of each, respectively. Proximal sources of variability, which are not shared between the two cells, enter after high-pass filtering and rectification that switches between the ON and OFF systems. The resultant signal provides the input to a leaky integrate-and-fire mechanism in each ganglion cell (*a* and *b*, at the bottom). Feedback to the outer layers has its gain adjusted by a signal related to the light, indicated by a light line with a curved terminal. The leakage time constant, τ , is adjusted by proximal common variability. See text for details.

OFF pathways; the signs of these pathways are not indicated, because that depends on whether they were pairs of on-center cells, off-center cells, or a pair comprising one of each.

Variability, whose sources are represented by the diamonds in the diagram, is introduced in at least two levels, distal and proximal to high-pass filtering. At the distal level, there is variability associated with the ON system and variability associated with the OFF system (denoted by the subscript *on* or *off*). The proximal source of variability that adds to each pathway after the combination of ON and OFF is indicated "Vp" and subscripted *a* or *b* according to which ganglion cell it influences. Note that this private variability may be shared with other ganglion cells that are not shown in this diagram (hence the lines fading to nowhere from these sources).

Light enters the receptor array at the top of the diagram, and is processed in the outer portion of the retina. This processing includes low-pass filtering (Toyoda, 1974; Levine, 1982). The signal splits into the ON and OFF pathways (labeled "ON" and "OFF"), each of which has added variability from the associated common source. Each combination of signal and variability is then high-pass filtered. Rectification, indicated by the graphs in boxes, provides a transition between the ON and OFF pathways. Proximal private variability (and possibly also common variability from a proximal source) is added to the signal that passes to the spike generating mechanism at the bottom.

Spike generation is by a leaky integrate-and-fire mechanism; the integral (in the box marked " $\int dt$ ") rises with input, but decays with time (the decay is indicated by the box marked "Leakage").

When the integral reaches a threshold value (at the box marked “Th”), an impulse is produced and the integrator is reset to its resting level to begin integrating toward the next impulse. The impulse trains generated by the two integrate-and-fire mechanisms are indicated “ R_a ” and “ R_b ” at the bottom of the figure.

Note that the receptive field surround is not represented in this figure. There are ON and OFF processes in the surround, but they are not congruent with those in the center. Low correlation could be explained if the surround is added by intervening neurons, which could add variability at the proximal level (Levine & Shefner, 1977b). It is possible that the private proximal sources of variability are actually associated with the input of the receptive field surround.

There are two additional features. The signal to the integrate-and-fire mechanism is also fed back (perhaps through interplexiform cells) to the level of the distal variability. This feedback has its gain adjusted by the outer retinal network. The non-linear gain adjustment is indicated by a thin line ending at a curve. This gain adjustment, comparable to that suggested by Shapley and Victor (1981), was proposed to account for the relative consistency of the percentage of cross-covariance in the overall variance (Ginsburg et al., 1984).

The other notable feature is that there is a proximal common variability that exerts a direct effect on the integrate-and-fire mechanism: it adjusts the time constant, τ , of the leakage. This non-linearity, also indicated by light lines and curved symbols, is what was required to explain details of the intervals proceeding and following impulses in the correlated impulse train, and also explained the relationship between relative latencies and cross-correlation lag (Johnsen & Levine, 1983; Levine, 1997).

The firing of retinal ganglion cells is quite variable. This variability has multiple sources, and interacts with retinal cells at various levels in various ways. However, it does not appear that this variability serves a particular function in the fish's retinal processing of visual information; if variability serves a useful function, it is apparently sculpted at higher processing levels to suit the needs of visual perception.

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