A Simple Coding Procedure Enhances a Neuron's Information Capacity

Simon Laughlin

Department of Neurobiology, Research School of
Biological Sciences, P. O. Box 475, Canberra City, A. C. T.
2601, Australia

Z. Naturforsch. **36 c,** 910–912 (1981);
received June 22, 1981

Neural Coding, Contrast, Fly Eye, Information Theory

The contrast-response function of a class of first order interneurons in the fly's compound eye approximates to the cumulative probability distribution of contrast levels in natural scenes. Elementary information theory shows that this matching enables the neurons to encode contrast fluctuations most efficiently.

Neurons carry and process information and there ought to be situations in which neural coding follows the dictates of information theory [1]. Large monopolar cells (LMC's) are first order interneurons of the insect compound eye. Like the analogous bipolar cells of the vertebrate retina, their graded responses are driven by small groups of receptors with the same field of view [2]. The compressive intensity-response function of the receptors, combined with lateral and self-inhibition, adjusts the LMC sensitivity to the background intensity so that their responses code contrast fluctuations rather than absolute intensity [3]. I show here that this interneuron's contrast-response function matches the range of contrasts encountered in natural scenes so as to increase the efficiency with which information is encoded.

A fundamental limitation upon neural coding is the restricted range of responses with which a neuron can represent the states of its inputs. For a graded potential cell like the LMC, the response range is ultimately limited by reversal potentials. How should a neuron weigh its inputs so as to best represent their states? If sensitivities are set too high then inputs will often saturate the response, and information will be lost through clipping. Conversely, when sensitivities are set too low, large parts of the response range are underutilised because they correspond to exceptionally large excursions of input. Information theory [4] suggests an efficient means of apportioning the neuron's limited response range: the inputs should be encoded so that all response levels are used with equal frequency. Under this condition the information carried by the responses can be maximised because the information channel achieves its maximum entropy [3, 4].

For the simplest case of a neuron representing a single input parameter with a single output parameter, this optimum can be attained when the input-output function corresponds to the cumulative probability function for the different input levels (Fig. 1), because equal output excursions correspond to equal probabilities of input. The technique of using a cumulative probability function as a

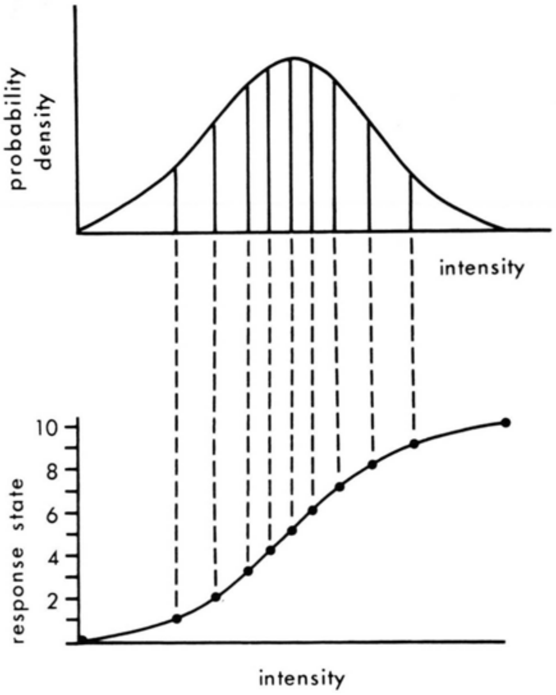

Fig. 1. The coding strategy for maximising a neuron's information capacity by ensuring that all response levels are used with equal frequency. Upper curve: – probability density function for stimulus intensities: Lower curve: – the intensity-response function that implements the strategy. In this example the neuron has 10 response states, corresponding to 10 "just noticeable differences" in response. The intensity-response function ensures that the interval between each response level encompasses an equal area under the intensity distribution, so that each state is used with equal frequency. In the limit where the states are vanishingly small this intensity-response function corresponds to the cumulative probability function for stimulus intensities.

Reprint requests to Dr. S. B. Laughlin.

0341-0382/81/0900-0910 $ 01.00/0

coding characteristic is used in digital image processing, and is called "histogram equalization" [5]. Note that this coding procedure amplifies inputs in proportion to their expected frequency of occurrence, using the response range for the better resolution of common events, rather than reserving large portions for the improbable.

To see if the first order interneurons of the blowfly's compound eye use this coding procedure I compared their contrast-response functions with the contrast levels measured in natural scenes, such as dry schlerophyll woodland and lakeside vegetation. Relative intensities were measured across these scenes using a detector which scanned horizontally, like the ommatidium of a turning fly. It consisted of a PIN photodiode, operating within its linear range, in the focal plane of a quartz lens. A combination of coloured glass filters (Schott, KG 3 + BG 38) was used to give the detector a spectral sensitivity similar to a fly monopolar cell [3]. The scans were digitised at intervals of 0.07° and convolved with a Gaussian point spread function of half-width 1.4°, corresponding to the angular sensitivity of a fly photoreceptor [6]. Contrast values were obtained by dividing each scan into intervals of 10, 25 or 50°. Within each interval the mean intensity, $\bar{I}$, was found, and substracted from every data point to give the fluctuation about the mean, ΔI. This difference value was divided by the mean to give the contrast, $\Delta I/\bar{I}$. The cumulative probability distribution of contrast levels (Fig. 2) was derived from 15000 readings. As expected, the range of contrasts encountered increased with the width of the interval used, but the difference between the two larger intervals, 25° and 50°, was small.

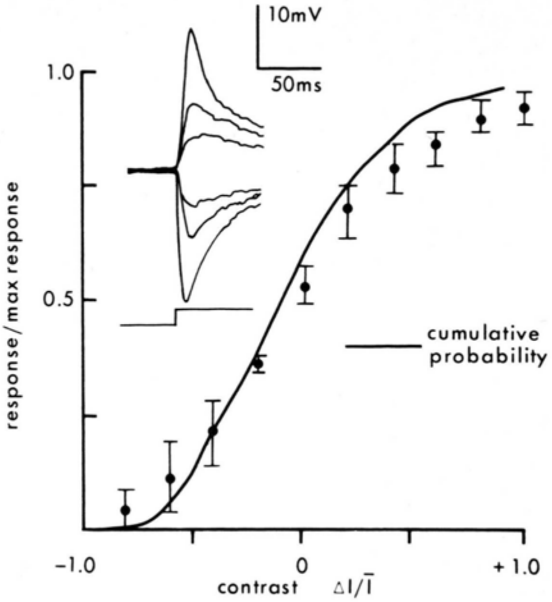

Fig. 2. The contrast-response function of light adapted fly LMC's compared to the cumulative probability function for natural contrasts (50° interval). Response is normalised with the maximum amplitude to light off as 0.0, and the maximum amplitude to an increment as 1.0. Data points averaged from 6 cells; range bars show total scatter. Inset shows the averaged responses of an LMC to four contrast steps (the cell hyperpolarises to increments and depolarises to decrements). The stimulus, a Siemens LD57C light emitting diode (LED) subtending 2° and filling the centre of the LMC's receptive field; was mounted in the centre of the reflecting screen of diameter 16°. LED and screen brightnesses were equalised by setting the mean LED intensity so that its substitution for the screen in the centre of the field generated a negligible response. Contrast steps were generated by setting the LED driving voltage to a new level for 100 ms, and the corresponding contrast determined by recording the driving voltages and referring these to the diode's voltage/intensity curve, determined *in situ*. Mean light levels where 2.5 to 3.0 log units above the intensity producing a half maximal response from the dark adapted LMC.

The interneuron's contrast-response function was measured using the techniques developed for intracellular recording in the intact retina of the blowfly, *Calliphora stygia* [3, 6]. Individual LMC's were light adapted by a bright steady background and the responses to sudden increments and decrements about this level recorded (Fig. 2). Repeated responses to the same stimulus were averaged to enhance the reliability of the data. The light adapted contrast-response function approximates to the sigmoidal form of the cumulative probability function for contrast levels in natural scenes (Fig. 2). This matching indicates that this class of neurons uses the strategy for efficient coding suggested by information theory. Since small departures from response equiprobability have a marginal effect on entropy [4], there should be little redundancy associated with the LMC response to natural scenes.

The successful application of a central concept from information theory, entropy, to a neuron's transfer function validates Barlow's suggestion that redundancy reduction is an important principle in neural coding [1]. In this context it is interesting that many of the bipolar [7] and ganglion cells [8] of the vertebrate retina have intensity-response functions similar to LMC's, suggesting that the efficient coding of the available information into neurons is an essential first step in visual processing. The strategy of matching a neuron's input-output function to the expected distribution of signals so as to increase the information capacity is equivalent to impedance matching, ensuring that the maximum amount of information is transferred between elements. For this reason the coding procedure described here might find a wider application among nervous systems.

Acknowledgements

I would like to thank Ray Stone for building and operating the light detector and Jo Howard, Richard Payne, M. V. Srinivasan, and Austin Hughes for their advice.

[1] H. B. Barlow, in: Sensory Communication (W. A. Rosenblith, ed.), 217 and 782, MIT Press, Cambridge, Mass., 1961.
[2] K. Kirschfeld, Fortschr. Zool. **21,** 229 (1973).
[3] S. B. Laughlin and R. C. Hardie, J. Comp. Physiol. **128,** 319 (1978).
[4] C. E. Shannon and W. Weaver, The Mathematical Theory of Communication, University of Illinois Press, Urbana, 1949.
[5] R. C. Gonzales and P. Wintz, Digital Image Processing, Addison-Wesley, Reading, Mass., 1977.
[6] R. C. Hardie, J. Comp. Physiol. **129,** 19 (1979).
[7] F. Werblin, J. Neurophysiol. **34,** 228 (1971).
[8] O. D. Creutzfeld, in: EEG Supplement 31, Recent Contributions in Neurophysiology (J.-P. Cordeau and P. Gloor, eds.), 159, Elsevier, Amsterdam 1972.

Verantwortlich für den Inhalt: A. KLEMM
Satz und Druck: Konrad Triltsch, Würzburg