Exp Brain Res (1981) 44: 437–440

Experimental Brain Research

Research Note

The Variability of Discharge of Simple Cells in the Cat Striate Cortex*

A.F. Dean[1]

The Physiological Laboratory, University of Cambridge, Downing Street, Cambridge, CB2 3EG, England

Summary. The relationship between the variance and mean rate of discharges of simple cells in the cat striate cortex has been examined when mean rate was varied by changing either stimulus spatial frequency or contrast. In both cases, the variance was related to the mean discharge rate by an exponent of about 1.15; the relation was thus roughly linear. The discharge variance was on average 1.7 times the mean rate for data obtained from measurements of the neurones' spatial frequency tuning curves, and 1.48 times the mean for data from the response-contrast determination. However, this difference was not statistically significant.

Key words: Response variability – Visual cortex – Cat

In recent years, considerable advances have been made in the analysis of the selectivity of cat striate cortical neurones for stimulus orientation, spatial frequency, temporal frequency and direction of movement. One aspect of striate neuronal behaviour which has received relatively little attention, however, is the statistical properties of the evoked discharges. Variations in responsiveness over a time course of minutes in the visual system have been reported by Henry et al. (1973) but little is known of the variability of discharge on a second to second timescale. One recent study has addressed this question (Tolhurst et al. 1981), but the data for both simple and complex cells was combined for presentation. The present study was therefore undertaken to examine quantitatively the statistical properties of a physiologically homogeneous neuronal class: simple cells.

Adult cats were anaesthetised by ventilating with 75% N_2O, 23% O_2, 2% CO_2, supplemented by an i.v. infusion of pentobarbitone sodium. Eye movement was minimized by paralysis with Flaxedil (gallamine triethiodide, May and Baker). The eyes were fitted with zero power contact lenses (entrance pupil 3 mm diameter) and focused onto a tangent screen. Extracellular recordings were made from neurones in the striate cortex using electrolytically sharpened glass-insulated tungsten micro-electrodes (Merrill and Ainsworth 1972). Further details are provided elsewhere (Movshon et al. 1978; Dean 1981).

Receptive fields were mapped using hand-held stimuli projected onto the tangent screen and classified as either simple or complex, according to the criteria of Hubel and Wiesel (1962). The tangent screen was then replaced by a display screen upon which were generated laterally moving sinusoidal gratings. The mean luminance of the screen was 300 cd/m^2.

A PDP 11/20 computer was used to implement the multi-histogram technique of stimulus presentation (Henry et al. 1973; Movshon and Tolhurst 1976). Typically, five blocks, consisting of the set of all stimuli and a "blank" (man luminance), would be presented. Within a single block, each stimulus was presented for a total of 20 temporal cycles, its position relative to the others being randomly assigned. The mean and variance of the total number of impulses elicited by each stimulus cycle in such groups of 20 cycles were then calculated. A modified power model regression analysis served to quantify the relationship between these two variables. As neither the mean nor the variance is an independent variable, the Y-onto-X regression slope (M_1) and the X-onto-Y regression slope (M_2) were combined to yield an "average slope" as ($M_1 + M_2$)/2. An "aver-

* This work was partially supported by an MRC project grant to D.J. Tolhurst and by the Wellcome Trust

1 Recipient of an MRC Research Scholarship

Offprint requests to: A.F. Dean (address see above)

0014–4819/81/0044/0437/$ 1.00

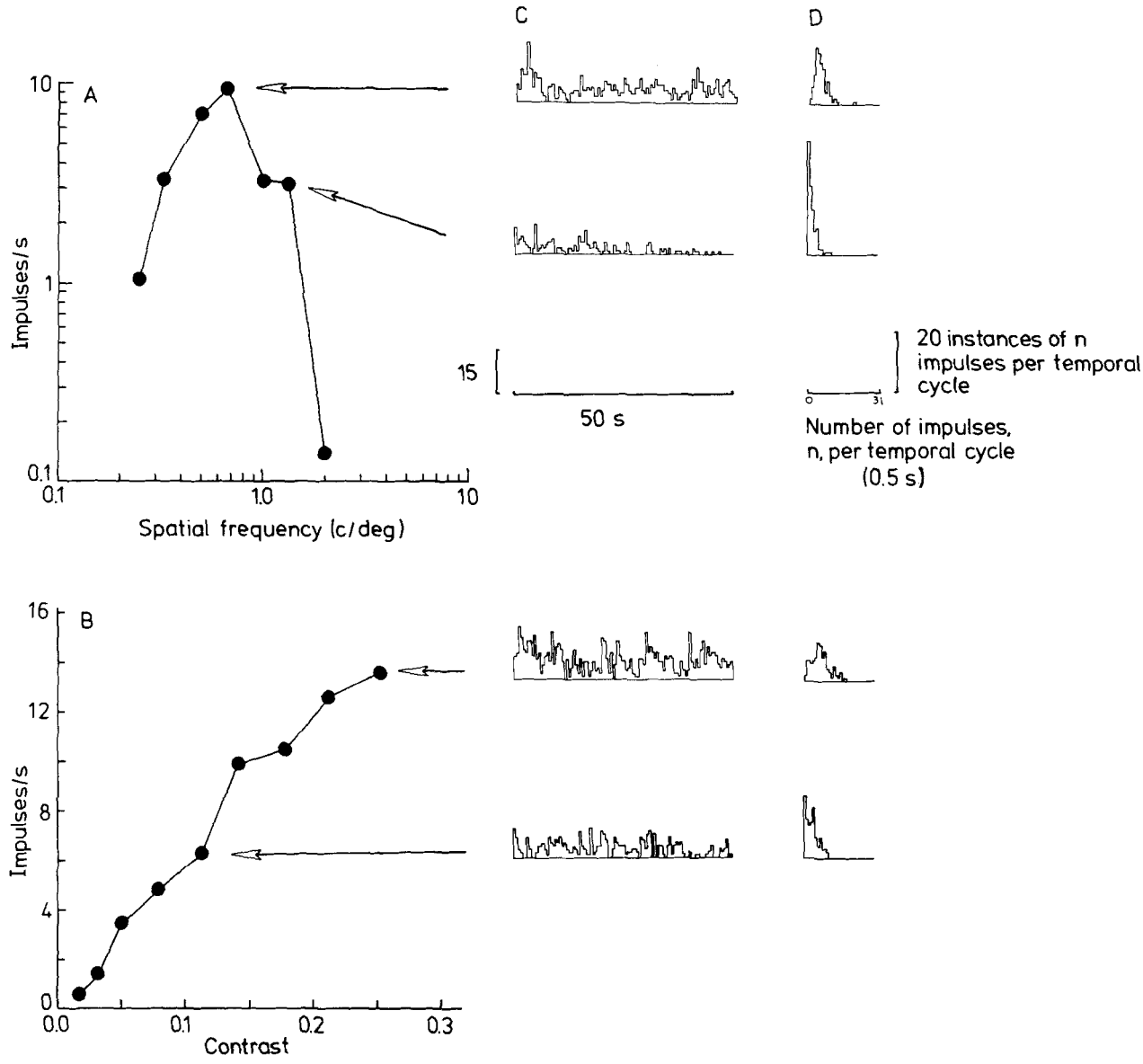

Fig. 1. A The relation between mean discharge and spatial frequency for a simple cell. The stimulus contrast and temporal frequency were held constant at 0.25 and 2 Hz, respectively. Each stimulus was presented for a total of 100 temporal cycles (50 s). **B** The relation between mean firing rate and contrast for the same neurone, measured at the optimal spatial frequency of 0.66 c/deg. The temporal frequency was again 2 Hz; 100 temporal cycles were presented at each contrast. **C** Histograms illustrating the variation in response over the course of 50 s of stimulation with the indicated stimuli. Each bin shows the total number of action potentials recorded in response to one temporal cycle (0.5 s). The vertical scale bar gives the number of impulses per temporal cycle. The horizontal bar shows 50 s. **D** Histograms for the same indicated stimuli showing the frequency of obtaining, within the analysis period of 0.5 s, the number of impulses, n, plotted horizontally. The first and last bins indicate the number of occurrences of zero and 31 action potentials per temporal cycle

age intercept" was also calculated, on the basis that a line of "average slope" is constrained to pass through the geometric means of the mean discharge values and the variance of discharge values. This intercept corresponds to the value of the variance when the mean is 1.

Mean values in the text are given with ± 1 standard deviation.

Thirteen simple cells were recorded. Each was subjected to a measurement of its spatial frequency tuning followed by a determination of the response-contrast relation at the optimal spatial frequency. Figure 1 illustrates the behaviour of a typical neurone. Figure 1A, B show, respectively, the spatial frequency tuning curve and the form of the response-contrast relation measured at 0.66 c/deg.

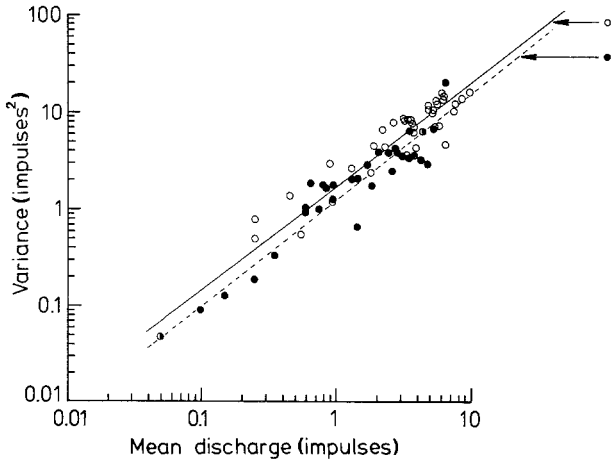

Fig. 2. The relationship between the mean and variance of the total number of impulses elicited by each cycle of the grating during the spatial frequency tuning measurement (filled circles; dashed line) and the response-contrast measurement (open circles; continuous line). Mean-variance data pairs were calculated from the responses to the groups of 20 consecutive cycles contained within each stimulus block. Calculation of the regression lines is described in the text. The correlation coefficients for the spatial frequency tuning and the response-contrast data are 0.962 and 0.947, respectively

The time-course of response variability is illustrated in Fig. 1C, which shows the number of impulses elicited by each of 100 temporal cycles of the grating. Clearly, response amplitude can vary considerably from one temporal cycle to the next (0.5 s). In addition, the second histogram from the top illustrates another aspect of simple cell behaviour that was frequently encountered: a drift in firing rate occurring over a much longer duration than that of the individual cycles. The time-course of this behaviour indicates that it is probably an example of the slow drifts originally described by Henry et al. (1973) and Tolhurst et al. (1981). Figure 1D shows, for the same stimuli, the form of the distributions of number of impulses elicited per temporal cycle. Observe that a reduction in mean response amplitude, whether achieved by lowering stimulus contrast or by altering the spatial frequency, is associated with an alteration in the form of the distribution from being roughly symmetrical to resembling an exponential decline. At low mean rates, the most frequently encountered number of action potentials per temporal cycle (0.5 s) was zero.

Figure 2 shows, for the same neurone, the relationship between the mean and the variance of the number of impulses per temporal cycle, calculated from each 20-bin pulse number histogram. Filled and open circles indicate data derived from the spatial frequency tuning measurement and the response-contrast experiment, respectively. The regression for the former data set (dashed line), had an "average slope" of 1.10 and an "average intercept" of 1.22, calculated as described above. The corresponding values for the latter data set (continuous line) were 1.08 and 1.68.

The range of "average slopes" encountered within the population of 13 neurones for the response-contrast data was from 0.92 to 1.34, with a mean value of 1.16 ± 0.11. The equivalent range for the spatial frequency tuning data was from 0.90 to 1.37, with a mean of 1.14 ± 0.13. A paired t-test revealed that the difference was not statistically significant ($t = 0.821$; $p > 0.1$). The values of "average intercepts" ranged from 0.83 to 2.71 for the response-contrast data, and from 0.85 to 3.03 for the spatial frequency tuning data; the mean values were 1.70 ± 0.62 and 1.48 ± 0.62, respectively. Again, the difference was not significant ($t = 1.187$; $p > 0.1$).

Although there is clearly a scatter of statistical parameters within the neurone sample, individuals show a significant positive correlation between the values of "average slope" that are obtained from the spatial frequency and the response-contrast experiments ($r = 0.72$; $t = 3.42$; $0.005 < p < 0.01$). The values of "average intercept" were similarly correlated ($r = 0.70$; $t = 3.25$; $0.005 < p < 0.01$).

Several important findings emerge from this study. Firstly, considerable variation is evident in the responses of simple cells to successively presented identical stimuli whose individual duration is as little as 0.5 s (Fig. 1C). Secondly, the variance of discharge is systematically related to the mean firing rate, and does not depend on the manner in which alterations of the mean rate are brought about (Fig. 2). More precisely, since the exponent of the relation linking variance (Y) and mean (X) is about 1.14 in the case of data derived from spatial frequency tuning measurements and 1.16 for response-contrast measurements, the two variables are approximately linearly related; the constants of proportionality ranging from about 1.48 to 1.70. Thirdly, the form of the distribution of the number of impulses per temporal cycle also appears closely related to the mean firing rate: whereas at low mean rates the distribution declines monotonically, "zero impulses" being the most common, at higher mean rates the form is approximately Gaussian (Fig. 1D).

The values of "average slope" are consistent with the range 1.0–1.4 recently reported by Tolhurst et al. (1981) in a similar study. However, the values of intercept which they obtained were somewhat higher, lying between 3 and 5. There is a plausible explanation for this discrepancy. Tolhurst et al. (1981) calculated the mean and variance of discharge

over durations of roughly 20 min. As they recognized, measurements over such durations are liable to contain an extra component of variance resulting from slow drifts in responsiveness (cf. Fig. 1C). This contamination was minimized in the present study by deliberately calculating values over much shorter intervals.

For the future, it will be instructive to examine the statistical parameters of geniculate neurones, in view of the considerable anatomical and physiological evidence indicating that they represent the major excitatory input to simple cells (Hubel and Wiesel 1962; LeVay and Gilbert 1976; Gilbert 1977).

Acknowledgements. I am grateful to D. J. Tolhurst for his help and criticism throughout this work, also to Prof. H.B. Barlow for valuable discussions. Peter Joyce, Mick Swann, Fiona Hake, and Peter Starling provided expert technical assistance.

References

Dean AF (1981) The relationship between response amplitude and contrast for cat striate cortical neurones. J Physiol (Lond) 318: 413–427

Gilbert CD (1977) Laminar differences in receptive field properties in cat primary visual cortex. J Physiol (Lond) 268: 391–421

Henry GH, Bishop PO, Tupper RM, Dreher B (1973) Orientation specificity and response variability of cells in the striate cortex. Vision Res 13: 1771–1779

Hubel DH, Wiesel TN (1962) Receptive fields, binocular integration and functional architecture in the cat's visal cortex. J. Physiol (Lond) 160: 106–154

LeVay S, Gilbert CD (1976) Laminar pattern of geniculocortical projection in the cat. Brain Res 113: 1–19

Merrill EG, Ainsworth A (1972) Glass-coated platinum-plated tungsten micro-electrodes. Med Biol Eng 10: 662–672

Movshon JA, Tolhurst DJ (1976) The use of a digital computer in the study of neuronal properties in the visual system. J Physiol (Lond) 249: 56–57P

Movshon JA, Thompson ID, Tolhurst DJ (1978) Spatial summation in the receptive fields of simple cells in cat's striate cortex. J Physiol (Lond) 283: 53–77

Tolhurst DJ, Movshon JA, Thompson ID (1981) The dependence of response amplitude and variance of cat visual cortical neurones on stimulus contrast. Exp Brain Res 41: 414–419

Received February 16, 1981 / Accepted August 28, 1981