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Short-term response variability of monkey striate neurons

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Neurons in striate cortex appear to respond in a more variable manner to visual stimulation of their receptive fields than do retinal ganglion or lateral geniculate nucleus (LGN) cells. The extent of this variability is of interest for both methodological and theoretical reasons. Methodologically, it is valuable to know what number of samples taken over what period of time adequately assesses a cell's response characteristics. Theoretically, some light may be shed on cortical connectivity by determining the relative variability of cell subgroups and the difference in variability between responses elicited by optimal and non-optimal stimuli.

We obtained a measure of response variability for 333 neurons in striate cortex and for 16 neurons in the LGN. The data were collected from 46 monkeys (*Macaca mulatta*) in the standard acute preparation; they were paralyzed with Flaxedil and were artificially respired with 30% O_2–70% N_2O. Only cells with receptive fields 2–5° from the fovea are included in this sample. The data collection and stimulus presentation system capable of producing visual stimuli in random order has been described elsewhere[5]. Variability data were collected over the 3–4 min period when the best orientation or length of an edge or bar was being assessed by sweeping a stimulus of optimal velocity across the receptive field using a waveform generator and a mirror galvanometer. All the impulses elicited during this sweep, which was typically 1 sec in duration per trial, were counted as the response. To obtain an index of variability the standard deviation of the response to 10 repeated presentations of a given stimulus was divided by the mean response and multiplied by 100. Low values indicate a cell with consistent responses and hence low variability; high values show high variability. Using a stimulus of optimal orientation, length, and velocity, the average index of variability for all units was 35.2 with a standard deviation of 20. Breakdowns of variability for simple (S-type) and complex (CX-type) cell groups appear in Fig. 1A. S-type cells are those oriented units which show spatially separated contrast specific subfields; CX-type cells are those oriented units which throughout their receptive fields respond to both light increment and light decrement[5]. These categories correspond generally to Hubel and Wiesel's[3] distinction between these two subgroups. Also included is a small sample of LGN units, studied in a similar manner, that had their receptive fields in the same part of the visual field.

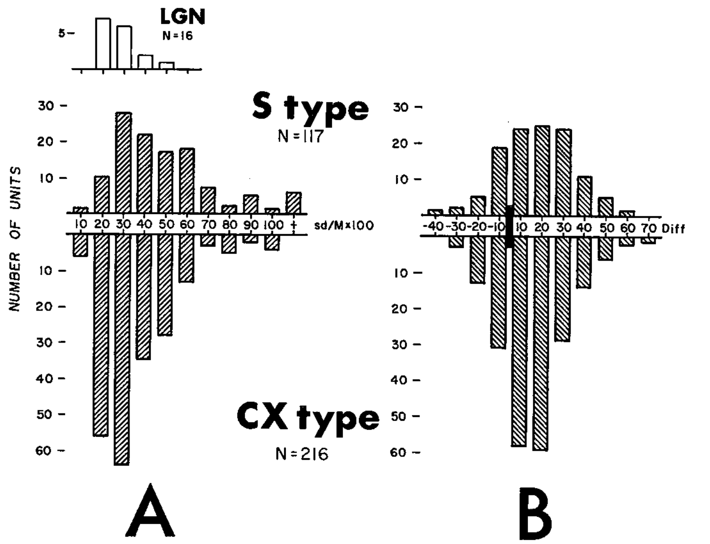

Fig. 1. A: the relative variability of LGN, S-type and CX-type cells. An index of variability was computed by dividing the mean number of responses to 10 presentations of a moving stimulus of optimal configuration by the standard deviation for those responses and multiplying this value by 100. LGN cells show the least relative variability, and S-type cells the most. B: the degree of variability in response rate of striate neurons to optimal *versus* non-optimal stimuli. The non-optimal stimulus was a bar oriented in such a way that its movement across the receptive field elicited half the number of responses as did its movement across the field at the optimal orientation. The variability index of the optimal stimulus was subtracted from the variability of the sub-optimal stimulus. The distribution centers around 20, which indicates that sub-optimal stimuli have greater relative variability than optimal stimuli. The histogram above the scale refers to S-type cells; the histogram below the line to CX-type cells.

These data show that CX-type cells are somewhat less variable than S-type cells. S-type cells had a mean variability index of 34.4 with only 33% showing a variability of 30 or less. CX-type cells had a mean variability of 26.3 and 58% had a variability less than 30. LGN cells show the least amount of variability. The difference between S-type and CX-type cells is statistically significant (*t*-test, $P < 0.05$) and is not inconsistent with the view that CX-type cells receive a convergent input from a greater population of visually driven cells than do S-type cells.

The response variability of cells in the various cortical layers differs. As one goes lower in the cortex, variability decreases. For layers 1–3, the average index of variability is 39.0; for layer 4, 32.1; for layers 5–6, 28.7. This trend for all cells is also true for CX-type cells; S-type cells show the trend to a lesser extent.

We also determined whether or not relative variability is increased when non-optimal stimuli are used. To assess this we obtained a similar variability index using an orientation which elicited half the number of responses as the optimal orientation. The variability index at the optimal orientation was subtracted from the variability index at this sub-optimal point. These data are shown in Fig. 1B. If the extent of variability for optimal and non-optimal stimuli were the same, the distribution should center around 0 (heavy line in graph). Instead, the distribution centers near 20, showing that on the whole cortical cells respond in a more variable manner to stimuli which are not appropriately oriented than they do to an optimally oriented stimulus. S-type and CX-type cells are quite similar in this respect.

Our variability index (SD $\div$ mean $\times$ 100) was based on 10 repeated trials of the optimal stimulus presented in the course of a random sequence of different orientations or lengths, generally totaling 90–120 trials over a period of 3–4 min. Thus the data presented may be said to represent short-term variability, and provide no information about the extent to which the response rate of neurons might change over longer time periods. Such changes may well be even greater since that has been shown to be case in the retina[4]. Henry *et al.*[2] have demonstrated marked changes over time in responsiveness in cat striate cortex.

Since the cells in monkey cortex show considerable variability over short-time periods, it is important that quantitative studies of cortex attempting to show differences in response rates use sufficient sample size to account for a standard deviation of 35% of maximum response rate or more. Randomization of stimulus presentation is another way of minimizing the effect of short-term changes in response rate.

Response variability may be an index of the amount of convergent excitatory input. It has been argued that simple cells in the cat receive a relatively sparse input from the LGN[1]. Complex cells, on the other hand, according to the hypothesis of Hubel and Wiesel[3], should be less variable in their responses since they receive convergent input from many simple cells. Our data concerning the relative variability of S-type and CX-type cells support this hypothesis. The fact that CX-type cells in layers 5 and 6 are least variable suggests considerable convergence upon these cells; their generally larger receptive fields are in consonance with this view.

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