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Short communication

MULTIUNIT ACTIVITY OF THE CAT LATERAL GENICULATE NEURONS EVOKED BY MOVING LIGHT PATTERN OF VARIABLE INTENSITY

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Abstract. The activity of groups of 2–5 cells with overlapping receptive fields (RFs) was recorded by one single electrode from the lateral geniculate nucleus. The histograms of responses to a moving complex stripe-pattern were qualitatively compared with the stimulus intensity change measured within the center of the RFs. We suggest that the intensity of the stimulus is matched by the "integrated" activity of several functionally related units.

The data concerning the pattern of lateral geniculate nucleus (LGN) single unit responses (3, 5–7) and the functional connections of the retina and LGN (9) allow the notion of a point to point transmission of visual information in these two structures (1, 4–8). According to this hypothesis a visual stimulus is reflected (with some inaccuracy) in the neuronal outputs of both these subcortical centers in the form of activity distributions (maps, reliefs of activity).

This experiment was performed with the aim of finding the relationship between the form and amplitude of activity map at a given, postsynaptic point in the LGN and the corresponding point intensity of a moving visual stimulus. It has been suggested before (8) that information about average brightness at a given point in the retina is transmitted simultaneously by many neighboring LGN neurons with overlapping

receptive fields. Thus, we recorded the responses of several (2 to 5) neighboring LGN units, simultaneously by a single microelectrode, in cases when their RFs overlap considerably. We considered in this experiment that post stimulus time histogram (PSTH) responses obtained in such a way reflect the activity map.

Twenty one recordings consisting of several units each were analysed in three cats. The animals had been prepared surgically one hour before the recording session. A pretrigeminal section was performed and a window in the skull was opened above the left LGN. Flaxedil paralysis and artificial respiration was applied. The pupils were maximally dilated by mixture of atropine and neosynephrine and the corneas were protected by contact lenses of +1 D in average, which focused the stimulus presented on a perimeter-like screen 70 cm in front of the cat's eye. Hubel-type tungsten microelectrodes were used for recordings. Spike-trains which could be easily recognized from noise were selected and counted simultaneously by PSTH-analyser. The stimulus was a slide of streak-like light pattern, consisting of several light and dark parallel stripes (see Fig. 1) moving on the darker background with a speed of 6°/s in two opposite (left and right) directions. The background and stimulus intensities could be varied (range 0–6 cd/m²) by changing the DC voltage supplying special bulbs and were measured using an SEI photometer.

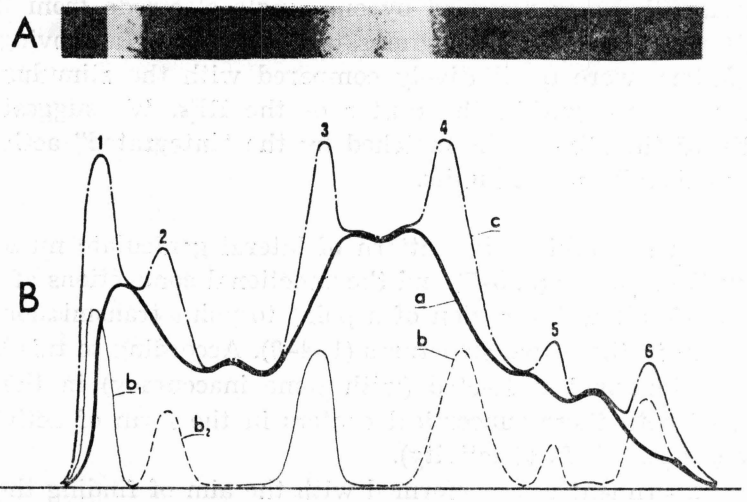

Fig. 1. The stimulus used in the experiment. A: the horizontal cut of a stripe slight. Its real dimensions were 10° height and 18° width; B: a, the appropriate intensity of the stimulus as measured by a photo-cell; b, the logarithm of the differential of the curve *a*; b_1 and b_2, positive and negative values of the curve *b*. The absolute values of the negative parts b_2 are drawn; c, the sum of the *a* and *b* curves; 1–6, the main peaks; See text for details.

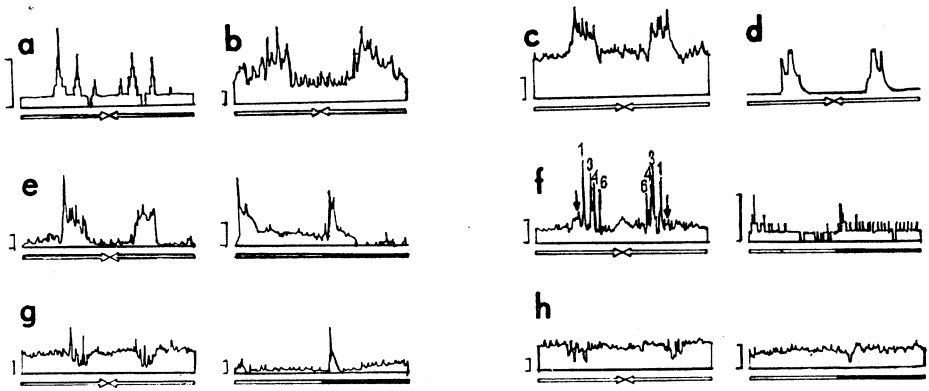

Fig. 2. PSTH of responses of cells to the moving stimulus and diffuse flash. a, single unit of the *on* type; b, single *off* cell; c, a group of five units (*on* and *off* center types); d, photo-cell response for the moving stimulus; e–h, double unit recordings, all consisting of one *on*-center and one *off*-center cell; e, g and h, cases with different *on* and *off* components in response to a diffuse flash; f, pair exhibiting similar *on* and *off* flash responses. Calibration for all histograms: 5 impulses per bin. The time base line for moving response histograms: 20 s; number of repetitions — 16. Arrows below histograms show the time and direction of movement; white-black bars indicate *on* and *off* phases of diffuse flash stimulation. The time base length for flash responses: 2s; number of repetitions — 32. The number of bins — 2000.

In Fig. 2 are shown the PSTHs of responses of LGN neurons to the stimulus moving across the RFs. Stimulus intensity changes in the averaged RFs center (Fig. 2*d*) were not simply followed by corresponding frequency changes in the histograms, either for the single unit (one cell) cases (Fig. 2*a, b*) or when groups of cells were investigated (Fig. 2*c, e, f, g*). A group of PSTHs could be, however, selected in which the responses to left versus right direction of stimulus movement were symmetric, and the shape of the histogram could be more easily compared with the stimulus intensity changes. It was found that in these cases (Fig. 2*c, f* and Fig. 3*A, B*) the appropriate PSTHs of responses to diffuse flash had *on* and *off* components similar in form and amplitude (i.e., primary responses for switching the light on and off). In the remaining group of recordings (Fig. 2*e, g, h*) when the *on* and *off* components of flash responses were different, even a qualitative analysis of responses for moving stimulus was hardly possible. It can be seen, for example, in Fig. 2*g, h* where the *off*-excitatory (Fig. 2*g*) or *off*-inhibitory (Fig. 2*h*) components are more pronounced than the corresponding *on*-components.

We assume that the recordings of similar *on* and *off* flash components represent the reality better since they are also closer to postulated quantitative equilibrium of *on* and *off*-type units in the LGN and other visual

structures. This also agrees with our finding that PSTHs of responses to moving stimuli obtained from the same recording points better imitated the activity maps which would have reflected punctate stimulus intensity. Thus, we selected data taking into account only the first group of PSTHs with "symmetrical" responses. Despite this selection, the comparison of PSTHs with consecutive stimulus intensity changes remained difficult because of: (i) inaccuracy of the overlap of the simultaneously investigated RFs; (ii) fast, neuronal adaptation (7) at the retinal and LGN levels; (iii) logarithmic type processes; (iv) spatio-temporal differentiation of signals within the RFs (apart from other reasons). It is hardly possible to estimate the influence of all these factors but the non-linear processes at the initial levels of visual system should be taken into account. For that reason the light intensity curve of the stimulus (Fig. 1*a*) was graphically differentiated and its logarithmic values were presented as curve *b* in Fig. 1. The last operation was done considering the existence of some thresholds in the system. The dashed parts in the *b* curve were drawn as positive because lowering of light intensity activates the *off*-system.

The calculated curve *b* of Fig. 1 approximately fits the shapes of some of the PSTHs (compare Figs. 2*f* and 3*A*). The remaining PSTHs of responses are, however, better approximated by the curve *c* in Fig. 1 (compare Figs. 2*c* and 3*B*). The *c* curve was obtained by adding the appropriate values of curves *a* and *b* in Fig. 1 which means that it combines both the light intensity value and its changes as described by *b* function.

As can be seen in Fig. 3 our PSTH data were better approximated by the *b* and *c* curves than by the light intensity curve as measured before the logarithmic and spatio-temporal changes were made by the system. It can be further seen in the Figs. 2 and 3 that consecutive (1 to 6) peaks of the curves *b* and *c* from Fig. 1 can be well identified in the PSTHs. The arrows point to the extra peaks on the histograms appearing as a result of an activation of receptive fields peripheries by the entering stimulus.

Figure 3 shows PSTHs of response from two groups of cells (A and B) consisting of three units each at different contrast levels. They are characteristic examples of two discussed above types of data, fitting either *b* or *c* curves from the Fig. 1. It was noticed that the flash responses of A-type groups had usually a more tonic characteristic of the responses to diffuse flash than those of the B-type. The latter responded to flash in more phasic-like manner (compare the lower-most histograms of Fig. 3).

Type A groups of cells always produced much higher amplitude of oscillation in response to the moving stripes than those of type B. In

both types, however, a decrease of the stimulus to background contrast diminishes the amplitude of the peak responses in lower contrast conditions. These findings agree well with electrophysiological and psychophysiological data concerning the well known enhancement of Mach effect with increasing contrast.

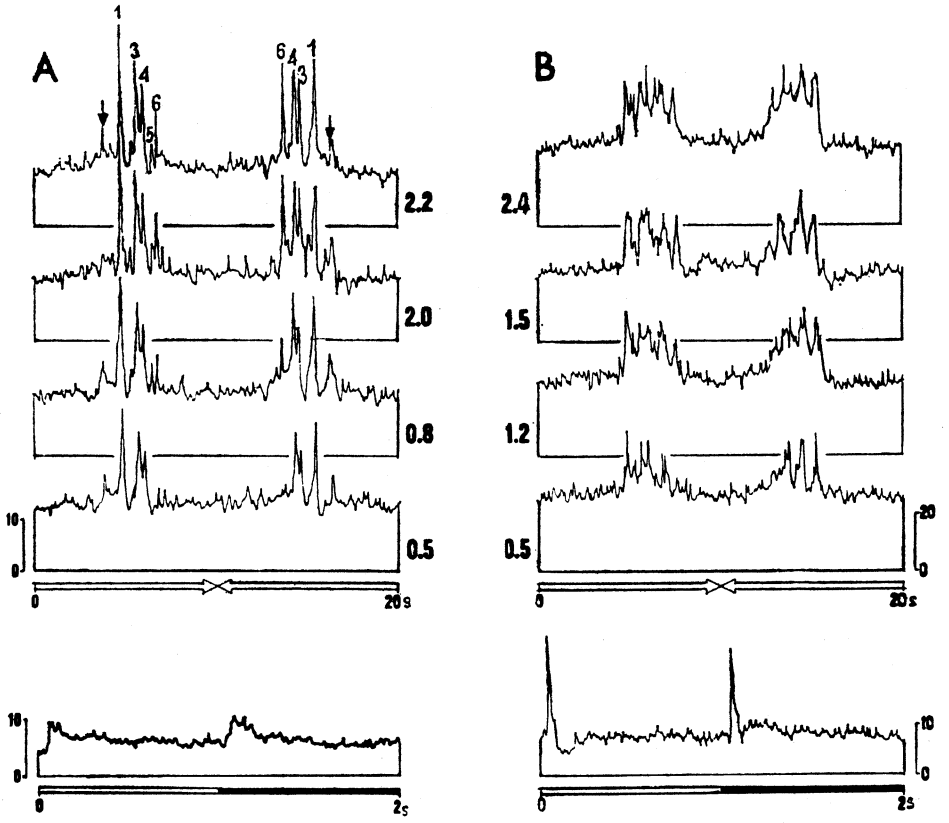

Fig. 3. PSTH of responses for moving stimulus of two groups of three cells each for different stimulus-to-background contrast values. Both groups consist of *on* and *off*-center cells. The lowermost histograms show responses to diffuse flashes. The numbers near the histograms show contrast values defined as the difference between the log intensity of the brightest stripe of the stimulus and the log intensity of the background when both were varied during the experiment. The main peaks of the histogram are numbered. Arrowed are extra peaks due to activation of RF periphery by the entering stimulus. Other explanation as in Fig. 2. See text for details.

Conclusions. We have shown that the punctate intensity of the visual stimulus can be transmitted from LGN to the cortex by the code of "integrated" activity of several units with overlapping RFs. These units

might be grouped in columns according to the IGN retinotopic organization (9). We understand that our approach to the problem of intensity coding by the cell population has some limitations. More advanced methods are needed for a better estimation of the actual processing.

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