ACTA NEUROBIOL. EXP. 1972, 32: 35-42

COLUMNAR ORGANIZATION OF VISUALLY DRIVEN NEURONS IN THE SUPERIOR COLLICULUS OF THE CAT

Krystyna DEC and Bella HARUTIUNIAN-KOZAK

Department of Neurophysiology, Nencki Institute of Experimental Biology, Warszawa, Poland

Abstract. The majority of microelectrode penetrations showed regular vertical arrangement of visually driven neurons. In 10% of penetrations, direction sensitivity of neurons, the responses to diffuse light and moving stimuli and the position of receptive fields were practically identical. In 70% of penetrations, neurons were similar in one or two of these respects. It is concluded that the vertical organization of neurons may be an elementary unit of collicular function.

INTRODUCTION

Data presented by Sprague et al. (1968) and our recent observations (Harutiunian-Kozak et al. 1970) indicate that there is some regularity in organization of neurons in the superior colliculus of the cat. The impression is that visually driven units in the superior colliculus are segregated into cell assemblies according to the positions of their receptive fields and that the shapes of these assemblies form more or less regular vertical columns.

Nevertheless the problem of columnar organization of neurons in the superior colliculus of the cat has not yet been investigated in detail. It was, therefore, interesting to study this problem and in particular the relationship between receptive field positions of neurons, their response characteristics and anatomical distribution.

MATERIAL AND METHOD

Experiments were performed on 25 unanesthetized cats, with pretrigeminal section (Żernicki 1964). 140 neurons in 36 penetrations were investigated.

The measurement of receptive fields and also the stimulating and recording procedure were described previously (Harutiunian-Kozak et al. 1970). The plotting of the blind spot and the area centralis was carried out by means of a narrow-beam (1°) reversible ophthalmoscope.

After each experiment, histological examination of the electrode track was made. The freezed blocks of tissue were sectioned in 30 μ sections and the electrode track was indentified. The lesions for localizing the electrode tip were performed by appyling a d-c 30 μa, during 15 sec.

RESULTS

Several parts of the superior colliculus were explored by vertical penetrations of a microelectrode. In each penetration responses of successive neurons were investigated and classified according to the classification of cells in the superior colliculus reported in a previous paper (Harutiunian-Kozak et al. 1970). Attempts were made to find some criteria which would help in the characterization of neural assemblies.

In 12 penetrations the microelectrode picked up no more than 2 or 3 neurons successively. Of 24 penetrations (where more than three neurons were recorded) 19 showed clear regularity in the organization and 5 penetrations showed no regularity. 13 penetrations were presented in figures as most typical for the superior colliculus neuronal organization.

In about 70% of cases, the neurons whose discharges were observed at successive depths, had several or sometimes one common feature. We considered such groups of neurons as regularly organized or columnar. In 10% of penetrations studied, a great similarity existed between the neurons. We called them "perfect columns". Nearly 20% of penetrations revealed a sequence of neurons without any order in organization ("mixed groups").

From 19 penetrations showing regular vertical organization in two penetrations cells, all had one common feature: they responded to the movement of the black spot, but had no response during the movement of the light spot. In three penetrations, the cells were not sensitive to the changes of diffuse light (light-flashes) but only to the moving stimuli. Sometimes we could observed well organized vertical group of neurons having nearly the same features, but lacking a prominent overlap in the positions of receptive fields.

In the experiment shown in Fig. 1 three penetrations were made in the anterior part of the colliculus superior. In the first track (Fig. 1*A*) there was a great overlap of receptive fields of consecutive neurons, but they differed slightly by their responses one from another. One of them was direction sensitive, and four were not. Two of them responded to

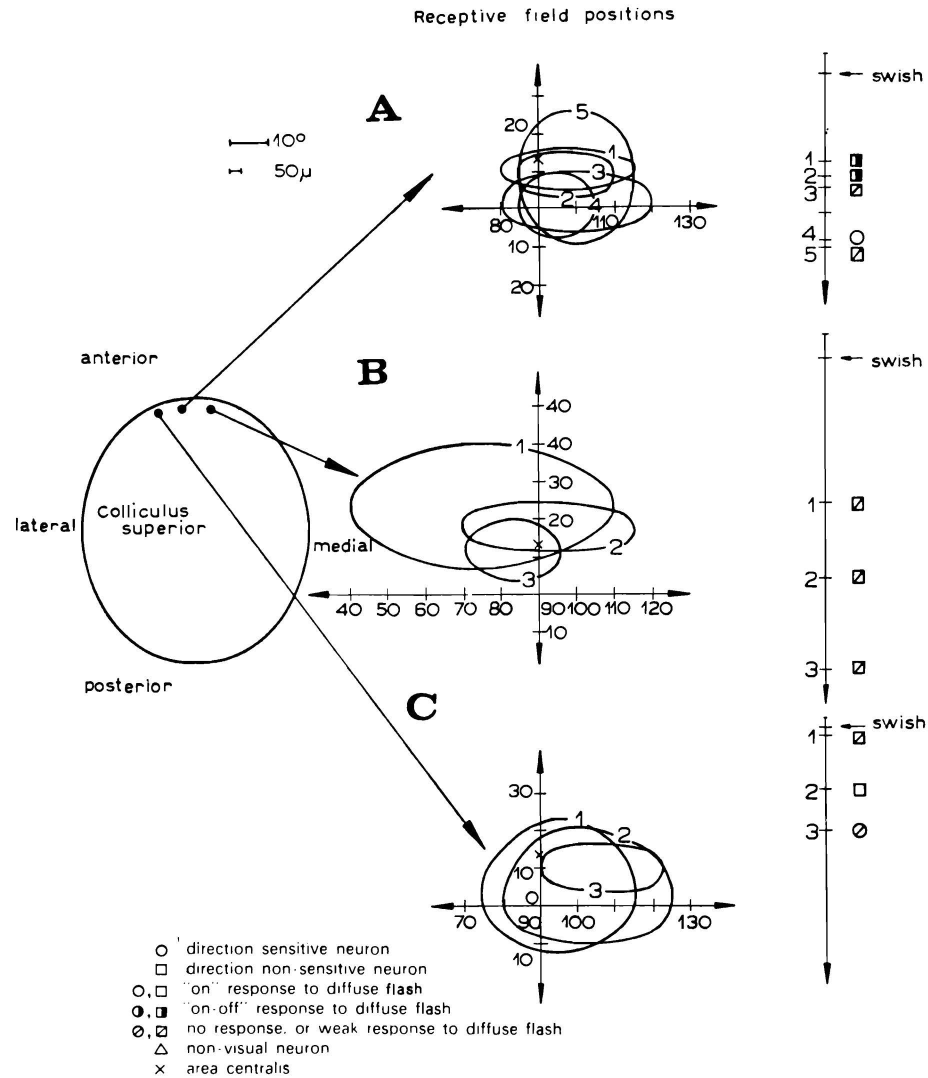

Fig. 1. Receptive fields and response characteristics of neurons in three penetrations of the microelectrode in the anterior part of the superior colliculus. Explanations for this and subsequent figures. The localization of successive neurons is shown on the right. The arrow indicates the beginning of swish reaction (summated response of many cells to the visual stimuli).

flashing light by the "on-off" manner, and two did not react to flash at all. Unfortunately in penetrations in Fig 1*B* and *C* few neurons were observed. In *B* all of them responded vigorously to the moving spots but were direction non-sensitive and also did not respond to the flashing light. The third track (Fig. 1C) presents the receptive fields of three neurons. The receptive fields have a prominent overlap, none of them responded to flashing light. So regularity is present. The difference exists in reactions of cells to moving stimuli. The first two were direction non-sensitive, one of them was direction sensitive.

One of the typical neuron organizations in the superior colliculus is shown in Fig. 2*A*. The microelectrode penetrated the lateral part of the colliculus superior and picked up nine neurons. All of them were direction non-sensitive and their receptive fields overlapped with each other. Differences became apparrent when flashing light was tested. Three neurons responded with "on" reaction to the flashing light, two with "on-off",

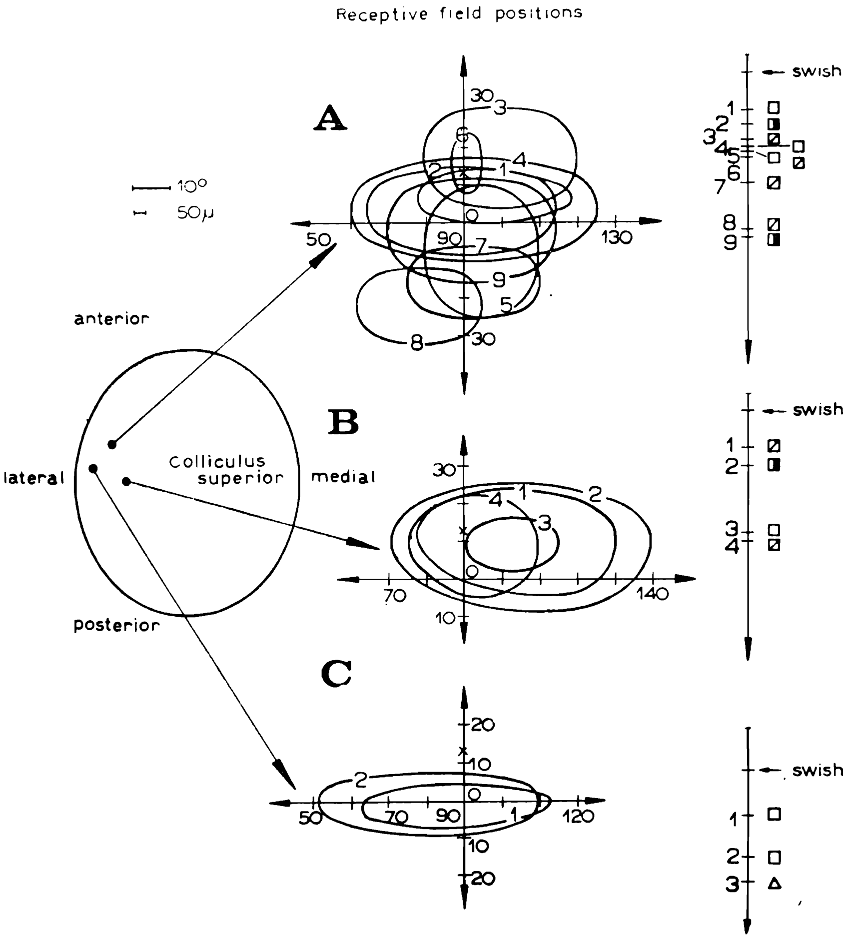

Fig. 2. Receptive fields and response characteristics of neurons in microelectrode penetrations in the lateral part of the superior colliculus.

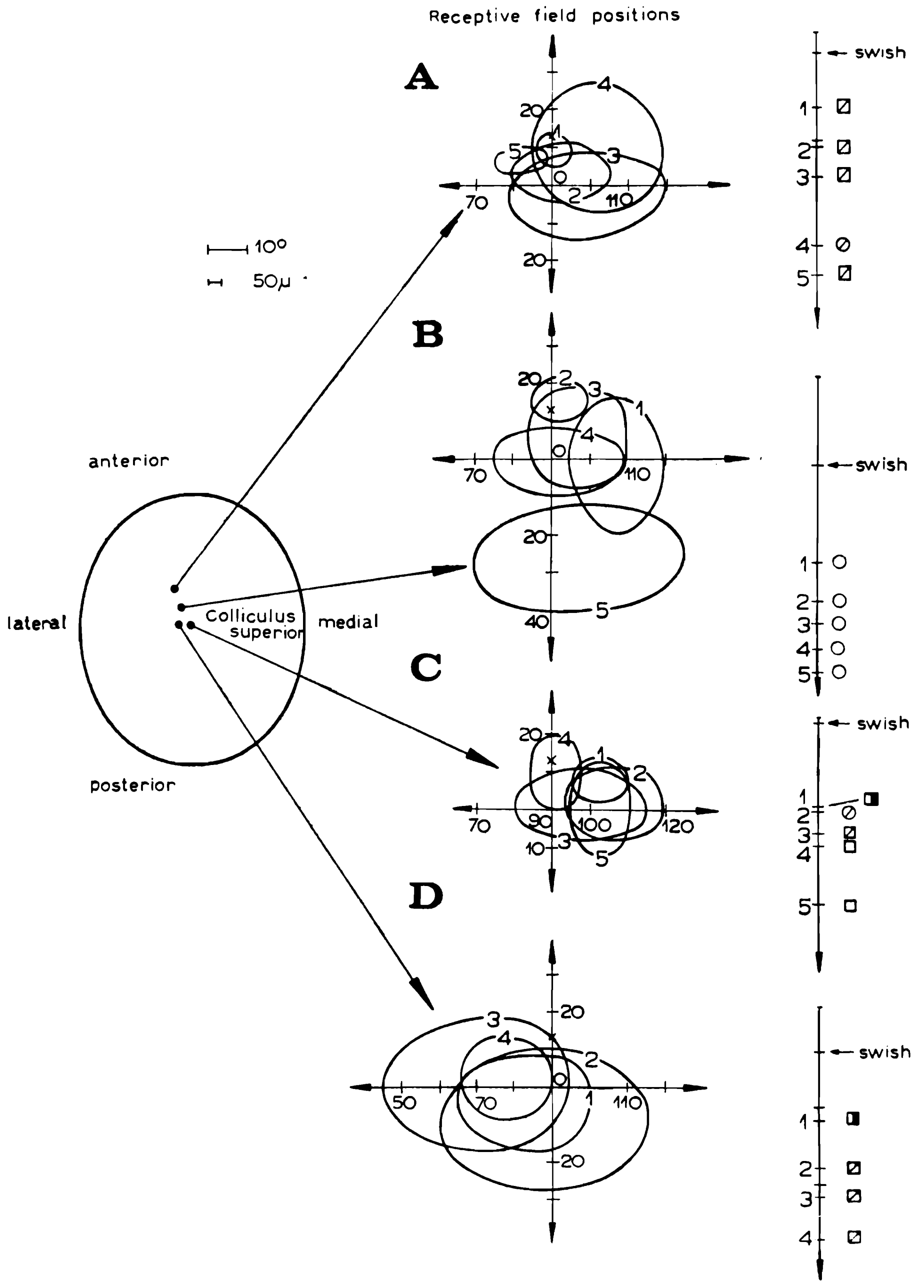

Fig. 3. Receptive fields and response characteristics of neurons in penetrations of the microelectrode in the middle part of the superior colliculus.

and four neurons did not respond to the flash at all. The same results were obtained in the penetration shown in Fig. 2*B*. In the next penetration (Fig. 2*C*), from three neurons observed two were sensitive to visual stimuli and were alike, the third one was not a visual neuron.

Figure 3 represents four penetrations of the microelectrode in the middle part of the colliculus superior. Two penetrations (*B* and *D*) showed well organized cell segregations, where all cells have the same functional characteristics, although some divergence in receptive field positions is evident in *B*. In penetrations *A* and *C* rather mixed groups of neurons were seen. In each penetrations between direction non-sensitive neurons, one direction sensitive neuron is interposed.

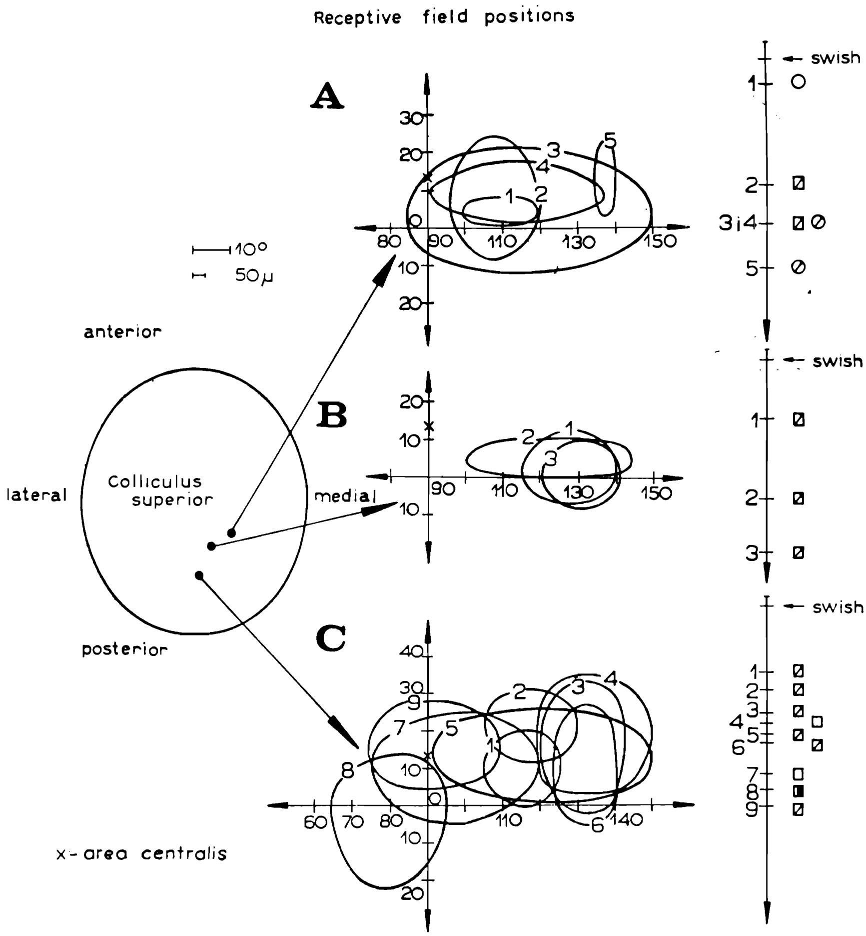

Fig. 4. Receptive fields and response characteristics of neurons in penetrations of the microelectrode in the posterocentral part of the superior colliculus.

Microelectrode penetrations in the posterocentral part of the superior colliculus are represented in Fig. 4*ABC*. In Fig 4*A*, five successive neurons with different functional characteristics were recorded. There was no regularity in their organization and they were classified as mixed groups. The next penetrations (Fig. 4*BC*), showed well organized cell segregations where all units had one common feature — all of them were direction-non sensitive. The differences between cells were observed in the third (*C*) penetration, when responses to the flashing light were tested. Although the majority of cells did not respond to the diffuse flashing light, some of them had "on" reaction, and one unit "on-off" reaction to the flash. Differences exist also in the positions of receptive fields (no overlap) which is clearly seen from the figure.

The surface curvature of the colliculus superior of the cat is very small and practically negligible. So deviations from the regular vertical organization of neurons were probably not caused by the oblique penetrations of the microelectrodes, and recordings from the neurons nearby columns.

DISCUSSION

The data presented in this paper confirm the concept that neurons in superior colliculus are organized into regions according to their functional characteristics, or receptive field positions. Recordings made during multiple microelectrode penetrations in different parts of colliculus superior make it clear that the regions have columnar structure, being oriented rather vertically.

Even in a regular segregation picked up by long microelectrode penetration, as a rule, the cells differ more or less one from another, and have only one or two common features typical for all of them. The impression is, that although vertical organization of visually driven neurons in the colliculus superior of the cat undoubtedly exist, it is not so perfect, as in the cortex (Mountcastle 1967), or in the superior colliculus of the ground squirrel (Michael 1967).

It may be questioned, whether such an organization of cells has any functional significance. A conclusion, that such a vertically linked group of cells is the elementary unit of cortical function was put forward by Lorente de Nó (1949), who emphasized that the vertical chains of neurons were capable of input-output activity without necessarily wide horizontal spread. Later Mountcastle (1957) and Hubel and Wiesel (1963) confirmed this hypothesis. It follows from their experiments that neurons in such vertical columns are capable of integrated activity of a complex order due to their interconnections. Such interconnection are easier to organize in the assemblies of neurons, where there is more or less similar afferent input.

As far as the visual system is concerned a regular order of neurons may facilitate to a great degree the processes of detection of visual stimuli. Experiments presented in this paper indicate that the elementary unit of the functional organization of the colliculus superior is a group of vertically linked neurons with more or less similar functional properties.

This investigation was partially supported by Foreign Research Agreement No. 05-275-2 of the U.S. Department of Health, Education and Welfare under PL 480.

REFERENCES

HARUTIUNIAN-KOZAK, B., KOZAK, W., and DEC, K. 1970. Visually evoked potentials and single unit activity in the superior colliculus of the cat. Acta Neurobiol. Exp. 30: 211–232.

HUBEL, D. and WIESEL, T. 1963. Shape and arrangement of columns in cat's striate cortex. J. Physiol. (London) 165: 559–568.

LORENTE de NÓ, R. 1949. Cerebral cortex: architecture, intracortical connections, motor projections. *In* J. F. Fulton (ed.), Physiology of nervous system. Oxford Univ. Press, Oxford p. 274–313.

MICHAEL, C. 1967. Integration of visual information in the superior colliculus. J. Gen. Physiol. 50: 2485–2486.

MOUNTCASTLE, W. 1957. Modality and topographic properties of single neurons in cat's somatic sensory cortex. J. Neurophysiol. 20: 408–434.

SPRAGUE, J., MARCHIAFAVA, P. and RIZZOLATTI, G. 1968. Units responses to visual stimuli in the superior colliculus of the unanesthetized mid-pontine cat. Arch. Ital. Biol. 106: 169–193.

ŻERNICKI, B. 1964. Isolated cerebrum of midpontine pretrigeminal preparation: a review. Acta Biol. Exp. 24: 247–284.

Received 11 June 1971

Krystyna DEC and Bella HARUTIUNIAN-KOZAK, Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa 22, Poland.