ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol. Exp. 1996, 56: 873-880

Spatial organization of receptive fields of cat's. Hippocampal visually driven neurones

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Abstract. According to the spatial configurations of receptive fields two broad groups of neurones in dorsal hippocampal region (HR) were distinguished. The receptive field borders of 22 cells have regular (R) smooth contours (squares or rectangles), usually with a horizontally oriented longitudinal axis. The second group was composed of neurones (20 cells) with irregular (IR) configurations of receptive fields. Some neurones (16 cells) of this group had relatively simple spatial configurations of receptive fields and 4 neurones had receptive fields with more intricate spatial configurations which formed complex geometrical shapes in the visual field. The exploration of the distribution of response properties a to stationary flashing spot over the RF surface revealed that the majority of cells with regular receptive fields have heterogeneous stationary structure with ON, ON-OFF and OFF subregions sequentially located in the receptive field, and these neurones, as a rule, were direction-sensitive. The neurones with irregular receptive fields, on the other hand, had a rather homogeneous structure of RFs when tested by a stationary flashing spot and only four neurones of 20 investigated were directionally sensitive.

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Key words: cat, hippocampal region, visually driven neurones, receptive field, movement sensitive cells

INTRODUCTION

Although there have been a number of studies describing the responses of single units in cat dorsal hippocampus (CA1 and CA3 areas) to visual stimulation (Vinogradova 1960, Brajnik and Vinogradova 1970, Brown and Horn 1977, Vinogradova and Dudaeva 1971, Gloveli and Ioseliani 1981, Harutiunian--Kozak et al. 1985, 1989, Kazarian et al. 1991), the knowledge of spatial properties of a hippocampal region (HR) neurone's receptive field (RF) is still far from complete. Detailed investigations of the spatial organization of RFs of visually driven neurones and their relation to specialized response properties of the cells are still lacking. At present, relatively little is known about the spatial configurations of RFs of HR neurones as well. Earlier we have studied the spatial organization of RFs of visually driven neurones in dorsal hippocampal region (HR) based on the responses to stationary flashing and moving dark and bright spots (Harutiunian--Kozak et al. 1985, 1989). The experiments which we present here were the continuation of these investigations.

The present paper describes the results of our experiments concerned with detailed exploration of RF configurations of hippocampal visually driven neurones and their response properties revealed by stationary flashing and moving visual stimuli.

METHODS

The experiments were carried out on 36 adult cats weighing 2.5-4 kg. A tracheotomy, fixation of the animal's head in a stereotaxic apparatus and pretrigeminal brain stem section was performed under ether anaesthesia (Żernicki 1968). Afterwards the animal was immobilized by Ditilin (diiodide dicholine ester of succinic acid), 7 mg/kg for an hour and maintained by artificial respiration (21 strokes/min.). A window was cut out of the skull overlying the dorsal hippocampus, and after durectomy it was filled with soft wax to avoid the pulsations of the brain. The pupils were dilated by applying 1% atropine sulphate and the corneas were covered by contact lenses (0 dioptric power) to avoid drying. Correction lenses were used when necessary. The body temperature of the animal was kept within 37°-38°C by means of an electric heating pad. The functional state of the animal was monitored by continuous recording of EEG and ECG. Arterial blood pressure was within 90-100 mm Hg.

The activity of single cells was recorded extracellularly by tungsten microelectrodes covered by vinyl varnish (Hubel 1957), with uninsulated tip of 2-5 μm. Responses of neurone were analysed by the ANOPS-101 analyzer using the program of Post--stimulus Time Histograms (PSTH). Special care was taken in discrimination of single spikes from the background noise. Only spikes with amplitudes of three times higher than background were chosen, with correspondingly adjusted trigger level. Usually 16 repetitions of stimulation were applied. Single unit discharges were also monitored using a loudspeaker during the course of the experiment.

The configurations and positions of single neurone RFs in the visual field were estimated using stationary flashing spots on the perimeter screen located at 1 m distance from nodal points of the eyes. As a first step, the RF borders and position in the visual field were determined by hand-held dark stimuli. Afterwards, a large surrounding area of the visual field where the RF under observation was located was explored point by point by means of flashing bright spots. This method allowed us to obtain the approximate configurations (shapes of contours) of the RFs. For the recording of neurone responses to a stationary flashing spot, we chose individually for each neurone the minimal diameter (0.1°-3°) for the testing spot that gave an adequate response. Next, the distribution of response characteristics to the stationary stimulation over the whole surface of the RF was performed. Although pretrigeminal brainstem section eliminated horizontal eye movements, nevertheless the vertical movements were preserved and could affect the results. Thus to avoid errors in RF measurements, as a rule, at the end of recordings of each neurone the RF position in the visual field was measured once more by hand-held

black stimuli. No shifts of RF positiones was observed. Dark and bright moving visual stimuli were applied using a conventional mirror-galvanometer system controlled by a trapezoidal pulse generator, and classifications of dynamic properties of neurones were performed according to their reactions to moving stimuli.

The contrast of a bright spot with respect to the background illumination was kept constant at 8 lx against 2 lx background during the entire experiment and, correspondingly, dark spots were of 2 lx illumination against 8 lx background. Under such conditions of stimulation the distortions of measurements caused by scattered light of visual stimuli were minimized.

At the end of each experiment a coagulation of the small brain area was made by the recording electrode. The brain was then perfused with 10% Formalin solution and after the proper fixation time (no less than a week) the recorded site was localized on the 30-40 μm histological sections.

RESULTS

Of all the 168 recorded neurones in HR, 54 were visually driven. Twelve neurones of these 54, which showed some habituation of responses to repetitive visual stimuli, were not included in this study. Thus the RF properties of 42 visually driven neurones in CA 1 (28 cells) and CA 3 (14 cells) regions of cat's HR have been studied. Single neurone activity was picked up by the penetration of the microelectrode through hippocampal CA_1 and CA_3 regions and visually driven neurones were observed scattered through all layers of the regions under investigation. No differences were found in the properties of neurones in CA_1 and CA_3 hippocampal regions, thus they are considered together in this study.

In order to analyse the spatial organization of RFs of visually responsive HR neurones we have followed our usual procedure of stimulating the cells by stationary and moving visual stimuli. Of all investigated neurones nearly 81% responded well to a stationary flashing light spot positioned in the centre of the RF. Three common types of responses to stationary visual stimuli were observed: OFF responses (14 cells) when the neurone reacted to light switched off (Fig. 1Aa), ON responses (3 cells), when the cell responded to the light switched on (Fig. 1Ab) and ON-OFF, (17 cells) when the neurone responded to both light on and light off (Fig. 1Ac).

Each neurone under investigation was further examined by moving visual stimuli which were bright and dark moving spots of various diameters, crossing the RF along its horizontal or vertical axis. Most (97%) of the neurones studied were sensitive to moving stimuli. Three groups of neurones were identified. The first group consisted of 28 neurones classified as direction non-sensitive, where a neurone responded with nearly equal number of discharges to the two opposite directions of stimulus

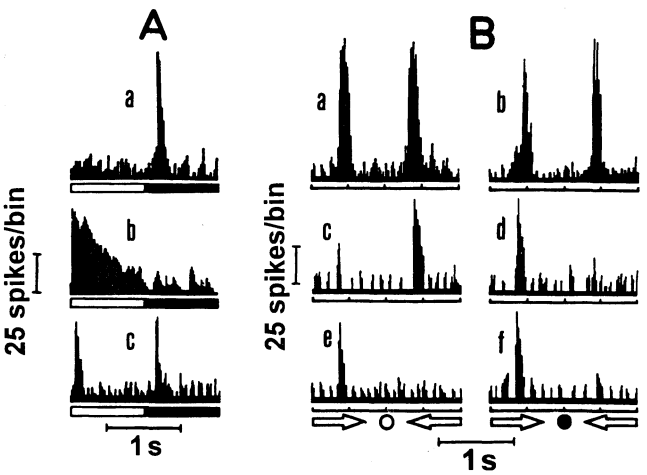

Fig. 1. Responses of hippocampal visually driven neurones to stationary and moving visual stimuli. A, PSTH of responses of three neurones to the stationary flashing spots positioned in the centre of the receptive field: a, responses of an "OFF" neurone; b, responses of an "ON" neurone; c, responses of an "ON-OFF" neurone. Light strip under the histograms indicate ON period of stimulation (1s) and black strip OFF period of stimulation (1s). Spot size 1^o of visual angle. B, PSTH of responses of three neurones to moving visual stimuli; a,b, responses of a direction non-sensitive neurone to bright (a) and dark (b) moving spots along the horizontal axis of the receptive field; c,d, responses of direction-sensitive neurone, which changed its prefered direction when contrasts of moving stimuli were changed; e,f, responses of a direction-selective neurone to the motion of bright (e) and dark (f) spots across the horizontal axis of the receptive field. The spot size 5^o of visual angle.

motion across the receptive field. A reversal of the contrast of the moving stimuli did not change the response patterns of these cells (Fig. 1Ba,b). The second group consisted of direction-sensitive neurones (12 cells) which were subdivided into two subgroups. The first subgroup comprised direction-asymmetric neurones (4 cells), which responded vigorously to motion in one direction (the preferred direction) and weakly or not at all to the opposite direction of the movement (null direction). This pattern, however, could be altered when the contrast of the moving stimuli was reversed (Fig. 1Bc,d). The second subgroup of direction-sensitive cells comprised the direction-selective neurones (8 cells), which do not change their preferred direction of responses depending on the contrast of the moving stimuli (Fig. 1B,e,f). After determination of general properties of a neurone under investigation, the whole surface of its RF was investigated using a flashing bright spot (0.1°-2° of diameter) positioned point by point within the RF and within its surroundings. The border line between the responsive test-zone of a RF and an unresponsive test-zone spatially close to the former one and situated outside of the RF was taken as a boundary edge of the RF under examination. Thus all the notions in this study about the RF's irregular configurations were defined according to the neurone responses to a flashing light spot. Such an exploration enabled us to outline in some approximation the spatial configurations of the borders, i.e. , the spatial configurations of the RFs studied.

According to the shapes of configurations outlined by stationary flashing spots two main groups of RFs were found. The first group (53%) comprised the RFs with regular boundaries (squares or rectangles) with the longer axis mainly in the horizontal orientation. These fields were classified as regular RFs (RRF). In this group were included also the neurones with extremely small RFs ($<1^{\circ}$), where a correct estimation of RF's border shapes was difficult to make, hence they were called point fields.

The other group of RFs (47%) was characterized by complex configurations of contours and they were classified as irregular RFs (IRF).

Regular receptive fields

The majority of the investigated neurones (22 cells) had RFs with regular boundaries, which could be considered as rectangles or squares when tested by flashing spots as well as hand-held dark stimuli. The boundaries of the RFs were determined first by means of hand-held dark visual stimuli and then by a flashing bright spot. Usually, they were located in the contralateral visual hemifield in the upper and lower quadrants, although some dispersion into the ipsilateral hemifield was observed. Figure 2 represents five examples of the RFs of this group. As demonstrated in this figure there are essential differences in the size and spatial position of RFs of a given neurone depending of the type of visual stimulus (dark or bright) used for the measurements. One could suggest that the observed differences are due to the scattered light when the bright stationary stimulus is applied. However in that case it should have been a more or less symmetrical distortion of RF's sizes and boundaries, which is not the case. For example, in Fig. 2A,a "dark" RF is quite asymmetrically located in the upper right hand part of the "bright" RF. The neurone presented in Fig. 2C has the "dark" RF in the extreme left hand part of the "bright" RF. In Figure 2B,D the "dark" RFs are nearly squares, but the "bright" RFs are

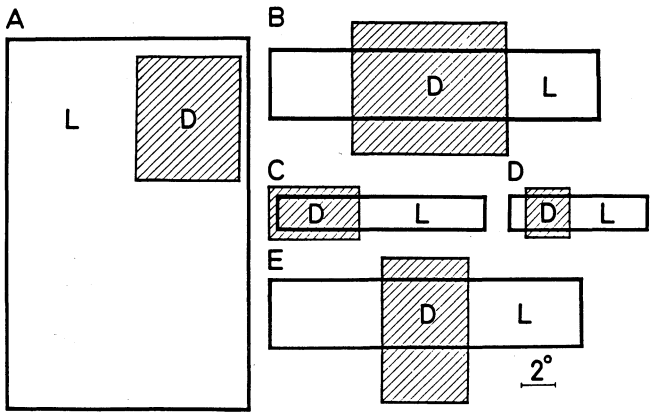

Fig. 2. Regular receptive fields. A-E, spatial configurations of receptive fields of five different neurones measured by hand-held dark visual stimuli (D), shadowed space and by stationary flashing spot (L), white space.

elongated rectangles, and in Fig. 2E the "dark" RF (D) has its longitudinal axis vertically oriented, whereas the longitudinal axis of the "bright" RF (L) is horizontally oriented. Usually 11% to 52% of the surface of the "dark" RFs overlapped spatially with "bright" RFs.

The examination of the distribution of cell response patterns to the stationary stimulation all over the RF has revealed that, in the majority of cases, regular RFs had a heterogeneous structure and are composed of subregions with different responses to the stationary stimulus. Figure 3 illustrates schematically the qualitative characteristics of neurones presented in Fig. 2. The stationary flashing bright spot positioned point-by-point on the RF surface revealed different subregions of RFs (ON-OFF, OFF and ON). Some RFs consisted of two subregions with ON-OFF and OFF responses situated side by side (Fig. 3A and F). Other RFs could have three or four sequences of intermittently located subregions. For example, the RF in Fig. 3D has four subregions: the ON-OFF response was elicited on the left hand periphery of the field, the OFF response elicited when the position of flashing light spot was shifted to the right hand, ON-OFF responses resulting from further shifting of the flashing spot and finally the right hand section of RF again gave pure OFF response. Apart from one example (Fig. 3B) all the regular RFs presented in Fig. 3 had heterogeneous structure and resemble the simple cells as described by Hubel and Wiesel (1965) in the striate cortex.

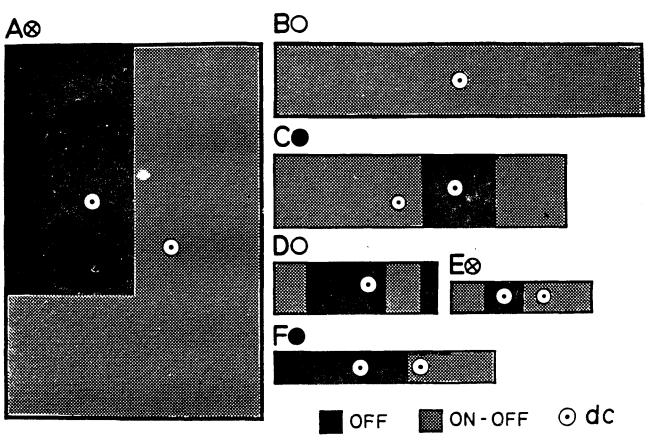

Fig. 3. Spatial distribution of response patterns to the flashing spot in regular receptive fields. A, RF tested point by point by flashing spot 3° in diameter. B-F, RFs tested by flashing spot 0.5° in diameter. Symbols on the right hand side of letters indicate the pattern of responses of each neurone to moving visual stimuli, across RF's horizontal axis. Cross, neurones responded only to stationary visual stimuli and are insensitive to the motion. Circle with cross, direction non-sensitive neurones. White circle, direction selective response. Black circle, direction asymetric response; dc, discharge centre. Explanations are the same for Fig. 5.

The discharge centers (the regions of the optimal responses in RF) of RFs were in most cases eccentrically located (Fig. 3A and C-F) and heterogeneous RFs could have more than one discharge centre where each subregion has its optimal response zone (Fig. 3 A,C,E and F).

All the neurones with regular type RFs (RRFs) were also tested by moving visual stimuli. Nearly 75% of them were direction sensitive. For example, neurones presented in Fig. 3B and D are directionally selective, i.e. , they didn't change direction selectivity when the contrast of moving stimuli was reversed. The neurones in Fig. 3C and F were directionally asymmetric, i.e., they changed the preferred direction when the contrast of moving stimuli was reversed. Receptive fields presented in Fig. 3A and E were direction non-sensitive.

Irregular receptive fields

The results of experiments revealed that 20 of 42 visually driven neurones, when tested by a stationary flashing spot, had irregular spatial configurations of RF borders and hence were called irregular receptive fields (IRFs). The most interesting were the neurones with extremely intricate configurations of RFs. Spatial configurations of three RFs of such type are presented in Fig. 4. These RFs differ significantly from one neurone to another. It is worthwhile to note that two unusual neurones were observed in this group, that had RFs consisting of two spatially separated subregions. These neurones resembled the double - field neurones described by Hubel and Wiesel (1971) in Siamese cats and by Stein et al. (1983) in normal cats. They were included in the group of irregular RFs (see Fig. 4A).

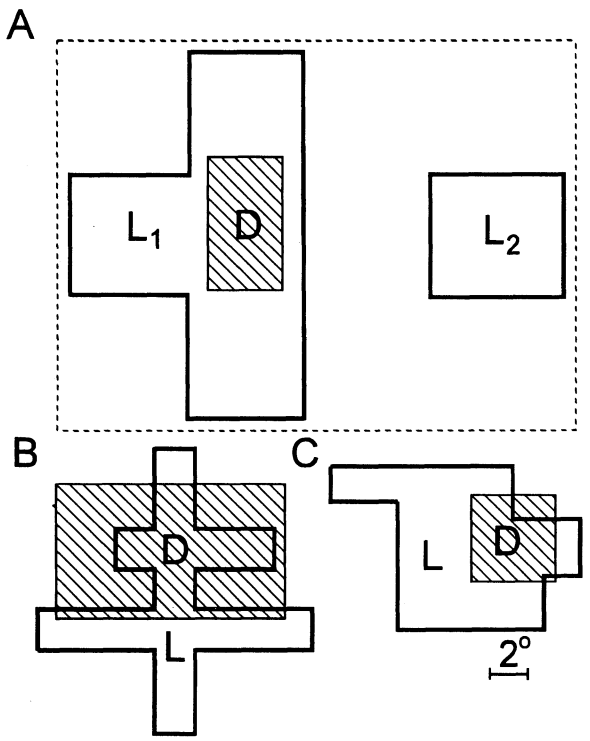

Fig. 4. Spatial configurations of irregular receptive fields. A, a receptive field which consists of two spatially separated regions, when tested by stationary flashing spot (L_1, L_2). Shadowed rectangle (D) indicates RF measured by dark stimuli. B,C, spatial configurations of two RFs with complex contours. Flashing light spot used in measurments was 0.5^o (C) and 0.1^o (B).

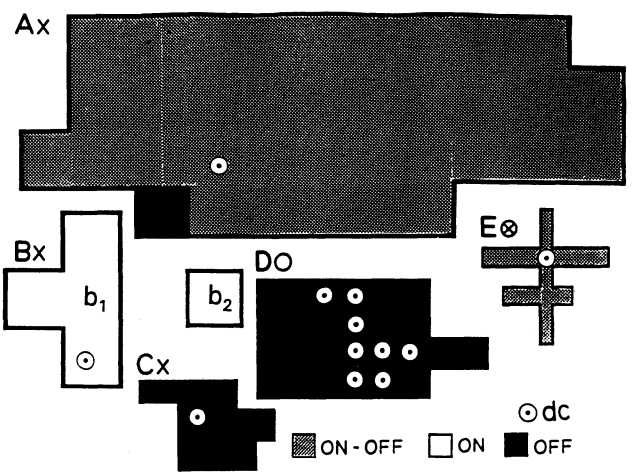

Fig. 5. Spatial distribution of response patterns to the flashing spot in irregular RFs. A, the RF with heterogeneous organization ON - OFF responses to the flashing spot (2^o in size) were recorded from the majority of the RF, only small region in lower left part of the field reveal OFF responses. The neurone did not react to moving visual stimuli. B-E, four RFs with homogeneous distribution of responses to the stationary flashing spot (0.1^o - 1^o of visual angle). B, movement non-sensitive neurone, both parts of the field (b_1, b_2) revealed ON responses to flashing spot. C,D, homogeneous OFF receptive fields. E, homogeneous ON-OFF receptive field.

As is seen from the figure the RF had an irregular configuration consisting of two spatially separated subregions shifted by 6^o of visual angle (Fig. 4AL_1 and L_2). Both subregions responded to the flashing light spot by ON responses (Fig. 5Bb_1 and b_2). The RF discharge centres of this group of neurones were generally located eccentrically. Sometimes the RFs could have several optimal response subregions spatially situated close to each other and forming a large space of optimal responses within the RF (Fig. 5D). The irregular RFs generally had a homogeneous structure and the majority of them had the same type of responses to a flashing bright spot throughout the RF surface (Fig. 5B-E). The neurone presented in Fig. 5A exhibited a small subregion in the left hand lower periphery of the RF with OFF characteristics of responses to the flashing light spot whereas the entire RF is ON-OFF. The majority of irregular RFs revealed less sensitivity to the stimulus motion. Several neurones (Fig. 5 A-C) did not respond to the moving spots across their RFs (crosses near the letters), the neurone shown in Fig. 5E had a weak reaction to the motion which was direction non-sensitive, but the neurone presented in Fig. 5D was direction-selective; this was only neurone in this group that exhibited directional sensitivity.

The distribution of geometrical centres of RFs (the crossing point of horizontal and vertical axes of the RF) in the visual field was mapped for 27 investigated neurones. As shown in Fig. 6 the regular RFs were situated mainly near the area centralis, whereas the majority of irregular RFs were situated further in the periphery of the visual field. In general, both types of RFs were located in the contralateral upper quadrant of the visual field with some scatter into the contralateral lower quadrant and ipsilateral hemifield.

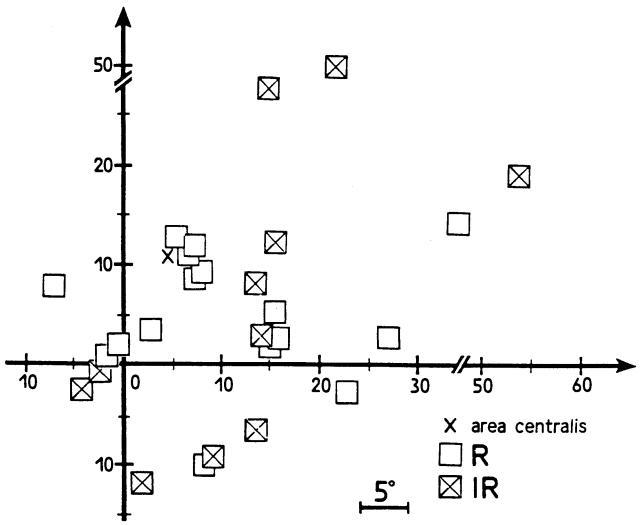

Fig. 6. The distribution of regular and irregular receptive field centres in the visual field.

DISCUSSION

On the basis of morphological investigations it has already been established that there exist pathways from the lateral geniculate body to the limbic cortex (Cuenod et al.1965, Marty et al. 1969, Mac Lean and Creswell 1970), and the limbic cortex in turn is the main source of afferent fibers to the hippocampus proper (Adey and Meyer 1952, Blackstad 1956, Mac Lean et al. 1968). Thus, visual sensory information reaches the hippocampus by polysynaptic pathways. In spite of this, as was shown by investigations of functional properties of hippocampal visually sensitive neurones (Kazarian et al. 1991), visual sensory input seems to preserve its organized character.

Recent studies of visual sensory information processing in hippocampal region (Gloveli and Ioseliani 1981, Harutiunian-Kozak et al. 1985, 1989, Kazarian et al. 1991) indicate that there is an obvious need for a more detailed knowledge of the spatial organization of RF properties of visually driven neurones in this limbic structure of the brain. It is well known that spatial organization of RFs is a key element in the mechanisms of central processing of visual information (Stevens and Gerstein 1976, Camarda et al. 1985, Peterhans et al. 1985, Hawken and Parker 1987, Galli et al. 1988, McLean and Palmer 1989). Thus the main focus of our investigation was the exploration of spatial configurations of the RFs of hippocampal visually driven neurones and their relation to functional properties of the neurones. Two main groups of RFs were distinguished according to their spatial configurations: regular (RRFs) and irregular (IRFs). Receptive fields in the RRFs group have rather regular configurations, being mainly horizontally oriented rectangles or squares. RFs in the IRFs group, on the other hand, had irregular intricate contours which form spatially complex geometrical shapes in the visual field. At first sight the explanation for these data seems to lie in their afferent input convergence, which might be apparently more complex for the irregular than for the regular receptive fields. Thus, it is possible that multiple convergence fibres conducting afferent information to a certain visually driven neurone in the HR due to the differential input create intricate border lines of IRFs. Alternatively, one could suggest that RRFs have more or less uniform visual inputs to the hippocampal neurones. But these suggestions look somewhat puzzling when the functional properties of hippocampal visually driven neurones are considered. The results of our experiments showed that neurones with RRFs surprisingly show a higher specialization in transferring information about the direction of moving stimuli. The IRFs, especially those of more complex configurations, seem to have simpler functional characteristics and they react almost homogeneously to stationary flashing bright spots over the entire surface of their RFs. The RRFs, on the contrary, have spatially more differentiated subregions, such as ON, ON-OFF or OFF sequentially located within the RF.

In general the receptive fields observed in our experiments seemed to show some resemblance to the simple cells of the striate cortex (Hubel and Wiesel 1965, Bishop et al. 1971, Sherman et al. 1975, Emerson and Gerstein 1977, Kato et al. 1978, Peterhans et al. 1985). Evidently the interpretation of present results could not be based merely on visual afferent convergention patterns taking into account that the visually driven neurones in hippocampus could be targets of afferent inputs of other sensory

modalities. Thus further investigations are necessary to elucidate the functional significance of visually driven neurones in hippocampal CA_1 and CA_3 regions.

ABBREVIATIONS

RF	receptive field
RRFs	regular receptive fields
IRFs	iregular receptive fields
EEG	electroencephalogram
ECG	electrocardiogram
HR	hippocampal region

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Received 2 February 1995, accepted 15 July 1996