Responses from outside classical receptive fields of dorsal lateral geniculate cells in rabbits

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Summary. The effects of stimuli at locations remote from classic receptive fields (CRF) of lateral geniculate cells were examined in rabbits. In anesthetized rabbits, small targets positioned well outside the CRF either facilitated or decreased responses evoked by a stimulus positioned within the most active area of the CRF in 51% of the cells tested, in spite of the fact that when presented in isolation the remote target failed to modify the spontaneous activity of the recorded cell. Late components of the discharge pattern evoked by the central stimulus were mostly influenced by the peripheral target. Focal or ectopic areas surrounding the CRF are thus identified. These areas were not a direct extension of the CRF, since the normal evoked response was unchanged when the remote stimulus moved closer to the CRF. Cells whose CRF were centrally located reacted with an augmented response in the presence of the additional stimulus, whereas units whose CRF was more eccentric exhibited a weaker response when the peripheral target was introduced in the visual field. We also investigated whether superior colliculus afferents to the lateral geniculate nucleus could be associated with these ectopic areas (EA). Depressing superior colliculus activity produced two types of results: (a) often the late component of the response pattern was modified; and (b) the influence of the remote stimulus disappeared with collicular blockade in 80% of tested neurons. These results provide evidence that the CRF of geniculate cells may be surrounded by satellite zones, which modify the responses to the central target when invaded by circumscribed stimuli. It appears that these focal areas constitute additional compartments of the receptive field organization. They are not due to a local horizontal circuit but are brought about by collicular afferents.

Key words: Receptive field – Lateral geniculate nucleus – Superior colliculus – Vision – Rabbit

Introduction

Since the pioneering work of Hartline (1938), Adrian (1941), and Kuffler (1953) sensory neurons have been characterized by their receptive fields (RFs). When a RF is invaded by a stimulus, the spontaneous firing rate of the neuron is modified. Classic dogma states that RFs have well-defined boundaries, and stimuli falling outside these borders do not influence the unit.

However, several investigations have challenged this concept over the past three decades. For instance, there have been reports suggesting that large targets introduced outside the classic RF (CRF) have detectable effects. (Mcllwain 1964, 1966) has demonstrated that a 20° disc located 90° of arc from the CRF could increase the firing rate of cat retinal ganglion cells, a phenomenon that he called the periphery effect (PE). These observations were confirmed by others (Levick et al. 1965; Cleland and Levick 1974; Barlow et al. 1977; Derrington et al. 1979; Rapaport and Stone 1988). In addition, Ikeda and Wright (1972) reported that phasic and Y-type cells are particularly sensitive to the presence of peripheral targets.

It was also reported that sudden shifts of gratings covering large portions of the visual field and surrounding the CRF produce modifications of retinal and geniculate cell responses (Krüger and Fischer 1973; Fischer et al. 1975; Krüger 1980). This observation was called the “shift effect” (SE) and was an additional modification to the response evoked by the gratings themselves (Fischer et al. 1975). While PEs and SEs are relatively frequent in cats and monkeys, in rabbits the situation is more controversial. Watanabe and Tasaki (1980) reported that 18% of ganglion cells react to remote stimuli, but Caldwell and Daw (1978) and Molotchnikoff et al. (1986) failed to observe such influences.

At the level of the superior colliculus, Rizzolatti et al. (1974) showed that, in cats, the addition of a small target up to 120° away from the CRF could reduce responses in the SC and suprasylvian cortex but not in the striate cortex (Rizzolatti and Camarda 1977). Pigeons also exhibited a similar phenomenon in the optic tectum (Frost et al. 1981).

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In all previous investigations, these peripheral effects were attributed to local lateral interactions that take place within the retina, lateral geniculate nucleus (LGN), or superior colliculus (SC). Allman et al. (1985) suggested that the so-called silent surround could yield excitatory responses and proposed that the CRFs include these supplementary areas.

The direct implication of these investigations is that the CRF, with its bipartite (center and surround compartments) organization may require a redefinition of its structure. The aim of the present investigation is to demonstrate that the CRF is surrounded by ectopic areas (EAs).

Our data suggest that the CRF is surrounded by remotely located islands or satellites, which can be excitatory or inhibitory. The influence of these “islands” emerges when small “mute” targets invade these focal areas and the responses to stimuli positioned within the CRF are modified. We call these supplementary targets mute because they fail to change cellular activity when applied alone, that is, without the simultaneous stimulation of the RF. Because the supplementary targets are small, our described phenomena contrast with PE and SE, in which peripheral stimuli are usually large. Furthermore, our results indicate that these remote influences cannot be due to interactions between cells within the LGN, because the inactivation of the SC suppresses these influences. Thus the influence of these islands may be conveyed by the colliculo-geniculate pathway. Consequently, collicular afferents which convey visual signals from retina to cortex contribute to receptive field organization of this thalamic station.

Materials and methods

Animal preparation

The general methods have been described elsewhere (Molotchnikoff and Cérat, 1990). Briefly, New Zealand rabbits, weighing between 2 and 3 kg, were prepared for recording neuronal activity in the dorsal LGN and SC. Most animals were first anesthetized with ketamine (60 mg/kg) in conjunction with acepromazine (1.6 mg/kg), then ventilated with a mixture of halothane (Fluothane) 0.5% and N₂O/O₂ (70/30) during the rest of the experiment. In a few experiments (20% of studied units), we used urethane (25%, 0.8 g/kg IV) to anesthetize animals. Results from both groups of experiments were identical and are combined here. Lidocaine hydrochloride (2% Xylocaine) was applied at all surgical and pressure sites. The animals were paralyzed with an injection of gallamine triethiodide (10 mg/kg h). Electrocardiogram (EKG) and rectal temperature were monitored throughout the duration of the experiments. Since rabbits are naturally hypermetropic (Barlow et al. 1964), the eye was covered with a contact lens (+6 D) to focus the image on the retina. The experiments were terminated with an overdose of sodium pentobarbital (Nembutal).

Glass microelectrodes filled with NaCl (20 MΩ direct current, DC) were employed to record cellular action potentials. The latter were amplified and conveyed to an audio monitor, a window discriminator, an oscilloscope and, finally, a computer for on- and off-line analysis.

Stimulation

For each recorded cell, the position of the RF, its dimensions, boundaries and the sensitivity of the unit to movement were determined with a hand-held ophthalmoscope whose slits or disk were projected onto a translucent screen. Then, the test (or central) stimulus, which was a light-emitting diode (LED), was positioned in the center of the activating area. This stimulus could be switched on and off. It subtended an angle of 2° of arc with an intensity of 6.5 × 10⁻¹ cd/m². In addition, a second, or conditioning, stimulus was introduced in the visual field, but well outside the limits of the CRF. This remote stimulus never came closer than 30° of arc perimeter from the RF center. This distance was chosen because, in rabbits, the largest geniculate RFs are 15° (Oyster et al. 1971). Thus a space of at least one uninvaded RF between the central and remote targets was maintained. The remote stimulus was generated on a cathode ray tube screen (P = 31), contrast 90%. In most cases, it was a slit of 8° × 2° whose intensity was 1.6 × 10⁻¹ cd/m². Both stimuli were under electronic control through function generators. In order to reveal the presence of ectopic zones, the conditioning stimulus was positioned at determined locations along the horizontal and/or vertical axis. In all cases, five to six equidistant sites were probed. The interstimulus distances were, in most cases, 30, 45, 60, 75, and 90° of arc; thus, the maximal exploring distance of the periphery of a given cell was 90° of arc. At each location, the slit moved for a distance of 3.5° arc in 100 ms, during which time it was turned on. It then reappeared at another location and was turned on again. In most experiments five remote areas were studied. These movements occurred in either centrifugal (moving away from the RF) or centripetal (approaching the activating area) directions. The sequence of loci was random. We employed a moving slit as a stimulus because it has been previously shown that such mobile targets are more efficient in modifying the test responses than stationary ones (Molotchnikoff and Cérat 1990). Hence, single cell activity was measured in four steps: (1) the spontaneous rate, that is, no stimulus present; (2) the conditioning stimulus presented on its own; (3) the test stimulus presented alone (repeated twice to assess cellular variability); (4) both stimuli applied concurrently, with the remote stimulus preceding the central target by 150–200 ms. This interval in the last stage was chosen because it had been demonstrated to evoke an optimal interaction of the paired stimuli (Molotchnikoff et al. 1986). These four steps were randomly interleaved. During the presentation of the remote target, in step 2, the cell’s action potentials were recorded and the collection of data was triggered by the remote stimulus; in no case did a neuron respond to the conditioning (remote) stimulus alone.

Collicular inactivation

In a separate series of experiments, a second micropipette was lowered into the superficial layers of the SC. This pipette was filled with lidocaine hydrochloride 2%. Chicago sky blue was added to the solution to reveal the location and the spread of the drug after appropriate histological treatment. This pipette was connected to a pressure pump to eject the inactivating drug and depress a small population of collicular cells. A silver wire, inserted in the pipette, permitted recording of multicell activity, or field potentials, under the ejecting tip in order to monitor inactivation and recovery and determine the coordinates of the activating area. In most cases, the geniculate (single unit) and collicular (multunit) pipettes were placed in retinotopic register, as evidenced by the fact that the same localized stimulus (LED) evoked responses at both sites.

Figure 1 illustrates the extent of the area from which no response was evoked after local collicular lidocaine injections. A moving slit (1° × 1°) swept the visual field in steps of 2°. The initial axis of motion is located 6° of arc above the activating area. The next axis of movement is 2° below, and so on. Thus, each trace on Fig 1 depicts neuronal activity for one axis of movement on the screen. Under the first column (Cont. 1), it is clear that the activating area lay between loci 3 and 6 (traces 3–6). This discharge area is shown by the upper concentric circles. The internal surface (radius 5°) represents the area.