EVIDENCE OF AN EXTENDED REPRESENTATION OF THE VISUAL FIELD IN THE SUPERIOR COLLICULUS OF THE RABBIT (*ORYCTOLAGUS CUNICULUS*)

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Summary: Electrophysiological mapping using multiple-unit criteria was employed to study the representation of the visual field in the superior colliculus of the rabbit. It was found that the contralateral superior colliculus of the rabbit has an extended representation beyond the representation of the zero vertical meridian or the line of decussation in the geniculostriate system. The amount of extended representation in the contralateral superior colliculus is coextensive with the extent of visual field represented ipsilaterally in areas 17 and 18 of the visual cortex. In agreement with previous findings, the representation of the visual field on the superior colliculus is extremely distorted. Finally, no evidence of an ipsilateral input can be produced.

Key words: extended representation visual field superior colliculus

INTRODUCTION

The orderly representation of the retina has been shown to be present in the central nervous system of all vertebrates investigated. In this rabbit, the general pattern of the visuotopic organization of the superior colliculus mimics the one obtained in the superior colliculus of most other mammals, i.e., the nasal field is represented anteriorly, the temporal field posteriorly, the upper visual field medially and the lower visual field laterally. However, like all other central visual structures of the rabbit, each superior colliculus has an expanded representation along the entire zero horizontal parallel of the contralateral visual field (12). This expanded representation corresponds well with the representation of the specialized structure of the retina, the visual streak, where the ganglion cells are most densely packed (5, 3, 18, 12).

Recently, many reports (20, 24, 26, 6, 14, 15) have suggested that the superior colliculus of some mammals, specifically those of non-primate mammals, have an extended representation of the visual field of the contralateral eye beyond the representation of the zero vertical meridian or the line of decussation of the geniculostriate system. This view is contrary to the traditional belief that the superior coliculus of mammals, like the dorsal lateral geniculate nucleus, represents only the contralateral hemifield (e.g. 1). In primates, however, evidences seem to suggest that the representation in the superior colliculus is limited to the contralateral half of the visual field in agreement with the previous concept (15, 13, 4, 8). Lane *et al.* (15) suggested that "at least two different basic types of visuotopic organization are found in the mammalian superior colliculus..." i.e., the organization similar to the representation in primates or in non-primate

mammals. To determine what kind of organization applies to the superior colliculus of the domestic rabbit, microelectrode mapping techniques using multiple unit criteria were employed to study the visuotopic representation in the superior colliculus of this animal.

MATERIALS AND METHODS

The experimental set-up and recording techniques were similar to those used by Montero *et al.* (21). Seven rabbits were anesthetized with urethane (125 *mgs*/100 *gms* body weight). Tracheostomy was routinely performed and the head was secured in a headholder in the Frankfurt horizontal plane. The visual cortex was bilaterally exposed. One eye was initially dilated with a parasympathetic blocking agent and was then immobilized to a metal ring. A translucent plastic hemisphere was used to represent the visual field. The immobilized eye was placed at the centre of the hemisphere so that all points on its surface were at equal distance from the eye. In all animals, the optic nerve head and the myelinated band of the ganglion cell axons was ophthalmoscopically projected into the translucent hemisphere. These retinal landmarks were periodically checked during the experiment to ensure stability of the immobilized eye.

Before mapping the contralateral superior colliculus, the zero vertical meridian or the line of decussation was determined in each experiment by recording from both the ipsi- and the contralateral visual cortex while stimulating only the immobilized eye. The contralateral superior colliculus was approached by penetrating through the overlying visual cortex. All recording sites were marked by microlesions to facilitate reconstruction of electrode tracts. After the experiment, the animal was perfused and the brain tissue processed histologically for cell and myelin stains.

RESULTS

The results obtained from electrophysiological mapping of the contralateral superior colliculus merits the conclusion that the total extent of 180 degrees of the visual field is represented in the contralateral superior colliculus of the rabbit. This includes the whole extent of the visual field of the eye that projects contralaterally as well as ipsilaterally to areas 17 and 18 of the visual cortex — a pattern similar to the subprimate type of organization described by Lane *et al.* (15). In addition, it has been possible to confirm Hughes' findings (12) that 1) the representation in the superior colliculus of the rabbit is topological, 2) there is an expanded representation along the zero horizontal parallel of the visual field in the superior colliculus which corresponds to the visual streak of the retina, and 3) no evidence of an ipsilateral input could be obtained in the superior colliculus.

The representation of the vertical meridian or the line of decussation was defined in every animal by mapping the corresponding portions of areas 17 and 18 of both cerebral hemispheres. Figure 1 represents receptive fields and the corresponding recording sites from the cerebral

hemispheres of animal 71-328. Penetrations 34 to 38 were in the ipsilateral hemisphere. The rest were in the contralateral hemisphere. The total extent of the ipsilateral

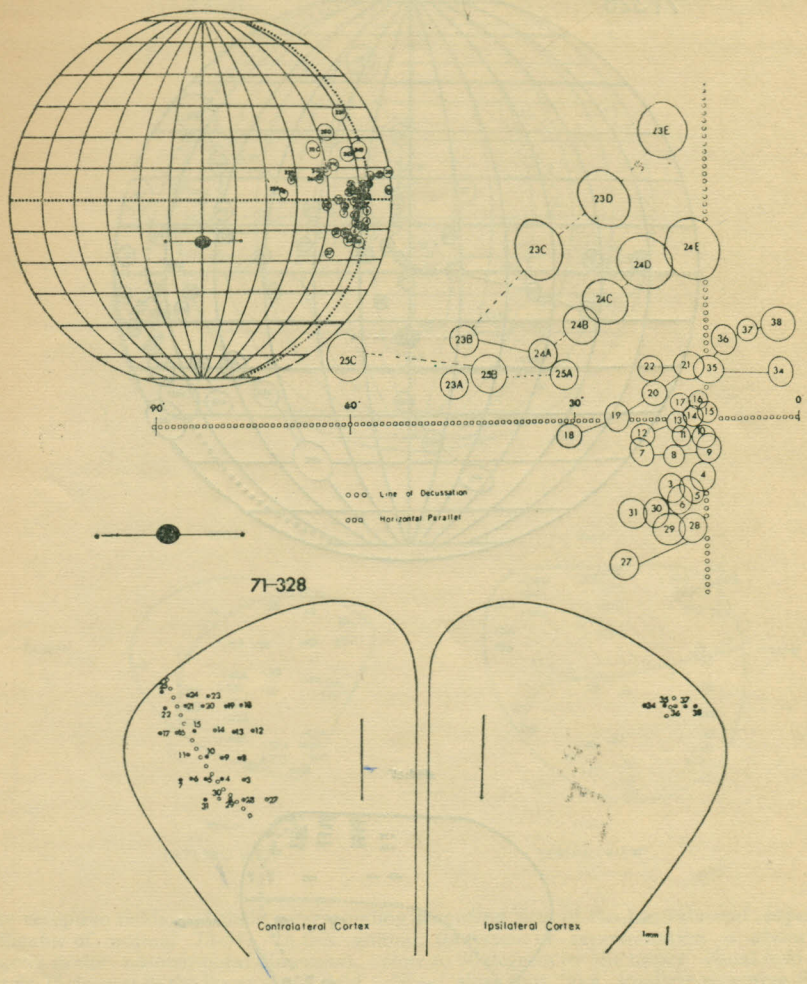

Fig. 1: The receptive fields and their corresponding recording sites of both the ipsi- and contralateral visual cortex of Rabbit 71-328. The extent of the ipsilateral representation (penetrations 34 to 38) is about 10-12 degrees. The vertical meridian is defined and represented by the open circle line.

receptive field representation was 10 to 12 degrees. The vertical meridian or the line of decussation was drawn through the part of the visual field where the ipsi- and the contralateral receptive fields overlapped. After the zero vertical meridian or the line of decussation was defined, the contralateral superior colliculus was mapped from the same animal as illustrated in Figure 2. In Figure 2, it can be seen that responses were obtained from penetrations 10, 11 ,16, 35 and 44 with receptive fields extending as much as 12 degrees nasal to the line of decussation defined experi-

mentally as already mentioned. These 12 degrees of the most nasal portion of the visual field representation are comparable in extent to the ipsilateral projection to areas

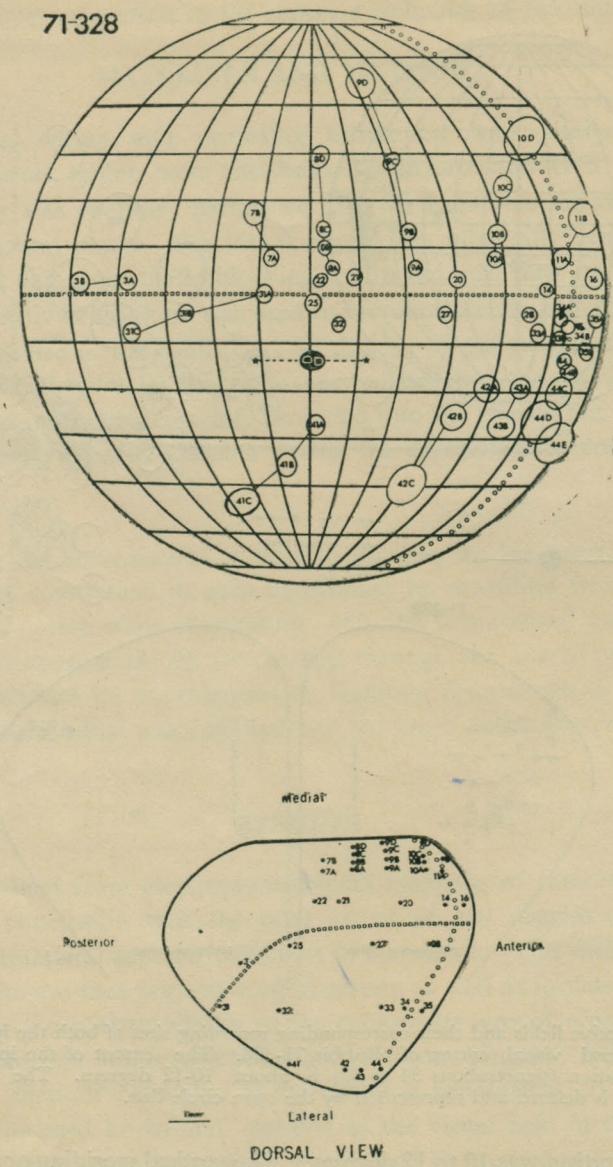

Fig. 2: The receptive fields and the corresponding recording sites of the contralateral superior colliculus of animal 71-328. Note that the representation in the contralateral superior colliculus is beyond the representation of the line of decussation defined as shown in figure 1 (penetrations 11b, 16, 35 and 44). It includes the representation of the whole eye in both the ipsi- and contralateral visual cortex.

17 and 18 of the visual cortex. The retinal landmarks were constantly examined so that data collected from any experimental animal whose eye was not well immobilized might be discarded.

Regarding the total extent of the visuotopic representation, Figure 3 gives the results of mapping the entire structure of the superior colliculus in animal 73-31. The receptive fields

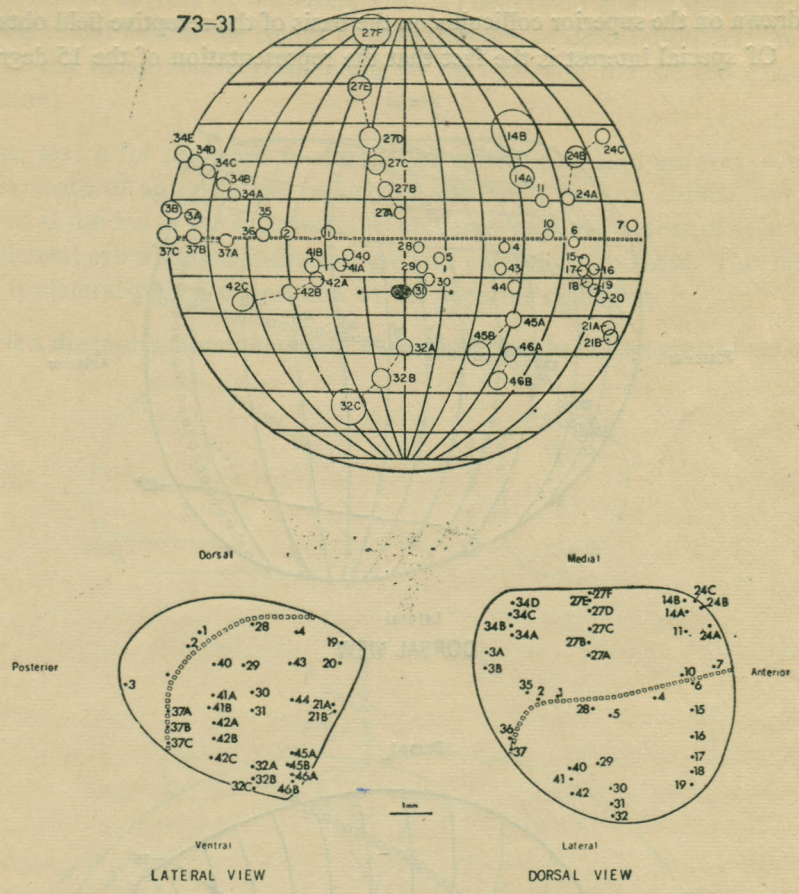

Fig. 3: The receptive fields and their corresponding recording sites of the contralateral superior colliculus of animal 73-31. In this animal, the extent of representation is about 180 degrees in the nasotemporal dimension, close to 90 degrees in the upper visual field and nearly 75 degrees in the lower visual field. Note also that the smallest receptive fields tend to be located near the zero horizontal parallel.

and their corresponding recording sites are displayed. It is clear that the upper visual field is represented medially, the lower visual field laterally, the nasal visual field anteriorly and the temporal visual field posteriorly. There are two points worth noting. First, the receptive fields beyond 20 degrees above and below the zero horizontal parallel are larger than those between these 20 degree parallels, even though the electrode was recording from cells in the same layer of the superior colliculus, namely the stratum griseum superficiale. The differences in receptive field sizes are less dramatic in the nasotemporal dimension of the visual field. Second,

there is an expanded representation of the visual field along the horizontal parallel corresponding to the representation of the visual streak, the specialized structure of the rabbit's retina. This expanded representation of the visual streak is particularly evident when the meridians and parallels are drawn on the superior colliculus on the basis of the receptive field obtained as shown in Figure 4. Of special interest is the fact that the representation of the 15 degrees below and

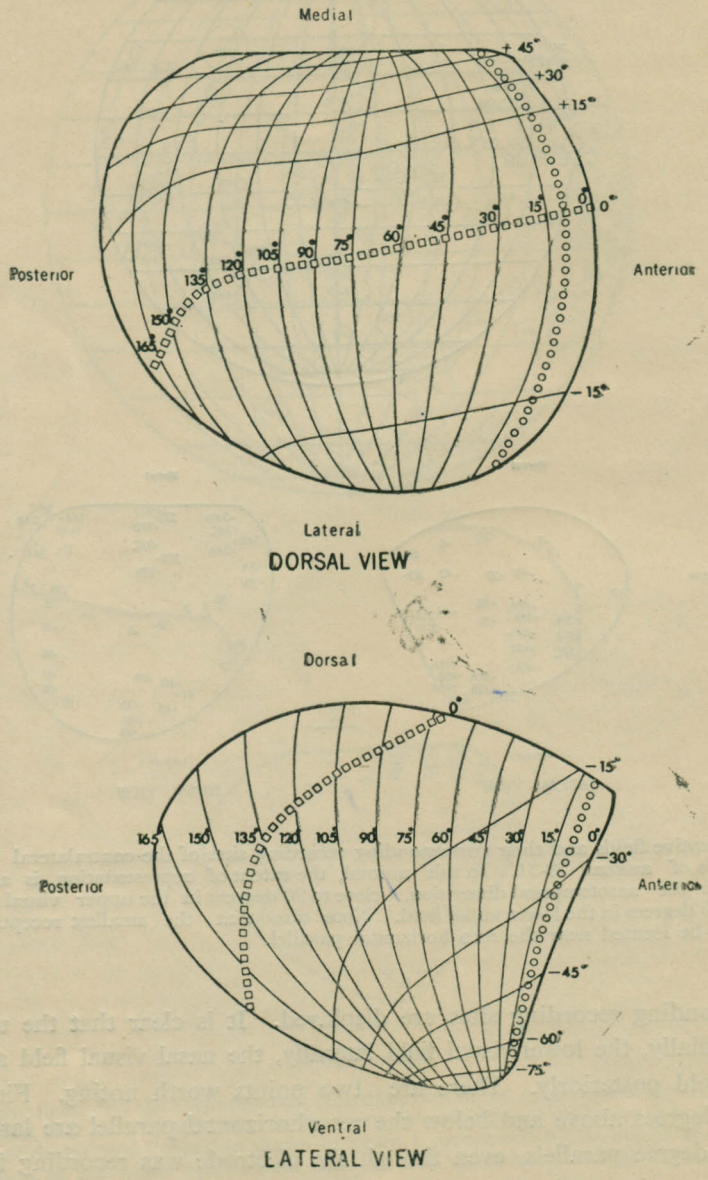

Fig. 4: Diagram of the representation of the visual field on the contralateral superior colliculus of the adult rabbit. Note 1) that the visual field is represented nasally beyond the line of decussation (indicated by the open circle line), 2) that there is a very great representation 15 degrees above and below the zero horizontal parallel, and 3) that there is no noticable expansion of the representation at the center of gaze.

above the zero horizontal parallel occupies more than half of the total 100 degrees visible on the dorsal aspect of the superior colliculus, and that only a small amount of tissue represents the upper and lower 60 degrees of the visual field. There is no special expansion of the representation of the visual field at the centre of gaze (the line of decussation) as compared to the representation of the visual field corresponding to the centre of the eye (80 degrees from the line of decussation).

Systematic search for responses to stimulation of the ipsilateral eye was conducted in all animals. No evidence of an ipsilateral input was obtained. In one animal, the contralateral eye was destroyed at the end of the experiment to obliterate any interference of neuronal response from the contralateral eye while the ipsilateral eye was carefully stimulated. The results yielded no evidence of ipsilateral retinal connection to the superior colliculus.

Figure 5 is a diagrammatic summary of the representation of the visual filed of the left eye

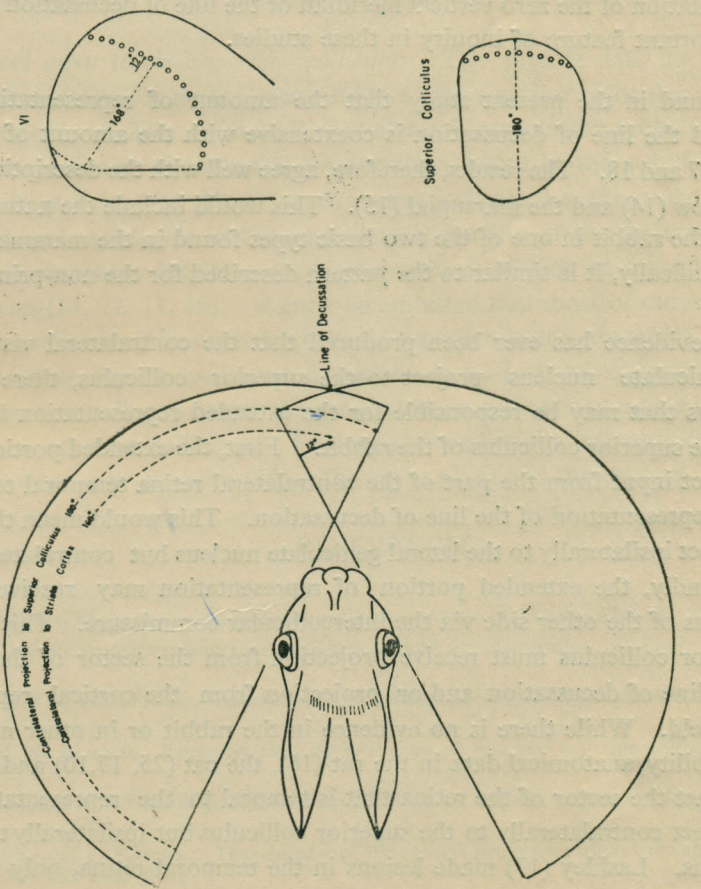

Fig. 5: Diagrammatic summary of the representation of the left eye on the right superior colliculus and in VI of the right hemisphere. The representation of the eye on the contralateral superior colliculus extends 12 degrees beyond the line of decussation (open circle lines on the brain).

in the right superior colliculus and the right striate cortex of the domestic rabbit. As can be seen, the entire visual field is represented in the superior colliculus, while in the striate cortex, the most temporal 168 degrees are represented contralaterally and the most nasal 12 degrees, are represented ipsilaterally (23).

DISCUSSION

A. *Extent of representation :* The superior colliculus of the rabbit represents the entire contralateral visual field. This extended representation of the visual field on the superior colliculus beyond the representation in the geniculostriate system has been reported for the cat (20, 24, 26, 6), the squirrel (14), the tree shrew (14), the marsupial (15) but not for primates (15, 13, 4, 8). Very extensive representation of the contralateral eye in the superior colliculus was noted in the ground squirrel (27), the rat (22) and the rabbit (12), although comparisons with the representation of the zero vertical meridian or the line of decussation in the visual cortex were not an important feature of inquiry in these studies.

It was found in the present study that the amount of representation in the superior colliculus beyond the line of decussation is coextensive with the amount of the ipsilateral projection to areas 17 and 18. The results, therefore, agree well with the description for the squirrel (14), the tree shrew (14) and the marsupial (15). This would include the nature of the visuotopic organization of the rabbit in one of the two basic types found in the mammalian superior colliculus (15). Specifically, it is similar to the pattern described for the non-primate mammals.

Since no evidence has ever been produced that the contralateral visual cortex or the contralateral geniculate nucleus project to the superior colliculus, there remain two other possible pathways that may be responsible for the extended representation beyond the line of decussation in the superior colliculus of the rabbit. First, the extended portion of representation may receive direct input from the part of the contralateral retina temporal to the region corresponding to the representation of the line of decussation. This would mean that the sector of the retina must project ipsilaterally to the lateral geniculate nucleus but contralaterally to the superior colliculus. Secondly, the extended portion of representation may receive input from the superior colliculus of the other side via the intercollicular commissure. This would require that the other superior colliculus must receive projection from the sector of the ipsilateral retina temporal to the line of decussation and/or projection from the cortical representation of the ipsilateral hemifield. While there is no evidence in the rabbit or in other mammals to exclude the second possibility, anatomical data in the rat (16), the cat (25, 17,10) and the tree shrew (10) suggest that in fact the sector of the retina that is tempral to the representation of the line of decussation project contralaterally to the superior colliculus but ipsilaterally to the dorsal lateral geniculate nucleus. Lashley (17) made lesions in the temporal retina, only in the sector representing the ipsilateral hemifield and found degeneration confined to the ipsilateral dorsal lateral geniculate nucleus and the contralateral superior colliculus.

B. *Distortion of representation :* In agreement with Hughes's careful study (12), the present results indicate that there is an expanded representation along the entire zero horizontal parallel in the superior colliculus, although there is no special expansion near the center of gaze as compared to the more temporal visual field corresponding to the center of the eye. Hughes (12) was also able to relate the degree of expansion near the zero horizontal parallel on the superior colliculus with the density of ganglion cells counted from a whole mount retina. This specialized features of the retina must play an important role to enable the species to meet special adaptive requirements. Brecher (2) has suggested that, since the rabbit is preyed upon and must constantly escape from predators, its protections are either 'freezing' to avoid being detected or 'flight'. During the 'freeze' condition, almost all the 360 degrees of the visual field of both eyes are very important in detecting movement in the horizontal plane, as is evidenced by the specialized region along the horizontal strip of the retina. Careful behavioural studies, which at present are quite scanty, may reveal other important environmental and adaptive requirements specifically related to the well developed visual streak of the rabbit.

C. *Ipsilateral input to the superior colliculus.* The present data do not provide any electrophysiological evidence for an ipsilateral input to the superior colliculus as is also true for several other species (27, 14, 22). This lack of ipsilateral input in the rabbit is in disagreement with the anatomical evidence of antegrade degeneration found in the superior colliculus after removal of the ipsilateral eye (7). However, evidences indicate that the ipsilateral degeneration is limited only to the deeper layer in the anterolateral portion of the structure (7). The lack of any physiological responses despite anatomical evidences of such an input has been reported in some other species (14, 22, 11, 19). It must be admitted that most of the explorations in the present study were confined to the stratum griseum superficiale and, therefore, it is believed that if physiological evidence for an ipsilateral projection is an important feature of inquiry, one has to look for responses in layers deeper than the stratum griseum superficiale and in the anterolateral part of the superior colliculus. Evidences for physiological responses to ipsilateral stimulation are convincing in primates (15), the cat (e.g., 6) and the opossum (e.g., 9).

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