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MICROELECTRODE ANALYSIS OF TRANSFER OF VISUAL INFORMATION BY THE CORPUS CALLOSUM [1]

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INTRODUCTION

Since the demonstration of the lack of interhemispheric transfer of visual discrimination learning following callosal and anterior commissure section (29, 23), the outstanding question has been to determine the nature of the information transmitted through these commissural systems. The most likely explanations considered have been either that i) learning and memory are transmitted in some kind of code through the corpus callosum from the trained hemisphere to the untrained side, or that ii) the basic sensory information needed in learning a discrimination is sent in duplicate form to the untrained hemisphere whereupon learning proceeds in concert with the ongoing processes of the directly trained hemisphere (30). Neurophysiological experiments carried out to date on cats (24, 25) monkeys (25, 9, 12) and man (14, 15) have not provided decisive evidence for either view.

The problem of whether there is an immediate carry-over of sensory information from one hemisphere to the other via the corpus

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Archives Italia de Biologia, 105, 583 - 596 the surface of the callosum. This was most likely due to operatory damage to the superficial parts of the corpus callosum.

Unresolved mass activity of the posterior third of the corpus callosum was little or not at all influenced by changes in diffuse illumination. Marked variations in gross callosal activity were on the contrary observed when patterned visual stimuli (generally waving a hand in front of the eyes) were introduced. Absence of response to diffuse illumination and clear responses to patterned visual stimuli were also found in all isolated units. The visual receptive field of approximately 60 units was satisfactorily identified, but only in 17 was the recording time sufficient to a thorough examination of response and field characteristics. At least two hours were in fact necessary to this purpose. Almost all the recorded units were spontaneously discharging at low frequency; yet no detailed study of spontaneous callosal activity has been performed. Action potentials from callosal units were always monophasic positive and of short duration (about 1 msec) (Fig. 2). These features are considered to be typical of axon-type spikes (11, 17). Axon-type, visually driven activity was continously recorded until the electrode was lowered by approximately 1 mm from the callosal surface; at this point it was replaced by the cell-type, visually unresponsive activity of the dorsal hyppocampus. Figure 3 shows a lesion in an area of the corpus callosum yelding typical axon-type spike activity.

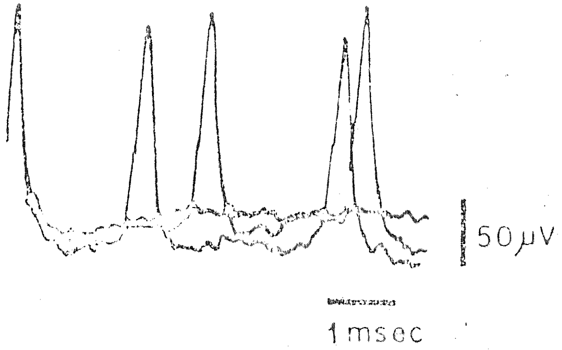

Fig. 2. — *Axon-type spikes recorded from fibers of corpus callosum.* Positivity up.

1. *Location and size of visual receptive fields of callosal neurons.* A most constant finding in the present experiments was the observation that visual stimuli evoked gross callosal-response only when presented along the midline of the visual field. Accordingly, the receptive fields of callosal units were all located in contact with or in close vicinity to the vertical meridian of the visual field. Figure 4 shows the spatial relationship between the vertical meridian and the receptive fields of the 17 units studied in detail; however, the map can be regarded as statistically representative of all the callosal receptive fields observed in this study. While many receptive fields fell within the area of clear vision (area centralis), evidence was obtained for callosal representations of regions along the vertical meridian situated as far as 50° from the areas centralis. Table 1 shows the size of the receptive fields of the 17 callosal units. It can be noted that while the great majority of fields were very small, there were three units responding to stimuli presented in an area extending from the vertical meridian to approximately 20° lateral. Of the 17 units studied in detail, three were driven from both eyes, the relative locations, size and organization of the receptive field being similar for the two eyes; nine were activated from one eye only and five showed a clear response to stimulation of one eye and

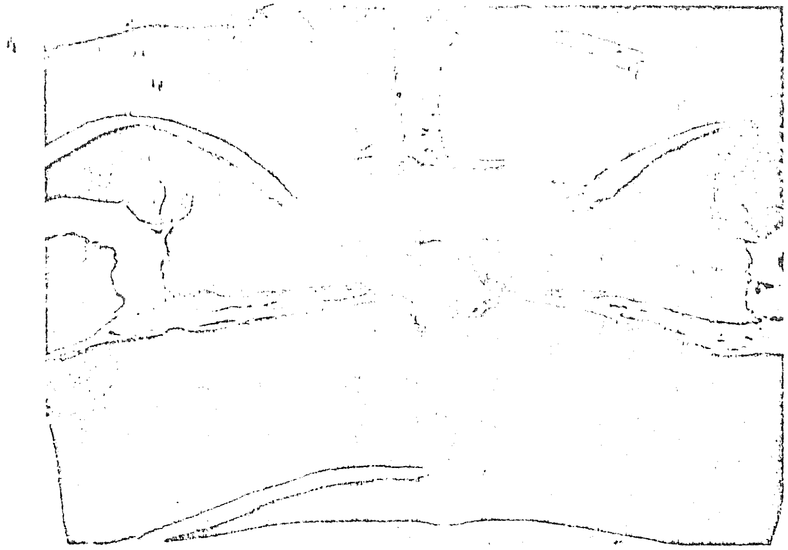

Fig. 3. — *Electrolytic lesion showing microelectrode position in corpus callosum.*

a much less evident response to stimulation of the other eye. While pure or predominantly monocular units appear to constitute the majority also in the remaining group of callosal neurons investigated in this study, a definite statistical conclusion cannot be reached.

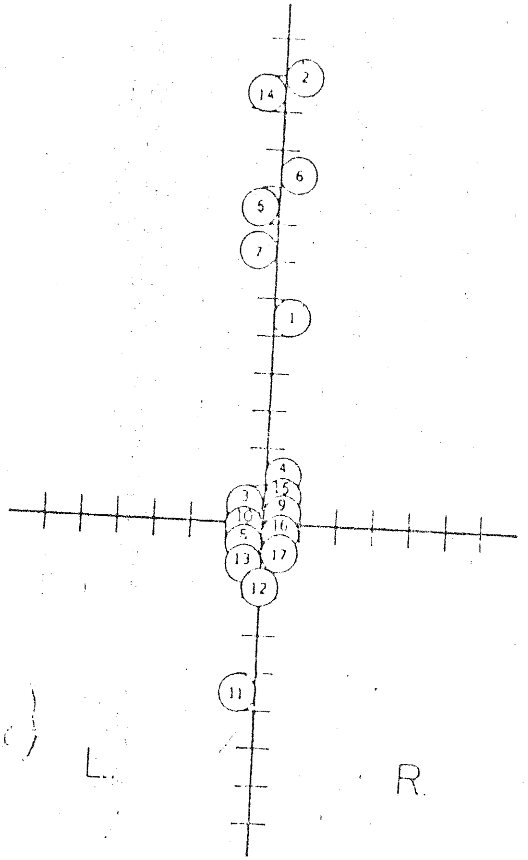

Fig. 4. – *Relation of receptive fields of callosal units to the vertical meridian of the visual field.*

Each circle indicates the position of the receptive field of the corresponding callosal unit (indicated by number) in the visual field, independently of its shape and size (for this see Table 1). In case of large receptive fields, the circle shows only the position of that part of the field located in close contact with the vertical meridian. Apparent absence of callosal receptive fields in the lower portion of the visual field is due to obstruction of vision of this area by the head holder (see Methods). The position of fields in area centralis is highly schematized; in fact, most fields in this area showed an almost total overlapping.

Each division on the coordinates corresponds to 2°.

TABLE I. – *Type, size, relation to eyes and position in visual field relative to vertical meridian of receptive fields of callosal units.*

Unit N.	Type	Driven from eye (s)	Size of field	Position in visual field
1	S	Both	4° × 3°30′	R
2	C	Predominantly L	6° × 9°	R
3	S	R	1°12′ × 1°12′	L
4	C	Predominantly R	4°12′ × 2°24′	R
5	S	Predominantly L	2°24′ × 1°48′	L
6	C	R	9° × 27°	R
7	C	R	12° × 3°30′	L
8	H	R	1°15′ × 36′	L
9	C	Both	3° × 12′	R
10	C	Both	9° × 18°	L
11	H	Predominantly R	2°24′ × 2°24′	L
12	C	R	3°40′ × 12′	vertical meridian
13	H	R	12′ × 4°18′	R
14	C	L	25° × 20°	L
15	S	L	4°18′ × 4°12′	R
16	H	R	3° × 10°12′	R
17	C	R	6° × 6°	R

Abbreviations: S = simple, C = complex, H = hypercomplex, L = left, R = right.

In the size column, the first figure gives the maximal length of the field, the second figure gives the maximal width.

The receptive field of unit N. 12 was so small that could not be assigned with certainty to either half of visual field.

In fact, some units might have been erroneously classified as monocular, because of the impossibility of a careful binocular examination due to the shortness of the recording time.

2. *Type of receptive fields.* — While all fibers recorded from the posterior third of the corpus callosum could be activated by visual stimuli, the organization of visual receptive field varied from unit to unit. It appeared evident that the criteria employed by Hubel and Wiesel (20) for the classification of the receptive fields of cells in cat and monkey visual cortex were also suitable in the case of callosal visual units. Accordingly, we have divided the population of visually driven callosal neurons into three groups: simple, complex and hypercomplex. The receptive fields of *simple* callosal neurons were divided into elongated excitatory and inhibitory regions, separated by straight lines. Explorations of these antagonistic regions with small spots of light yelded pure on or off responses respectively. Effects of algebraic summation were observed when larger areas of excitatory and inhibitory regions were separately or simultaneously

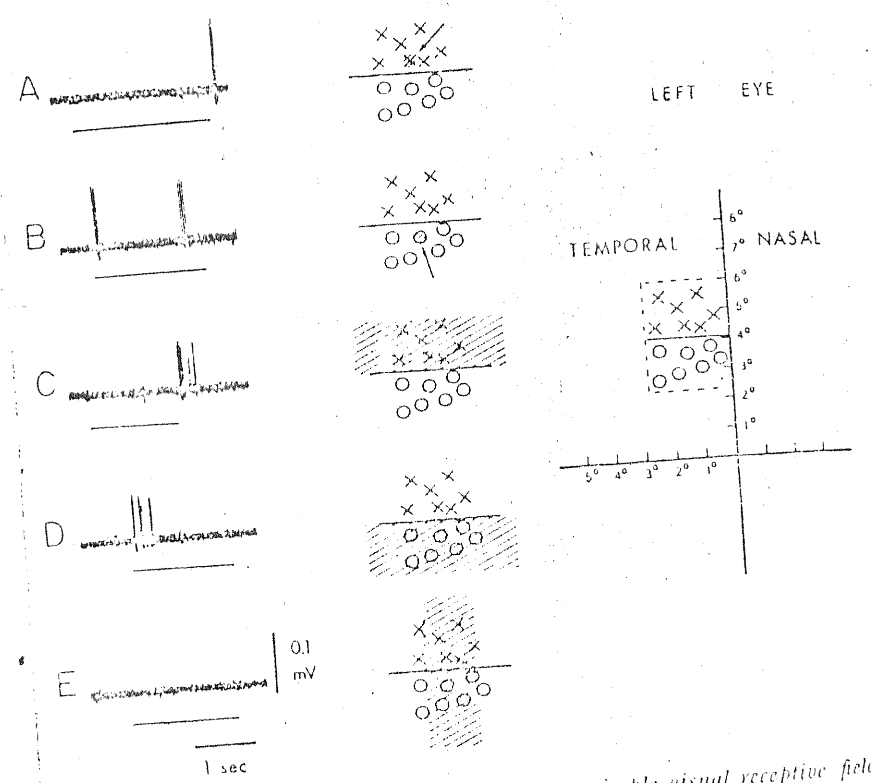

Fig. 5. – *Example of callosal unit having a simple visual receptive field.*

This unit was driven from left eye only. The receptive field (shown at the right of the figure) was divided by a straight line in an upper excitatory region and a lower inhibitory region. *A* and *B* show off and on responses to small (12') spots of light shone in the positions indicated by the arrows in the drawings at the right of the records. Similar on and off responses were recorded upon illumination of other points marked with circles and crosses respectively. *C* and *D* show increased off and on responses to stimuli covering the entire excitatory and inhibitory areas respectively (spike amplitude is reduced compared to *A* and *B* because the records were taken several minutes after the latter). *E* shows absence of response to simultaneous illumination of both antagonistic areas of the receptive field.

illuminated (see Fig. 5). Simple receptive fields were in all cases very small.

Complex callosal neurons had generally larger receptive fields. They were little or not at all activated by small spots of light; the adequate stimulus was generally a slit, or a bar, or an edge of a given width and presented with a given inclination; varying the lenght of the stimulus beyond the limits of the receptive field was without effect. Moving the proper stimulus in one direction normal to the preferred inclination gave generally the most powerful activation; a movement of the stimulus in the opposite direction was ineffective (Fig. 6).

Those callosal neurons showing a greater complexity in the organization of their receptive field were classified as *hypercomplex*. An example of a hypercomplex unit is shown in Fig. 7. An upward vertical movement of a narrow rectangular band of light was the most effective stimulus, regardless of its position in the receptive field. When the stimulus was made larger, but was still restricted to the receptive area, there appeared to be no increase, and possibly a decrease, of the response. Extension of the borders of the stimulus beyond the boundaries of the receptive field suppressed the response. All these features typically distinguish hypercomplex from complex units.

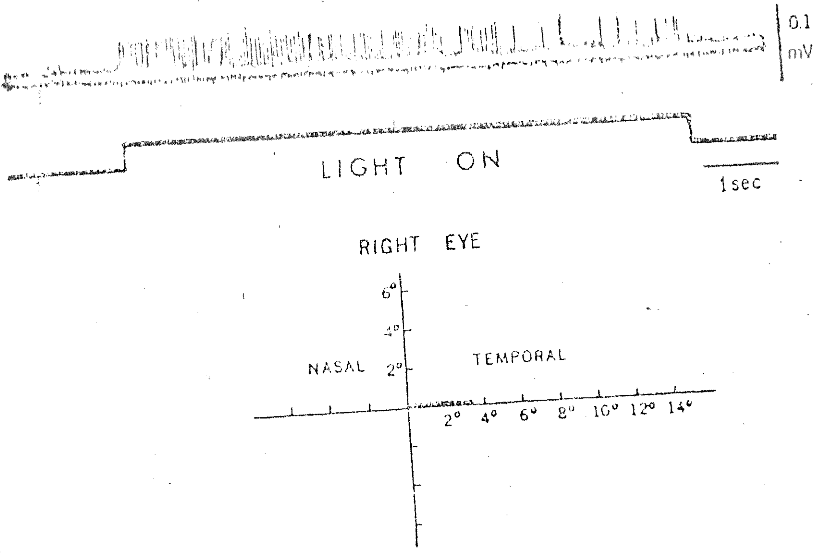

Fig. 6. – *Example of callosal unit having a complex visual receptive fields.*

This unit was driven from right eye only. It did not respond to spots of light shone in the receptive field. The optimal stimulus was a horizontal edge (light up) shone in the receptive field (shown at bottom of figure). The length of this edge could be prolonged beyond the vertical boundaries of the receptive field with full preservation of the response.

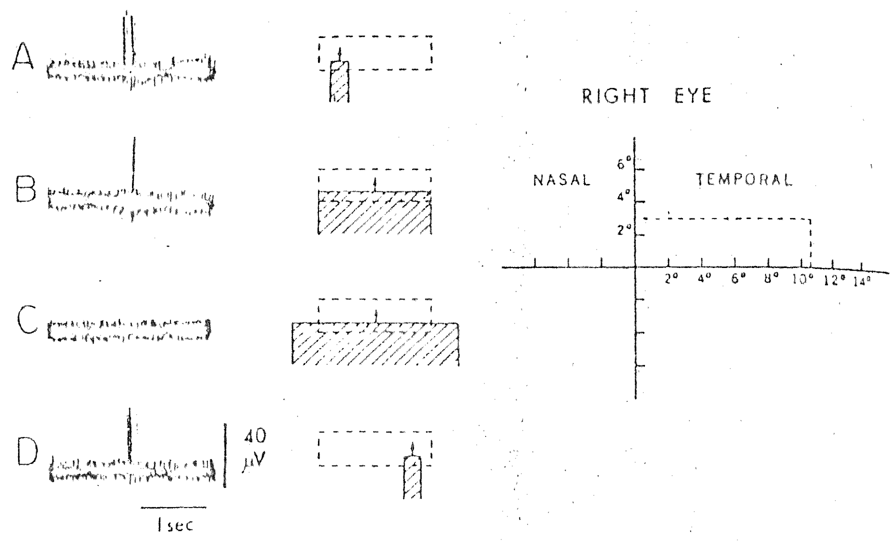

Fig. 7. - *Example of callosal unit having a hypercomplex receptive field.*

This unit was driven from the right eye. The best stimulus was a narrow (1° 15′) band of light moved vertically upward anywhere in the receptive field (shown at right of figure); see *A* and *D*.

Increasing the width of the stimulus within the boundaries of the receptive field led to a decrease of the response (see *B*); absence of response was observed upon extension of the width of the stimulus beyond the boundaries of the receptive field (see *C*).

Out of 17 units, three were classified as simple, four as hypercomplex, the remaining as complex (Table 1).

3. *Anteroposterior organization of the visual portion of the corpus callosum.* - Both gross and unitary visual responses were recorded solely from the posterior third of the corpus callosum. In one cat, showing a marked callosal responsiveness to visual stimuli, successive penetrations into the corpus callosum were made by moving the electrode forward in steps of 0.5 mm starting from the caudal edge of the splenium. Visual responses disappeared when the distance between the electrode and the splenial tip was 2.5 mm.

We have no evidence of a patterned anatomical distribution of the fibers in the corpus callosum according to their type of response. However, it was often seen that adjacent units had their receptive fields in the same region of the visual field.

DISCUSSION

The results show that the cells whose axons form the posterior third of the corpus callosum can be activated by appropriate visual stimuli. The organization of the visual receptive fields of these callosal neurons is in no way distinguishable from that described as generally typical of the cells in the visual cortex of the cat (20). Evidence for the existence of simple, complex and hypercomplex types of callosal visual receptive fields has in fact been obtained in this study, suggesting that the three groups of callosal neurons, identified according to these response properties, belong respectively to visual areas 17, 18 and 19 (see 20). This is consistent with the anatomical finding that at least some parts of all of the three divisions of cat visual cortex project to the opposite hemisphere via the corpus callosum (28, 27, 20).

In the present experiments all the callosal receptive fields were located along the vertical midline of the visual field. This would suggest that, among the visual cortex neurons, only those connected with the vertical meridian of the retina send their axons to the corpus callosum. In agreement with this finding, it has been reported that in cats submitted to unilateral section of the optic tract, some cells in the visual cortex homolateral to the section can still be activated, via a callosal relay, by visual stimuli presented along the vertical meridian of the visual field (8, 34). These cells are only found in a region at the boundary between areas 17 and 18, one which normally receives projections from the vertical meridian of the retinae (30, 31). It is this same area, which is impinged upon by the great majority of the posterior callosal afferences (10). From the foregoing, it would appear that the representation of the visual world upon the cerebral cortex is on a continuum, the neurons associated with the vertical meridian and their callosal connections being the *trait d'union* necessary for bringing together the two half visual fields. Such a hypothesis implies that, at the unit level, there ought to exist a class of priviledged cortical neurons "looking at" areas crossing the vertical meridian of the visual field, the contralateral and homolateral pieces of information being carried over to them by respectively the direct geniculo-cortical and the indirect callosal pathways. Hubel and Wiesel (20) have shown that neurons having receptive fields extending somewhat into the homolateral field of vision are indeed to be found in the cat visual cortex, but do not regard this evidence as conclusive because of possible inaccuracies in defining the vertical meridian. The most direct way to demonstrate that the existence of such receptive fields is associated with callosal mechanisms, would be to map the receptive area of these neurons in a split-chiasm cat by first stimulating the homolateral eye, followed by the contralateral one. A study aimed at this purpose is presently under way in this laboratory (2).

When the present results are interpreted in light of split-brain studies, it would now appear not necessary to postulate that learning and memory are transmitted from one hemisphere to the other via the callosum as is commonly suggested. From the foregoing, it would appear that it is the information related to the vertical meridian that is immediately transmitted to the other side of the brain via the corpus callosum. When the optic input is artificially restricted to one hemisphere as in split-chiasm animals with one eye occluded, the callosal visual input is the only way by which the other hemisphere receives a map of the visual world. Thus, interocular transfer of learned visual pattern discrimination in split-chiasm animals would be best explained by assuming that the untrained hemisphere actually perceives the discriminanda presented to the opposite trained eye. This carry-over of visual information from one eye to the opposite hemisphere would, of course, present limitations related to the narrowness of the receptive area. Such limitations could reasonably be held responsible for the lack of interocular transfer seen on some visual pattern discriminations in split-chiasm animals (24, 9, 25).

The foregoing considerations, while offering a parsimonious interpretation of the callosal transfer of visual discriminations, by no means exclude the possibility that other more complicated kinds of information, equally or more important for visually guided behavior, visual learning and memory, can be exchanged through the corpus callosum. For example, callosum-sectioned humans cannot, using their dominant left hemisphere with its speech mechanisms, describe any visual event occurring in the left visual field (14, 15). Yet, the normal right-handed person, if called upon to do so, can give a running verbalization of objects and symbols presented not only just to the left of fixation, but also in any other point in the left visual field. With this in mind one must conclude that the right hemisphere's visual sphere is so carefully analyzed by the speech and language mechanisms residing in the left dominant hemisphere on the basis of elaborate information supplied by the corpus callosum.

SUMMARY

Responses to patterned visual stimuli were recorded with tungsten microelectrodes from single fibers of the posterior third of the corpus callosum in midpontine pretrigeminal cats. Visual receptive fields of these units were similar to those observed with cells in cortical areas 17, 18, 19. However, callosal visual receptive fields were all located along the vertical meridian of the visual field. The datum is discussed in relation to *a)* the possible interhemispheric association of the right and left halves of the visual field and *b)* the interhemispheric transfer of visual pattern discriminations in animals with lateralized optic input.

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