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Binocular interaction and disparity coding in area 19 of visual cortex in normal and split-chiasm cats

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Abstract. Binocular disparity, resulting from the projection of a three-dimensional object on the two spatially separated retinae, constitutes one of the principal cues for stereoscopic perception. The binocularity of cells in one hemisphere stems from two sources: (1) the ganglion cells in the homonymous temporal and nasal hemiretinae and (2) the contralateral hemisphere via the corpus callosum (CC). The objectives of this study were, on one hand, to determine whether disparity-sensitive cells are present in a "higher order" area, namely area 19 of the visual cortex, of the cat and, on the other hand, to ascertain whether the CC contributes to the formation of these cells. As in areas 17–18, two types of disparity-sensitive neurons were found: one type, showing maximal interactive effects around zero disparity, responded with strong excitation or inhibition when the stimuli presented independently to the two eyes were in register. These neurons are presumed to signal stimuli situated about the fixation plane. The other type, also made up of two subtypes of opposed valencies, gave maximum responses at one set of disparities and inhibitory responses to the other set. These are presumed to signal stimuli situated in front of or behind the fixation plane. Unlike areas 17–18, however, disparity-sensitive cells in area 19 of the normal cat were less finely tuned and their proportion was lower. In the split-chiasm animal, very few cells were sensitive to disparity. These results, when coupled with behavioral data obtained with destriate animals, indicate that (1) area 19 is probably less involved in the analysis of disparity information than area 17, (2) the disparity-sensitive neurons that are sensitive to disparity are not involved in the resolution of very fine three-dimensional spatial detail, and (3) the CC only determines a limited number of these cells in the absence of normal binocular input.

Key words: Area 19 – Corpus callosum – Split chiasm – Spatial disparity – Binocular interaction – Cats

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Introduction

Several studies have shown that cells in the visual cortex of monkeys and cats exhibit significant interactive effects when both eyes are stimulated simultaneously at slightly disparate retinal loci. Poggio and Fisher (1977) have shown that cells in the visual cortex of monkeys can be subdivided into two functional classes: (a) those which seem to prefer stimuli situated within Panum's fusional area, some of which show excitation while others show inhibition when the two stimuli exhibit zero or near-zero disparity; and (b) those which react to stimuli situated either in front of or behind the fixation plane. The latter were called either near and far units, respectively, or crossed and uncrossed disparity detectors. These units are present in many visual areas, where their proportion sometimes exceeds that of the primary visual cortex (V1; Poggio and Fisher 1977; Maunsell and Van Essen 1983; Poggio 1984; Poggio and Poggio 1984; Poggio et al. 1985, 1988; Burkhalter and Van Essen 1986; Felleman and Van Essen 1987; Hubel and Livingstone 1987; Livingstone and Hubel 1987a,b; Hubel and Wiesel 1970).

The existence of these neurons probably constitutes one of the most important, if not the essential, neural basis for stereoperception. Proof of this physiological-functional relationship is necessarily indirect, although a number of converging lines of evidence appear to support this view. Electrophysiologically, Poggio and colleagues have shown that in areas V1, V2, and V3 of the alert monkey cells can be differentially excited with dynamic random-dot stereograms (Poggio 1984; Poggio and Poggio 1984; Poggio et al. 1985, 1988). At the behavioral level, a number of studies have shown that cats (Fox 1981; Lepore et al. 1986; Ptito et al. 1986) and monkeys (Bough 1970; Cowey et al. 1975; Sarmiento 1975; Harwerth and Boltz 1979a,b) can carry out discriminations using disparity information contained in random-dot stereograms. Removing these "depth" neurons, moreover, by raising animals with some kind of eye misalignment (Packwood and Gordon 1975), abolished stereoscopic discrimination based on disparity. A second pro-

cedure for reducing the binocular input is to either split the optic chiasm, which leaves only the corpus callosum (CC) as the second source of input to a cell or to section both the chiasm and the callosum, which results in purely monocular cells being ipsilaterally activated through the temporal hemiretina. A chiasm split can have one of two possible effects: if disparity-sensitive cells cannot be mediated by the callosum, the loss of depth perception based on disparity should ensue; if the callosum does determine some of these cells, then only combined chiasm and callosum section would completely abolish stereoperception. Using random-dot discriminations with cats, we have shown (Lepore et al. 1986; Ptito et al. 1986) that discrimination becomes poor, but not totally impossible, following chiasmatomy and that it is completely wiped out upon subsequent callosal section. An alternate procedure for eliminating disparity-sensitive cells is to ablate the anatomical structure which contains them. After having lesioned most of areas 17–18, we (Ptito et al. 1992) have shown that this type of discrimination did in fact break down completely.

A number of researchers have shown that cells sensitive to spatial disparity are quite numerous in areas 17–18 of the cat (Barlow et al. 1967; Pettigrew et al. 1968, Joshua and Bishop 1970; Bishop and Henry 1971; Bishop et al. 1971; Cynader and Regan 1978; Von der Heydt et al. 1978; Fisher and Kruger 1979; Regan et al. 1979; Ferster 1981; Cynader and Regan 1982; Regan and Cynader 1982; Gardner and Raiten 1986; Maske et al. 1986a,b; Gardner and Cynader 1987; Le Vay and Voigt 1988). Using a different stimulating procedure, moreover, it has been shown that cells in visual cortex not only code for spatial disparity but also for relative phase differences (Freeman and Ohzawa 1990; Ohzawa et al. 1990; De Angelis et al. 1991). We have also established (Lepore et al. 1992) that splitting the chiasm considerably reduced the number of disparity-sensitive cells, but did not eliminate them altogether. It would thus appear that disparity-sensitive cells in areas 17–18 can be partially mediated through the CC.

Only one experiment has looked for the presence of disparity-sensitive cells beyond areas 17–18 (Pettigrew and Dreher 1987). It has shown that area 19 contains cells that are indeed tuned to disparity and that they are, in agreement with the results obtained in monkeys, more numerous than in areas 17. One surprising finding, however, was that they might be principally sensitive to divergent disparities, leading the authors to suggest a modular, parallel organization for disparity sensitivity: the X system (area 17) codes mainly for stimuli on the fixation plane; the Y system (areas 17 and 18) is responsible for crossed disparities; the W system (area 19) analyzes uncrossed disparities The first purpose of the present study was to confirm and extend these results.

The apparent anatomofunctional parallelism between cat and monkey organization might, however, not apply to the callosal system. While cats exhibit extensive interconnections between areas 17, the striate cortices of the monkey appear to be only marginally callosally interconnected or not at all (Cusik and Kaas 1986). Moreover, in the cat, although the callosal zones in area 19 extend well beyond the regions where the vertical meridian is represented, up to about 20° of eccentricity (Innocenti 1980; Segraves and Rosenquist 1982a,b), the receptive fields (RFs) for the two eyes are juxtaposed or contiguous across this meridian (Antonini et al. 1985). In the monkey, the anatomical distributions show that the projections not only relate to the vertical meridian but also to homo-areal regions which are not continuous across the midline (Cusik and Kaas 1986). This would suggest that callosal function might be different in the monkey and in the cat. In a previous study (Lepore et al. 1992), we showed that disparity-sensitive neurons could be mediated through the callosum in the cat. Does this also apply to area 19? The second purpose of this study, therefore, was to determine whether disparity-tuned neurons are present in area 19 of split-chiasm cats.

Materials and methods

Subjects

The experiment was carried out on 20 cats weighing between 2 and 4 kg each. Although the animals came from a local supplier, they were quarantined upon arrival to give them the opportunity to adapt to local laboratory conditions. They were in good health and had no apparent malformations or pathological disorders. All manipulations were carried out in accordance with the guidelines proposed by the Canadian Council on Animal Care.

Material and procedure

The optic chiasms of eight cats were sectioned using the transbuccal approach (Myers 1955). The animals were then allowed to recuperate for a minimum of 4 weeks.

On the day of recording, each cat was injected with atropine (Atro-Sol, 0.2 mg/kg) to reduce bronchial secretions, after which they were anesthetized with a gaseous solution of nitrous oxide, oxygen (N_2O: O_2 70:30), and Fluothane (2–3% of total gaseous mixture). The animal was then intubated and the saphenous vein was cannulated in order to administer 5% dextrose in lactated Ringer solution to maintain blood pressure and hydration. A small bone flap overlying area 19 was removed and a small incision was made in the dura overlying the cortex representing the center of the visual field (about A 0–P 6 and L 6–11; see Tusa et al. 1979). Pressure points and wounds were next infused with a local anesthetic (xylocaine 2%) and the Fluothane anesthesia was lowered to 0.5%. Gallamine triethiodide (Flaxedil, 200 mg) and d-tubocurarine (Tubarine, 20 mg) dissolved in 30 ml dextrose solution (5%) in lactated Ringer were continuously infused (5.6 ml/h) through the saphenous vein cannula to maintain paralysis of extraocular muscles. Respiratory rate was controlled so as to maintain constant, physiological levels of expired CO_2 (3.5–4.5%). Temperature was also kept constant (37°C) with the help of a heating waterpad, thermostatically controlled with a rectal thermoprobe. Heart rate and, occasionally, electroencephalographic activity (EEG) were also monitored during the experiment.

Recording was carried out with tungsten microelectrodes that had an impedance of 3–6 MΩ measured at 1000 Hz. A neutral contact lens with a 3-mm artificial pupil was placed on each eye to prevent dehydration and improve image resolution. When necessary, the optic quality of the eyes was also ensured by the use of appropriate dioptric lenses which focussed the image on the retinae. Moreover, the optic axis of one of the eyes was deviated using a Risley biprism so that the RFs of the two eyes would be located on widely separated coordinates on the tangent screen, placed at 171

cm from the animal. Two projectors were placed behind the animal. The two stimuli were equated for brightness, and an appropriate computer-controlled optic bench system ensured the independent and precise control of the other parameters: stimulus velocity and directionality, bar length and width, position and orientation in space, stimulus onset, and duration of sweep.

Upon isolating a cell, the stimulation procedure adapted from Henry et al. (1967) was used. In order to determine the probable position of the area centralis (Fernald and Chase 1971) each optic disk was projected on the screen. The area centralis was considered to be situated approximatively 16° medially and 7.5° below the isoelevation line of the center of each disk (Bishop et al. 1962). This approximation is commonly used in these types of studies because it is quite impossible to precisely determine the location of the area centralis. The RF ("minimal response field," Barlow et al. 1967) of each eye was next precisely mapped using the narrow slit of an ophthalmoscope. The best stimulus parameters (directionality, velocity, orientation, and size), as estimated from the output of the audio monitor, were determined for the dominant eye. Each cell was classified in terms of simple, complex or end-stopped category (Hubel and Wiesel 1962, 1965a,b; Henry 1977; Dreher 1986). Ocular dominance (OD) was defined (Hubel and Wiesel 1962) for each cell on a scale from 1 (contralateral eye only) to 7 (ipsilateral eye only). In order to class the binocular cells among the five intermediate categories, an index of binocularity was calculated using the formula: $B=[I/(I+C)]\times 100$, where I represents the response to stimulation of the ipsilateral eye and C, that of the contralateral eye. The index thereby obtained allowed for the classification using the following criteria: class 2, $B=1$–20; class 3, $B=21$–40; class 4, $B=41$–60; class 5, $B=61$–80; class 6, $B=81$–99. In order to stimulate the unresponsive eye of an apparently monocularly driven cell, its RF was estimated to be situated at the same spatial coordinates as that of the RF of the responsive eye.

Disparity sensitivity was next tested. First each eye was tested separately. Stimulation was carried out using the optic bench system: a bar having the best estimated dimensions was swept at optimal velocity in the two directions orthogonal to the best orientation. Stimulus velocity varied between 0.67°/s and 7.41°/s, each sweep covering 6.67°. Each stimulus was presented five times and the peristimulus time histograms were derived from the summed responses to these five stimulations in the preferred direction. Following the examination of the monocular responses, the binocular responses were tested at null and disparate presentations. Disparity was created experimentally by delaying the initiation of one of the two stimuli as follows. The two stimulus bars were positioned equidistant from the center of the RF of each eye: when the two bars started moving at the same time, they crossed the centers of the RFs simultaneously, and disparity was null. However, if the initiation of the sweep of one bar was delayed with respect to the other, the two bars would be situated at non-corresponding points in each RF at any particular time. Depending on the direction of motion, this delay simulated either crossed or uncrossed disparity. Beside the zero condition, 14 other conditions were tested, with disparity varying from $-3°$ to $-1°$ and from $+1°$ to $+3°$ in 1° steps, whereas it varied in 0.2° steps from $-1°$ to $+1°$. Disparity, therefore, is defined relative to the RFs and not to the coordinate reference points of the eyes. Although these two measures would generally coincide, small errors in alignment are possible, and zero disparity should not be understood in absolute terms. That is the reason why analyses concerned with response type (i.e., the response profiles, see below) are the most meaningful. All conditions were presented in a pseudorandom fashion, each being interleaved with every other a total of five times. The interval between each sweep was at least 10 s. The action potentials evoked by the five stimulations in the preferred direction for each condition were summed by the computer. Peristimulus time histograms were derived by dividing response time into 50 bins of equal length.

In this type of study, it is important to insure that the eyes do not move during the recording period; this was done as follows. The precise positions of the RFs were determined first before carrying out the quantitative protocol, and again immediately after having completed the protocol. Any measurable displacement in the location of either field resulted in the data being discarded (for monocular cells, only the position of the RF of the dominant eye was evaluated). Second, the position of the eyes was estimated from the relative positions of the optic disks (Fernald and Chase 1971). Since the diameter of the optic disk at this screen distance was fairly large, the major blood vessels radiating from the disk were also taken as reference points (Pettigrew et al. 1979). This evaluation was carried out just before and immediately after having tested the cell on the quantitative protocol. Again, any obvious displacement of the eyes led to the results being rejected. In addition, the different estimates taken at various intervals during the recording session gave indications as to whether any gross displacement of the eyes had taken place during the long hours of recording. These displacements were found to be generally very small over the average 30-h recording session. This method, therefore, constitutes a useful index of both short- and long-term stability of eye position, and the results indicate that fairly stable positions were obtained throughout the experiment.

At the end of the experiment, each cat was deeply anesthetized with 6% Fluothane, after which it was perfused through the heart with an isotonic saline solution followed by formalin (10%). The brain was removed, placed in formalin, and later prepared for histology. In order to verify the completeness of the chiasma section, the block containing this structure was cut in coronal sections 20 μm thick. Every second section was kept and stained using the Kluver-Barrera method (Kluver and Barrera 1953).

Electrode penetrations were all within area 19, identified according to the maps of Otsuka and Hassler (1962), Hubel and Wiesel (1965a) and Tusa et al. (1979). Only the results of those animals which showed complete chiasm transection are presented in this report.

Results

Only cells which gave robust responses to the stimuli were submitted to the complete protocol. Since this generally required more than 2 h, cells which could not be tested on all parameters were not retained for the present analysis. Thus, a total of 117 cells are described, 65 cells for normal cats and 52 for split-chiasm cats. Only central vision was examined, because it is in this region that callosal and depth function are presumed to operate. The various distributions are not therefore representative of all of area 19, especially of those portions of the area which are not callosally connected.

Receptive field properties

The cells were classified into simple, complex, or end-stopped categories. No simple cells were found in either group of animals. The majority of cells was classified as complex (normal cats 40/65, split-chiasm cats 42/52) because they had RFs with spatially overlapping on and off regions. An important proportion of cells showed strong end-zone inhibition (normal cats 25/65, split-chiasm cats 10/52).

The RF sizes (in deg^2) were generally quite small. Complex cells had a slightly larger average RF (normal cats 5.4, split-chiasm cats 4.1) than end-stopped cells (normal cats 3.4, split-chiasm cats 2.8). These differences were confirmed statistically using an analysis of variance (normal cats $F=24.48$, $P<0.01$; split-chiasm cats $F=4.29$, $P<0.05$).

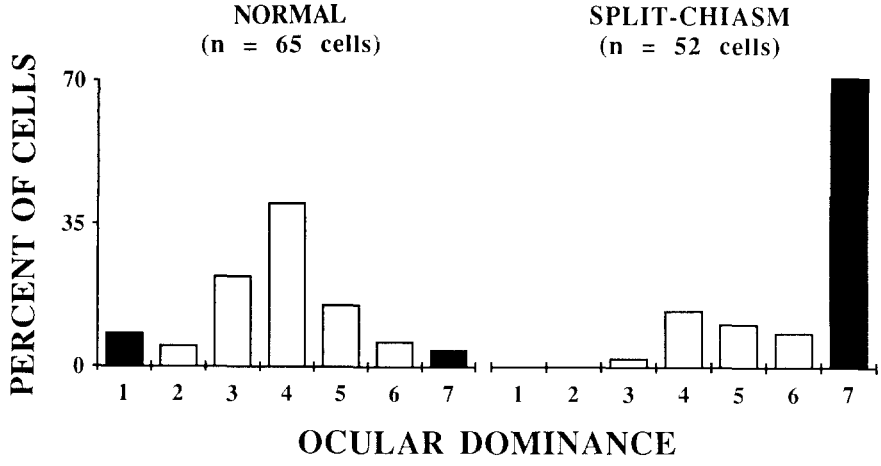

Fig. 1. Ocular dominance distribution for normal (*left*; $n=65$ cells) and split-chiasm (*right*; $n=52$ cells) cats. *Light bars*, binocular cells; *dark bars*, monocular cells. Cells in category *1* represent units driven exclusively through the contralateral eye, and category *7*, those excited by stimulation of the ipsilateral eye. The other categories correspond to intermediate eye dominances (see text for definition), where category *4* shows the cells which respond equally well to either of the two eyes

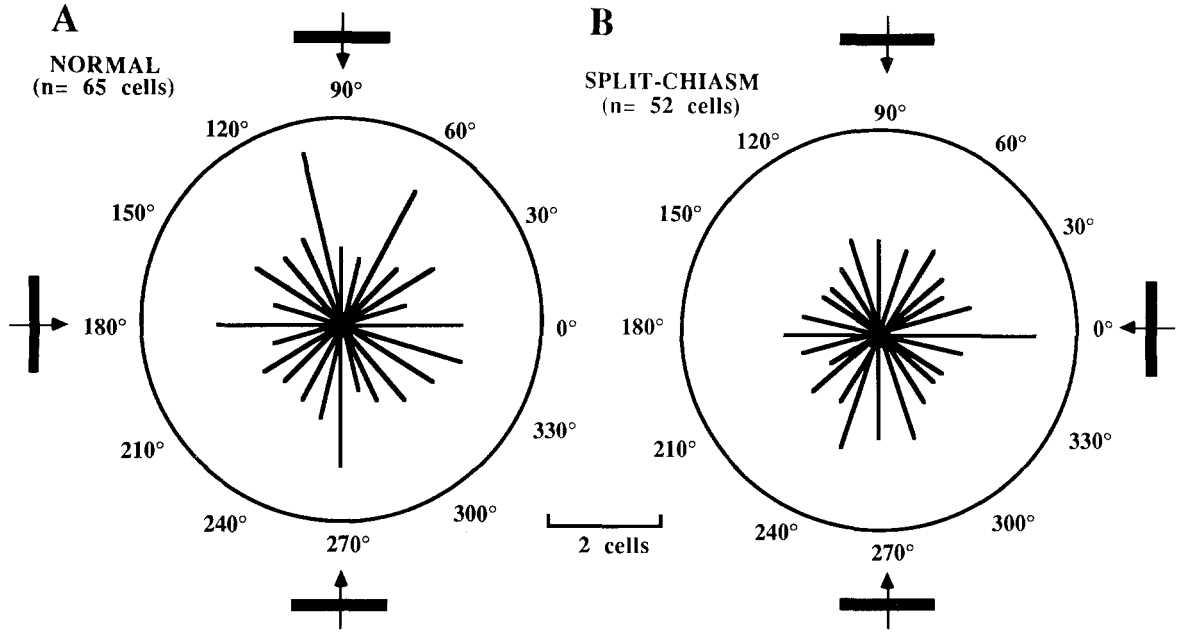

Fig. 2. Orientation tuning of cells in area 19 for normal (*left*) and split-chiasm (*right*) cats. The *radial lines* indicate the preferred orientation of a cell. The length of each line is proportional to the number of cells which preferred this to any other orientation of the stimulating bar

The OD distributions obtained for all cells are shown in Fig. 1. In the normal group, most cells were binocularly driven (88%), with a clear preponderance of class 4 units and a slight bias in favor of the contralateral eye. In the split-chiasm animals, OD is shifted towards the ipsilateral eye, 35 out of the 52 cells sampled responding exclusively to this eye and 9 others preferring this to the other eye (classes 5 and 6). This distribution is statistically different from that of the normal cats ($\chi^2=40.8$, $P<0.05$). However, not all contralateral activation was abolished by the surgery. Although no cell was responsive exclusively to contralateral eye stimulation, 17 of 52 could be driven through the two eyes. The amount of contralateral eye influence through the callosum is more important than that which can be deduced from these OD data. A number of cells which were classed monocular when each eye was stimulated separately showed strong binocular interactions when the two eyes were stimulated simultaneously (see below). Therefore, it is clear that the CC contributes significantly to the binocular activation of cells in area 19 of the cat.

Orientation preference was estimated as being that orientation of a slit, varied in approximately 15° steps, which produced the best response, as determined by ear. It appeared from the present study that no strong anisotropy in favor of the major axes existed for either normal or split-chiasm animals. This is illustrated in Fig. 2. The two distributions were, within the limits presented above, similar to each other ($\chi^2=6.75$, $P>0.05$).

Binocular interaction and disparity sensitivity

Binocular interaction. Stimulation was carried out in the present experiment under two viewing conditions: monocular viewing, where each eye was stimulated sepa-

Table 1. Number and proportion of disparity-sensitive cells recorded in area 19 in normal and split-chiasm cats

Cells	Normal			Split-chiasm		
	Monocular	Binocular	%	Monocular	Binocular	%
Tuned excitatory	1	4	8	1	4	9
Tuned inhibitory	–	3	5	1	3	8
Far cell	–	4	6	–	–	–
Near cell	–	10	15	1	3	8
Insensitive	4	24	43	25	2	52
Unclassified	3	12	23	7	5	23
Total	8	57		35	17	

rately, and binocular viewing, whereby both eyes were stimulated simultaneously. In the latter case, the timing between the initiation of the two stimuli was adjusted so as to create a predetermined spatial disparity. If binocular interaction consisted of only linear summation, then the response to the simultaneous stimulation of the two eyes should be equivalent to the sum of the responses of each eye stimulated separately or possibly to that produced by stimulation of the dominant eye. Moreover, the binocular response of apparent monocularly driven cells should equal the monocular response. Discharge rates obtained during simultaneous stimulation which are smaller or larger than these responses would indicate nonlinear binocular interactions either of the inhibitory or of the excitatory type.

Results of simultaneous binocular stimulation are presented in Table 1, which separates cells according to their response profiles to various stimulus disparities. In the normal animals, 28 cells (43% classified as "insensitive") showed no binocular interactions in the sense that the binocular response was essentially similar to that of the dominant eye; 24 of these were binocularly driven cells. The remaining cells, which constituted 57% of the sample in area 19, showed some form of binocular interaction. It is interesting to point out that of the eight cells that were categorized as being monocularly driven, four showed some binocular interaction.

Chiasm transection drastically reduced the number of binocular cells. Moreover, most monocular cells (25/35 or 71%) showed no interaction even when the two eyes were stimulated simultaneously. Binocularity in general, and the nature of the residual binocular interaction in particular, appear to be the parameters most affected by the chiasma transection. Whereas the former could have been predicted, given the nature of the surgery, the qualitative changes in the remaining binocular cells could not easily have been anticipated, given the apparent normalcy of all the other parameters tested (orientation selectivity, RF size and organization, ipsilateral and contralateral discharge rates, and excitability).

Disparity tuning. Response profiles for the disparity continuum (–3° to +3°) were derived from the poststimulus time histogram obtained at each disparity. Examples illustrating how these disparity profiles were computed are presented in Fig. 3. Thus, the response to ipsilateral and contralateral stimulation, as well as to stimulation at each disparity, is used to derive a disparity-specific histogram (Fig. 3, left). The summed discharges contained within each histogram give the ordinate value at a particular disparity (see insets on the right of Fig. 3). In these examples, two cells from normal cats (Fig. 3A,D) and two cells from split-chiasm cats (Fig. 3B,C) are shown.

Despite some differences in response profiles, it was clear that, in the normal cat, a significant proportion of cells (22 cells or 34%) could be grouped into four classes according to their response profiles to the disparate stimulation. Examples of each of these are presented in Fig. 4. Since these sensitivity profiles resembled in most respects those previously described by Poggio and Fisher (1977) and Poggio and Poggio (1984) for the monkey cortex, the same terminology was employed to characterize them. One class of cells responded with strong excitation to a very narrow range of disparities; these were labeled "tuned excitatory". Some units showed a strong inhibitory response to precise spatial disparities; these were labeled "tuned inhibitory". Another class of cells gave a strong excitatory response to one set of disparities and an inhibitory one to another. Depending on the direction of this excitation/inhibition, they corresponded to the "near" and "far" cells of Poggio and Fisher (1977) and Poggio and Poggio (1984). The relative proportions of each of these subsets for the normal cat are given in Table 1. This table shows that all four classes of disparity-sensitive cells are present in this area.

Results for the split-chiasm cats are also represented in Table 1. Three points can be made. First, as previously pointed out, the proportion of monocular cells increased drastically. Second, proportionately more of these monocular cells are "truly" monocular in the sense that no interaction was demonstrated during simultaneous stimulation of the two eyes (monocular cells: 25/35 "insensitive" in the operated animals vs 4/8 "insensitive" in the normal cat). Third, as can be expected from the surgery which completely disconnects the nasal hemiretinae, no far cells were found in the operated animals. Representative examples of the three classes of disparity-sensitive cells found in these cats are given in Fig. 5.

A substantial number of cells (23% in each group), labeled "unclassified", showed some form of binocular interaction, essentially of the excitatory type. However, no consistent repeatable response profile could be

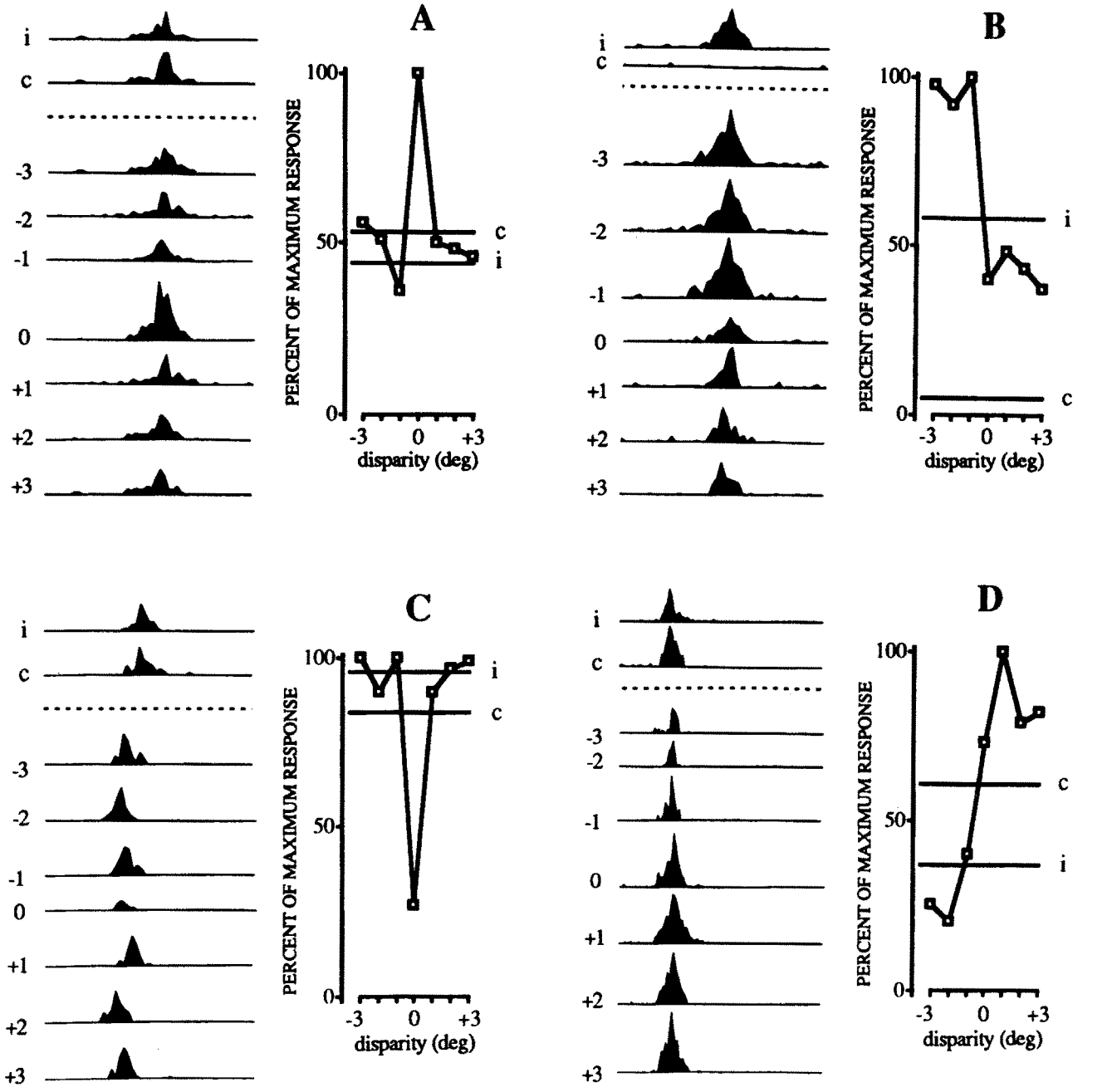

Fig. 3A–D. Examples of peristimulus time histograms from which were derived the sensitivity profiles of the four typical disparity-sensitive cells. **A, D** Normal cat; **B, C** split-chiasm cat. Beside the response to the seven disparities, the response to monocular ipsilateral (*i*) and contralateral (*c*) eye stimulation is also shown at the top of each set of histograms. **A** Tuned excitatory cell; **B** near cell (monocular); **C** tuned inhibitory cell; **D** far cell

derived which would have permitted a grouping of a number of units into some identifiable class. Examples of two of these cells for each group are presented in Fig. 6 (normal cats, Fig. 6A,B; split-chiasm cats, Fig. 6C,D). The cells shown in Fig. 6A and C have profiles which most closely resemble tuned inhibitory cells in that a clearly lower discharge was obtained at 0° disparity in comparison with that evoked at the other disparities. However, even the lowest binocular response was never smaller than that of the individual monocular responses. Similarly, cells illustrated in Fig. 6B and D resemble tuned excitatory cells, since they show maximal response at or close to 0° disparity. However, these were not classified as such, because the responses at larger disparities did not clearly decrease to the levels of the monocular responses.

The response profiles for the cells represented in Figs. 3–6 were derived from the histograms obtained at disparities which varied in 1° steps (see abscissae of the different figures). However, in order to titre out cells which might be sensitive to very fine disparities from those sensitive only to coarser disparities, all cells were tested between −1° and +1° in steps varying by 0.2°. These results are presented in the insets of Figs. 4–6. As expected, no cell

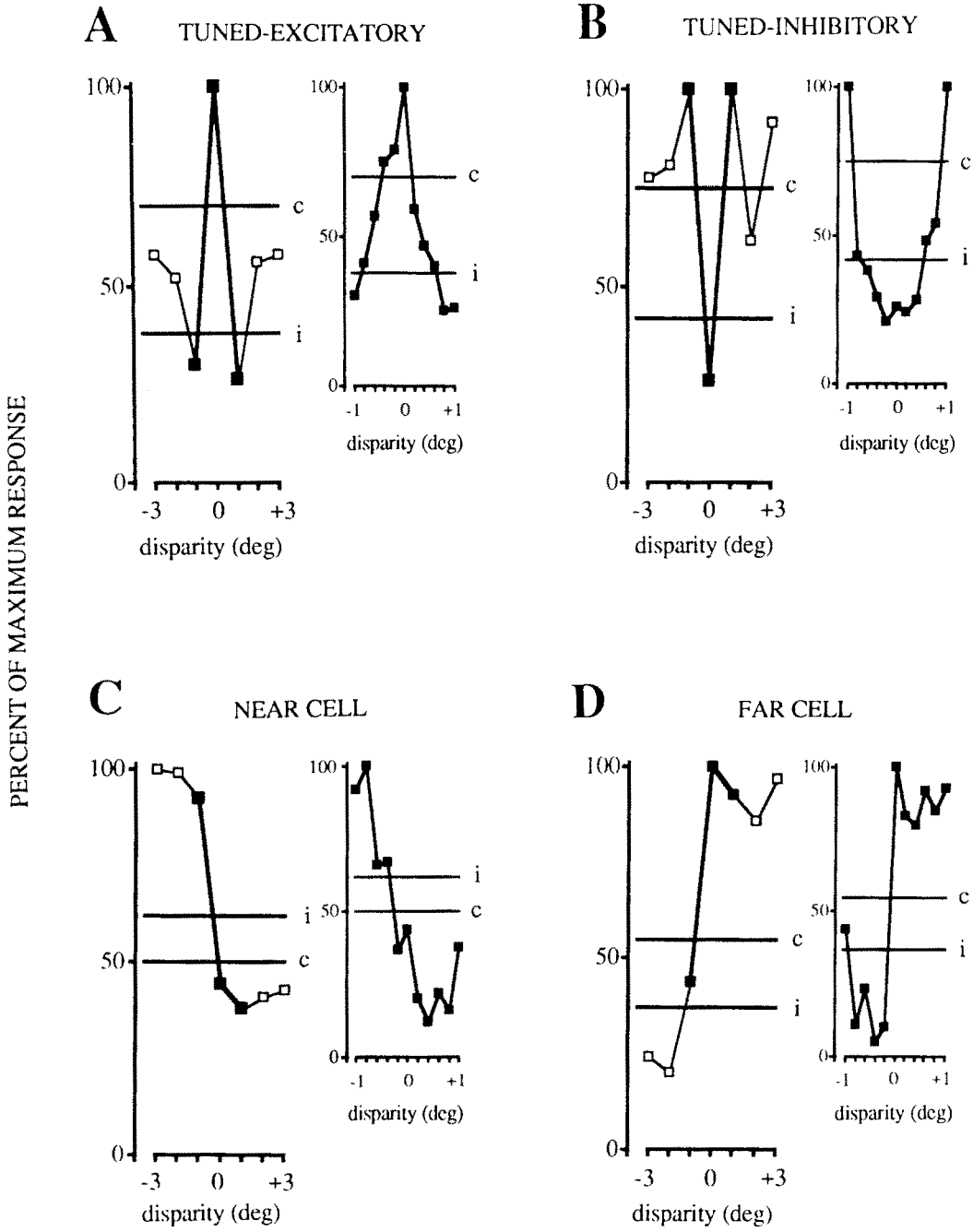

Fig. 4A–D. Representative examples of the four subtypes of disparity-sensitive cells found in area 19 of the normal cat. The tuned excitatory (**A**) and tuned inhibitory (**B**) cells are those which prefer the stimulus on the fixation plane, the former responding with excitation and the latter with inhibition to binocular stimulation. The near cell (**C**) and far cell (**D**) are those units which are excited at one set of disparities and inhibited at another set. The spatial arrangement of the stimuli are such that one can presume that the first subtype prefers stimuli situated in front of the fixation plane and the second, stimuli which appear behind the fixation plane. The profiles which are represented in the larger graphs (*left in each subset* **A–D**) show the responses to five disparities varying from $-3°$ to $+3°$ in 1° steps. The responses of the cells to disparities between $-1°$ and $+1°$ are highlighted. They are, moreover, illustrated in more detail in the slightly smaller graph on the *right in each subset*, which shows the responses to the 11 disparities tested between $-1°$ and $+1°$ in 0.2° steps. The response to monocular ipsilateral (*i*) and contralateral (*c*) eye stimulation is also displayed

which had been classified as "insensitive" in either group showed any additional interactive effect even at these finer disparities. It was expected, on the other hand, that some of the "unclassified" cells might show more typical profiles when more points were sampled. The results shown in the insets to the narrower 0.2° steps are very much in agreement with those obtained at the wider disparities (i.e., 1° steps). No cell originally placed in the "unclassified" category because of its response properties so altered its profile that it could be assigned to one of the four disparity classes.

Most profiles of the disparity-sensitive cells also did not change class even when the additional points between $-1°$ and $+1°$ were inserted in the curve. At best, they only accentuated or sharpened the curves. However, one set of results did occasionally emerge, and it is shown in Fig. 7. The cell from a normal cat represented in Fig. 7A would probably have been classed as a far cell if it had been tested only at disparities varying between $-1°$ and $+1°$ (see inset). It was instead clearly a tuned excitatory cell if the disparities tested extended to 3° on either side of null disparity. Similarly, the cell represented in Fig. 7B obtained in a split-chiasm cat showed a near profile between $-1°$ and $+1°$ and a tuned excitatory profile at the larger disparities. A small minority of all cells tested behaved in this manner (normal cats, two cells; split-chiasm cats, one cell).

The results were also examined to determine whether a relationship existed between disparity subtype and position on the OD scale. The results are presented in Table

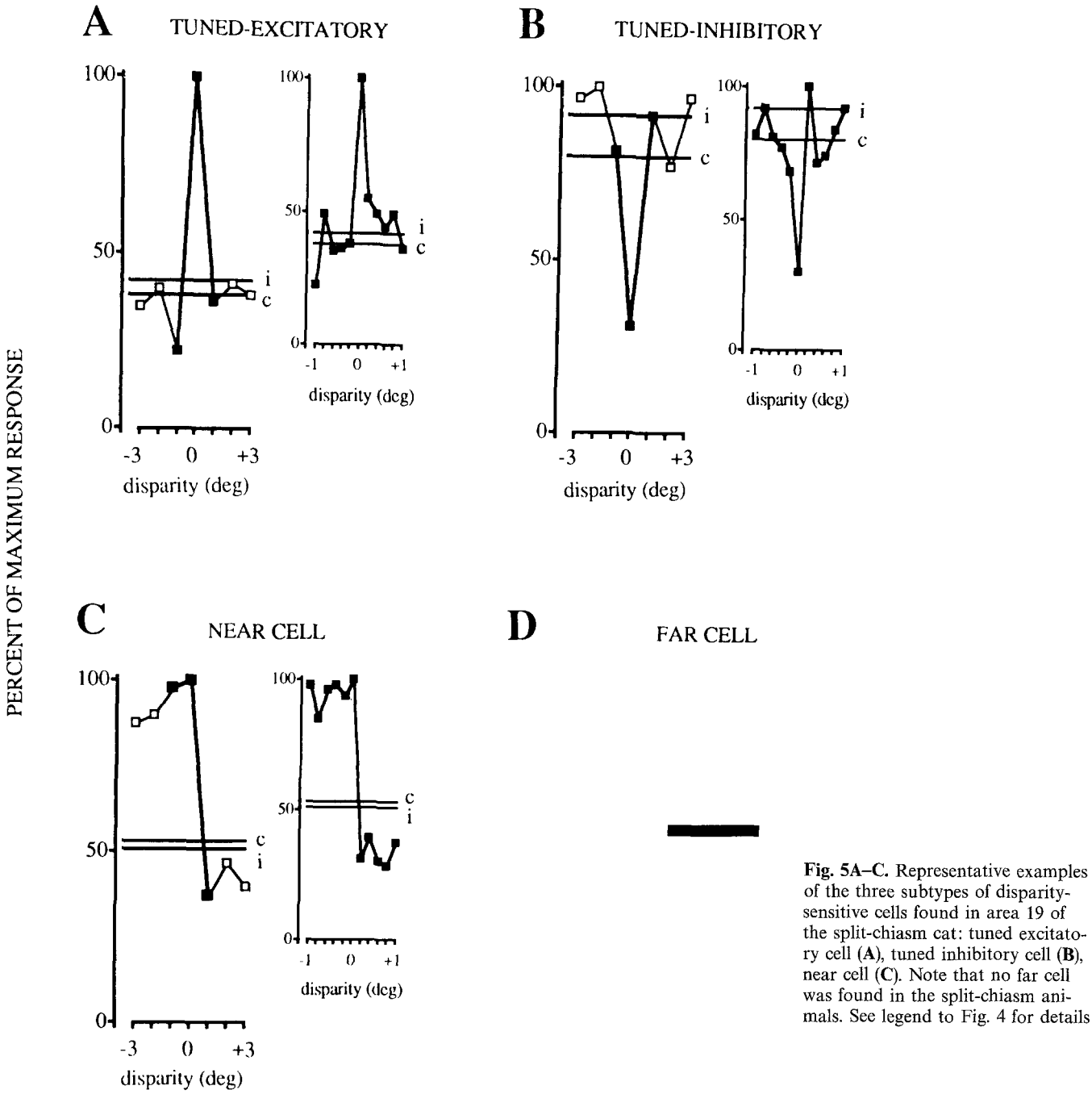

Fig. 5A–C. Representative examples of the three subtypes of disparity-sensitive cells found in area 19 of the split-chiasm cat: tuned excitatory cell (**A**), tuned inhibitory cell (**B**), near cell (**C**). Note that no far cell was found in the split-chiasm animals. See legend to Fig. 4 for details

2. The data obtained from the normal group of cats demonstrates essentially that all tuned cells were mainly found among the balanced OD classes. The split-chiasm group shows a somewhat unbalanced dominance in favor of the ipsilateral eye.

The orientation selectivity of individual bar stimuli presented in Fig. 2 showed no anisotropy in favor of any particular axis. However, convincing evidence has been advanced (Freeman and Ohzawa 1990; Ohzawa et al. 1990; De Angelis et al. 1991) which suggests that putative simple and complex depth cells not only process spatial disparity but also phase relationships. Moreover, they showed that a strong anisotropy in favor of vertical orientations characterizes these cells. Although our stimulation procedure does not allow us to comment on possible phase disparities of cells in area 19, the results do permit a comparison between spatial disparity and orientation preference. All cells which were clearly tuned to orientation were subdivided in terms of their disparity sensitivities. The results are shown in Table 3. Since orientation was tested in approximately 15° steps, the three axes (vertical, horizontal, oblique) were defined as principal axis $\pm 15°$ It is clear from this table that, although no overall orientation anisotropy exists in area 19 when all neurons are considered (Fig. 2), a strong bias is present for cells showing disparity tuning to be particularly sensitive to vertical orientations.

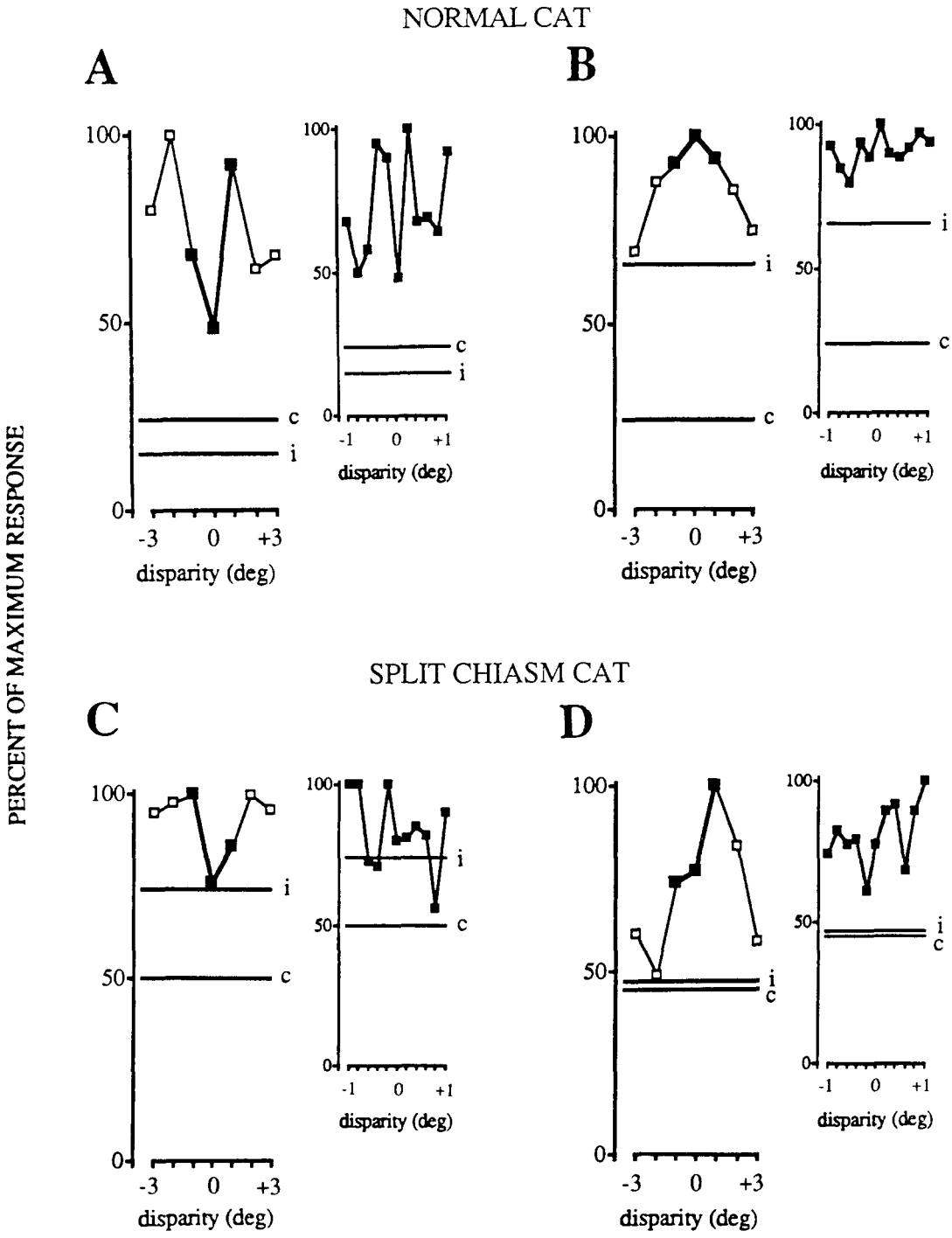

Fig. 6. Examples of atypical cells which showed binocular interactions in the normal (**A**, **B**) and split-chiasm (**C**, **D**) cats. These cells displayed response profiles which did not satisfy all the characteristics of the subclass that they most closely resembled. Thus, the units represented in **A** and **C** behaved as tuned inhibitory cells, since they showed strong inhibition at or near 0° disparity. However, their responses never decreased below the monocular responses. This, moreover, is not due to the fact that not enough points were sampled, since their response within the critical −1° to +1° interval also did not decrease below monocular levels (see *smaller graphs on the right*). **B** Probably a tuned excitatory cell, but with such wide tuning that the responses on either side of the extreme disparities tested are still higher than the monocular levels. **D** Some characteristics of a tuned excitatory cell, but with a maximum somewhat removed from 0° disparity and some properties of a far cell, but without a clear inhibition to one set of disparities. See legend to Fig. 4 for details

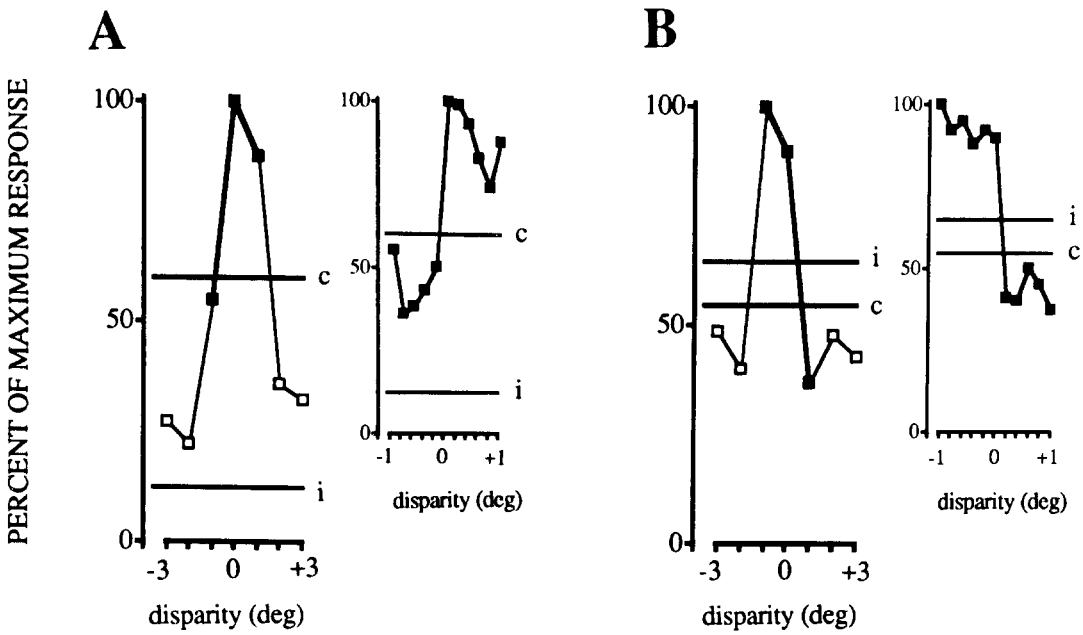

Fig. 7. Examples of two rare cells recorded in the normal (**A**) and split-chiasm (**B**) cats. These cells satisfy all the characteristics of tuned excitatory cells when the profiles to the larger disparities are considered. However, if only the fine disparities situated between $-1°$ and $+1°$ had been considered, one cell (**A**) would have been classed as a far cell and one cell (**B**) as a near cell. See legend to Fig. 4 for details

Table 2. Ocular dominance and number of disparity-sensitive cells in area 19 in normal and split-chiasm cats

Cells	Ocular dominance						
	1	2	3	4	5	6	7
Normal cats							
Tuned excitatory	1	–	1	3	–	–	–
Tuned inhibitory	–	–	–	2	1	–	–
Far cell	–	–	1	2	1	–	–
Near cell	–	–	2	5	2	1	–
Insensitive	2	2	8	10	3	1	2
Unclassified	2	1	2	4	3	2	1
Split-chiasm cats							
Tuned excitatory	–	–	1	2	1	–	1
Tuned inhibitory	–	–	–	–	1	1	1
Far cell	–	–	–	–	–	–	–
Near cell	–	–	–	2	–	1	1
Insensitive	–	–	–	1	1	1	25
Unclassified	–	–	–	2	2	1	7

Table 3. Orientation and number of disparity-sensitive cells recorded in area 19 in normal and split-chiasm cats

Cells	Orientation		
	Vertical	Horizontal	Oblique
Normal cat			
Tuned excitatory	4	0	1
Tuned inhibitory	3	0	0
Far cell	4	0	0
Near cell	9	0	1
Insensitive	0	12	14
Unclassified	0	5	12
Split-chiasm cat			
Tuned excitatory	3	0	1
Tuned inhibitory	2	0	0
Far cell	0	0	0
Near cell	3	0	1
Insensitive	4	12	8
Unclassified	5	5	2

Discussion

The present experiment had two main objectives: first, to determine whether disparity-sensitive cells are present in area 19 of the cat and, second, to examine whether these interactions can be assured through combined thalamocallosal inputs to a cell, independently of normal binocular thalamocortical convergence. The results indicate that disparity-sensitive cells are present in this area, although their proportion appears to be smaller than in areas 17–18 and their tuning characteristics less well defined. Following chiasmatomy, there was a drastic reduction in the number of neurons sensitive to disparity and an increase in the number of monocularly driven cells. These results are substantially different from those obtained under similar experimental conditions in areas 17–18.

Receptive field properties and chiasma transection

RFs in the control group showed all the properties typical of the area. Sectioning the optic chiasm abolished input to visual cortex coming from the contralateral

nasal retina. This constituted a reduction of over 65% of total visual input to the cortex and resulted in complete elimination of all direct contralateral thalamocortical activation of individual cells. Approximatively 14% of units were unresponsive in the operated animals compared to 3% in the control group. Cell classification did not seem to be greatly affected by the chiasm transection. The distribution obtained for the normal cat is not uncommon for this cortical area (Hubel and Wiesel 1962, 1965a; Henry 1977; Albus and Beckmann 1980; Duysens et al. 1982a,b; Dreher 1986). The same type of RF organization prevails in the split-chiasm cat (Antonini et al.1985). The OD distribution obtained for the normal group is typical for this brain region (Hubel and Wiesel 1965a; Antonini et al. 1985; Albus and Beckmann 1980; Duysens et al. 1982a,b). The distribution found for the split-chiasm group shows that OD was shifted towards the ipsilateral eye, the largest single category of cells sampled responding exclusively to this eye. The contralateral eye input is presumed to arise in the opposite cortex and pass through the CC, as we have demonstrated experimentally for other areas (Lepore et al. 1988). One should not, however, consider the absolute proportion of binocular cells as representative of all area 19, nor even of the region of cortex under study. On the one hand, this proportion probably underestimates the number of binocular units in the target cortex, since only those units which gave robust response to at least one eye were examined in detail. A poorly responsive unit would not be tested because it could generally not be examined for the complete protocol which lasted for about 2 h and often longer. On the other hand, the ratio is probably higher than that which would be obtained if total area 19 were sampled evenly. This is due to the purposeful bias of recording from the region of central vision, where we had expected disparity-sensitive units and callosal activation to be most abundant. These OD results are not unlike those reported by Antonini et al. (1985) in similarly prepared animals. A post hoc statistical analysis comparing our results with those reported by these researchers showed the proportions to be similar ($\chi^2 = 10.63$, $P > 0.05$). The overall results concerning these RF properties testify, therefore, to the redundant nature of the contralateral thalamic and callosal inputs, and they show that the callosal pathway can act for this "higher order" area as a transcortical extension of the sensory pathway.

Binocular interaction and disparity tuning

The principal objective of this study was to examine the nature of binocular interaction in normal cats and to see whether these properties extend to converging inputs mediated partially through the callosal pathway. In the normal cat, most cells were binocularly driven (about 88%). Moreover, of the eight cells which appeared to be monocular, four showed binocular interactions when the two eyes were stimulated simultaneously. This indicates that most, if not all cells in this select region of cortex are sensitive to binocular stimulation, provided that the stimulation procedure is appropriate. In this sense, the results confirm and extend those reported by others for this area (Hubel and Wiesel 1965a; Duysens et al. 1982a; Rapaport et al. 1982; Leventhal and Hirsch 1983).

Results obtained in the monkey led to the expectation that disparity tuning would be one of the dominant characteristics of cells in area 19. This was not found to be the case in cats. Whereas, using identical stimulation procedures (Lepore et al. 1992), nearly 71% of the cells in areas 17–18 showed disparity tuning, only 34% of the cells in area 19 demonstrated this property. The degree of tuning of the disparity-sensitive cells also differed between these areas. Areas 17–18 cells had sharply defined profiles such that cells sensitive to stimulation on the fixation plane (the tuned excitatory and tuned inhibitory cells) had narrow half-widths and far and near cells had very pronounced slopes separating the excitatory and inhibitory profiles. These characteristics persisted, in an attenuated but appropriate manner, even following chiasmatomy. In area 19, on the other hand, despite the fact that similar ranges of disparities were examined, most cells were more widely tuned. They almost completely disappeared following the section of the chiasm.

The results obtained in area 19 of the normal cat differ in some respects from those obtained in the only other study which has looked at this problem using a comparable approach. Pettigrew and Dreher (1987) found that cells in this area which were tuned to disparity were more numerous than in area 17. A second point of disagreement concerns the relative proportions of the four subclasses of disparity-tuned neurons: whereas our results point to a fairly homogeneous distribution among the four classes, Pettigrew and Dreher (1987) suggest that cells in this area might be particularly sensitive to uncrossed disparities. There is no obvious explanation for these differences. Although their results agree more with those obtained in the monkey as far as overall number of disparity-sensitive cells in this higher order area are concerned, ours seem to fit more closely with those obtained in this animal as far as the relative distribution of the four subclasses are concerned.

Given the results from electrophysiological analysis, as well as the behavioral results showing that subtotal areas 17–18 lesions abolish stereoscopic discrimination based on disparity (Ptito et al. 1992), it would appear that area 19 is minimally involved in the analysis of disparity information. This was unexpected, but explainable. Area 19 receives its inputs not only in a hierarchical fashion from areas 17–18 but also in parallel from many subcortical sources, such as the medial interlaminar nucleus (MIN) and the C-laminae of the dorsal lateral geniculate nucleus (d-LGN), the geniculate wing, and the lateral posterior- (LP)-pulvinar complex (Rodieck and Brening 1983; Stone 1983; Rosenquist 1985; Dreher 1986). Cells in the LP-pulvinar complex generally have large RFs and coarse tuning properties (Chalupa and Fish 1978; Chalupa et al. 1983; Casanova et al. 1989; Chalupa and Abramson 1989), which makes them inappropriate to signal the fine spatial characteristics of disparity-tuned neurons. Much less is known about the RF properties of cells in the MIN. However, cells of the C-laminae of d-LGN mainly belong to the W class (Rodieck and Brening

1983; Stone 1983; Dreher 1986). These cells, which constitute a generally heterogeneous class, are also those which are usually termed "sluggish," "hard to drive," and are not thought to be involved in the analysis of fine spatial detail (as the X-type cells, for example). The electrophysiological results in recipient area 19 are therefore a reflection of the poorly defined spatial properties of these projection cells. This interpretation, however, as was the case with the results, differs from that of Pettigrew and Dreher (1987), who postulate that it is precisely this W-cell input which is responsible for the formation of the disparity-sensitive neurons.

The results are nonetheless surprising if one uses the lower to higher order argument to justify RF properties of cells in the terminal area, since area 19 receives a large input from cells in areas 17–18, which are themselves well tuned to spatial disparity. One would have assumed that this lower order property would be maintained at the subsequent station of the "functional stream" (Van Essen 1985; Van Essen et al. 1992). The results are also surprising because they point to a significant difference between cat and monkey functional organization. This difference is, however, paralleled at the anatomical level, the monkey visual pathways being more serially organized than the cat's.

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