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Monocularly Induced 2-Deoxyglucose Patterns in the Visual Cortex and Lateral Geniculate Nucleus of the Cat: II. Awake Animals and Strabismic Animals

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Abstract

In the course of experiments studying the organization of ocular dominance columns in the visual cortex of cats, we noticed that—contrary to common belief—labelling with 2-deoxyglucose after monocular stimulation failed to induce a pattern of ocular dominance columns but resulted in a rather homogeneous 2-deoxyglucose uptake throughout area 17 in anaesthetized and paralysed animals. We wondered whether 2-deoxyglucose columns could be obtained in awake animals and/or in strabismic animals, which have a more pronounced segregation of ocular dominance columns. To this end, we investigated 2-deoxyglucose patterns after monocular stimulation in three groups of animals: (i) in awake normally reared cats, (ii) in awake strabismic cats and (iii) in anaesthetized and paralysed strabismic cats. Additionally, we labelled ocular dominance columns with intraocular [^{3}H]proline injections. In all cats, monocular stimulation induced 2-deoxyglucose patterns that were in precise register with the proline-labelled ocular dominance columns in layer IV. Regions of increased 2-deoxyglucose uptake extended in a columnar fashion through all cortical layers. In contrast to normally reared animals, in strabismic cats, the expression of 2-deoxyglucose labelled ocular dominance columns was not abolished by anaesthesia or paralysis. However, there was a difference between the 2-deoxyglucose patterns in the awake normally reared cats and the strabismic animals. In the former, the patches of 2-deoxyglucose labelling were smaller and occupied less territory than the afferents of the stimulated eye in layer IV. Together with the results of the previous study, these data indicate that in awake normally reared and in awake and anaesthetized strabismic cats, but not in anaesthetized and paralysed normally reared animals, monocular stimulation activates selectively neurons in columns that are in register with the termination sites of afferents from the stimulated eye. This suggests the existence of a mechanism in normally reared animals which restricts cortical activation after monocular stimulation to territories that are in register with the afferents from the stimulated eye. This mechanism appears to be effective only when the animals are awake and actively exploring their environment. This and the fact that the active columns were narrower than the terminal fields of the stimulated eye suggest an active inhibitory process, perhaps related to mechanisms of selective attention. The observation that ocular dominance columns persist in strabismic cats even under anaesthesia can be accounted for by the lack of binocular convergence in these animals.

Introduction

In the visual cortex of the cat, the geniculo-cortical afferents conveying signals from the two eyes terminate in alternating regions of layer IV known as ocular dominance columns (Hubel and Wiesel, 1962, 1969). In a number of studies, these columns have been visualized by labelling the afferents of the lateral geniculate nucleus (LGN) (Shatz *et al.*, 1977; Shatz and Stryker, 1978; LeVay *et al.*, 1978; Löwel and Singer, 1987; Anderson *et al.*, 1988). According to Kossut *et al.* (1983) and Tieman and Tumosa (1983) it is also possible to obtain functional maps of ocular dominance columns by 2-deoxyglucose (2-DG) autoradiography. Monocular but not binocular exposure of freely moving cats to a complex laboratory scene induced columnar patterns of increased 2-DG uptake in area 17 (Kossut *et al.*, 1983; Tieman and Tumosa, 1983). In the course of experiments studying the organization of ocular dominance columns, we noticed, however, that—contrary to common belief (LeVay and Nelson, 1991)—labelling with 2-DG after monocular stimulation failed to induce a pattern of ocular dominance columns but resulted in a rather homogeneous 2-DG uptake throughout area 17 in anaesthetized and paralysed cats (Löwel and Singer, 1993). We interpreted this somewhat suprising finding as indicating that in the cat visual cortex binocular convergence seems to occur so early in cortical processing that monocular stimulation with many different orientations leads to a rather homogeneous activation of cortical tissue.

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This result and its interpretation—although at odds with the above-mentioned reports—fits electrophysiological data about the degree of binocularity of visual cortical neurons. In a number of studies, most of which have been performed in anaesthetized and paralysed animals, it has been shown convincingly that in the cat, the majority of neurons in area 17—even in the input layer IV—respond to stimulation of both eyes i.e. are binocularly driven (Hubel and Wiesel, 1962; Albus, 1975; Shatz and Stryker, 1978). If the homogeneous 2-DG labelling induced by monocular stimulation is indeed due to early binocular convergence then 2-DG labelling should lead to very different results in strabismic cats. In these animals, the optical axes of the two eyes cannot be aligned and the images on the two retinae cannot be brought into register. As a consequence binocular convergence breaks down and most of the cells in the visual cortex become responsive exclusively to stimulation of either the right or the left eye (Hubel and Wiesel, 1965). In addition, it has been shown recently that the columns of the right and left eye are no longer interconnected by the network of tangential intracortical fibres (Löwel and Singer, 1992a) and that responses of cells in different ocular dominance domains can no longer synchronize (König *et al.*, 1990, 1993). This predicts that in strabismic animals monocular stimulation should activate only restricted regions of the cortex and hence should lead to 2-DG patterns reflecting the ocular dominance domains of the stimulated eye. In order to test this prediction we extended our monocular 2-DG experiments to animals in which divergent strabismus had been induced surgically at the age of 2–3 weeks.

The second goal of the present study was to resolve the discrepancy between our results (Löwel and Singer, 1993) and those of the other groups who reported 2-DG columns after monocular stimulation in normally reared cats (Kossut *et al.*, 1983; Tieman and Tumosa, 1983). These groups used awake cats while our previous experiments were performed in anaesthetized and paralysed animals. This raised the possibility that anaesthesia and paralysis might influence the topography of activation patterns resulting from monocular stimulation. We have therefore performed the 2-DG experiments in both normal and strabismic cats and also in awake, behaving animals. Some of the results of the present study have been published in abstract form (Löwel and Singer, 1992a,b).

Materials and methods

A total of 10 cats were used in this study (see Table 1). In seven kittens, divergent strabismus was induced surgically at the age of 2–3 weeks. At the age of 2–3 months, four of them and three age-matched normally reared cats were subjected to a 2-DG experiment with monocular stimulation (Sokoloff *et al.*, 1977) while being awake and freely exploring the laboratory. In two strabismic and one normal cat, the ocular dominance columns were additionally labelled by intraocular [^{3}H]proline injections (Grafstein, 1971; Wiesel *et al.*, 1974). The remaining three strabismic cats were subjected to a 2-DG experiment with monocular stimulation while being anaesthetized and paralysed as described in the accompanying paper (Löwel and Singer, 1993).

Surgical procedures and visual stimulation

For the induction of strabismus, anaesthesia was induced with ketamine hydrochloride (10 mg/kg body wt) and xylazine hydrochloride (2.5 mg/kg) injected intramuscularly, and maintained with ketamine hydrochloride injected intraveneously. In all seven kittens, the medial rectus muscle of the left eye was severed in order to induce divergent strabimus.

For transneuronal labelling of ocular dominance columns in layer IV, one normally reared (B0) and two strabismic cats (B9 and B10) were anaesthetized as above (ketamine/xylazine) and were then given an injection of 2–2.5 mCi of [^{3}H]proline (in 50 μl of saline) in one eye (the right eye in cats B9 and B10, and the left eye in cat B0). Two weeks later, the animals were prepared for the monocular 2-DG experiments as described below.

TABLE 1. Conditions for the monocular 2-DG experiments and proline injections

Cat	Rearing	2-DG experiment		Injected eye
		State	Open eye	
B5	strabismic	awake	right	–
B6	strabismic	awake	right	–
B9	strabismic	awake	left	right
B10	strabismic	awake	right	right
B11	strabismic	anaesthetized and paralysed	right	–
B12	strabismic	anaesthetized and paralysed	right	–
B13	strabismis	anaesthetized and paralysed	right	–
B7	'normal'	awake	right	–
B8	'normal'	awake	left	–
B0	'normal'	awake	right	left

In four strabismic (B5, B6, B9 and B10) and three normally raised 2- to 3-month-old cats (B7, B8 and B0), one eye was occluded and a venous catheter implanted under halothane anaesthesia (1–4% halothane in a mixture of 70% N_2O/30% O_2). After full recovery from anaesthesia, 2-deoxy-D-[U-^{14}C]glucose (2-DG, Amersham, sp. act. 310 mCi/mmol; 100–120 μCi/kg) was injected and the cats were allowed to move freely around in the laboratory for effective monocular stimulation.

The remaining three strabismic cats (B11, B12 and B13) were prepared for a 'conventional' 2-DG experiment (under anaesthesia and paralysis) as described in detail elsewhere (Freeman *et al.*, 1987; Löwel *et al.*, 1987; Löwel and Singer, 1983). Visual stimulation of these animals was monocular and consisted of moving square wave gratings which covered the central 20° of the visual field. A 1.5° wide strip along the vertical meridian was stimulated with horizontal contours only whereas the orientation of the grating in the remaining visual field changed every 5 s in 45° steps (spatial frequency: 1, 0.5 and 0.15 cycles/degree; velocity: 2 cycles/degree).

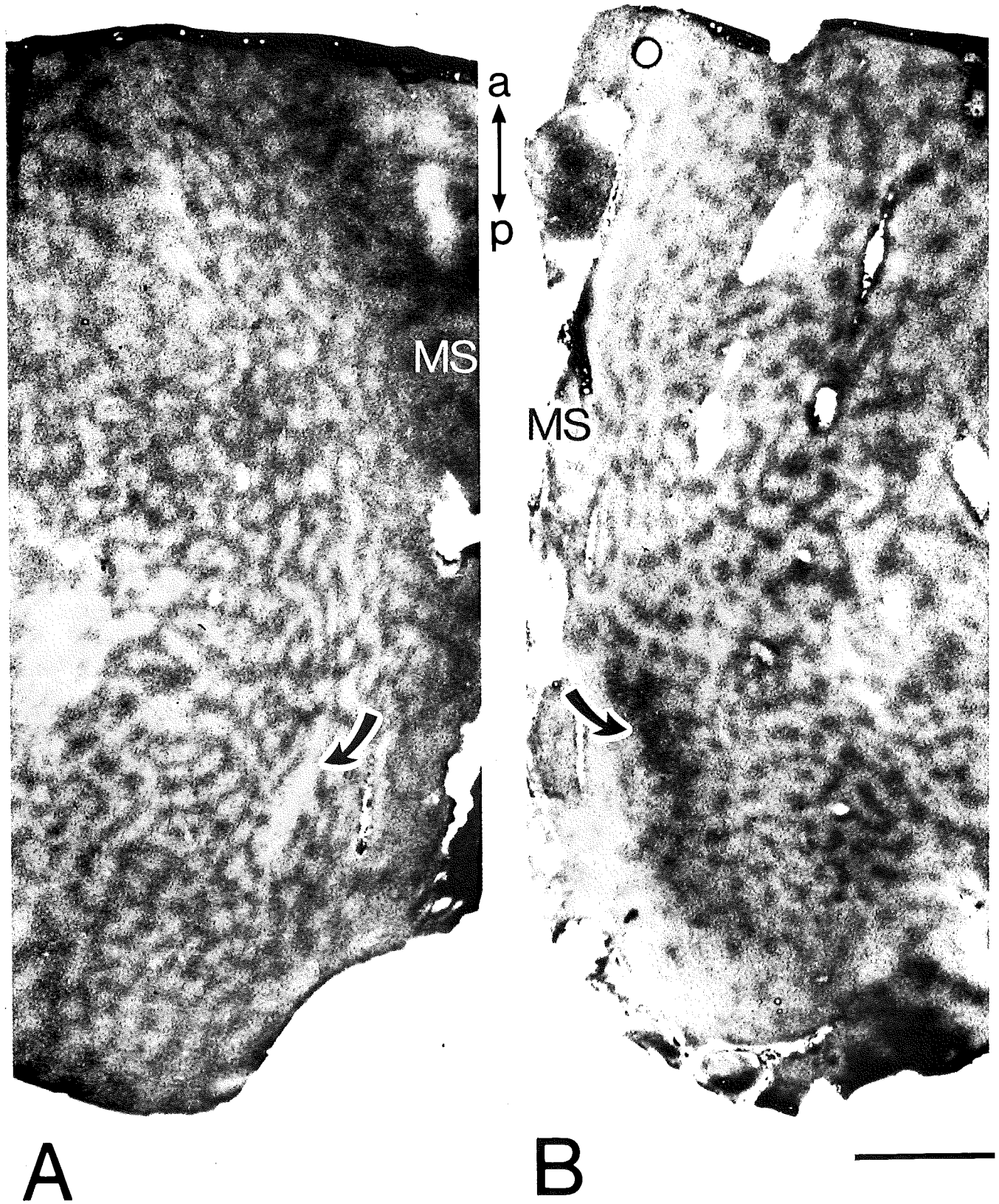
Histological procedures were identical to those described in the accompanying paper (Löwel and Singer, 1993).

Results

In all awake strabismic cats, monocular stimulation induced 2-DG patterns that were in precise register with the terminal labelling in layer IV (Fig. 1; see also Löwel and Singer, 1987, 1992a; Anderson *et al.*, 1988). The 2-DG labelling extends in columns through all cortical layers and these columns are precisely superimposed on the termination sites of the active terminals in layer IV (Fig. 1C and D). Accordingly, the 2-DG patterns display all the characteristic features of ocular dominance domains. (i) The optic disc representations of the stimulated and unstimulated eye are identifiable in the posterior third of both hemispheres as demarcated oval regions which are solidly labelled ipsilateral (right) and unlabelled contralateral (left) to the open eye (Fig. 1A and B; Fig 2). (ii) The monocular segment is indicated by uniform labelling at the medial border of the area 17 contralateral to the stimulated eye and by the absence of labelling at comparable eccentricity on the ipsilateral side. (iii) The territories of the open eye tend to be larger in the contra- than in the ipsilateral hemisphere. These features

of the ocular dominance system are expressed equally well in all layers. This is illustrated for the cortical representation of the contralateral eye's blind spot in Figure 2. There was no detectable increase in 2-DG uptake at that location (no 'filling in') in either supragranular, granular or infragranular layers.

Contrary to our observations in normally raised cats (Löwel and



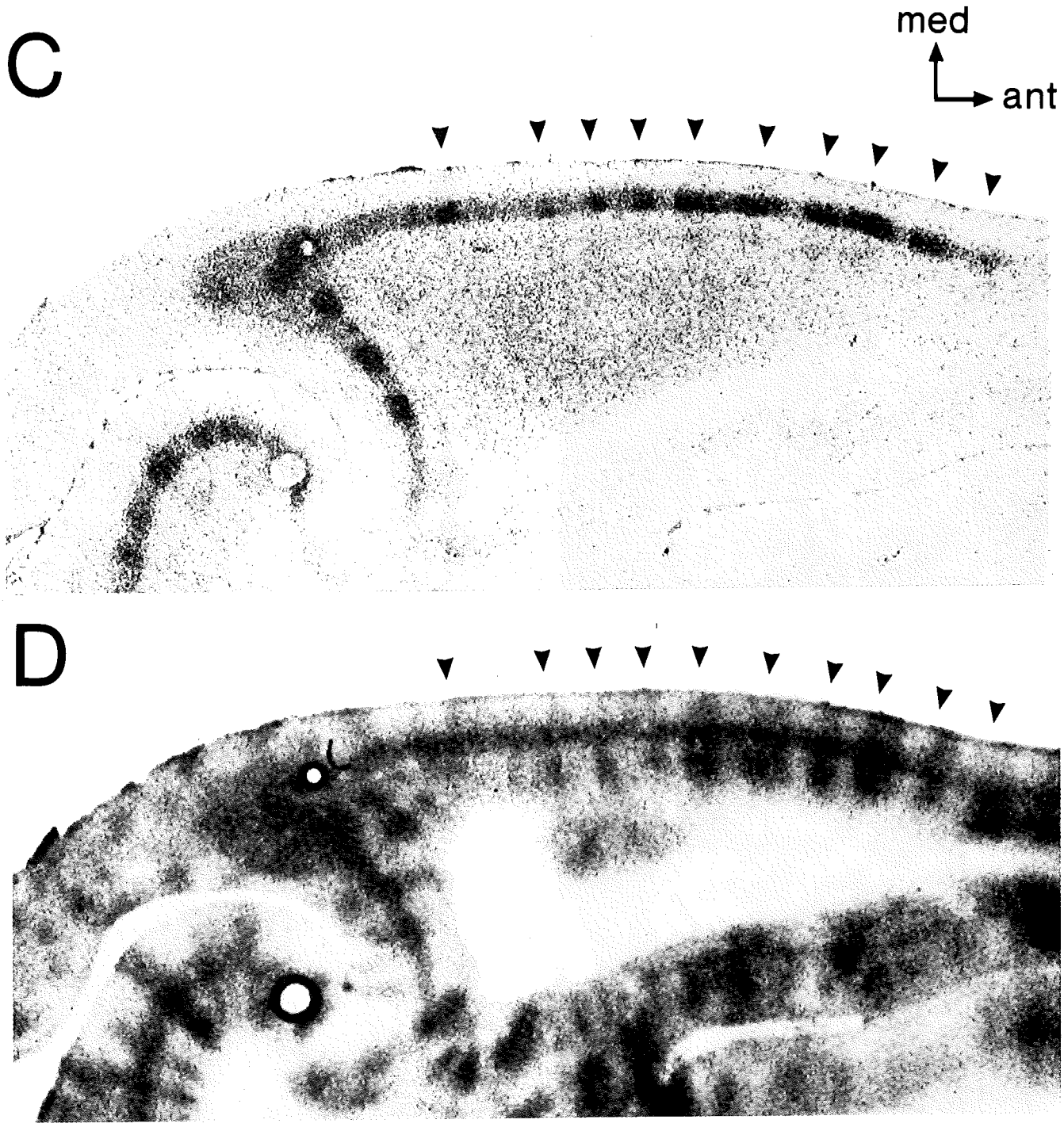


FIG. 1. Ocular dominance columns in the visual cortex of awake strabismic cats. (A, B) 2-DG autoradiographs of supragranular flat-mount sections from the unfolded left (A) and right (B) hemisphere of a strabismic cat that had been stimulated through the right eye. Note that sharp delineation of active (dark grey) and inactive (light grey) territories. The optic disc representations are indicated with arrows. Note that the territories of the open eye tend to be larger in the contralateral hemisphere (A) than in the ipsilateral one (B). (C, D) Comparison of ocular dominance columns in a horizontal section through the medial bank of right area 17 as revealed by transneuronally transported [^{3}H]proline injected into the right (normal) eye (C) and 2-DG labelling after right-eye stimulation (D). The two autoradiographs are from the same section. The columns of increased 2-DG uptake are in register with the right-eye territories in layer IV (arrowheads). Abbreviations: a/ant, anterior; p, posterior; med, medial; MS, monocular segment. Scale bars represent 5 mm (A, B) or 2 mm (C, D).

Singer, 1993), monocular stimulation induced clearly visible 2-DG patterns in area 17 of strabismic cats even when these animals were anaesthetized and paralysed. Figure 3A shows a section through layer IV of the hemisphere contralateral to the stimulated eye which reveals sharply delineated ocular dominance domains. As in the awake strabismic cats, the territories of the contralateral eye (the dark regions)

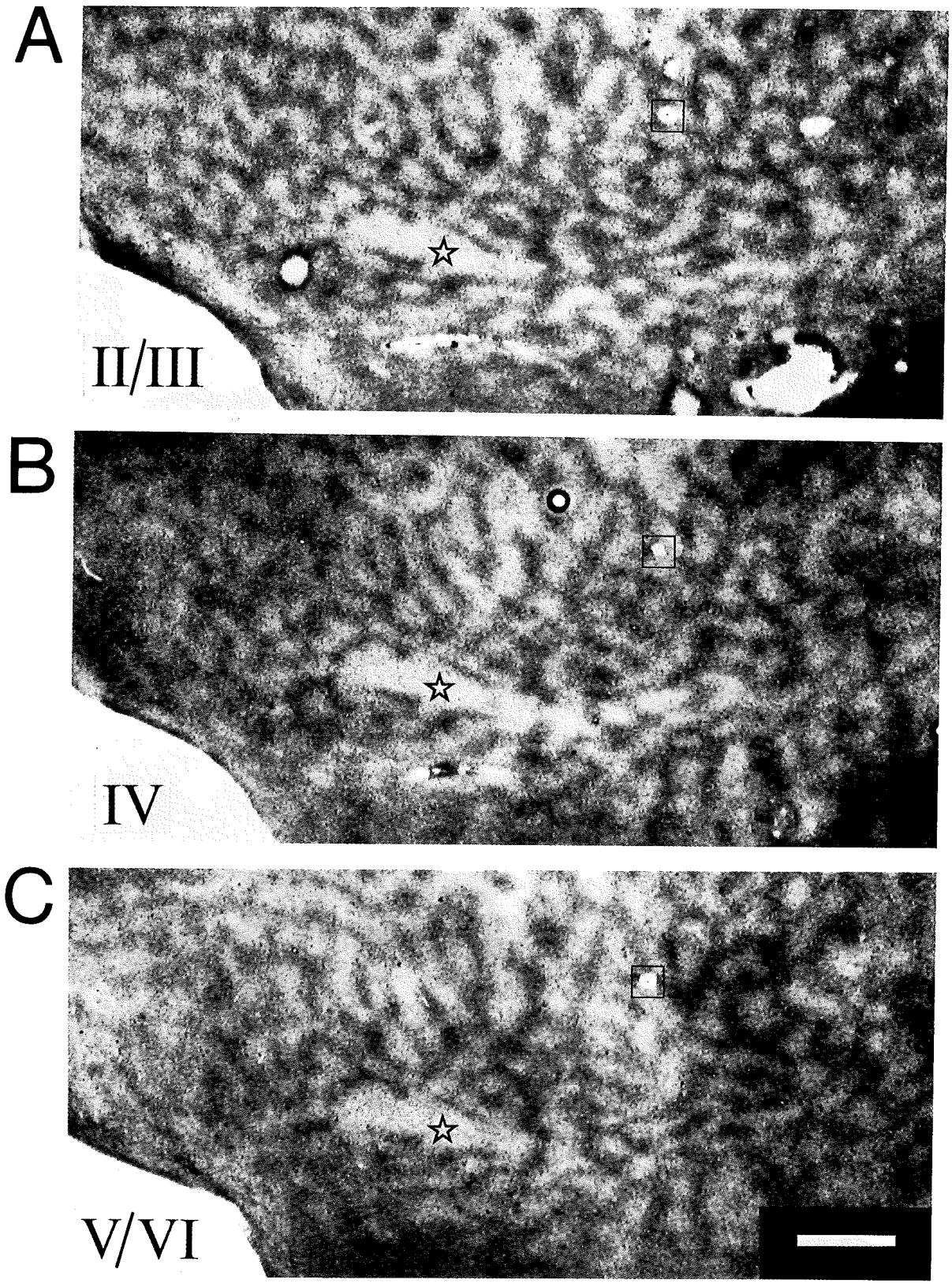


FIG. 2. 2-DG-labelled ocular dominance columns in the vicinity of the optic disc representation in different layers of area 17. The hemisphere contralateral to the stimulated eye in a strabismic cat is illustrated. (A–C) The optic disc representation (asterisk) appears as a pale oval-shaped region irrespective of whether the autoradiograph is taken from layers II/III (A), IV (B) or V/VI (C). The marked white spot to the upper right side of the optic disc representation is one of the needle holes used for aligning the sections. Scale bar, 2 mm.

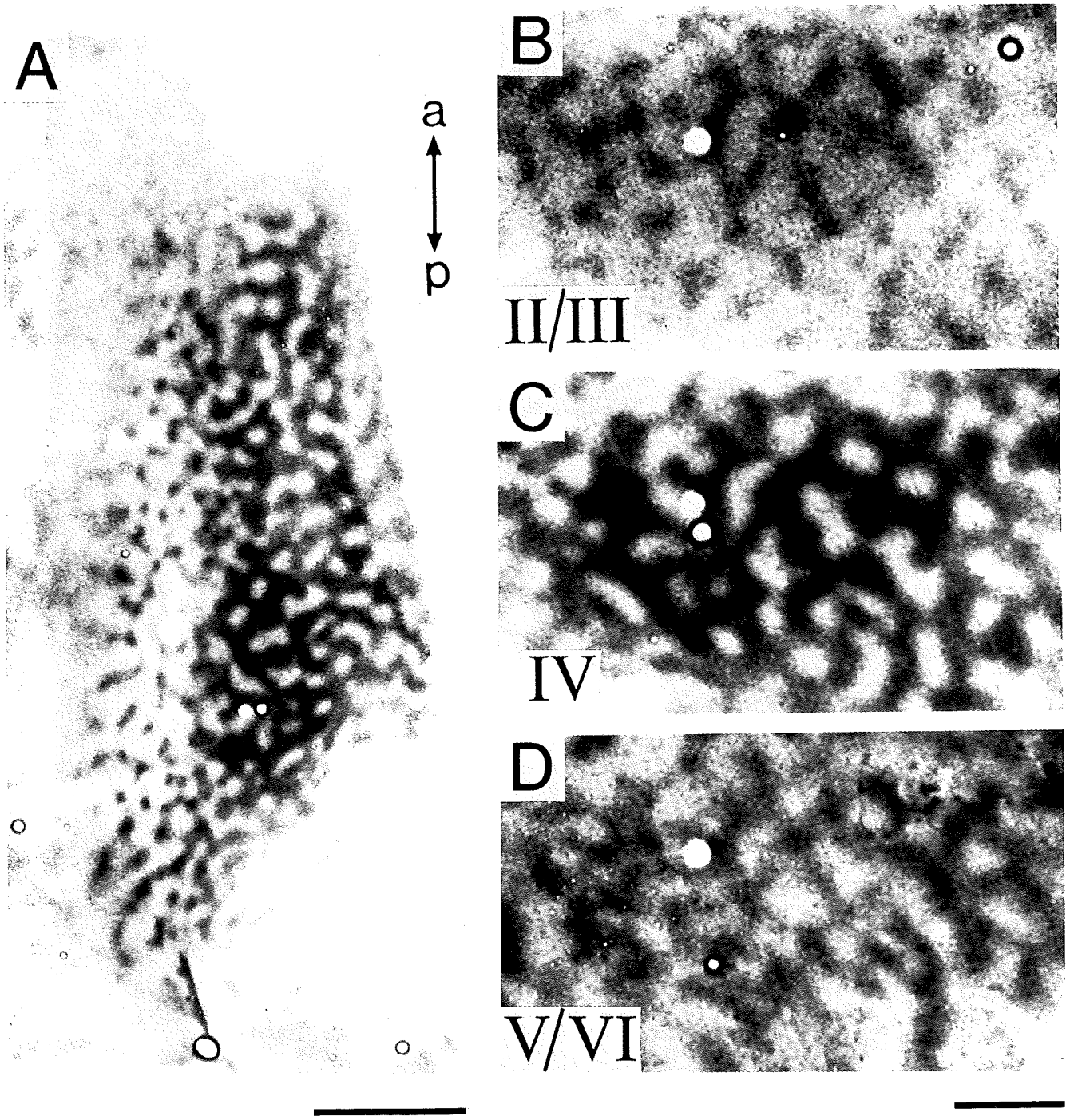


FIG. 3. Monocular 2-DG patterns in the visual cortex of an anaesthetized and paralysed strabismic cat. (A) Overall pattern of ocular dominance domains in a hemisphere that was stimulated with many different orientations through the contralateral eye. (B–D) Detail of the ocular dominance pattern in layers II/III (B), IV (C) and V/VI (D). Note that the width of the ocular dominance domains decreases in supragranular layers (B). The white spot visible in B, C and D is one of the needle holes used for aligning the sections. Abbreviations as in Figure 1. Scale bars represent 5 mm (A) or 2 mm (B–D).

occupy more cortical surface area than the weakly labelled territories of the unstimulated ipsilateral eye. The 2-DG pattern again extends in columns through all cortical layers. The most prominent difference in comparison with the non-anaesthetized (strabismic) cats is that the width of these columns decreases in supragranular layers (compare (Fig. 3B–D). Since only the central 20° of the visual field were stimulated (see Materials and methods), the optic disc representations and the monocular segments that are located more peripherally are not visible on the autoradiographs.

In the three normally reared cats that were awake during 2-DG exposure, monocular stimulation also induced columnar 2-DG patterns (Fig. 5). This is in marked contrast to anaesthetized and paralysed animals, in which we found homogeneous increases in 2-DG labelling following monocular stimulation (Löwel and Singer, 1993). The 2-DG

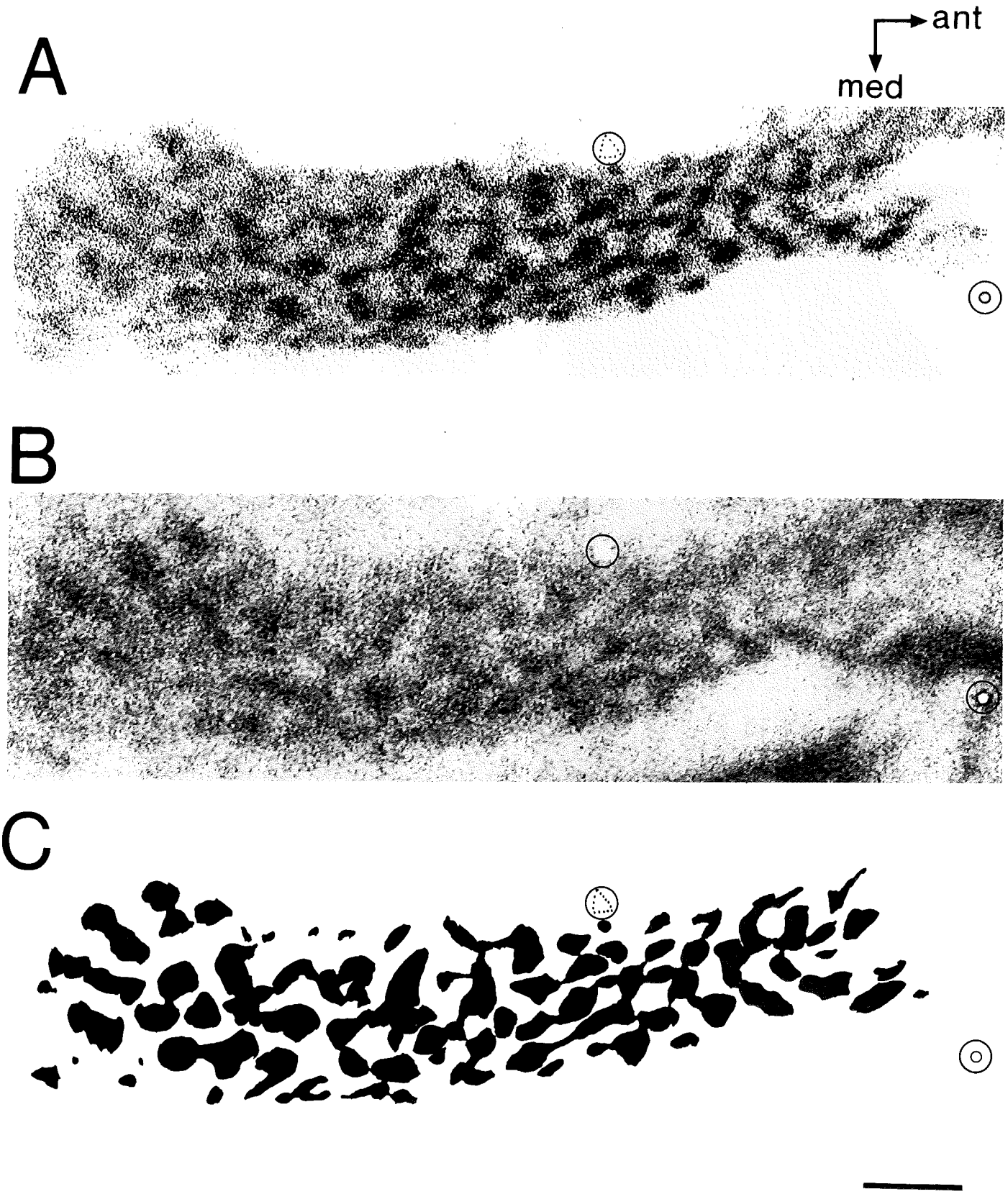
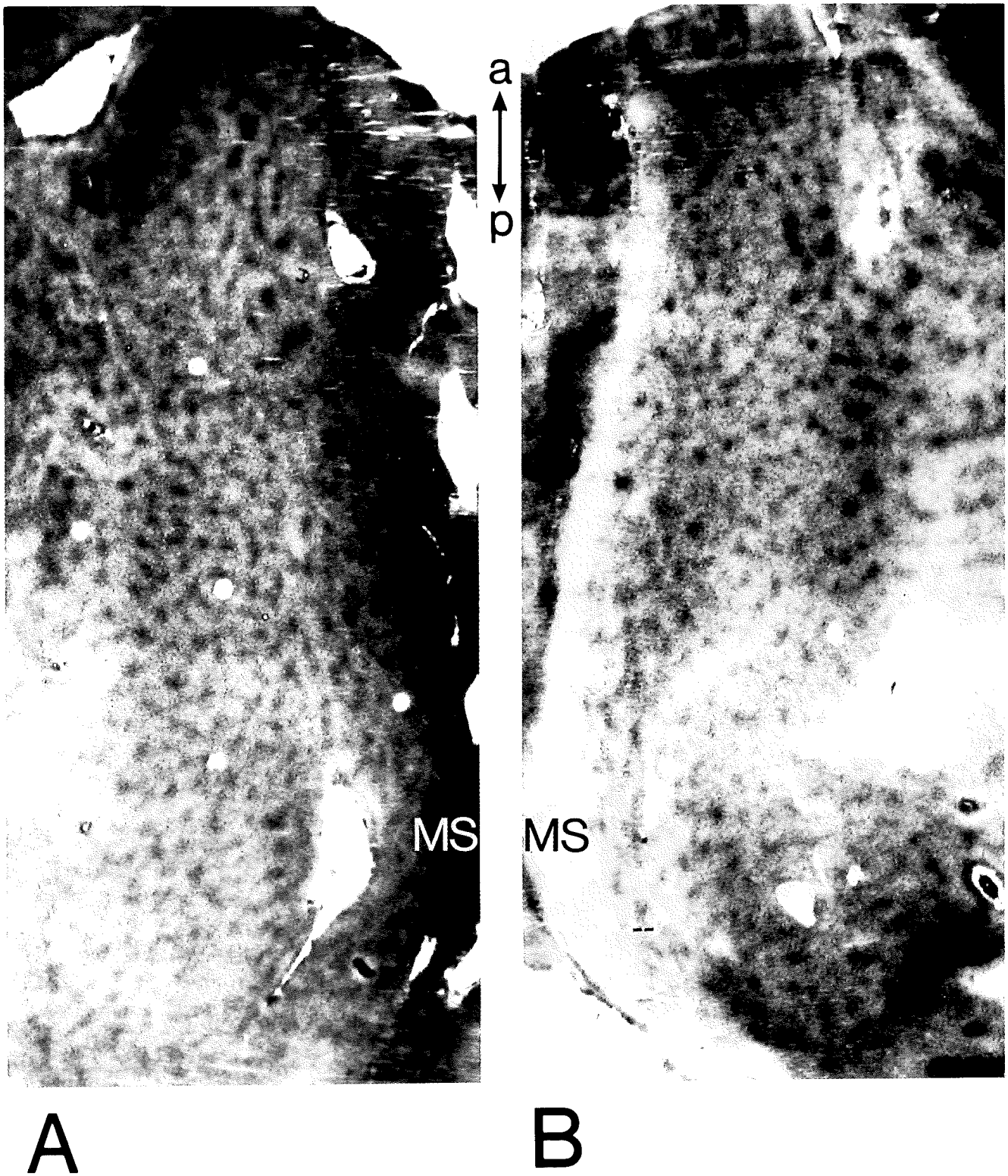


FIG. 4. Ocular dominance domains in the visual cortex of normally raised cats. Comparison of ocular dominance domains as revealed by transneuronally transported [^{3}H]proline injected into the left eye (A) and 2-DG labelling after right-eye stimulation (B). The hemisphere ipsilateral to the injected eye (contralateral to the stimulated eye) is illustrated. Both autoradiographs are from the same flat-mount section. Note that the [^{3}H]proline pattern (A) is in register with the left-eye domains (light patches in B). Circles indicate the locations of an air bubble (right) and a hole in the tissue (up) used for aligning the autoradiographs. (C) Schematic drawing of the proline pattern in A. Abbreviations as in Figure 1. Scale bar, 2 mm.

columns were again in precise register with the ocular dominance territories of the stimulated eye (Fig. 4). In the illustrated case, proline had been injected into the left unstimulated eye so that domains of increased [^{3}H]proline-labelling correspond to zones of weak 2-DG-labelling and vice versa. The monocularly induced 2-DG patterns in the normal awake cats differ in a number of features from those in the strabismic animals. In the former, the 2-DG patterns have a more patchy appearance in both hemispheres: the patches of labelling are smaller and occupy less territory than the afferents of the stimulated eye in layer IV. This is especially obvious in the hemispheres



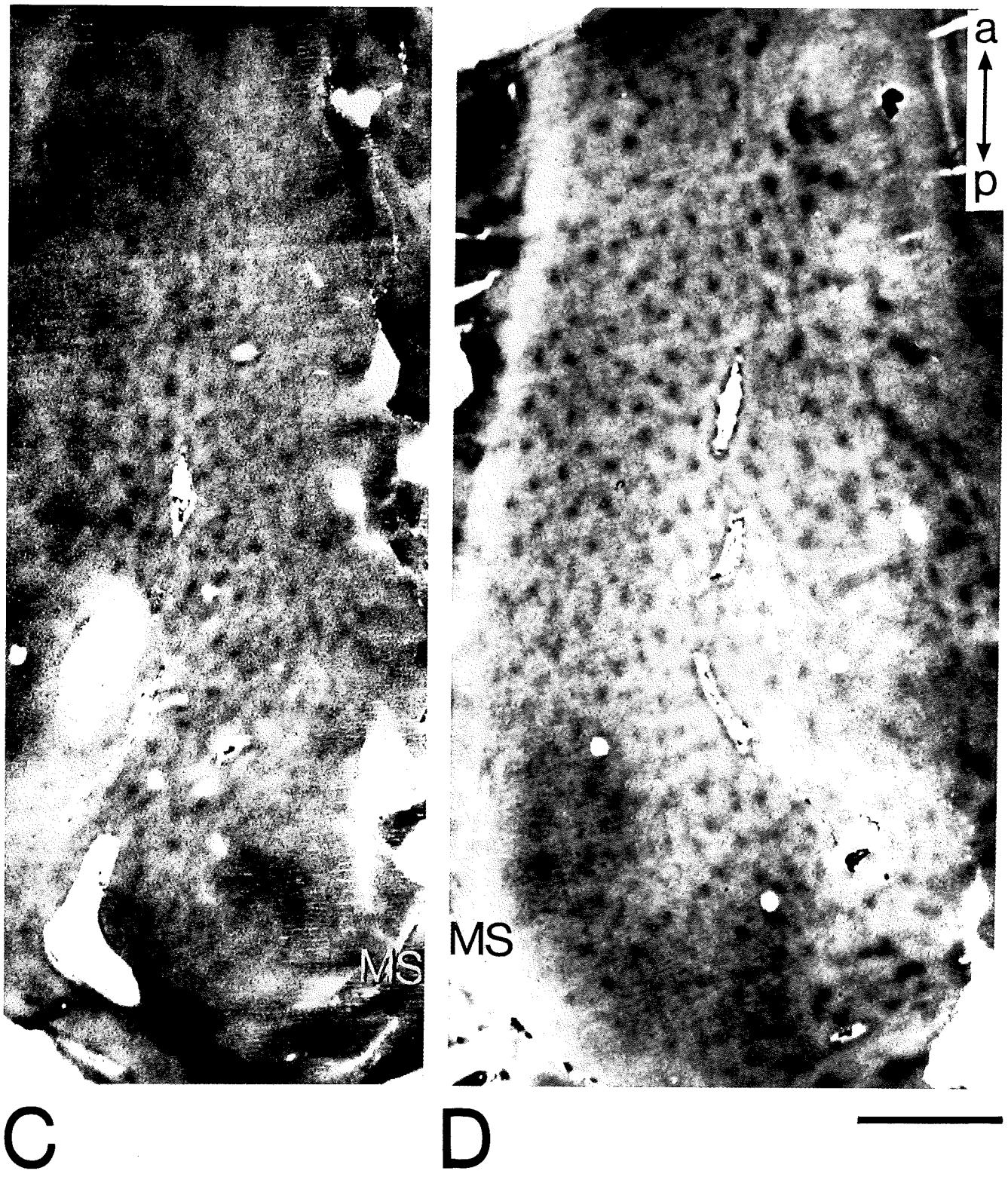


FIG. 5. Ocular dominance domains in the visual cortex of awake, normally raised cats. (A–D) 2-DG autoradiographs of flat-mount sections from supragranular layers of two monocularly stimulated animals. Unfolded hemispheres contralateral (A, C) and ipsilateral (B, D) to the open eye. Note that the 2-DG patterns look very patchy in all hemispheres. In comparison with the strabismic animals, characteristic features of ocular dominance columns are less well discernible: (i) the open-eye territories (dark 2-DG patches) do not tend to be larger in the contralateral hemispheres (A, C) than in the ipsilateral ones (B, D) (compare with Fig. 1A); (ii) the blind spots are not detectable at all; and (iii) only the monocular segments (MS) are visible: indicated by uniform labelling at the medial border of the contralateral area 17 (A, C) and by the absence of labelling at comparable eccentricity on the ipsilateral side (B, D). The large white holes are artefacts. Abbreviations as in Figure 1. Scale bar, 5 mm.

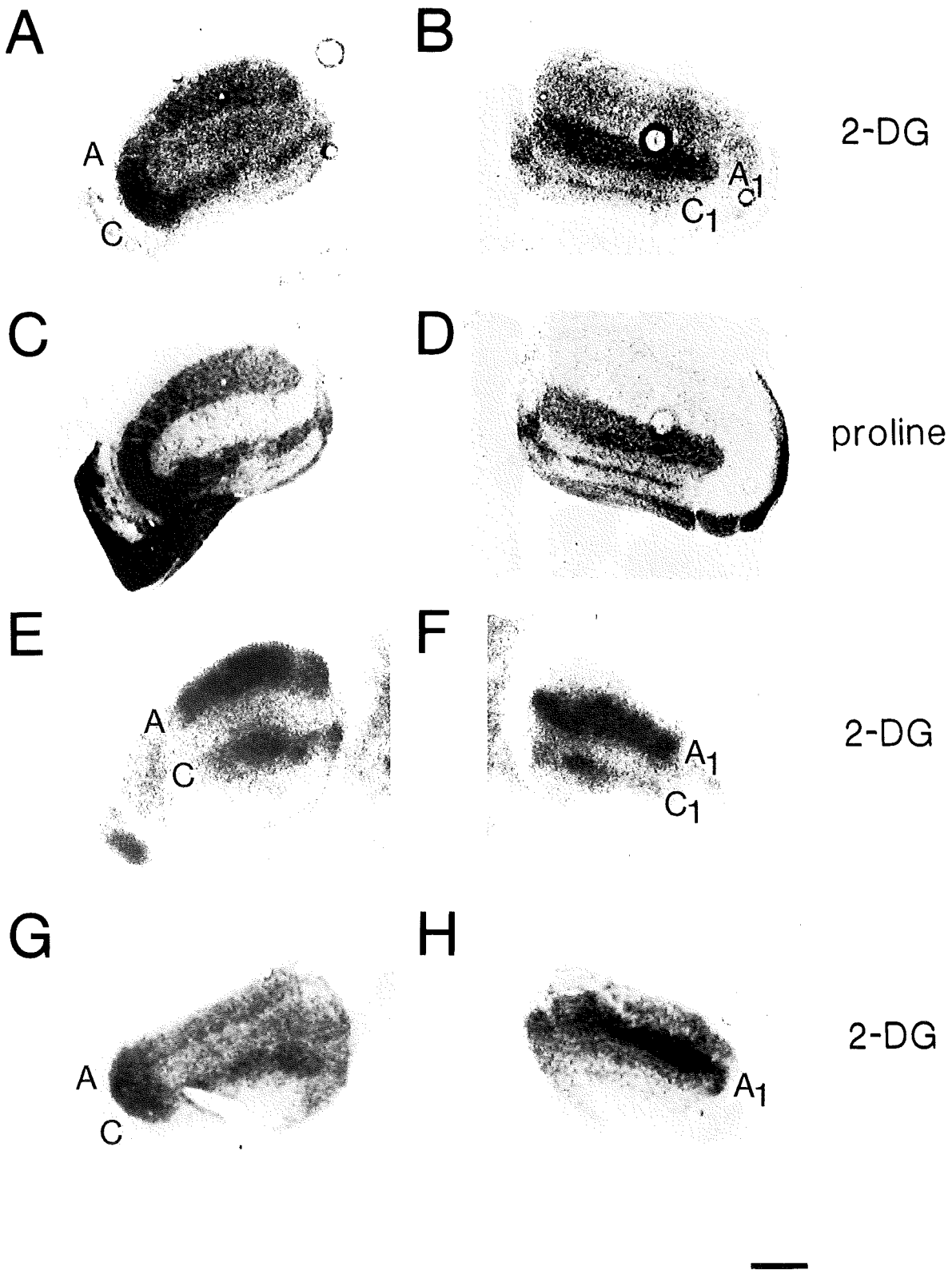


FIG. 6. Monocular 2-DG labelling and proline patterns in the LGN of awake strabismic (A–D), anaesthetized strabismic (E, F) and awake, normally reared cats (G, H). Hemispheres contralateral to the open (and injected, C) eyes are displayed in the left column (A, C, E, G), those ipsilateral to the open (and injected, D) eyes in the right column (B, D, F, H). Note that 2-DG labelling is highest in layers A and C contralateral to the open eye (left column) and in layers A_1 and C_1 ipsilateral to the open eye (right column). Note in addition that in the anaesthetized strabismic animal (E, F), only the central 20° of the visual field was stimulated (see Materials and methods). Scale bar, 1 mm.

contralateral to the stimulated eye (compare Fig. 5A and C with Figs 1A and 3A). In contrast to previous anatomical investigations of ocular dominance domains in layer IV, which have always demonstrated that more cortical tissue is devoted to the representation of the contralateral eye (Shatz and Stryker, 1978; Tieman and Tumosa, 1983; Löwel and Singer, 1987), we never observed this kind of asymmetry in the monocularly induced 2-DG patterns in our normally raised cats: in both hemispheres of these animals, the 2-DG columns appeared as 'dark islands in a grey sea' and occupied less than half of the cortical surface area. Another difference concerned the optic disc representations: these were not distinguishable in non-granular layers and only barely visible within layer IV. The representations of the monocular segments, by contrast, were clearly discernible by uniform labelling at the medial border of hemispheres contralateral to the open eye (Fig. 5A and C) and by the absence of labelling at comparable eccentricity on the ipsilateral side (Fig. 5B and D).

In the LGN, the monocularly induced 2-DG patterns were quite similar in all experimental animals. Irrespective of rearing conditions and the state of wakefulness, 2-DG uptake was highest in layers A_1 and C_1 ipsilateral to the open eye and in layers A and C contralateral to the open eye (Fig. 6). Regions of increased 2-DG uptake were in register with the [^{3}H]proline-labelled laminae of the stimulated eye (compare Fig. 6A and B with C and D).

Discussion

The present results demonstrate that in the visual cortex of normally reared cats, but not in that of strabismic cats, monocularly induced 2-DG patterns critically depend on the state of wakefulness of the animals. Although the vast majority of visual cortical neurons in cats with normal visual experience are binocularly driven (Hubel and Wiesel, 1965; Noda *et al.*, 1971; Albus, 1975; Shatz and Stryker, 1978), monocular stimulation induced 2-DG patterns in register with ocular dominance columns if the animals were awake. As shown in the accompanying paper (Löwel and Singer, 1993) this is not the case in anaesthetized and paralysed cats. In contrast, in strabismic animals, in which most cells in area 17 are monocular (Hubel and Wiesel, 1965) and interactions betwen territories served by different eyes are reduced (König *et al.*, 1990, 1993; Löwel and Singer, 1992a), monocular stimulation induced 2-DG patterns characteristic of ocular dominance columns irrespective of whether the animals were awake or not.

Do monocular 2-DG columns correspond to ocular dominance domains?

Before discussing the differential effects of anaesthesia on the visualization of columnar systems in normal and strabismic cats the question needs to be addressed whether the observed 2-DG patterns correspond to the ocular dominance columns. In the case of the awake animals, one could also imagine that the patterns reflect other variables such as eye movements. Lang and Henn (1980) described columnar 2-DG labelling in cat area 17 even after visual stimulation with random dot patterns (Julesz type) and corrugated cardboard, stimuli that do not contain any oriented components. The authors concluded that spontaneous eye movements in an otherwise static scene might have contributed to the cortical activity distribution. Similar influences of eye movements could also be imagined for monocular activity patterns: for example, the prevailing horizontal eye and head movements that cause a horizontal image shift on the retina could activate preferentially cortical neurons sensitive to vertical orientations in which case one might expect to see labelled orientation columns. However, these possibilities seem to be excluded because both Tieman and Tumosa (1983) and Kossut *et al.* (1983) have shown homogeneous radioactive labelling in area 17 of awake cats after binocular stimulation. Their results and those of the present study rather indicate that the monocularly induced patterns reflect ocular dominance columns. Firstly, the ocular dominance domains identified by [^{3}H]proline transneuronally transported from the stimulated eye were in precise register with territories of increased 2-DG labelling. Secondly, the characteristic features of ocular dominace maps such as the representations of the monocular segments are present in the 2-DG patterns.

Influence of anaesthesia on cortical 2-DG patterns

The evidence that monocular stimulation induces columnar patterns of increased 2-DG uptake in area 17 of normally reared cats if these are awake is in accordance with the previous reports by Kossut *et al.* (1983) and Tieman and Tumosa (1983). The inability to obtain ocular dominance columns in anaesthetized cats with normal binocularity (see Löwel and Singer, 1993) thus cannot be attributed solely to early binocular convergence but must also be related to anaesthesia and/or paralysis. It is known that anaesthesia diminishes cortical responsiveness and [^{14}C]2-DG uptake (Sokoloff *et al.*, 1977). However, this does not seem to impede the visualization of columnar systems in general, since orientation domains (Livingstone and Hubel, 1981; Löwel and Singer, 1993) and in strabismic cats also the ocular dominance columns can be visualized readily under anaesthesia and paralysis. Livingstone and Hubel (1981) investigated the effects of different states of wakefulness on the processing of visual information in the cat. Using the 2-DG method, they compared the patterns of orientation domains induced in two paralysed cats, one being awake and the other in slow-wave sleep. Under both conditions, columns of increased 2-DG uptake were visible, the only difference being a somewhat weaker labelling in infragranular layers in sleeping cats. One is therefore led to postulate a mechanism that restricts neuronal activity to eye-specific columns that is effective when the animals are awake and freely moving and inactivated by anaesthesia and paralysis. The nature of this mechanism is unknown but it is likely that it is related to phenomena of interocular suppression and eye-specific selective attention. However, one question remains unresolved: was our failure to see ocular dominance columns in our anaesthetized animals (Löwel and Singer, 1993) a function of the type of anaesthetic used? It is possible that other anaesthetics such as barbiturates might favour the visualization of ocular dominance columns. Barbiturates increase inhibitory interactions and this could cause a better delineation between active and inactive regions.

Comparison between activation patterns in normal and strabismic cats

The 2-DG columns in normally raised and strabismic cats differ in that regions of increased 2-DG labelling were more restricted in the former than in the latter. One possibility is that this compression of active territories is again due to interocular interactions. A recent psychophysical investigation by Denny *et al.* (1991) supports this hypothesis. The authors measured spatial sensitivity of human foveal vision and the influence of interocular interactions upon monocular vision. They demonstrated that monocular sensitivity to gratings is reduced by tonic suppression from the other (photically) unstimulated eye. Attenuation of this input by light adaptation or pressure blinding was found to improve markedly the sensitivity of the other eye. A similar interocular interaction may have been responsible for the compression of territories activated by the stimulated eye in our normally reared animals. The finding that zones of increased 2-DG

uptake were not compressed in strabismic cats but corresponded well to the width of the proline-labelled ocular dominance territories in layer IV is compatible with the reduced interocular interactions in these animals. Here the termination zones of thalamic afferents from the two eyes are segregated more readily in layer IV (Shatz *et al.*, 1977) and tangential connections between ocular dominance territories served by different eyes are markedly reduced (Löwel and Singer, 1992a). An additional explanation for the reduced width of the open-eye territories in normally raised cats could be that some binocular neurons (i.e. those concerned with disparity coding and binocular fusion) are less active or even inhibited under monocular viewing conditions. Monocular stimulation would then activate only a subpopulation of the binocular cells together with the purely monocular cells connected to the stimulated eye and this could be responsible for the observed sculpturing of the 2-DG columns. This interpretation is compatible with the results from the strabismic cats: in these animals, binocular neurons are drastically reduced in number, so that monocular stimulation would activate all neurons dominated by the open eye and hence label the respective ocular dominance columns entirely.

These special conditions of strabismic animals account also for the finding that ocular dominance territories were sharply delineated in the 2-DG patterns following monocular stimulation even when the animals were anaesthetized and paralysed. In these cats, monocular stimulation always activates only the fraction of cells located in columns innervated by the stimulated eye. The most prominent effect of anaesthesia and paralysis was that it reduced the width of the columns in supragranular layers. The most likely reason for this effect is a reduction of excitability which is expected to affect polysynaptic responses more than monosynaptic responses and hence should reduce preferentially the activity in supragranular layers. This agrees with previous evidence that anaesthesia attenuates and reticular stimulation particularly facilitates polysynaptic responses in supragranular layers (for review see Singer, 1979). An additional possibility is that anaesthesia reduced feedback from other cortical areas. The feedback projections terminate preferentially in supragranular layers (for review see Felleman and Van Essen, 1991), thereby perhaps further decreasing excitability in these laminae.

Concluding remarks

Taken together, the results of this and the previous study indicate the existence of a mechanism that can restrict responses to monocular stimulation in cats with normal binocularity to territories that are sufficiently segregated to allow for a distinct patterning of 2-DG uptake. This mechanism is most likely based on active suppression of neuronal responses since it is blocked by anaesthesia. The neurons suppressed by this mechanism must be located mainly in columns related to the unstimulated eye because the labelled territories are in register with the afferents from the stimulated eye. We propose that this eye-specific suppression is the result of top-down influences from 'higher' cortical areas. Such top-down effects have been proposed in the context of binocular rivalry in order to account for the suppression of non-matched stimuli thus preventing these stimuli from reaching conscious awareness (Logothetis and Schall, 1989; see also Blake, 1989). How the eye-specific suppression suggested here is realized and whether it involves only cortical mechanisms or also back projections to the geniculate where both eyes are segregated is still unknown. The present findings would suggest that these questions can only be approached in awake, visually attentive animals because the suppression mechanism does not appear to function in anaesthesia. Whether the postulated top-down inhibitory mechanism or some intrinsic inhibitory processes are responsible for the observed sculpturing of the monocularly induced 2-DG patterns in normally raised cats remains to be determined. It is nevertheless imaginable that in a cortex with pronounced binocularity (such as cat area 17), any 'eye-specific' suppression could extend into the most binocular regions of the opposite eye dominance columns, namely the border regions between the two sets of columns.

Acknowledgements

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Abbreviations

2-DG 2-deoxyglucose
LGN lateral geniculate nucleus

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