

THE LAYOUT OF FUNCTIONAL MAPS IN AREA 18 OF STRABISMIC CATS

K.-F. SCHMIDT¹* AND S. LÖWEL¹

Leibniz-Institute for Neurobiology, Project Group "Visual Development and Plasticity," Brenneckestr. 6, D-39118 Magdeburg, Germany

Abstract—Strabismus (or squint) is both a well-established model for developmental plasticity and a frequent clinical symptom. To analyze experience-dependent plasticity of functional maps in the brain we used optical imaging of intrinsic signals to visualize both orientation and ocular dominance domains in cat area 18. In strabismic animals, iso-orientation domains exhibited a pinwheel-like organization, as previously described for area 18 of normally raised animals and for area 17 of both normally raised and strabismic cats. In area 18, mean pinwheel density was similar in the experimental (2.2 pinwheel centers per mm² cortical surface) and control animals (2.3/mm² in normally raised animals), but significantly lower than in area 17 of both normally raised and strabismic cats (2.7–3.4/mm²). A comparison of orientation and ocular dominance domains revealed that iso-orientation domains were continuous across the borders of ocular dominance domains and tended to cross these borders at steep angles. Thus, the orientation map does not seem to be modified by experience-dependent changes in afferent activity. Together with our recent observation that strabismus does not enhance the segregation of ocular dominance domains in cat area 18, the present data indicate that the layout of functional maps in area 18 is less susceptible to experience-dependent manipulations than in area 17. © 2006 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: area 18, strabismus, development, orientation domains, visual cortex.

The advent of optical imaging techniques has allowed the most comprehensive visualization of orientation maps to date (e.g. Hübener and Bonhoeffer, 2002, for a recent review). Because multiple recordings can be made in a living animal, it is possible to compare, in the same cortical region, the neuronal responses to a variety of visual stimuli. These analyses have revealed that iso-orientation domains are arranged radially around singularities, with each orientation appearing once per singularity (Blasdel and Salama, 1986; Grinvald et al., 1986; Bonhoeffer and Grinvald, 1993; Shmuel and Grinvald, 2000). In addition, the topographical relationships between orientation maps and other functional systems such as ocular dominance and

spatial frequency have been analyzed in both normally raised animals (Hübener et al., 1997; Basole et al., 2003; Buzás et al., 2003) and in animals with experimentally modified vision (Löwel et al., 1998; Crair et al., 1997; Sengpiel et al., 1998; Engelmann et al., 2002).

In area 17 of normally raised cats, most neurons are binocularly driven and their orientation preference is virtually identical for the two eyes. This match is essential for stereoscopic vision. In contrast, in area 17 of strabismic cats, neurons are responsive almost exclusively to stimulation of either the left or the right eye (Hubel and Wiesel, 1965), the segregation of thalamocortical afferents into alternating ocular dominance columns is enhanced (Shatz et al., 1977; Löwel, 1994) and horizontal interactions between different ocular dominance columns are severely reduced compared with normally raised animals (Löwel and Singer, 1992, 2002; König et al., 1993). Furthermore, optical imaging of intrinsic signals revealed clearly segregated ocular dominance domains in area 17 of strabismic but not in normally raised cats (Löwel et al., 1998; Engelmann et al., 2002).

While the effect of strabismus on the functional architecture of area 17 has been extensively studied far less is known about experience-dependent plasticity in the immediately adjacent visual cortical area 18. In particular, functional cortical maps have not yet been analyzed in detail. Since evidence is indicating that area 18 may play a special role in binocular vision by containing a visuotopic map representing only the part of the visual field in which binocular overlap is possible (Tusa et al., 1979) we recently studied the effect of strabismus on ocular dominance maps in area 18. Interestingly, in strabismic cats, visual cortical activity maps after stimulation of the left or the right eye were much more similar in area 18 (Schmidt and Löwel, 2006) compared with area 17 of strabismic cats so that the segregation of functional ocular dominance domains was not enhanced as described for area 17 (Löwel et al., 1998; Löwel and Engelmann, 2002). This was surprising because electrophysiological recordings from single neurons in area 18 of strabismic cats have revealed a marked loss of binocularly driven units compared with normally raised animals (Cynader et al., 1984; Chino et al., 1988), and the loss in cortical binocularity was comparable in magnitude to the effect described for area 17 (Hubel and Wiesel, 1965; Van Sluyters and Levitt, 1980; Berman and Murphy, 1982).

While optical imaging of intrinsic signals has visualized the layout of iso-orientation domains in area 18 of normally raised cats (Bonhoeffer and Grinvald, 1993; Shmuel and

¹ Present address: Institut für Allgemeine Zoologie und Tierphysiologie, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, D-07743 Jena, Germany.

*Correspondence to: K.-F. Schmidt, Institut für Allgemeine Zoologie und Tierphysiologie, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, D-07743 Jena, Germany. Tel: +49-3641-949131; fax: +49-3641-949102.

E-mail address: karl.schmidt@uni-jena.de (K.-F. Schmidt).

Grinvald, 2000) the functional architecture in animals with modified visual input has not been analyzed in detail.

Here we have examined the layout of orientation domains and their topographical relationship to ocular dominance domains in area 18 of strabismic cats using optical imaging of intrinsic signals. We show that orientation preference maps exhibit a pinwheel-like organization as previously described for normally raised cats in area 18 (Bonhoeffer and Grinvald, 1993) and for both strabismic and normally raised cats in area 17 (Hübener et al., 1997; Crair et al., 1997; Löwel et al., 1998; Engelmann et al., 2002). In addition, pinwheel densities and topographic relationships between ocular dominance and orientation preference maps are not different in area 18 of strabismic and normally raised animals. Our results indicate that the layout of area 18 maps is more robust against experience-dependent modifications than in area 17. These results may be applicable only to the feline visual cortex where parallel but somewhat different thalamic afferents project to areas 17 and 18, but not to primates.

EXPERIMENTAL PROCEDURES

Fifteen cats from 10 different litters of the colony of the Leibniz-Institute for Neurobiology in Magdeburg, Germany, were included in the present study. In eight of the cats, a divergent squint angle, and in one cat, a convergent squint angle was induced surgically at postnatal days 17 or 18 (Sireteanu et al., 1993; Roelfsema et al., 1994; Löwel et al., 1998; Schmidt and Löwel, 2006). For statistical analyses we used only the animals with a divergent strabismus. Six normally raised cats served as control animals. All animals were >8 weeks of age at the time of the imaging experiments. The animals were kept in family groups in large rooms with an outdoor facility and many opportunities for climbing and jumping.

All animal experiments have been performed according to the German Law on the Protection of Animals and the corresponding European Communities Council Directive of November 24, 1986 (86/609/EEC). The experiments were designed to minimize the number of animals used and their suffering.

Squint induction

The squint induction was carried out under anesthesia induced with an i.m. injection of ketamine (10 mg/kg, Ketanest®, Parke-Davis, Berlin, Germany) and xylazine hydrochloride (2.5 mg/kg, Rompun®, Bayer AG, Leverkusen, Germany) as previously described (Löwel et al., 1998; Schmidt and Löwel, 2006). For the induction of squint the tendon of the medial (divergent squint) or lateral (convergent squint) rectus muscle of the left eye (of the right eye for convergent squint) was cut. The angle of the resulting squint was determined repeatedly during early postnatal development using the corneal reflex method (Sherman, 1972; Olson and Freeman, 1978; von Grünau, 1979). The ratio of the distance between the corneal reflexes over the distance between the pupils is a reliable indicator of eye alignment (Sherman, 1972; Sireteanu et al., 1993). The ratios of our eight divergent squinters were always below 0.93 (between 0.91 and 0.87), the ratio of the convergent squinter above 1.02 (1.05) and thus in the range for squinters throughout the critical period (von Grünau, 1979; Sireteanu et al., 1993). Since, in addition, ratios did not change over time, an effective squint was induced in all animals.

Optical imaging

For optical imaging, anesthesia was induced with an i.m. injection of ketamine and xylazine hydrochloride as described above and maintained throughout the experiment using N_2O/O_2 anesthesia (50% N_2O /50% O_2), supplemented with halothane (0.8–1.2%, Eurim Pharma, Piding, Germany). The ECG, pulmonary pressure, end tidal CO_2 (3–4%), and rectal temperature (37–38°C) were continuously monitored. The animal's head was fixed in a stereotactic frame by means of a metal nut cemented to the skull. For optical imaging of area 18 a craniotomy (15×6 mm) was performed centered at Horsley-Clarke coordinate A7.

Visual stimulation, data acquisition and data analysis

Animals were stimulated monocularly with high-contrast square-wave gratings of four equally spaced orientations (0°, 45°, 90°, and 135°) moving at a speed of 2 cycles/s with a spatial frequency of 0.15 cycles/degree presented on a monitor at a distance of 25 cm. Stimuli were presented to both eyes in a random order. The animals' eyes were refracted appropriately using corrective corneal contact lenses with artificial pupils with a diameter of 3 mm. The imaging setup, data acquisition and analyses procedures have been described in detail previously (Engelmann et al., 2002; Schmidt and Löwel, 2006). Briefly, we used the ORA 2001 system (Optical Imaging Inc.) for collecting intrinsic signals, "episodic stimulation" during data acquisition and both "cocktail blank" procedures and "differential imaging" to calculate functional maps (Blasdel and Salama, 1986; Bonhoeffer and Grinvald, 1996; Löwel et al., 1998; Schmidt and Löwel, 2006). All displayed orientation (angle and polar maps) and differential maps for orientation are the sum of the respective left and right eye maps.

Quantitative analyses of map layout

The location and density of orientation pinwheel centers were determined as described in detail elsewhere (Löwel et al., 1998). Briefly, the positions of putative pinwheel centers correspond to the crossings of the 0°/90°, with the 45°/135°-orientation contours, respectively. For every single point we checked by visual inspection whether it represented a proper orientation center in the corresponding angle map. Points around which iso-orientation domains did not exhibit a clear radial organization were discarded from further analysis. Using this semi-automatic method, no orientation centers can be missed and only clear examples of pinwheel centers enter the quantitative spatial density analysis. The average size of the quantitatively analyzed cortical region was similar for both strabismic (8.8 mm²) and normally raised animals (9.0 mm²; no significant size difference: $P=0.69$, t -test).

To characterize the local geometric relationship between iso-orientation domains and ocular dominance borders, we analyzed the statistics of their intersection angles using Spearman's rank correlation test (see Löwel et al., 1998; Engelmann et al., 2002).

RESULTS

We recorded visual cortical activity maps in area 18 of both strabismic and normally raised cats in 4.8×3.6 mm large areas using optical imaging of intrinsic signals. Recordings were made both ipsilateral and contralateral to the squinting eye. Examples of the blood vessel patterns of the imaged cortical areas are illustrated in Fig. 1 (first row). We computed differential maps for orientation (90°/0° and 135°/45°) to illustrate the layout of orientation maps for both normally raised and strabismic cats (Fig. 1, 2nd and 3rd row). The imaging data reveal that maps contain both linear zones with the elongation approximately parallel to

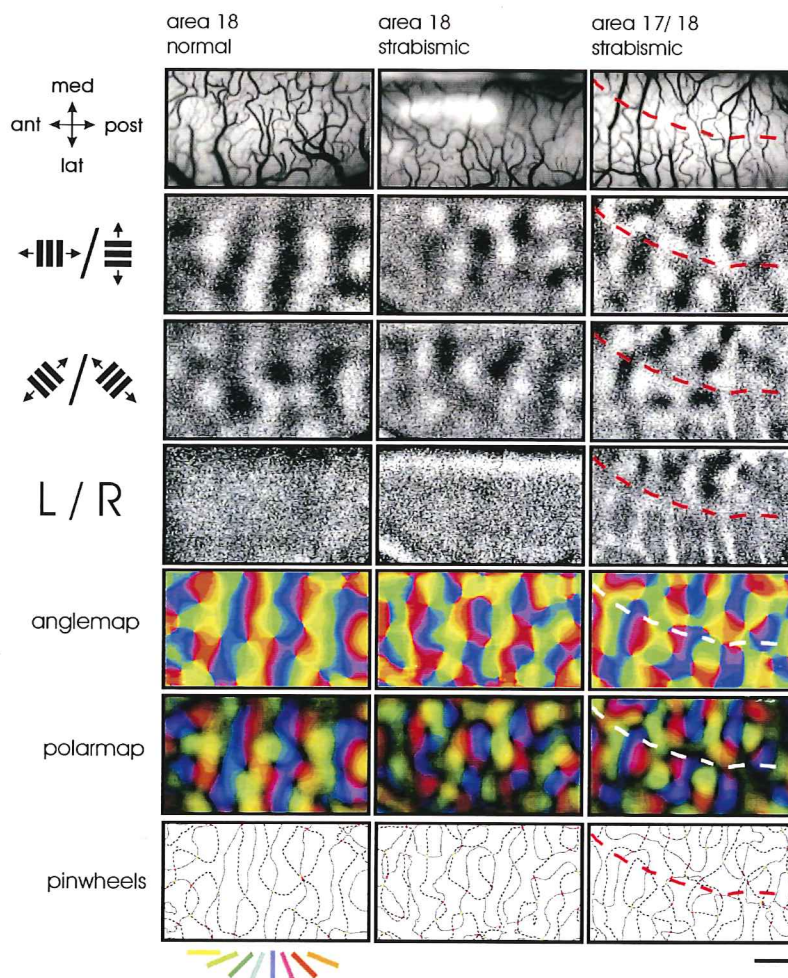


Fig. 1. The layout of orientation domains in area 18 of normally raised (first column) and strabismic cats (2nd and 3rd column). Blood vessel patterns of the imaged cortical areas (4.8×2.7 mm) are shown in the top row. Cortical activation patterns were visualized by optical imaging of intrinsic signals while the animals were stimulated through the left and right eye with moving oriented gratings of 0° , 45° , 90° and 135° . To illustrate the layout of orientation and ocular dominance maps we computed differential maps for both orientation (all maps induced by visual stimulation with vertical divided by all maps induced by visual stimulation with horizontal gratings, (left 90° +right 90°)/(left 0° +right 0°), 2nd row; and (left 135° +right 135°)/(left 45° +right 45°), 3rd row) and ocular dominance (all left eye activity maps divided by all right eye activity maps, L/R, 4th row). Fifth row: Orientation preference ("angle") map of the same piece of cortex: The preferred orientation for every region of the imaged cortex is color-coded according to the scheme at the bottom left of the Fig. 6th row: Orientation "polar" maps in which the brightness additionally codes the selectivity of the intrinsic signal at a particular cortical location. Seventh row: Quantitative analysis of the locations and spatial density of orientation (pinwheel) centers: The pinwheel centers correspond to the crossings of the dotted with the broken lines. Optical recordings in the left two columns are from area 18, those in the right column are from the border (indicated by the dashed line) between areas 17 (upper part=medial cortex) and 18 (lower part=lateral cortex). In all cases, data from the left cortical hemisphere are illustrated. Abbreviations: ant, anterior; lat, lateral; med, medial; post, posterior. Scale bar=1 mm.

the medio-lateral axis of the brain and more patchy activity domains. In line with previous analyses, the topology of orientation maps can be described as a coexistence of linear and radial organization (Shmuel and Grinvald, 2000). For a comprehensive analysis of orientation preference, we computed two different types of orientation preference maps by vectorial summation of the responses to the different stimulus orientations: angle maps and polar maps (Blasdel and Salama, 1986; Bonhoeffer and Grinvald, 1993; 1996). In angle maps (Fig. 1, 5th row), a color-code is used to display the orientation that elicited the maximal response at a particular cortical region. In polar maps, the selectivity of the signal is additionally encoded by the brightness of the color (Fig. 1, 6th row). In

area 18 of all our normal and strabismic animals, angle and polar maps displayed a pinwheel-like organization of iso-orientation domains, as previously described for both areas 17 and 18 of a variety of mammals (e.g. Blasdel and Salama, 1986; Bonhoeffer and Grinvald, 1993; Chapman et al., 1996; Bosking et al., 1997; Hübener et al., 1997).

To further investigate the layout of orientation preference maps, we determined the spatial density of the pinwheel centers in area 18. Quantitative comparison of the optically recorded maps revealed that pinwheel densities were similar for strabismic and normally raised animals: in normally raised animals, the pinwheel density was 2.3 ± 0.32 ($n=7$) per mm^2 of cortical surface area; in strabismic animals, there were 2.2 ± 0.28 ($n=10$) pinwheels/ mm^2 cor-

Table 1. Pinwheel densities in area 18 of strabismic (S1–S8) and normally raised cats (N1–N6)

Cat/hemisphere	Age (months)	Pinwheel density (1/mm ²)	Cortical area (mm ²)
S1/LH	2	2.2	8.1
S2/RH	2	1.9	8.9
S3/RH	2	2.1	9.6
S3/LH	2	2.3	7.7
S4/RH	2	2.7	8.4
S4/LH	2	2.5	8.7
S5/LH	3	1.7	8.6
S6/LH	2	2.2	8.9
S7/LH	2	2.2	10.0
S8/LH	2	2.3	8.8
Mean±SD		2.2±0.28	8.77±0.68
N1/LH	8	2.1	9.5
N2/RH	4	2.6	7.3
N3/LH	2	2.6	8.6
N4/LH	2	2.7	9.3
N5/RH	2	1.8	10.2
N6/RH	2	2.3	10.3
N6/LH	2	2.3	7.5
Mean±SD		2.3±0.32	8.95±1.21

Age, age at time of optical imaging, Cortical area (mm²), size of the cortical area used for quantitative analyses of pinwheel densities. LH, left hemisphere, Pinwheel density (1/mm²): density of pinwheel centers per mm² cortical surface. RH, right hemisphere,

tical surface. Data from individual animals are given in Table 1. The pinwheel density in area 18 of our cats is thus significantly ($P<0.001$, two-tailed t -test) lower than in area 17 of normal and strabismic cats (2.7–3.4 pinwheels/mm²;

Löwel et al., 1998; Engelmann et al., 2002). More direct evidence for different pinwheel densities in areas 17 and 18 is given in Fig. 1 (right column). In this experiment, optical imaging was performed at the border region between areas 17 and 18. Here, pinwheel density was about 3.0 pinwheels/mm² in area 17 (medial part of the visual cortex, corresponding to the top of the image) and 1.9 pinwheels/mm² in area 18 (lateral part of the visual cortex, corresponding to the lower part of the image).

While strabismus clearly enhances the segregation of ocular dominance domains in area 17 compared with normally raised cats, we recently observed that this is not the case in visual cortical area 18. To quantify these effects we calculated cross-correlation coefficients for maps obtained by left eye versus right eye activation. The mean cross-correlation coefficients in area 18 were 0.68 ± 0.12 (mean±S.D., $n=8$) for control and 0.64 ± 0.14 (mean±S.D., $n=10$) for strabismic animals. Thus no significant difference for the segregation of columns in area 18 between normal and strabismic animals was found as previously described for area 17 (Löwel et al., 1998; Engelmann et al., 2002; Schmidt and Löwel, 2006, see Fig. 1, 4th row). This can be illustrated by showing that differential maps for orientation exhibit a high contrast in area 18 of both normally raised and strabismic cats, but differential maps for ocular dominance are of low contrast in area 18 and only show a high contrast in area 17 of strabismic animals.

To analyze the topographical relationship between orientation and ocular dominance domains in area 18, we therefore needed to drastically enhance the contrast of the ocular dominance maps. These analyses revealed that

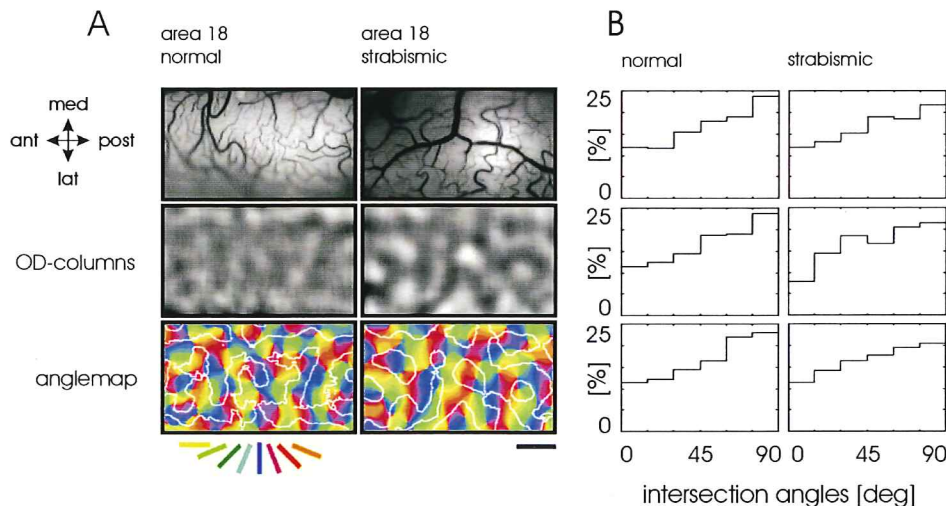


Fig. 2. Spatial relations between ocular dominance (OD) and orientation domains in cat area 18. (A) Topographic relationship between OD and iso-orientation domains in area 18 of normally raised (left column) and strabismic cats (right column). Top row: Blood vessel patterns of the imaged cortical areas (4.8×2.7 mm). Second row: Contrast-enhanced map of OD domains: Regions activated by the left eye (dark gray regions) are less strongly activated by the right eye (lighter gray regions). Third row: Superposition of the orientation "angle" map (see color-code at the bottom of the figure) and the borders between adjacent OD domains (indicated by the white lines). Note that iso-orientation domains are continuous across OD borders in both groups of animals. B: Histograms of intersection angles between iso-orientation and OD contours in area 18 of normally raised (left column) and strabismic cats (right column). Data from three pairs of littermates (three rows) are illustrated. x Axis: intersection angle in degrees from 0° to 90°, divided into six classes (0–15°, 15–30°, 30–45°, 45–60°, 60–75°, 75–90°). y Axis: percentage of intersection angles in the respective class. Note that intersection angles between 75° and 90° are most abundant in all cases. In all cases, data from the left cortical hemisphere are illustrated. Abbreviations as in Fig. 1. Scale bar=1 mm.

iso-orientation domains were continuous across the borders of ocular dominance domains in both normal and strabismic animals (Fig. 2A, middle and lower row). A similar topographical relationship has been described previously for area 17 of normal and strabismic cats (Hübener et al., 1997; Löwel et al., 1998; Engelmann et al., 2002). Quantitative analyses demonstrated that iso-orientation contours tended to intersect the borders of adjacent ocular dominance domains at steep angles. The histograms of intersection angles of three pairs of littermates are displayed in Fig. 2B, illustrating a preponderance of angles between 75° and 90°. In these typical cases, between 20 and 24% of all intersection angles fell within this range. Spearman's rank correlation test revealed a strong positive correlation ($r > 0.9$) between the steepness of intersection angles (from 0° to 90°) and percentage per class in normal and in strabismic animals. In addition, we calculated average intersection angles for all animals and obtained no statistically significant difference between control and experimental animals ($P = 0.17$, unpaired *t*-test). The mean of the intersection angles was $50.9^\circ \pm 0.9^\circ$ (mean \pm S.D., $n = 8$) for normal animals and $50.0^\circ \pm 1.7^\circ$ (mean \pm S.D., $n = 10$) for strabismic animals. Our analysis thus indicates that the topographical relationship between iso-orientation and ocular dominance domains in area 18 is not modified by strabismus, as previously shown for area 17 (Löwel et al., 1998; Engelmann et al., 2002).

DISCUSSION

The main results of the present study are i) that orientation preference maps in area 18 of strabismic and normally raised cats are similar with respect to overall organization and pinwheel density and ii) that strabismus does not interfere with the topographical relationship between orientation and ocular dominance domains in area 18.

As previously described for cat area 17 (Löwel et al., 1998; Engelmann et al., 2002) the layout of orientation preference maps in area 18 does not display any obvious experience-dependent alterations between normally raised and strabismic animals. Quantitative analyses of the orientation maps revealed similar overall organization and similar average pinwheel densities in experimental and control groups. Interestingly, there seems to exist a general population difference because the absolute pinwheel densities reported in the present study (area 18: 2.3/mm² in normal, and 2.2/mm² in strabismic animals) are much higher than the values reported for area 18 of normally raised cats by Bonhoeffer and Grinvald (1.2 pw/mm², Bonhoeffer and Grinvald, 1993; Bonhoeffer et al., 1995). Supporting this argument, we have previously reported that in area 17 of cats from our Magdeburg colony, the average pinwheel density was about 3.4 pw/mm² (Engelmann et al., 2002) and thus again significantly higher than pinwheel densities reported by other groups (Bonhoeffer et al., 1995; Rao et al., 1997; Löwel et al., 1998). Possible explanations for this interesting observation are either i) that genetic factors may influence quantitative features of functional cortical maps as recently demonstrated for column

spacing in littermate comparisons (see Kaschube et al., 2002) or ii) that the particular environment of the Magdeburg colony with the animals living in family groups in large rooms with outdoor facilities may exert an influence on cortical development (Sale et al., 2004). Increased pinwheel densities of visual cortical orientation maps result in more hypercolumns per mm² of cortical surface which in turn could influence visual acuity of the animals. While raising animals in so-called enriched environment causes a variety of changes in brain circuitry and behavior, we have not yet tested this possibility systematically. Previous behavioral tests of our animals' visual capabilities with the jumping stand apparatus have not revealed visual acuities beyond the normal range (Engelmann et al., 2002).

Why are there no obvious experience-dependent changes in map layout in visual cortical area 18 compared with the immediately adjacent area 17? The most salient difference between the two areas is that area 17 predominantly receives X-cell input while area 18 is dominated by Y-cell input (Stone, 1983; Orban, 1984). Y-cells possess both larger receptive fields and larger thalamocortical afferent arbors terminating in layer IV which might influence the degree of decorrelation between left and right eye inputs in the two areas. While binocularly driven neurons are severely reduced in both areas 17 and 18 of strabismic cats (Hubel and Wiesel, 1965; Smith et al., 1979; Van Sluyters and Levitt, 1980; Berman and Murphy, 1982; Cynader et al., 1984; Chino et al., 1988; Sengpiel et al., 1994), electrophysiological experiments have nevertheless revealed a number of findings that may underlie the observed differences in susceptibility to changes in afferent activity patterns. When both eyes are stimulated together, many apparently monocular cells have been shown to display substantial binocular interactions (Bishop, 1973; Cynader and Regan, 1978; Cynader et al., 1984; Chino et al., 1988). Interestingly, in area 18, binocular facilitation was similar in both strabismic and normally raised animals, and the major effect of strabismus consisted of a reduction in strength of binocular inhibition (Cynader et al., 1984) while in area 17, the majority of neurons showed interocular suppression (Sengpiel et al., 1994). Thus there exists a clear difference in the effect of strabismus on binocular interactions in the two visual areas, with the reduced inhibition in strabismic area 18 favoring common activation of cortical neurons which may make layout changes—at least for ocular dominance domains—more difficult.

Since different functional maps are not independent of each other, displaying rather fixed geometrical relationships (Hübener et al., 1997), the layout of one system could serve as the scaffold for the layout of another system. This is consistent with the observations of the present study: as previously shown for area 17 of both strabismic and normally raised cats (Hübener et al., 1997; Crair et al., 1997; Löwel et al., 1998; Engelmann et al., 2002) orientation and ocular dominance domains have a particular topographical relationship also in area 18: iso-orientation contours intersect the borders between adjacent ocular dominance columns at steep angles thus further indicating a systematic topological relation between the two maps as

originally suggested by Hubel and Wiesel (1977). A similar geometry of the functional domains has also been described for macaque monkey striate cortex (Bartfeld and Grinvald, 1992; Obermayer and Blasdel, 1997). This arrangement is well adapted because it permits coverage of a particular point in the visual field with all relevant combinations of orientation preference and ocular dominance in the smallest possible volume of cortex (Swindale, 1991; Hübener et al., 1997). One may speculate that this arrangement is therefore too precious for the animals' visual capabilities and protected against experience-dependent modifications.

There is one other clear difference between visual cortical areas 17 and 18: its shape or geometry. While area 18 is a very narrow but elongated strip of cortical tissue immediately adjacent to area 17, area 17 itself is much larger and more pear-like in shape. A model for the self-organization of orientation maps (Wolf et al., 1996) offers an explanation for the observed susceptibility differences in areas 17 and 18 by taking this particular geometry into account. Based on this theoretical study which models visual cortical orientation maps as attractors of a cortical learning dynamics, narrow areas (such as area 18) offer fewer degrees of freedom for potential layout changes than larger two-dimensional areas (such as area 17) (Wolf et al., 1996; Wolf and Geisel, 1998).

Taken together, our results strongly indicate that the layout of functional maps in visual cortical area 18 is less susceptible to changes in afferent activity patterns compared with area 17. These results may be applicable only to the feline visual cortex where parallel but somewhat different thalamic afferents project to areas 17 and 18, but not to primates. In addition, the topographical relationship between orientation and ocular dominance domains is similar in both areas 17 and 18 and similarly resistant to experience-dependent layout modifications, indicating that this particular geometrical arrangement is of functional significance for visual information processing most likely by ensuring optimal coverage of different visual attributes (Hübener et al., 1997). Finally, our results are also consistent with theoretical considerations suggesting that experience-dependent map changes may not only depend on the statistics of corticofugal activity patterns but are also influenced by factors such as the geometry of cortical areas or the nature of intracortical interactions.

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There is one other clear difference between visual cortical areas 17 and 18: its shape or geometry. While area 18 is a very narrow but elongated strip of cortical tissue immediately adjacent to area 17, area 17 itself is much larger and more pear-like in shape. A model for the self-organization of orientation maps (Wolf et al., 1996) offers an explanation for the observed susceptibility differences in areas 17 and 18 by taking this particular geometry into account. Based on this theoretical study which models visual cortical orientation maps as attractors of a cortical learning dynamics, narrow areas (such as area 18) offer fewer degrees of freedom for potential layout changes than larger two-dimensional areas (such as area 17) (Wolf et al., 1996; Wolf and Geisel, 1998).

Taken together, our results strongly indicate that the layout of functional maps in visual cortical area 18 is less susceptible to changes in afferent activity patterns compared with area 17. These results may be applicable only to the feline visual cortex where parallel but somewhat different thalamic afferents project to areas 17 and 18, but not to primates. In addition, the topographical relationship between orientation and ocular dominance domains is similar in both areas 17 and 18 and similarly resistant to experience-dependent layout modifications, indicating that this particular geometrical arrangement is of functional significance for visual information processing most likely by ensuring optimal coverage of different visual attributes (Hübener et al., 1997). Finally, our results are also consistent with theoretical considerations suggesting that experience-dependent map changes may not only depend on the statistics of corticofugal activity patterns but are also influenced by factors such as the geometry of cortical areas or the nature of intracortical interactions.

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