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Optical imaging in cat area 18: Strabismus does not enhance the segregation of ocular dominance domains

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While early-onset strabismus leads to clearly segregated domains of the left and the right eye in cat primary visual cortex (area 17), far less is known about experience-dependent plasticity of ocular dominance in area 18. We therefore used optical imaging of intrinsic signals to analyze the influence of strabismus on cortical maps in cat area 18. Monocular visual stimulation of the left and right eye with moving square wave gratings of four different orientations induced patchy activity maps. Unlike our previous observations in cat area 17, the monocular activity maps in area 18 of strabismic cats were rather similar so that functional ocular dominance domains were not clearly segregated. Imaging of the 17/18 border region confirmed this observation and revealed a sudden change in the segregation of the left and right eye domains across the border. Our results demonstrate that modified visual input can have different consequences for different visual areas: while the decorrelation of activity between the two eyes (as induced by strabismus) clearly enhances the segregation of ocular dominance domains in cat area 17, area 18 does not show this effect although electrophysiological studies have confirmed that the percentage of binocularly driven neurons is as reduced as in area 17.

Introduction

Strabismus is a common clinical condition in which the visual axes of the two eyes do not meet at the fixation point and the two retinal images cannot be brought into register. If strabismus is present in early postnatal life, this alteration leads to a breakdown of binocular convergence and the correlation of neuronal activity from both eyes is severely reduced. As a consequence, neurons become responsive almost exclusively to stimulation of either the left or the right eye (Hubel and Wiesel, 1965) and the segregation of geniculocortical afferents into alternating ocular dominance columns is enhanced in area 17 of strabismic as compared with normally raised cats (Shatz et al., 1977; Löwel, 1994). In area 17 of strabismic cats, monocular visual stimulation induces activity patterns extending in columns through all cortical layers, and these columns are in precise register with the afferents of the stimulated eye in layer IV (Löwel and Singer, 1993a,b). In addition, neuronal synchronization and horizontal interactions between different ocular dominance domains are severely reduced compared to normally raised animals (König et al., 1993; Löwel and Singer, 1992; Löwel and Engelmann, 2002). Finally, optical imaging of intrinsic signals revealed clearly segregated ocular dominance domains in area 17 of strabismic but not in normally raised adult 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 area 18. In particular, ocular dominance domains have not yet been analyzed in detail. The most salient difference between the two visual cortical areas is that area 17 is dominated by X-cell input while area 18 receives essentially Y-cell input (see Stone, 1983; Orban, 1984, for an overview). Y-cells possess both larger thalamocortical afferent arbors terminating in layer IV and larger receptive fields which both might influence the degree of decorrelation between left and right eye inputs induced by strabismus in the two areas.

Furthermore, evidence is indicating that area 18 may play a special role in binocular vision. Area 18, unlike area 17, contains a visuotopic map representing only the part of the visual field in which binocular overlap is possible while the monocular visual field in the periphery is not represented (Tusa et al., 1979). Electrophysiological recordings from single neurons in area 18 of strabismic cats revealed a marked loss of binocularly driven units compared to normally raised animals (Cynader et al., 1984; Chino et al., 1988). This loss in cortical binocularity is comparable in magnitude to the effect described for area 17 (Hubel and Wiesel, 1965; Van Sluyters and Levitt, 1980; Berman and Murphy, 1982).

Here, we have examined the layout of ocular dominance domains in area 18 of strabismic cats using optical imaging of intrinsic signals. We show that activity maps induced after stimulation of the left or the right eye with moving gratings were much more similar than in area 17 of strabismic cats thus resembling those visualized in area 18 of normally raised animals. In contrast to area 17, functional ocular dominance domains are thus not clearly segregated in area 18 of strabismic cats. These results indicate that early-onset strabismus can have different consequences in different areas of the visual

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cortex and that area 18 seems to be less susceptible to experience-dependent changes in ocular dominance map layout.

Materials and methods

Squint induction

16 kittens from 8 different litters of the colony of the Leibniz-Institute for Neurobiology in Magdeburg were included in the present study. In seven of the kittens, a divergent squint angle and in one kitten, a convergent squint angle were induced surgically at postnatal days 17 or 18 (Löwel and Singer, 1992; Löwel et al., 1998; Roelfsema et al., 1994). Eight normally raised cats served as controls. The squint induction was carried out under anesthesia induced with an intramuscular injection of ketamine (10 mg/kg, Ketanest®, Parke-Davis, Berlin, Germany) and xylazine hydrochloride (2.5 mg/kg, Rompun®, Bayer AG, Leverkusen, Germany). After incision of the conjunctiva, the tendon of the medial (divergent squint) or lateral (convergent squint) rectus muscle was located and cut. In all strabismic animals, 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). To this end, the animals were manually restrained, several flashlight snapshots of the cats head were taken, and the ratio of the distance between the corneal reflexes over the distance between the pupils was determined on the photoprints. This ratio is a reliable indicator of eye alignment (Sherman, 1972; Sireteanu et al., 1993). The ratios of our divergent squinters were always below 0.93, those of the convergent squinters always above 1.02 and thus in the range for squinters throughout the critical period (von Grünau, 1979; Sireteanu et al., 1993).

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).

Optical imaging

Surgery

Anesthesia was induced with an intramuscular injection of ketamine and xylazine hydrochloride as described above and maintained throughout the experiment using nitrous oxide/oxygen anesthesia (50% N_2O/50% O_2), supplemented with halothane (0.8–1.2%, Eurim Pharma, Germany). The ECG, pulmonary pressure, end tidal CO_2 (3–4%), and rectal temperature (37–38°) were continuously monitored. The animals 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 was performed centered at Horsley–Clarke coordinate A7. All experiments were performed when the animals were at least 2 months old (range 2–12 months).

Visual stimulation

Animals were stimulated monocularly with high-contrast square-wave gratings (subtending 90 × 60° visual field) of four orientations (0, 45, 90, and 135°) moving at a speed of 2 cyc/s with a spatial frequency of 0.15 cyc/degree. Stimuli were generated by EZV-Stim software (Optical Imaging Inc., Rehovot, Israel) and presented on a LG Electronics Flatron 295 LCD-monitor (luminosity 180 cd/m^2; contrast 300:1; refresh rate 85 Hz; resolution 1600 × 1200 pixel) at a distance of 25 cm. The eyes were treated with atropine and Neosynephrine® and refracted appropriately using corrective corneal contact lenses with artificial pupils with a diameter of 3 mm.

Data acquisition and analysis

The cortical surface was illuminated by means of two adjustable light guides attached to a tungsten-halogen lamp (Spindler and Hoyer, Göttingen, Germany) equipped with interference filters for different wavelengths. The vascular pattern of the cortex was visualized at 546 ± 10 nm (green), cortical activity maps at 707 ± 10 nm (red). During data acquisition of intrinsic signals, the camera was focused 650–750 μm below the cortical surface. A tandem-lense was used for imaging (Ratzlaff and Grinvald, 1991). The ORA 2001 system (Optical Imaging Inc.), equipped with a cooled Theta CCD system (384 × 288 pixel chip from Thomson-CSF) was used for collecting the intrinsic signals. We acquired a series of frames every 12 s, whereby a grating of a given orientation was presented for 2 s in a static mode, followed by 4.2 s of data acquisition during which the grating was moved in both directions along the axis orthogonal to its orientation. We used episodic stimulation during data acquisition (7 frames of 600 ms duration). The first frames were excluded from further analysis. The stimulus presentation was monocular, an eye shutter was used to conceal the eyes. A single stimulus trial consisted of 2 × 8 stimulus conditions (4 grating orientations for the left and the right eye) and 8 isoluminant blanks presented in a random sequence. Twelve trials were usually presented to obtain a map, so that every stimulus was shown 24 times. We first calculated "single condition maps" in which the images acquired during presentation of a particular stimulus were divided by the sum of all different stimulus conditions ("cocktail blank procedure"; see Bonhoeffer and Grinvald, 1993, 1996; Löwel et al., 1998; Engelmann et al., 2002). Differential maps for ocular dominance and orientation were calculated by summing all left eye activity maps divided by all right eye activity maps (L/R) respectively all maps induced by visual stimulation with vertical divided by all maps induced by visual stimulation with horizontal gratings (vertical/horizontal).

Quantitative analysis of map layout

To compare the layout of left and right eye activation maps, we computed cross-correlation coefficients for all single condition maps of individual animals (4 left and 4 right eye maps) on a pixel by pixel basis and calculated a mean value per animal. The cortical activation patterns of all experimental animals ($n = 16$) were used for this quantitative analysis. In addition, we used 12 hemispheres (7 squinting and 5 normal) from 10 kittens from previous area 17-studies for quantitative comparisons of map layout (Löwel et al., 1998; Engelmann et al., 2002). Statistical significance was tested using Mann–Whitneys U test.

Results

Using optical imaging of intrinsic signals, we recorded activity maps in area 18 of strabismic and normally raised control cats in 4.8 mm × 3.6 mm large areas. 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 Figs. 1–3.

In area 18 of normally raised animals, visual stimulation of the left and right eye with moving gratings revealed patchy activity maps resembling those previously described in kitten area 18

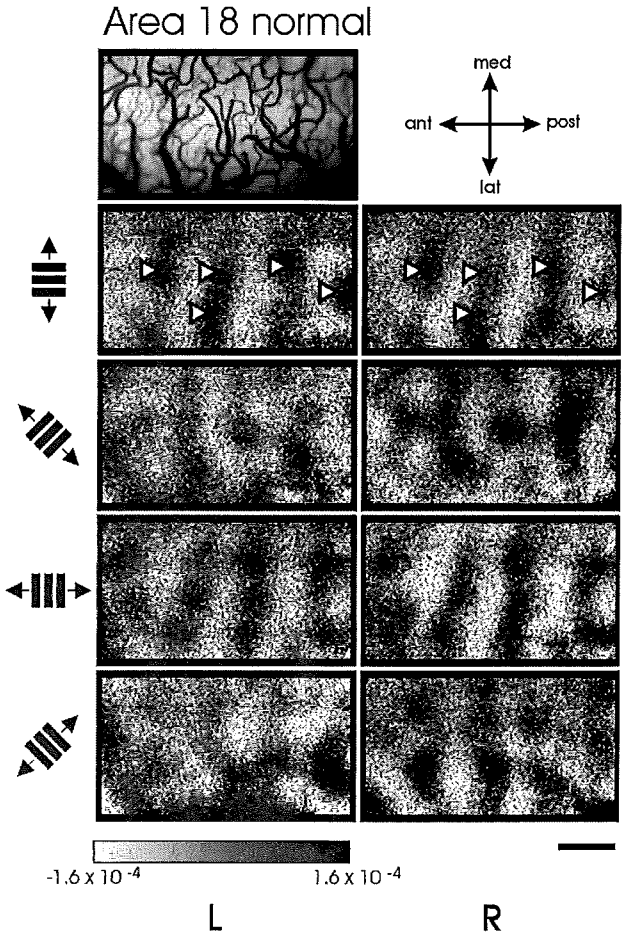

Fig. 1. Monocular iso-orientation domains in area 18 of a normally raised cat. The blood vessel pattern of the imaged cortical area (4.8 × 2.7 mm) is shown at top left. Cortical activation patterns were visualized by optical imaging of intrinsic signals while the animal was stimulated through the left (L, left column) and the right eye (R, right column) with moving gratings of 0°, 45°, 90°, and 135° orientation (from top to bottom). Note that the activity patterns were rather similar for left and right eye stimulation (compare left and right columns as indicated by white arrowheads). The scale of grey levels represents the fractional changes of the response patterns. Abbreviations: ant = anterior; lat = lateral; post = posterior; med = medial; Scale bar = 1 mm.

(Gödecke and Bonhoeffer, 1996). As expected for normally raised animals, the monocular orientation domains were rather similar in layout (compare left and right column in Fig. 1) so that segregated ocular dominance domains could not be visualized (Fig. 4A). Surprisingly, the same result was obtained in area 18 of strabismic animals, both for convergent and divergent squinters: monocular visual stimulation with moving gratings induced rather similar activity maps for the left and the right eye (compare left and right column of Fig. 2) so that functional ocular dominance domains were not clearly segregated (Fig. 4C). Notably, this result was obtained consistently in *all* single experiments and all individual trials. As a control for the signal-to-noise ratio of our experiments, we additionally computed differential maps for orientation. For both normally raised and strabismic cats, these maps showed a clear segregation of domains preferring vertical and horizontal gratings (Figs. 4B and D), confirming the excellent signal-to-noise ratio of our recordings.

The result of overlapping activity maps for the left and right eye in strabismic cats in area 18 is totally different from results obtained previously in area 17. In area 17 of strabismic cats, activity maps of the two eyes were clearly segregated and ocular dominance domains of the left and the right eye were complementary (Löwel et al., 1998; Engelmann et al., 2002). To quantify these qualitative observations, we computed cross-correlation coefficients for left/right eye map comparisons in all experimental animals of the present study. In addition, we analyzed cortical activity maps of the left and right eye obtained in cat area 17 in previous studies (Löwel et al., 1998; Engelmann et al., 2002). Fig. 5 illustrates that cross-correlation coefficients between left and right eye maps for strabismic and control animals are very similar in area 18, but significantly different in area 17, corroborating our previous qualitative observations: in area 18, the mean cross-correlation coefficient was 0.68 ± 0.12 (mean ± SD; $n = 8$) for control and 0.64 ± 0.14 ($n = 8$) for strabismic animals. The difference was statistically not significant ($P = 0.44$; two-tailed U test). In contrast, in area 17, the mean cross-correlation coefficient

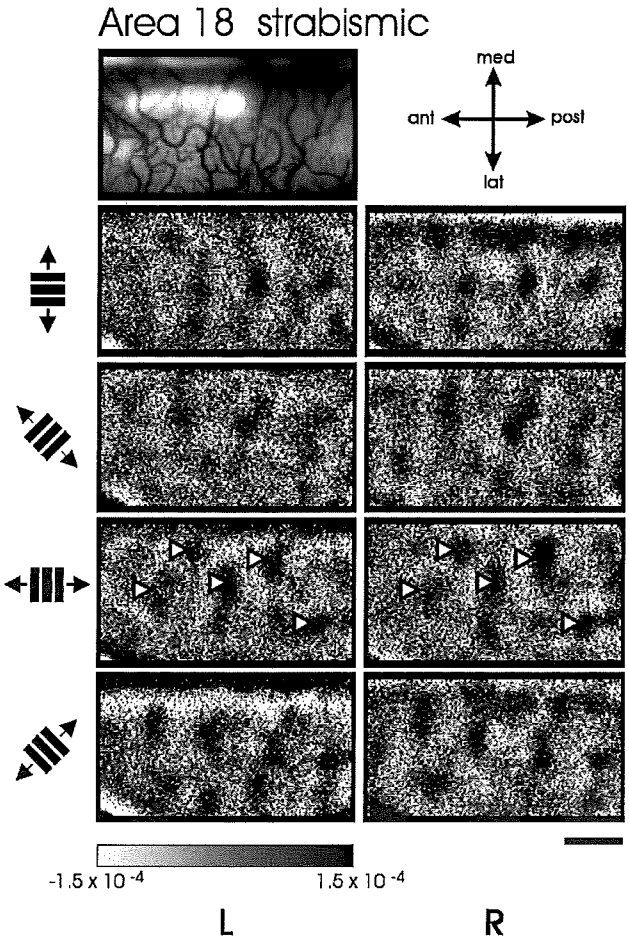

Fig. 2. Monocular iso-orientation domains in area 18 of a strabismic cat (sibling of the cat in Fig. 1). The blood vessel pattern of the imaged cortical area (4.8 × 2.7 mm) is shown at top left. Cortical activation patterns were visualized by optical imaging of intrinsic signals while the animal was stimulated through the left (L, left column) and the right eye (R, right column) with moving gratings of 0°, 45°, 90°, and 135° orientation (from top to bottom). Note that the activity patterns were rather similar for left and right eye stimulation (compare left and right columns as indicated by white arrowheads). Abbreviations as in Fig. 1. Scale bar = 1 mm.

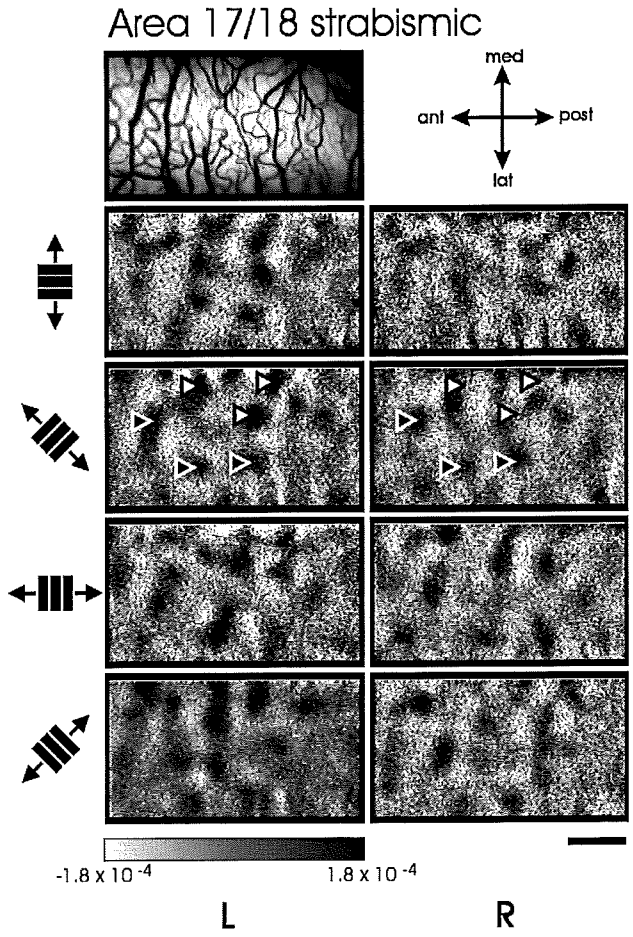

Fig. 3. Monocular iso-orientation domains at the border between areas 17 and 18 of another strabismic cat. The blood vessel pattern of the imaged cortical area (4.8 × 2.7 mm) is shown at the top left. Cortical activation patterns were visualized by optical imaging of intrinsic signals while the animal was stimulated through the left (L, left column) and the right eye (R, right column) with moving gratings of 0°, 45°, 90°, and 135° orientation (from top to bottom). Note that the activity patterns were clearly different for left and right eye stimulation only in the upper part of the visualized cortical region (medial part of the visual cortex), corresponding to area 17: in this region, the white arrowheads point to dark domains after left eye stimulation (left column) and to light grey domains after right eye stimulation (right column). In contrast, in the lower part of the field of view (lateral visual cortex), corresponding to area 18, the black arrowheads point to dark domains irrespective of the stimulated eye (compare left and right columns). Abbreviations as in Fig. 1. Scale bar = 1 mm.

for normal animals was 0.61 ± 0.13 ($n = 5$) and 0.14 ± 0.13 ($n = 7$) for strabismic animals. This difference was statistically significant ($P < 0.01$; two-tailed U test). Cross-correlation coefficients for strabismic cats in area 18 and for normal cats in areas 17 and 18 were not significantly different (strabismic 18/normal 17: $P = 0.94$, normal 18/normal 17: $P = 0.28$; two-tailed U test), while the 17/18 comparison for strabismic cat maps was highly significant ($P = 0.0003$; two-tailed U test). The magnitude of the strabismus and the cross-correlation coefficients were not correlated (area 18: $r = 0.08$, area 17: $r = 0.09$).

To check the consistency of our results with previous studies, we additionally imaged the border region between areas 17 and 18 (around Horsley–Clarke coordinate A3) in strabismic cats. In these experiments, the differing distribution of activity spots in the two visual cortical areas was directly visualized: while in area 17, the activity spots induced by stimulation of the left and the right eye were nonoverlapping and thus clearly segregated (white arrowheads in Fig. 3), monocular activity spots in area 18 were overlapping (black arrowheads in Fig. 3). Furthermore, the imaging data revealed that the segregation of left and right eye domains changes relatively abruptly across the border: while in area 17, ocular dominance domains appear clearly segregated (clear black-and-white pattern at the top of Fig. 4E), this segregation disappears in immediately adjacent regions in cortical area 18 (rather homogeneous activity distribution at the bottom of Fig. 4E). In contrast, differential maps for orientation are equally strong in both cortical areas (Fig. 4F; see also Figs. 4 B,D). The latter observation is very important in showing (i) that the absence of well segregated ocular dominance domains in area 18 is not due to a bad signal-to-noise ratio of the recorded optical signal and (ii) that the visual stimulus used was able to strongly activate both visual cortical areas.

Thus, although electrophysiological studies have shown that strabismus leads to a breakdown of cortical binocularity in both areas 17 and 18 (Hubel and Wiesel, 1965; Van Sluyters and Levitt,

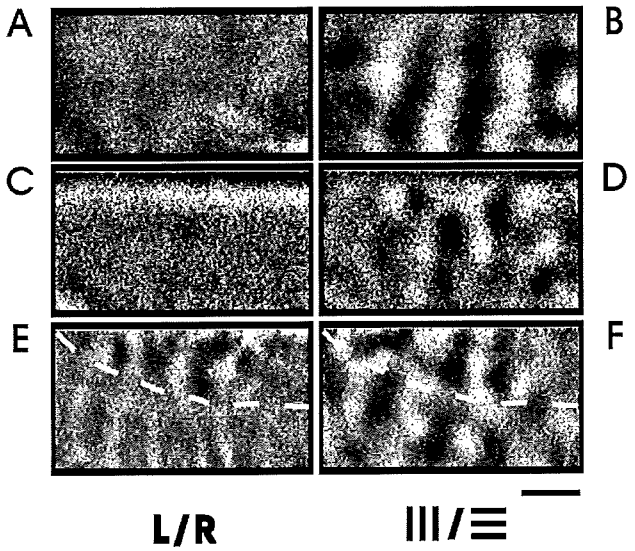

Fig. 4. Differential maps for ocular dominance (all left eye activity maps divided by all right eye activity maps (L/R; left column)) and orientation (all maps induced by visual stimulation with vertical divided by all maps induced by visual stimulation with horizontal gratings (vertical/horizontal; right column)) in one normal (A,B) and two strabismic cats (C,D and E,F). In panels A–D, cortical area 18 is visualized, in panels E and F, cortical activation patterns at the border between areas 17 and 18 (dashed white line) are illustrated. In panels E and F, area 17 corresponds to the upper (medial visual cortex) and area 18 to the lower part of the field of view (lateral visual cortex) as in Fig. 3. Note that ocular dominance domains are not clearly segregated in area 18 of both normal and strabismic cats (A and C; rather homogeneous activation) while differential maps for orientation of the same piece of cortex have a high contrast (B and D) signifying excellent signal-to-noise ratio of the imaging experiments. Note further that ocular dominance domains are clearly segregated in area 17 (high contrast differential labeling in the upper part of the field of view in panel E), while this segregation disappears in immediately adjacent regions in cortical area 18 (rather homogeneous grey labeling in the lower part of the visualized cortical region in panel E). In contrast, orientation domains are clearly visible on both sides of the 17/18 border (F). Scale bar = 1 mm.

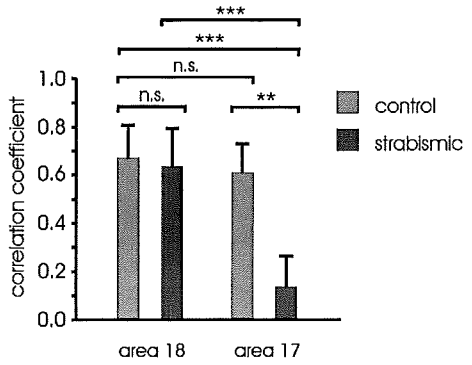

Fig. 5. Quantitative analyses of the similarity of left and right eye activation patterns in strabismic and normally raised animals. Mean and SD of cross-correlation coefficients are given. Area 18-maps from the present study are compared with previously obtained area 17-maps from our laboratory (Löwel et al., 1998; Engelmann et al., 2002). In area 18, cross-correlation coefficients for left/right eye map comparisons of control (0.68 ± 0.12, mean ± SD; $n = 8$) and strabismic animals (0.64 ± 0.14, $n = 8$) were not significantly different ($P = 0.44$; two-tailed U test). In contrast, in area 17, the mean cross-correlation coefficient for normal animals was 0.61 ± 0.13 ($n = 5$) and 0.14 ± 0.13 ($n = 7$) for strabismic animals. This difference was statistically significant ($P < 0.01$; two-tailed U test). Cross-correlation coefficients for strabismic cats in area 18 and for normal cats in areas 17 and 18 were not significantly different (strabismic 18/normal 17: $P = 0.94$, normal 18/normal 17: $P = 0.28$; two-tailed U test), while the 17/18 comparison for strabismic cat maps was highly significant ($P = 0.0003$; two-tailed U test).

1980; Berman and Murphy, 1982; Cynader et al., 1984; Chino et al., 1988), optically imaged activity maps induced by stimulation of the left and the right eye get clearly functionally segregated only in area 17 but not in area 18 of strabismic animals. Thus – unlike area 17 – monocular orientation maps in cat area 18 are rather similar in both normal and strabismic animals.

Discussion

The major finding of the present study is that in area 18 of strabismic cats activity maps induced by stimulation of the left and the right eye are overlapping. Functional ocular dominance domains are thus *not* clearly segregated and rather resemble those visualized in normally raised animals. This is in sharp contrast to our previous observations in area 17 of strabismic cats, where left and right eye activity maps are complementary and ocular dominance domains are clearly segregated (Löwel et al., 1998; Engelmann et al., 2002). These results indicate that modified visual input can have different consequences for different visual cortical areas: while the decorrelation of activity between the two eyes (as induced by strabismus) clearly enhances the segregation of ocular dominance domains in area 17, neuronal activity maps in area 18 do not show this effect.

It is well agreed that cat area 18 receives direct projections primarily from geniculate Y-cells while area 17 is dominated by X-cell input and that Y-cells possess both larger thalamocortical afferent arbors and larger receptive fields (Stone and Dreher, 1973; Harvey, 1980; Sherman and Spear, 1982; Humphrey et al., 1985a,b). In principle, one could argue that the larger thalamocortical afferent arbors in area 18 necessitate larger strabismic angles to decorrelate the inputs from the two eyes compared to area 17. However, all our experimental animals had large strabismic angles and nevertheless their left and right eye activity maps were rather similar. This is surprising given that binocular excitatory convergence onto single cells is as markedly reduced in area 18 as it is in area 17 of strabismic cats (Cynader et al., 1984; Chino et al., 1988). Interestingly, however, the spatial properties of area 18-neurons in strabismic cats, including receptive field size and spatial frequency tuning, did not differ from those in normal controls—in sharp contrast to area 17-neurons (Chino et al., 1983, 1988).

In general, the most obvious effect of early strabismus is the substantial reduction in the number of cells activated by stimulation of the two eyes. While binocularly driven neurons are common in area 18 of normal cats, only about 10–25% of the neurons in strabismic cats fall in this category (Cynader et al., 1984; Chino et al., 1988). This observation is similar to the loss of binocular convergence observed by many other investigators in cortical area 17 (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). Interestingly, this susceptibility to binocular breakdown by strabismus appears to distinguish areas 17 and 18 from several other visual areas such as the superior colliculus and the lateral suprasylvian area in which only little change in the distribution of ocular dominance is found after strabismus.

Electrophysiological recordings have nevertheless revealed a number of findings that may underlie the observed differences in ocular dominance map layout between areas 17 and 18 of strabismic cats. While binocular excitatory convergence onto single cells is markedly reduced in both areas 17 and 18 of strabismic cats, many apparently monocular cells have been shown to display substantial binocular interactions when both eyes are stimulated together (Bishop, 1973; Cynader and Regan, 1978; Cynader et al., 1984; Chino et al., 1988). In fact, Cynader et al. (1984) have found that binocular facilitation in area 18 was as marked in the population of cells studied in strabismic cats as it was in normal animals. The major effect of strabismus was even a reduction in the strength of binocular inhibition when units were tested with sideways motion (Cynader et al., 1984). When tested with stimuli with varied disparities and directions of motion in depth about 50% of the area 18-neurons in strabismic cats displayed modulations of 2:1 or more in firing rate as a function of the parameters of binocular stimulation. While these units were diminished in number compared to normal animals, they provided strong evidence for residual stereoscopic capacities in at least some area 18-neurons in strabismic cats. In sharp contrast, strabismus virtually abolished the disparity-specific binocular interactions in area 17 that are such a distinctive feature of normal striate neurons, but left pronounced, nonspecific interocular suppression in the majority of cells (Sengpiel et al., 1994). In numbers, less than 10% of all area 17-neurons showed any enhancement of the monocular response and only 5% exhibited genuine facilitation (Sengpiel et al., 1994). Thus, in area 17, the majority of cells showed interocular suppression while a reduction of binocular inhibition was dominating the experience-dependent changes of binocular interactions in area 18 of strabismic cats. This reduced inhibition in strabismic area 18 may increase the likelihood of common activation in visual cortical neurons thus making segregation of ocular dominance columns more difficult.

The present study shows that, in area 18, left and right eye activity maps are rather similar in both control and strabismic cats. Since the thalamocortical afferents of the two eyes in cortical layer

IV are segregated (Shatz et al., 1977; Löwel and Singer, 1987; Anderson et al., 1988; Löwel, 1994), this might seem to be a contradiction which it is not. As previously shown, cortical activity maps in supragranular layers of area 17 can be rather independent of the ocular dominance pattern in cortical layer IV (Löwel and Singer, 1993a). In fact, thalamocortical afferents are clearly segregated also in area 17 of normally raised cats (Shatz et al., 1977; Anderson et al., 1988; Löwel and Singer, 1987) while nerve cell responses are overwhelmingly binocular (Hubel and Wiesel, 1962). Furthermore, functional ocular dominance domains cannot be visualized with 2-deoxyglucose autoradiography after monocular visual stimulation in anesthetized normally raised animals (Löwel and Singer, 1993a) while they are readily visible using the same techniques in strabismic animals (Löwel and Singer, 1993b). Finally, optical imaging of intrinsic signals also revealed a clear difference in the visual cortical activity maps between normal and strabismic cats in area 17: while left and right eye activity maps are rather similar in normal adult cats (Engelmann et al., 2002), they clearly differed in strabismic animals (Löwel et al., 1998; Engelmann et al., 2002). Interestingly, in area 17, horizontal intracortical fibers contact neurons driven by both the left and the right eye in normally raised animals while the fibers extend preferentially between domains of the same ocular dominance in strabismic animals (Löwel and Singer, 1992; Schmidt et al., 1997; see also Tychsen et al., 2004). Whether the same holds true for visual cortical area 18 is presently not known. Given the results of the present study, one would rather expect similar selectivities for horizontal fibers for both control and strabismic animals but a definitive answer can only be given after further experiments.

The different susceptibilities of areas 17 and 18 to strabismus are reminiscent of differing effects previously found in reverse-suture experiments. Electrophysiological studies have shown that area 17-neurons that regain input from a previously sutured eye exhibit independent orientation preferences (Blakemore and Van Sluyters, 1974; Movshon, 1976), whereas orientation maps in area 18 of reverse-sutured kittens were nearly identical for the left and the right eye as visualized by optical imaging of intrinsic signals (Gödecke and Bonhoeffer, 1996). While these observations suggest that the cortical mechanisms which produce binocular selectivity in cat area 18 are somewhat impervious to environmental manipulations, a model for the self-organization of orientation maps (Wolf et al., 1996) offers an alternative explanation and accounts for these differences in areas 17 and 18 in terms of the geometry of the involved visual cortical areas. Based on modeling studies of visual cortical orientation maps as attractors of a cortical learning dynamics, narrow areas offer fewer degrees of freedom for layout changes of cortical maps than larger two-dimensional areas. Thus, models of activity-dependent map formation predict very similar orientation maps in narrow and elongated areas such as area 18 and maps with different and more variable patterns in areas with more extended geometries such as area 17 (Wolf et al., 1996; Wolf and Geisel, 1998).

In summary, our mapping data indicate that ocular dominance maps in area 18 are less susceptible to experience-dependent manipulations than in area 17. Thus, modified visual input can have different consequences for different visual cortical areas. In addition, our observation supports theoretical considerations suggesting that plastic map changes may not only depend on the statistics of afferent activity patterns but can also be strongly influenced by other factors such as the nature of intracortical interactions and the geometry of cortical areas.

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