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CENTRIFUGAL MOTION BIAS IN THE CAT'S LATERAL SUPRASYLVIAN VISUAL CORTEX IS INDEPENDENT OF EARLY FLOW FIELD EXPOSURE

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SUMMARY

1. Neurones in the postero-medial part of the cat's lateral suprasylvian visual cortex (area PMLS) show an overall preference for centrifugal motion, suggesting that the PMLS may be specialized in the analysis of expanding optic flow fields associated with forward locomotion.

2. We examined whether the visual experience young kittens normally receive during forward locomotion guides the development of the centrifugal preference in the PMLS.

3. Seven kittens were reared in the dark and exposed to either expanding or contracting flow fields for at least 100 h during their 4th–11th weeks of life. Specific experience was achieved by exposing kittens either to flow field patterns generated on a screen or by actually moving them forward or backward in a carousel.

4. Our results show that although the development of directional selectivity in the PMLS requires visual experience, the centrifugal bias is independent of specific visual exposure. The preference for centrifugal motion among PMLS cells was just as evident in kittens exposed to contracting as in kittens exposed to expanding flow fields.

5. We conclude that the preference for centrifugal motion in the PMLS is not the result of anisotropic stimulation kittens receive during locomotion in early ontogeny, but is probably innately determined as a phylogenetic adaptation.

INTRODUCTION

As we move around, successively fixating various objects, the orientation and position of our eyes in the environment is constantly changing. The arising shifts and deformations of the image on our retina – the optic flow – could themselves be very useful sources of information about our environment (Gibson, 1950, 1958, 1966; Lee,

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1980; Koenderink, 1986). Evidence that analysis of the optic flow field guides human locomotion can be derived from a number of psychophysical findings. The perception of self-motion relies on optic flow information even when this is in conflict with that from other modalities (Lee, 1980). Furthermore, apparent self-motion depends on the flow of the part of the display that is perceived as the background (Ohmi & Howard, 1988). Finally, the direction of self-motion can be judged from an optic flow pattern, even during pursuit eye movements (Warren & Hannon, 1988).

In cats, the overall organization of response properties of neurones in the posteromedial part of the lateral suprasylvian visual cortex (PMLS) appears to make this area suitable for flow field processing. In this part of the extrastriate cortex, the neurones' direction preferences depend on the location of their receptive fields in such a way that many cells respond optimally to stimuli moving away from the area centralis (Rauschecker, von Grünau & Poulin, 1987*a*; Rauschecker, 1988). The resulting radial organization of direction preferences is accompanied by an increase in the preferred velocity with eccentricity (Rauschecker *et al.* 1987*a*). These preferences correspond to the displacement of the retinal image when moving in the direction in which one is looking.

There are many examples of environmental influences on the development of kitten visual cortex. Each neurone in the striate cortex responds best to stimuli with specific properties. By introducing specific biases in exposure during early postnatal development the distribution of many response properties can be changed (Blakemore & Cooper, 1970; Hirsch & Spinelli, 1970; Stryker, Sherk, Leventhal & Hirsch, 1978; Rauschecker & Singer, 1981; for review see Wiesel, 1982; Frégnac & Imbert, 1984; Rauschecker, 1990). Of particular relevance to the present study is the finding that cats raised in an environment with continuous motion in one direction later show a preponderance of neurones preferring that direction of motion (Cynader, Berman & Hein, 1975; Tretter, Cynader & Singer, 1975; Daw & Wyatt, 1976), and that cats raised in stroboscopic light show reduced direction selectivity (Cynader, Berman & Hein, 1973; Rauschecker & Schrader, 1987). Here we try to advance our knowledge about visual plasticity and the effects of environment outside the striate cortex.

The aim of the present study is to determine whether specific environmental stimulation is necessary for the development of the centrifugal organization of directional preferences in cat PMLS. In particular, we want to know whether the centrifugal bias is a result of the anisotropic distribution of flow patterns over a young kitten's retina during locomotion. As kittens mainly walk forwards (i.e. in the direction in which they are looking), the distribution of contour displacements on the retina could underly the development of the centrifugal directional bias. Such an explanation has been suggested for the bias towards centrifugal motion in human vision (Georgeson & Harris, 1978; Ball & Sekuler, 1980) as well as monkey middle temporal visual area (Albright, 1989), but has never been studied experimentally.

In our experiments, kittens were exposed to either expanding or contracting flow fields, and the resulting directional preferences of PMLS neurones were examined. We consider the three most likely outcomes. (1) Exposure to expanding flow fields (real or simulated forward motion) results in a centrifugal bias; exposure to contracting flow fields (real or simulated backward motion) results in a centripetal bias. This outcome would demonstrate that the centrifugal bias which is normally found is a result of the fact that kittens usually walk forwards. (2) In both cases PMLS neurones show no directional specificity at all. This outcome would suggest that self-induced movements are essential for extrastriate visual development. In striate cortex the development of stimulus specificity appears to depend on a correspondence between retinal stimulation and eye movement proprioceptive input (Buisseret, Gary-Bobo & Milleret, 1988). PMLS development may similarly depend on feedback concerning bodily displacement. Considering that the PMLS may play a role in visually guided locomotion, it is not unlikely that the bodily displacement must be self-induced (Held & Hein, 1963). (3) In both cases PMLS neurones show a centrifugal bias. This would demonstrate that although visual experience is necessary for neurones to develop directional specificity (Spear, Tong & Sawyer, 1983), the distribution of directional preferences is independent of experience. It would not necessarily imply that the centrifugal bias is functionally unrelated to flow fields during locomotion. However, the bias is innately determined and arises through evolutionary rather than individual development.

METHODS

Visual exposure

Two litters of kittens were born and raised in a completely dark room with a double-door arrangement. Between $3\frac{1}{2}$ weeks and about 3 months of age they received a total of 100–112 h of specific visual exposure in daily sessions of approximately 3 h, after which the response properties of PMLS neurones were examined using standard techniques (Rauschecker *et al.* 1987*a*).

Kittens were exposed to flow fields in two different ways (Fig. 1). The first litter of three kittens was exposed to flow fields presented on a large screen using an ATARI Mega ST4 computer (frame rate 70 Hz) and an Electrohome EDP 58XL video projection system. Each kitten's head and body was restrained so that their eyes were at a distance of 20 cm from the screen. The horizontal extent of the visual field during exposure was 60 deg; the vertical extent was 46 deg. The computer simulated rectilinear 3-D motion of the kitten at a speed of 0·5–4·3 m/s through a space filled with rectangular surfaces ('objects') of various sizes. The simulated objects, which were moving toward or away from the kitten, were programmed to pass the kittens below, above and on both sides at distances of 30–240 cm. On the screen, the rectangles moved radially in forty-eight directions, size and speed of motion varying over a wide range with eccentricity. The stimuli gave human observers a strong impression of motion in space. One kitten was exposed exclusively to centrifugal and two kittens exclusively to centripetal motion.

The four kittens of the second litter were exposed to a normally illuminated room with many visible real objects. During exposure, the animals were continuously moved either facing forwards (two kittens) or facing backwards (two kittens) in a specially designed carousel. Of course, the retinal flow while sitting in a carousel contains not only a translational component (expansion or contraction from forward or backward motion respectively), but also a rotational one (leftward or rightward movement of the visual world). However, the magnitude of the rotational component for a given translational velocity depends on the radius or distance from the centre of rotation (approaching zero at a distance of infinity). We thus designed a carousel that had relatively long arms and fixed the kittens in little hammocks at a distance r of 80 and 100 cm from the centre of rotation, 50 cm above the ground. This had also the effect that, in order to get a reasonable centrifugal flow field corresponding to real speeds of self-induced locomotion ($v = 0{\cdot}3$–$0{\cdot}8$ m/s), relatively moderate speeds of rotation ($f = v/2\pi r = 3{\cdot}8$–$7{\cdot}5$ r.p.m.) could be used. In addition, to eliminate any remaining bias for leftward or rightward movement, the carousel moved clockwise and anticlockwise on alternate days, while each kitten always either moved forwards or backwards. The kittens passed about 10 cm from the closest objects and several metres from the farthest.

After the first few days of exposure the kittens got used to the equipment and rarely complained about being restrained. They were supervised throughout each exposure session, so that they could be woken up whenever necessary. Special care was taken that the kittens received no accidental exposure with stimuli other than intended; in particular, animal care, feeding, cleaning, and preparation for exposure, were all performed in the dark.

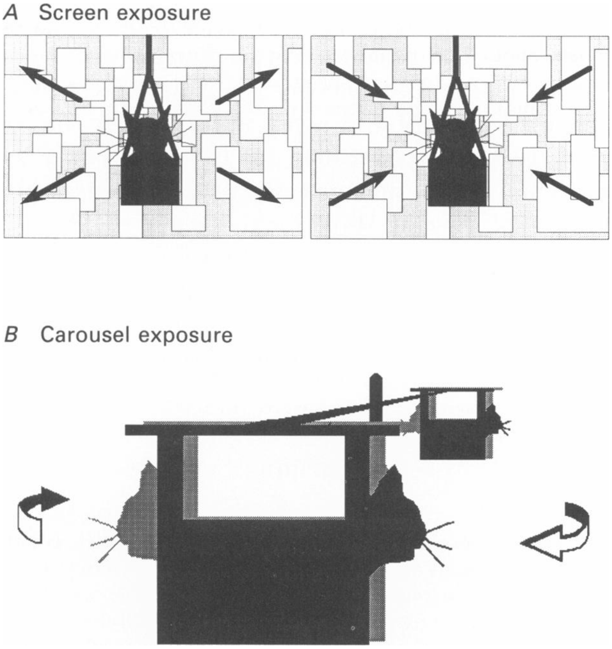

Fig. 1. Schematic representation of the exposure conditions. *A*, screen exposure: kittens are restrained in the dark during exposure sessions in front of a large screen on which either expanding or contracting flow fields are displayed. Rectangles of light move and change size in a manner simulating forward or backward motion. The flow field patterns are generated by a computer and projected onto the screen by means of a video projector (see text). *B*, carousel exposure: kittens either face forward or backward in a carousel, which moves with varying speed.

Recording procedure

For surgery, kittens were anaesthetized with ketamine hydrochloride (Ketanest) and xylazine (Rompun) after premedication with atropine sulphate. In some cases this was supplemented with methohexital (Brevimytal). After tracheotomy, the kitten was placed in a stereotaxic head holder and the skull was opened over the suprasylvian sulcus (A0–A10; L10–L16). From then on, the animals were artificially respirated, and anaesthesia was maintained by adding 0·4–1·0% halothane to the 70/30 mixture of N_2O/O_2. Paralysis was ensured by continuous infusion of gallamine triethiodide (Flaxedil). Body temperature was kept at 38 °C and end-tidal CO_2 was kept between 3·6 and 4·0%. The EEG and ECG were used to monitor the kittens' condition and state of anaesthesia. Contact lenses protected the kittens' eyes. The nictitating membranes were retracted with neosynephrine and the pupils dilated with atropine. When necessary the eyes were focused with spectacle lenses and aligned with Risley prisms. Extracellular recordings were obtained using 1·5 M-potassium citrate-filled glass microelectrodes with an impedance of about 7 MΩ (for further details see Rauschecker *et al.* 1987*a*). All except for one track were in the right hemisphere. In one kitten (forward exposure in carousel) recordings from thirty cells in a single oblique track through striate cortex (area 17) confirmed that this area had developed normally, having small, well-oriented receptive fields with good responses. No bias in the distribution of orientation or direction preferences was apparent in this sample.

Visual stimuli

Visual stimuli were initially either presented with a hand-held lamp or were back-projected on the screen (144 × 90 cm at 114 cm from the kittens' eyes) with the same video equipment that was used to provide the expanding and contracting flow fields for exposure (see above). The computer program could present spots or bars of almost any dimensions, and allowed us to switch easily from light stimuli on a dark background to dark stimuli on a light background. Contrast $((I_{\max}-I_{\min})/(I_{\max}+I_{\min}))$ was 80%. The stimuli were projected onto the screen with the video projector. We mainly used spots with diameters between 2·5 and 17 deg of visual angle which could be moved across the screen with a variety of speeds and directions either manually, by moving the ATARI's 'mouse', or automatically, by instructing the computer to do so.

Once the extent of the receptive field was determined and stored, the computer could be instructed to direct selected stimuli through the receptive field centre in order to help find the optimal stimulus size, velocity, and direction. The computer was also used to evaluate directional tuning, ocular dominance, and surround inhibition. We distinguished five ocular dominance classes (see Fig. 3 and Rauschecker *et al.* 1987*a*). Surround inhibition was assessed by evaluating the effect of increasing stimulus size. When informed that the experimenters were confident of having found the optimal stimulus, the computer program saved all parameters, including the position of the receptive field and the optimal direction of motion.

The criteria for determining the optimal stimuli (direction, velocity, etc.) were the same as in a previous study on normal animals (Rauschecker *et al.* 1987*a*). Responses were first assessed by listening to an audio monitor while the stimuli were automatically swept across the screen, and when necessary by recording raster displays and peristimulus time histograms. For the latter procedures, the ATARI delivered a synchronizing signal triggering data aquisition by a PDP 11/34 computer, which was then used for quantitative assessment of the response. Whenever we compared quantitative and qualitative estimates of the preferred direction of a cell, the two were in excellent agreement, as has also been noted by other authors (e.g. Blakemore & Zumbroich, 1987; McCall, Tong & Spear, 1988).

Data analysis

Recording was performed in a semi-blind procedure: one of the experimenters (E.B.) knew which group the kitten that was being recorded from belonged to, while the other (J.P.R.) did not. The findings of the two experiments were analysed separately and compared. There were no significant differences between data collected by the two experimenters. Recording sites were verified by examining the electrode tracks in 80 μm Cresyl Violet-stained sections. Tracks that did not pass through the PMLS were excluded from further analysis.

Cells were divided into four groups on the basis of their responses: (1) cells that were not responsive to any of the visual stimuli that we tried; (2) visually responsive cells for which we were unable to define a distinct receptive field; (3) cells with a distinct receptive field but no clear optimal direction of stimulus movement; and (4) cells that clearly preferred motion in a certain direction (including both DS and DB cells, as defined by Rauschecker *et al.* 1987*a*). The third group included cells that responded to motion irrespective of the direction, cells that also responded to stationary flashed stimuli, and cells which responded best to motion in two opposite directions with no clear preference for either direction.

For the directionally selective cells (group 4) directional tuning was determined, and an '*axial direction preference*' was calculated by subtracting the polar angle of the receptive field centre from the conventional direction preference (Rauschecker *et al.* 1987*a*). Axial direction preference thus corresponds to the angular difference between a line along the preferred direction and a line connecting the area centralis with the receptive field centre (see Fig. 4). For conventional direction preferences, movement to the right was defined as 0 deg, to the left as 180 deg, upward motion as 90 deg, downward motion as 270 deg. For axial direction preference, 0 deg corresponds to precisely centrifugal motion (away from the area centralis) and ± 180 deg to centripetal motion (towards the area centralis). For further analysis, the cells were then subdivided into three groups on the basis of their axial directional preferences: (A) centrifugal cells, preferring motion within ±45 deg of the direction away from the area centralis; (B) centripetal cells, preferring motion towards the area centralis to within ±45 deg; (C) circular cells: all other cells (with randomly distributed axial direction preferences half of the cells would fall into this group).

All frequency distributions (nominal or ordinal data) were tested statistically with χ^2 tests. Whenever comparing exposure groups, an overall test of the effect across groups was performed as well as separate analysis of the effects of exposure method (screen or carousel) and exposure direction (forward or backward). The relationships between electrode depth and eccentricity of the receptive field, eccentricity and size of the receptive field, and eccentricity and optimal stimulus speed were evaluated with linear regression. Whenever data were available on an interval scale, two-way analyses of variance (ANOVA) were used to evaluate the effects of exposure type (screen or carousel) and exposure direction (forward or backward motion) on the different variables. This was the case for receptive field size and eccentricity as well as for the optimal speed of the stimulus. The significance of peaks in the distribution of axial direction preferences (e.g. whether there was a preference for centrifugal motion) was tested with statistical methods specifically designed for periodic variables (*V* test; Batschelet, 1981).

RESULTS

Response selectivity

We recorded activity from 478 visually responsive cells in thirty-eight electrode tracks through the area PMLS of seven kittens. In 387 neurones directional selectivity could be determined. Of these, 270 cells (70%) clearly preferred motion in one direction. In the Methods section we have defined four categories for the characterization of response selectivity. Table 1 shows the distribution of cells into these categories for each exposure group. Before data were combined from different animals, homogeneity was tested using the χ^2 test, and no significant differences were found between animals within a group. For the pooled data, no significant difference was found between the distribution for the two directions of motion (forward *vs.* backward) during exposure ($\chi^2_{[\mathrm{d.f.}=3]} = 1{\cdot}09$). However, kittens exposed to motion on the screen had a somewhat higher proportion of unresponsive cells than kittens that received their experience in the carousel (26 rather than 11%). A similar tendency was found for the other categories, so that, taken together, a significant difference in response selectivity was found between screen and carousel kittens ($\chi^2_{[\mathrm{d.f.}=3]} = 28{\cdot}44$; $P < 0{\cdot}001$).

TABLE 1. Response specificity of PMLS cells for kittens in different exposure groups. Number of cells per category is given

Exposure method...	Screen		Carousel		
Direction	Forward	Backward	Forward	Backward	Total
No response	19	62	23	6	110
Vague receptive field	15	40	26	10	91
No optimal direction	19	35	29	34	117
Directionally selective	36	88	79	67	270
Total	89	225	157	117	588

Surround inhibition

The presence or absence of surround inhibition was evaluated in most of the directionally selective cells ($n = 203$). If the response was clearly reduced or disappeared altogether when stimulus size was increased, the cell was considered to have strong surround inhibition. If the effect of increasing stimulus size was very weak and thus could not be determined unequivocally, the cell was registered as having unclear or weak surround inhibition. If the cell's response did not change when stimulus size was increased, the cell was reported to have no surround inhibition. As shown in Fig. 2, the kittens exposed in the carousel showed significantly more surround inhibition than those with screen exposure when tested with the χ^2 test ($\chi^2_{[\mathrm{d.f.}=2]} = 6{\cdot}06$; $P < 0{\cdot}05$). Again, the direction of exposure had no effect. In each case, animal-to-animal variability within a group was small: χ^2 tests revealed no significant differences, so data could be combined.

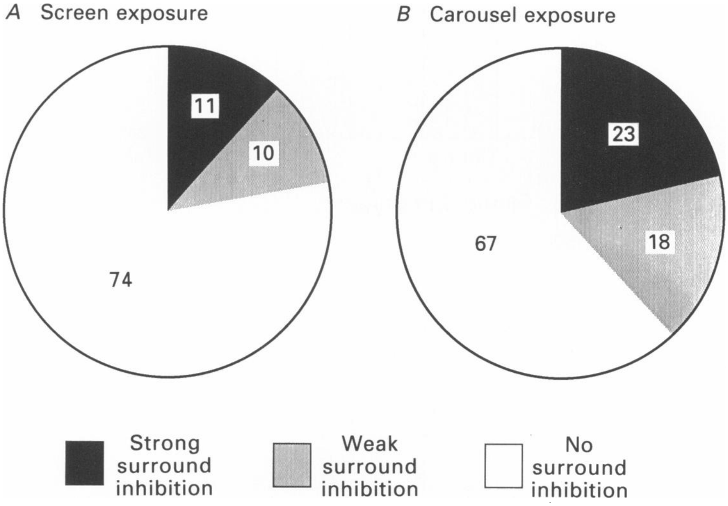

Fig. 2. Amount of surround inhibition in PMLS cells for screen-exposed (*A*) and carousel-exposed (*B*) kittens. Numbers of cells are given as indicated in the legend. For further explanation see text.

Ocular dominance

Ocular dominance distributions of PMLS cells were normal in all kittens. Both for screen and carousel exposed kittens, more cells reacted better to stimulation of the contralateral ($n = 106$) than of the ipsilateral eye ($n = 11$), and most cells (159/204 = 78%) could be driven by either eye (Fig. 3). Chi-squared tests revealed no significant differences between the groups nor between individual animals within a group. As in normal cats (Rauschecker *et al.* 1987*a*), cells often reacted to simultaneous stimulation of both eyes much more vigourously than to stimulation of each eye alone, i.e. they showed binocular facilitation.

Directional selectivity

Distribution of direction preferences

Seventy per cent (270/387) of all cells tested for directional selectivity showed a clear preference for one direction of motion. This is slightly less than in normal cats, in which 90% or more of PMLS units have a preferred direction (Rauschecker *et al.* 1987*a*). A slight over-representation of preference for movement into the lower quadrant (180–270 deg) was found in the distribution of direction preferences (104/270 = 39% as compared to an expected proportion of 25%). The majority of direction-selective cells (211/270 = 78% as opposed to an expected 50%) had their receptive field centres also situated in this part of the visual field.

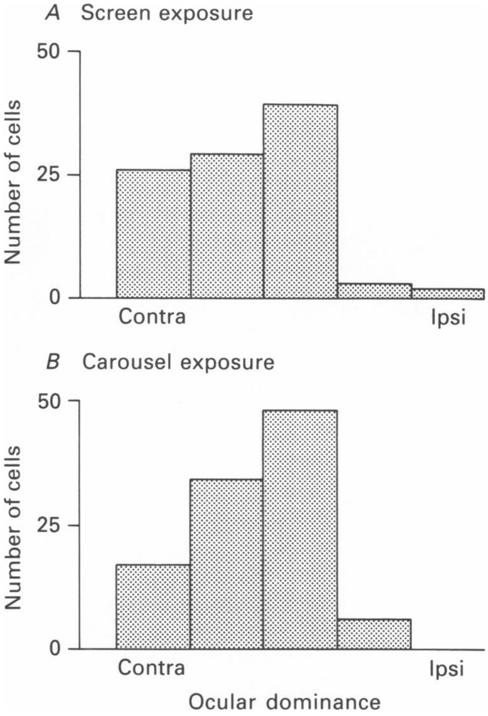

Fig. 3. Ocular dominance distributions for PMLS cells in screen (*A*) and carousel kittens (*B*). Ocular dominance groups are (from left to right): response to stimulation of the contralateral eye only, response predominantly to stimulation of the contralateral eye, approximately equal response to stimulation of either eye, response predominantly to stimulation of the ipsilateral eye, response to stimulation of ipsilateral eye only.

Distribution of axial direction preferences

The most relevant parameter of our study is the distribution of axial direction preferences of the selective cells in the PMLS. Axial direction preference relates conventional direction preference to the location of the receptive field centre. When axial direction preferences were calculated in the way described in Methods (see also Fig. 4 and Rauschecker *et al.* 1987*a*), a preference for centrifugal motion was apparent for all exposure groups (Fig. 5). In every single kitten, there was a higher number of cells with centrifugal than with centripetal preference (Table 2). When individual kittens were tested against each other with the χ^2 test, no significant difference was found in this respect between screen-exposed and carousel-exposed kittens. Data from both exposure methods could thus be combined. As shown in Fig. 6, the centrifugal bias was just as clear for kittens exposed to real or simulated backward motion (contracting flow fields; Fig. 6*B*) as for those exposed to forward motion (expanding flow fields; Fig. 6*A*). In fact, three of the four kittens exposed to contracting flow fields showed the clearest individual preference for centrifugal motion when tested with circular statistics (*V* test; see Methods). As a group, both kittens with forward exposure ($V = 0{\cdot}138$; $n = 115$; $P < 0{\cdot}05$) and kittens with backward exposure ($V = 0{\cdot}247$; $n = 155$; $P < 0{\cdot}001$) significantly favoured centrifugal motion.

For further statistical analysis the cells were divided into three classes (centrifugal, centripetal, or circular, as defined in the Methods section). Again, the exposure condition did not affect the distribution of the cells between these three classes, as shown in Table 2 ($\chi^2_{[\mathrm{d.f.}=6]} = 4{\cdot}69$). Analysis of this distribution for pooled screen *versus* pooled carousel exposure ($\chi^2_{[\mathrm{d.f.}=2]} = 3{\cdot}11$) gave no indication that the method of exposure affected the distribution of preferred directions. Similarly, combined data for real and simulated forward motion did not differ significantly from combined data for real and simulated backward motion ($\chi^2_{[\mathrm{d.f.}=2]} = 1{\cdot}53$). Kittens in the latter group still had over 40% centrifugal cells, although this only represents 25% of all possible directions. For each of the four exposure groups the distribution was significantly different from what one would expect with a random distribution of axial direction preferences.

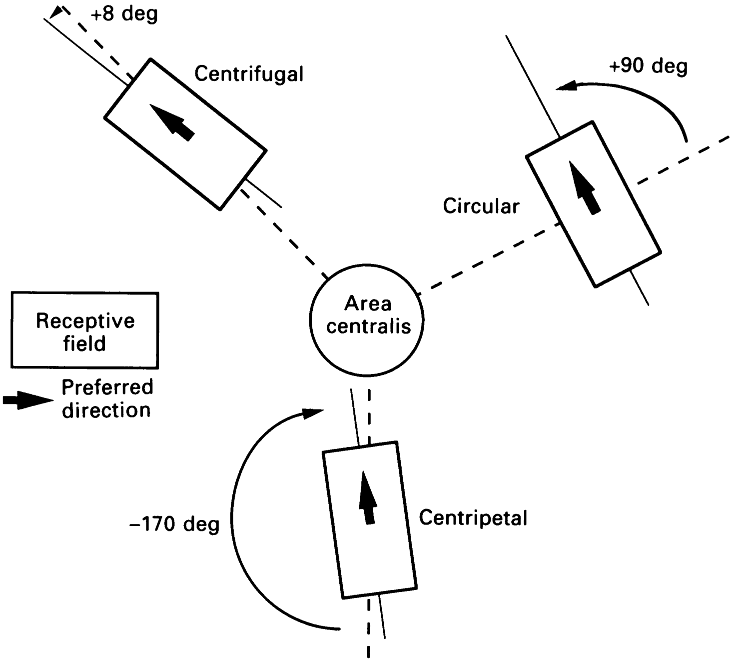

Fig. 4. Schematic illustration for determining axial direction preference. The axial direction preference of a cell (difference from centrifugal direction of motion) is the angle between a line connecting the centre of the area centralis with the centre of the receptive field and a line along the preferred direction. Axial direction preference thus depends on the preferred direction as well as on the position of the receptive field.

Direction tuning

For most directionally selective cells direction tuning was determined quantitatively to the nearest multiple of 22·5 deg. There was no significant difference in the distribution of axial direction preferences between narrowly tuned cells (responding only within 45 deg to either side of the optimal direction), cells of medium tuning (that responded within 90 deg to either side), and widely tuned cells ($\chi^2_{[\mathrm{d.f.}=4]} = 3{\cdot}31$). There was also no significant difference between the four exposure conditions in the distribution of these tuning categories ($\chi^2_{[\mathrm{d.f.}=6]} = 4{\cdot}12$; see Table 2). Altogether, the tuning was less sharp than in normal cats studied in the same laboratory using similar methods: there about half of the units showed 'narrow' tuning (within ±45 deg) and less than 20% had responded to directions differing by more than 90 deg from the preferred one (Rauschecker *et al.* 1987*a*).

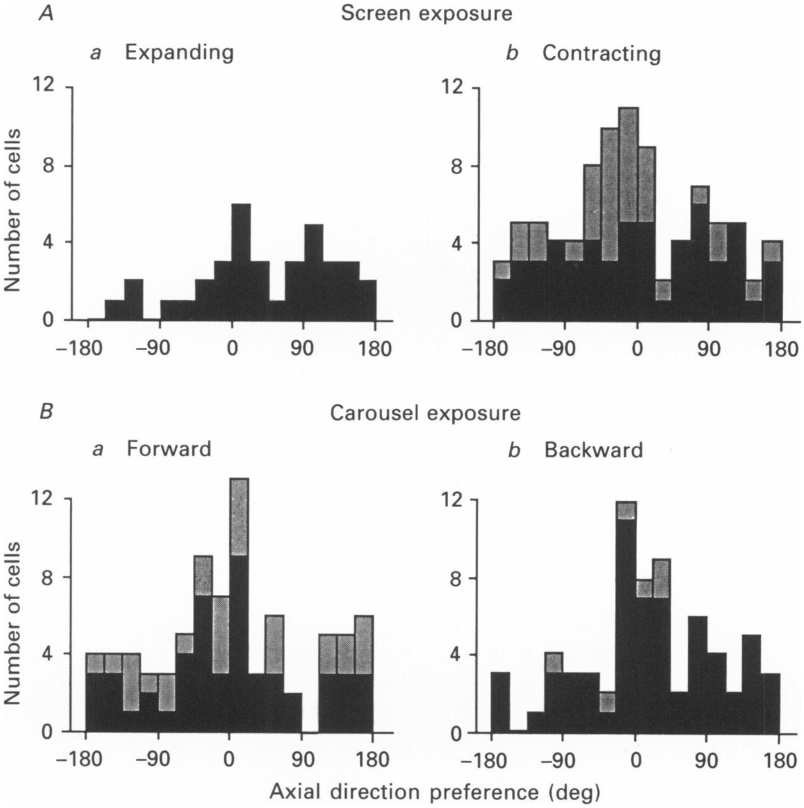

Fig. 5. Distribution of axial direction preference for each of the exposure conditions. Results from kittens exposed to simulated forward (*Aa*) and backward (*Ab*) motion on the screen are shown on top, real forward (*Ba*) and backward (*Bb*) motion in the carousel on the bottom of the figure. Data for individual kittens are indicated by different shading. Axial direction preferences were divided into sixteen bins of 22·5 deg, with 0 deg representing motion directly away from the area centralis.

Eccentricity dependence of the centrifugal bias

In general, the optic flow due to ego-motion is slower near the area centralis than in the periphery of the visual field. On the other hand, PMLS neurones typically prefer higher stimulus velocities (greater than 5 deg/s; Spear & Baumann, 1975; Rauschecker *et al.* 1987*a*). If cells with a preference for centrifugal motion are indeed functionally related to the processing of optic flow from self-motion, there is reason to expect a stronger centrifugal bias for greater eccentricities. Such an eccentricitydependent effect has indeed been described for the centrifugal bias in monkey middle temporal visual area (Albright, 1989) and cat lateral posterior nucleus (Friederichs, 1988; Rauschecker, 1988). To test for an interdependence between receptive field eccentricity and axial direction preference we divided the cells into four eccentricity classes. In all, forty-nine cells had their receptive fields centred within 10 deg of the centre of the area centralis, forty-nine cells between 10 and 20 deg eccentricity, seventy-four cells between 20 and 30 deg, and fifty-three cells beyond 30 deg. The preference for centrifugal motion increased significantly with the distance from the area centralis ($\chi^2_{[\mathrm{d.f.}=6]} = 14{\cdot}39$; $P < 0{\cdot}05$) (Fig. 7).

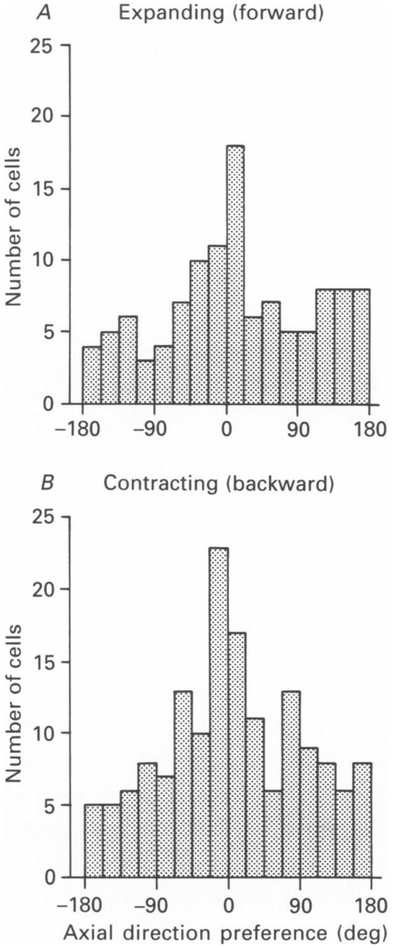

Fig. 6. Distribution of axial direction preferences for kittens exposed to expanding (*A*) or contracting (*B*) flow fields. For each direction of exposure, data from screen- and carousel-exposed kittens are pooled. Both groups of animals show a clear preference for centrifugal motion (*V* test; see text) with no significant difference between them.

Since this eccentricity dependence of the centrifugal bias could have influenced our comparison of the different exposure groups, we evaluated mean eccentricity together with receptive field size and optimal stimulus velocities separately for each exposure group (Table 3). The result was reassuring in that the mean eccentricity did not differ between any of the groups. It was interesting, in addition, that neither combined group (forward or backward) showed a centrifugal bias for cells with receptive field centres within 10 deg of the area centralis.

Receptive field size and stimulus speed

For each exposure group, Table 3 shows the average receptive field size, eccentricity, and optimal stimulus velocity. Optimal velocity was determined in the semi-quantitative way described in the Methods section. In the pooled data, screen-exposed kittens had somewhat larger receptive fields and preferred higher stimulus speeds than did carousel-exposed kittens. A two-way analysis of variance for method and direction of exposure showed a main effect of the method on the optimal speed ($F = 75{\cdot}13$; $P < 0{\cdot}001$) and on receptive field size ($F = 4{\cdot}43$; $P < 0{\cdot}05$). All other main and interaction effects were not significant at a 5% level. If individual kittens are considered by calculating mean values for each animal, a significant difference ($P < 0{\cdot}05$) is found under the *t* test and the Mann–Whitney *U* test for optimal speed, but not for receptive field size.

TABLE 2. Directional selectivity for different exposure groups. Numbers of cells are given (individual animals in parentheses)

Exposure method...	Screen		Carousel		
Direction	Forward	Backward	Forward	Backward	Total
Axial direction preference					
Centrifugal	14	32 (14/18)	32 (22/10)	31 (26/5)	109
Centripetal	6	14 (9/5)	19 (12/7)	11 (11/0)	50
Circular	16	42 (32/10)	28 (16/12)	25 (24/1)	111
Direction tuning					
Narrow < ±45 deg	10	25	21	22	78
Medium < ±90 deg	11	33	22	17	83
Wide > ±90 deg	15	30	36	28	109

Total number of cells per exposure group corresponds to the number given in Table 1 for 'directionally selective' cells.

As previously found in normal cats (Rauschecker *et al.* 1987*a*), the relationship between receptive field eccentricity and receptive field size was not significant, neither for each group separately nor for all groups together. Unlike in normal cats, no clearly positive correlation was found between eccentricity and optimal velocity. This is due to the fact that a broad range of velocities was represented at every eccentricity, which might have been caused by the specific experience. In all penetrations eccentricity shifted significantly with electrode depth (cf. Palmer, Rosenquist & Tusa, 1978; Rauschecker *et al.* 1987*a*) at a rate of $-5{\cdot}6$ deg/mm ($t = 11{\cdot}49$; $P < 0{\cdot}001$).

Histological verification

Of the 270 directionally selective cells, 214 were confirmed histologically to be in the PMLS. The remaining fifty-six were either in the lower part of the sulcus where the PMLS–PLLS border is not clear, or were in electrode tracks that could not be

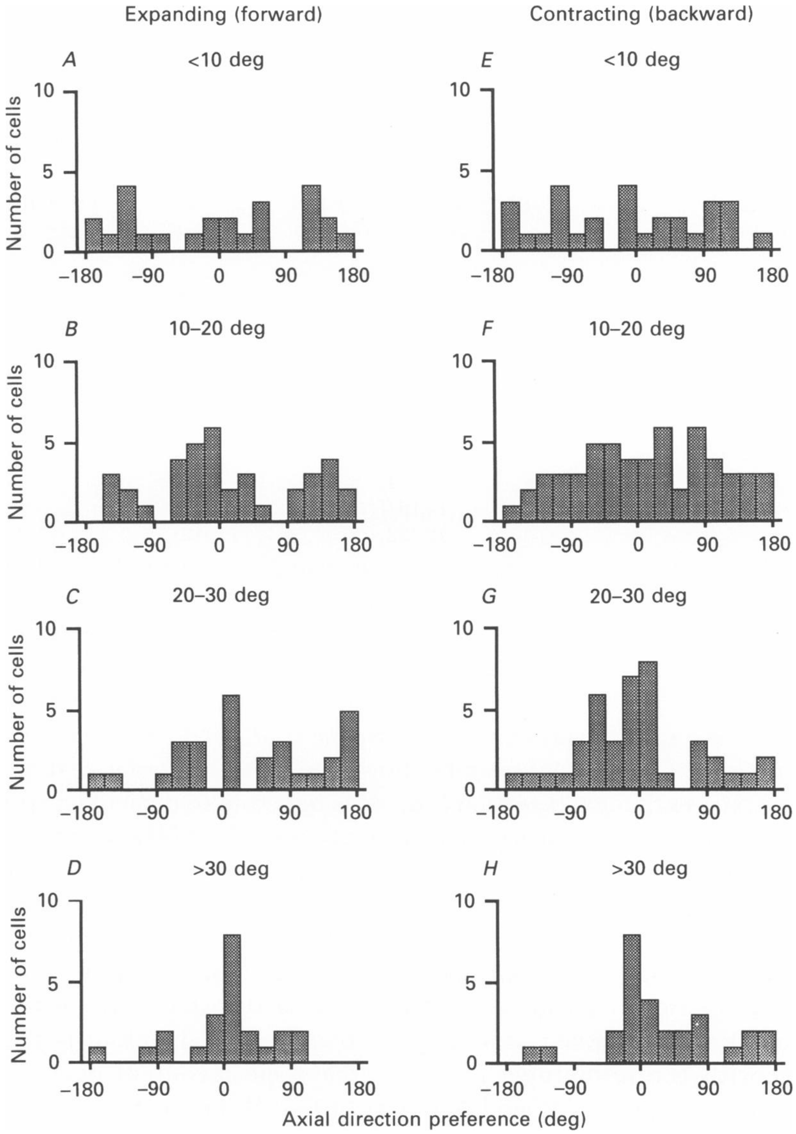

Fig. 7. Distribution of axial direction preferences for different ranges of eccentricity. Data for kittens exposed to real or simulated forward motion are displayed on the left (*A–D*), to real or simulated backward motion on the right (*E–H*). Eccentricity ranges are: *A* and *E*, less than 10 deg; *B* and *F*, 10–20 deg; *C* and *G*, 20–30 deg; *D* and *H*, over 30 deg. For both exposure groups, a centrifugal bias is found only for eccentricities beyond 10 deg.

retrieved. Six of the thirty-eight tracks were not found in the histological sections. By comparing these tracks' stereotaxic co-ordinates with those of identified tracks, we concluded that they probably were in the PMLS. If not in the PMLS, these cells must have been situated in the nearby postero-lateral part of the lateral suprasylvian visual area (PLLS), for which a centrifugal bias has also been reported (Blakemore & Zumbroich, 1987; Rauschecker *et al.* 1987*a*). The fifty-six unverified cells' direction preferences were no different from those of the 214 directly confirmed cells ($\chi^2_{[\mathrm{d.f.}=2]} = 0{\cdot}03$). Furthermore, there was again no difference between the dis-

TABLE 3. Size, eccentricity, and optimal stimulus speed ($n = 270$) of PMLS receptive fields for each exposure group (mean and standard deviations)

Exposure method...	Screen		Carousel	
Direction	Forward	Backward	Forward	Backward
Eccentricity (deg)	19 ± 10	21 ± 11	20 ± 12	20 ± 10
Size (deg^2)	138 ± 106	149 ± 118	117 ± 83	116 ± 78
Speed (deg/s)	76 ± 27	67 ± 30	43 ± 23	42 ± 20

tribution of axial direction preferences after exposure to forward as compared to backward motion when only considering cells whose origin was shown histologically to be in the PMLS ($\chi^2_{[d.f.=2]} = 1{\cdot}58$).

DISCUSSION

The development of various single-unit response properties in the striate cortex of the cat depends on the environment (Blakemore & Cooper, 1970; Hirsch & Spinelli, 1970; Cynader *et al.* 1975; Daw & Wyatt, 1976; Rauschecker & Singer, 1981; see Rauschecker, 1990, for review). Much less is known about visual development in the extrastriate cortex, but it is quite certain that development of direction selectivity in area PMLS requires visual experience (Spear *et al.* 1983; see Sherman & Spear, 1982, for review). Our present results show that a higher-order feature of PMLS organization, its centrifugal direction bias, does not seem to depend on specific visual experience. This preference for centrifugal motion in the PMLS has been described in detail recently (Rauschecker *et al.* 1987*a*, *b*), and it would be conceivable that it is generated during ontogeny by the expanding flow fields kittens normally see during forward locomotion. However, independent of the type of exposure, whether they experience expanding or contracting flow fields, all kittens showed a preference for centrifugal motion. We conclude, therefore, that the centrifugal direction bias in PMLS is innately determined as a 'computational map', much as is the case on a lower level with the retinotopic map and the basic layout of ocular dominance columns in area 17 (Hubel, Wiesel & LeVay, 1977; Rakic, 1981).

Visual exposure: role of eye and head movements

Two types of restricted visual exposure were used. During screen exposure, kittens were restrained and shown rectangular stimuli moving on a dark background along paths that simulated linear vection of the kitten through a visual environment. However, the kittens were free to make eye movements. In the second type of exposure using a specially designed carousel the same limitation applied, and the kittens even retained some freedom to move their heads. However, as the kittens are actually moving during carousel exposure, this is probably a better simulation of the normal condition. With the circular motion of the carousel we were confined to using relatively low speeds. In order to keep the rotational component of the flow field stimulation to a minimum, the carousel was built with fairly long arms ($r = 1$ m). In addition, the rotation was clockwise and counterclockwise on alternate days, while each kitten was always either facing forwards or backwards.

Eye and head movements have the effect of shifting the local centre of expansion or contraction (the 'singularity' of the flow field, or focus of outflow) away from the area centralis (see below, and Gibson, 1950; Regan & Beverley, 1982; Warren & Hannon, 1988). However, the *global* radial outflow is only little affected, and it is this global outflow which is used to determine, for instance, the direction of heading in humans moving on a ground plane (Gibson, 1950; Warren & Hannon, 1988). Of course, during locomotion kittens also cannot be assumed to continuously look exactly in the direction of motion.

If the development of the centrifugal bias in the PMLS did depend on experience, but eye movements and residual head rotation had made the selective exposure ineffective, the kittens of both groups should have shown no centrifugal bias at all. However, all kittens did show the centrifugal bias. The optic flow associated with rotation of the head and eyes only adds a constant displacement to the flow pattern (Warren & Hannon, 1988) and, since rotations occur equally to either side, it shows no net retinal asymmetry. A radial outflow pattern and thus a centrifugal bias could only be generated by systematic changes in the distance between the observer and surfaces in the environment. We can be quite certain, therefore, that the centrifugal bias in our kittens is not a result of the exposure, but develops independently.

Of course, none of the types of 3-D motion which the kittens experienced were self-induced. According to the classical experiment of Held & Hein (1963), visually guided behaviour develops normally only with active, self-induced movement. Assuming a direct functional role of the area PMLS in these forms of behaviour, it cannot be ruled out completely, therefore, that flow field exposure resulting from active locomotion would lead to different results.

Development of response specificity in the PMLS

The PMLS develops very rapidly during the first 3 or 4 weeks of life, and does not reach maturity until at least 8 weeks (Jones, Spear & Tong, 1984; Benhamida, 1987; Zumbroich, Blakemore & Price, 1988). Visuotopic organization and ocular dominance distribution appear to be fully developed as soon as cells become visually responsive, whereas the percentage of directionally selective cells and of cells showing surround inhibition increases during the first weeks of a kitten's life (McCall *et al.* 1988; Price, Zumbroich & Blakemore, 1988). This does not necessarily imply that the sensitive period for the effects of environment is over by then, as the comparison with area 17 shows: most cells there are selective after 4 weeks of normal visual experience (Pettigrew, 1974), but are still prone to the effects of deprivation for at least another 8 weeks.

Binocularly deprived cats have much fewer visually responsive cells in the PMLS than normal cats, and the responsive cells have abnormally large receptive fields and very often respond exclusively to stimulation through the contralateral eye. Direction selectivity is lost altogether (Spear *et al.* 1983). Rearing kittens under stroboscopic illumination reduces the number of directionally selective PMLS cells, while leaving other properties intact (Spear, Tong, McCall & Pasternak, 1985), just as it does in the striate cortex (Cynader *et al.* 1973; Rauschecker & Schrader, 1987).

Some signs of the selective experience could also be found in the present study. Judging by the percentage of directionally selective cells and of cells showing surround inhibition, the PMLS was quite mature in our kittens, but it had not fully reached the adult level. This could be attributed to the limited exposure time or to the circumscribed environment our kittens encountered. When carousel-exposed kittens were compared to screen-exposed kittens, the following differences were found: carousel kittens had a higher proportion of cells with directional selectivity and vigorous response (Table 1), showed more surround inhibition (Fig. 3), and, on average, had smaller receptive fields (Table 3). In addition, the ocular dominance distribution of screen-exposed kittens appeared to be shifted towards the contralateral eye (Fig. 2). All these differences might be interpreted in such a way that carousel kittens experienced more variation in their environment than did screen kittens and therefore showed signs of greater maturity. However, such a conclusion has to be drawn with great caution, because all the statistical differences are calculated from pooled data using χ^2 tests. For a firmer statement more individual data in a higher number of animals would be needed. One effect which is highly robust under various statistical evaluation, however, is the lower average of optimal velocities after carousel exposure (Table 3). This difference is probably related to the slower speeds of motion experienced during carousel than during screen exposure.

Altogether, the results can be taken to confirm that the environment is certainly relevant for the development of specificity in the PMLS, even if it does not guide the realization of the centrifugal bias.

Pathways involved in the centrifugal bias

A directional bias in the rearing environment induces a preponderance of cells responsive to that direction of motion in striate cortex (Tretter *et al.* 1975) but does not have the same effect in the superior colliculus (Cynader *et al.* 1975). The PMLS receives a large part of its input from the superior colliculus via the lateral posterior nucleus of the thalamus. The distribution of axial direction preferences in the lateral posterior nucleus is also not uniform and many cells show surround inhibition (Chalupa & Abramson, 1988; Friederichs, 1988; Rauschecker, 1988). This suggests that directional selectivity and the centrifugal bias in the PMLS could be determined, at least to some extent, by the superior colliculus–lateral posterior pathway. If this were the case, our present results could simply reflect a lower degree of plasticity in these subcortical structures.

However, the PMLS also receives both direct and indirect input from other cortical visual areas (for a summary see Rosenquist, 1985). Lesion studies show that directional selectivity depends on input from areas 17, 18 and 19, both in the superficial laminae of the superior colliculus (Stein, 1988) and in the PMLS (Spear, Tong & McCall, 1988). Measurements of response latencies and laminar analysis of PMLS cells with regard to axial direction preference support the conclusion that the centrifugal direction bias is generated intracortically (Rauschecker *et al.* 1987*b*). However, PMLS directional selectivity recovers after early occipital lesions (Spear *et al.* 1988), implying that although this input does usually determine directional selectivity, it is not indispensable. A conclusion on the involved pathways is therefore premature.

Flow fields during locomotion or object motion

Are the neurones in areas PMLS with their centrifugal organization of direction preferences really related to the processing of optic flow, as it results from locomotion? For the present study we obviously assume that it is, but other possible functions have to be considered. For example, the PMLS could be more involved in the analysis of object motion rather than self-motion. Some PMLS neurones have indeed been shown to respond to real or simulated three-dimensional object motion (Toyama, Komatsu, Kasia, Fujii & Umetani, 1985). This is reminiscent of the kind of 'looming detectors' suggested previously (Koenderink, 1986; Regan, 1986) and could come about by co-operative convergence from a number of unidirectional receptive fields with radial preference. Under certain conditions, e.g. with only one object in view, there is no difference between the optic flow resulting from motion of an observer towards the object and that from the object moving towards the observer.

Inhibition of responses by in-phase motion of a textured surrounding also indicates an involvement in the processing of object motion relative to the background or of discriminating figure from ground (von Grünau & Frost, 1983). However, this double-opponent mechanism could also be useful for the processing of flow fields resulting from self-motion: it could help to eliminate components due to eye and head rotation (uniform displacement of the whole image) from the optic flow due to locomotion (expansion and other deformation of the image). In other words PMLS cells could participate in extracting the translational component from a more complex optical flow field.

A decomposition of the optic flow into its translational and rotational components is also needed for the analysis of motion parallax (Clocksin, 1980). The same problem has to be solved for determining the direction of self-motion ('heading') in the presence of eye movements. This task can be performed correctly by human observers moving across a ground plane with a precision of 1 deg of visual angle (Warren & Hannon, 1988), which could be explained by models based on differential motion of image elements (Rieger & Lawton, 1985). It may be just this kind of function that area PMLS subserves.

Phylogenetic origin of the centrifugal bias

If the development of the centrifugal bias is not the result of visual experience during ontogeny, a phylogenetic origin has to be postulated. Assuming that the centrifugal bias is indeed involved in flow field processing, an evolutionary specialization appears very reasonable. Flow field analysis probably guides visuomotor behaviour in a wide variety of species (Wagner, 1982; Frost, 1985). Since forward locomotion is a ubiquitous feature of animal behaviour, special purpose devices for the analysis of the resulting optic flow may be among the oldest mechanisms in the evolution of seeing, and may even have evolved independently several times. More generally speaking, it is obvious that the global functional characteristics specifying a certain type of sensory map must be innately determined, in order to warrant reproducible patterns of sensory processing. Epigenetic factors may then be involved in the tuning of *local* features.

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