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Development of visually guided behaviour requires oriented contours

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Kittens do not learn to use visual information to guide their behaviour if they are deprived of the optic flow that accompanies their own movements. We show that the optic flow that is required for developing visually guided behaviour is derived from changes in contour orientations, rather than from velocity patterns. We used several tests to assess visually guided behaviour. The performance of kittens that had only been allowed to see isolated dots of light was indistinguishable from that of kittens that had received no visual exposure at all. Kittens that had seen streaks of light performed better on several tasks. We discuss this finding with relation to the visual pathways that are presumably involved.

When a kitten moves around, the image on its retina is constantly changing. These changes are systematic, depending both on the movements the kitten makes and the positions of surrounding surfaces [5, 12]. In their classical 'carousel' experiment, Held and Hein [11] demonstrated that kittens only learn to use vision to guide their behaviour if they are allowed to walk around. Moving them around passively is not sufficient. The carousel experiment demonstrates that kittens must learn the relationship between their own movements and changes in the image on the retina: the optic flow.

Kittens that were free to walk around under 1.8 Hz stroboscopic illumination also did not develop normal visually guided behaviour [10]. The only visual response they showed was visually triggered extension (extending their forelimbs in anticipation of contact when carried towards a surface), which kittens even developed if they were exposed during periods of total immobilization or with diffusers in front of their eyes. Stroboscopic illumination prevents vision of motion, but does not prevent the kittens from experiencing the effects of their displacements on perspective or texture gradients. It is clear, therefore, that optic flow is involved in the development of visually guided behaviour.

Can we specify which aspects of the optic flow are required? Kittens that were free to rotate their eyes (and heads), but whose bodies were restrained during exposure to light, also developed visually triggered extension, but no other form of visually guided behaviour [10]. Vertical and horizontal eye movements shift the image on the retina; and torsional eye movements rotate the image. However, the relative positions and orientations of contours in the visual field will not change. Displacements of the image on the retina, therefore, can provide feedback on such eye movements, but cannot provide information about the structure of the environment.

When a kitten moves around, the image on its retina changes in a manner that depends on its displacements, as well as on the structure of the surrounding. These changes could provide the kitten with feedback on its own (direction of) motion, as well as providing it with information on the distance and orientation of surrounding surfaces. The former could be derived from the global distribution of directions of motion in the retinal image (the direction of heading is given by the focus of expansion; after accounting for eye movements). The latter, requires more precise analysis of each part of the retinal image.

In the cat, visual feedback on locomotion could be provided by cells in the lateral suprasylvian visual cortex. These cells are selective for the direction of motion, have large receptive fields, and motion away from the area centralis is over-represented [16] (although not all studies confirm the latter [2]). The development of these cells' response properties coincides with the time that kittens start to show visually guided behaviour [15]. However, the preference for centrifugal motion — that suggests a

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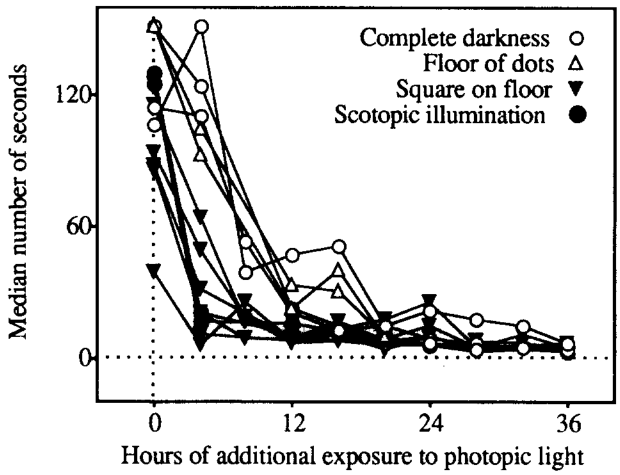

Fig. 1. Time taken to find the food under photopic illumination. Symbols show median values for each kitten. The data can be divided into two categories on the basis of performance after 4–12 h of additional exposure: kittens exposed to dots of light performed no better than those kept in total darkness, whereas kittens exposed to squares of light and those exposed to scotopic illumination clearly found the food faster. Variability within exposure groups is modest despite the fact that the kittens were not always from the same litter and received different amounts of experience with the task itself (between the additional exposure periods the kittens were either tested under scotopic or under photopic illumination or both).

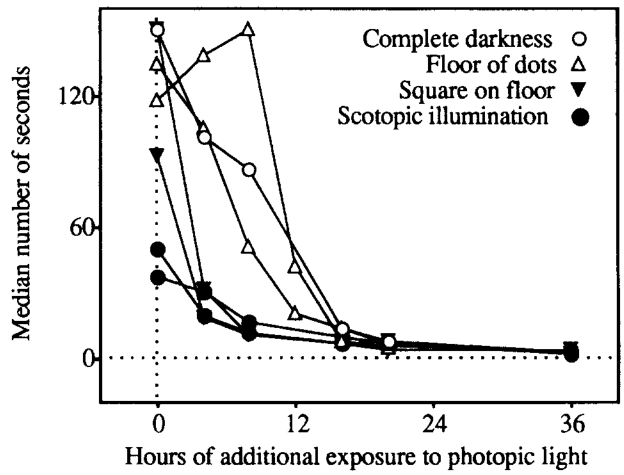

Fig. 2. Time taken to find the food under scotopic illumination. Performance was very similar to that under photopic illumination. The only clear difference was on the first testing session, when the kittens that had been exposed to scotopic illumination performed considerably better under scotopic than under photopic illumination. This effect disappeared after 4 h of photopic exposure.

role in optic flow analysis — was found not to be the result of kittens' predominant exposure to expanding flow fields during locomotion [3].

Local direction and velocity of motion are the most straightforward parameters for deriving distances and orientations of surrounding surfaces from the optic flow. However, differences in velocity along surfaces' contours, as the result of motion of the observer, will result in changes in the contours' orientations, as well as changes in the length of, and distances between, different contours. Considering that human subjects are not very good at discriminating between velocities [4], it is quite likely that these changes in orientation, size, and distance are used to evaluate the optic flow [12]; instead of the local velocity information itself.

In the primary visual cortex of the cat, most cells have small receptive fields, and respond to contours of a specific orientation. It seems reasonable, therefore, that changes in orientations and in the distance between contours — as the result of the kitten's displacements — should also be analysed in the primary visual cortex, or at least on the basis of information from this area. In the present study, we show that the changes in contour orientation that accompany the kitten's displacements are essential for the development of visually guided behaviour. This matches the fact that the distribution of preferred orientations in the primary visual cortex is shifted by selective exposure [1], and requires experience with oriented contours to develop normally [17].

Thirteen kittens (from 4 litters of the same mother) were raised in complete darkness from several hours after birth. Once they were 3–4 weeks old, each of them spent several hours a day in a specially designed environment. The environment was a wooden cube (except for the case mentioned below) with sides of 60 cm. The inside of the cube could be completely dark (3 kittens); could be illuminated from above at a scotopic (1.2×10^{-3} lx) level (2 kittens); or could have either 20 dots (2 kittens) or 4 streaks (6 kittens) of light on its floor.

The dots of light were produced by green light emitting diodes (LEDs; 5 mm diameter). Twenty dots were distributed at random under a transparent sheet of perspex covering the floor of the cube. The LEDs were placed within holes in the wooden floor, so that only the tops were visible.

The streaks of light were made by passing light from similar LEDs through thin perspex fibres which had been roughened with sand-paper to allow the light to escape along the whole length. The streaks of light were arranged so that they formed a square. This square coincided with the edges of the cube for four of the kittens, and did not do so for another two. In the latter case, the exposure took place in a glass, rather than wooden, cube of the same dimensions; and the perspex fibres (providing the streaks of light) were just below the glass floor. We found no differences between the two conditions, so they are presented as one group. The LEDs were driven at a current that made the dots and streaks invisible to the unadapted human eye, but clearly visible after several minutes of dark adaptation. The kittens could never touch the LEDs or fibres.

Once each kitten had been exposed to a certain visual environment for 49 h (within 3 weeks for all but 2 of the dark reared controls; exposure increasing from 1 to 3 h per day depending on how long the kittens could be separated from their mother without distress), various aspects of visually guided behaviour were examined. All kittens were first tested under photopic illumination. The kittens of the last two litters were also tested under scotopic illumination, because there is some evidence that the two systems develop independently [6].

We examined whether kittens extend their paws when moved towards the horizontal surface of a table (visually triggered extension [9]), and, if so, whether they are able to guide the extended paw towards one of the prongs of an interrupted surface (visually guided reaching [9]). Depth perception was tested with a visual cliff [7], requiring a descent (7 cm) onto a transparent surface in one of two directions. A checkerboard pattern with squares of 5 by 5 cm was directly below the surface on the shallow side, and 80 cm below it on the deep side. We examined ocular pursuit (often combined with head movements) by moving our hand silently in front of the kitten's eyes; and comparing the response with that for the same motion while making a small noise by sliding our fingers across each other. In the latter case, which was included to make sure that the kittens were able to make the required eye movements, all kittens followed the hand with their eyes.

TABLE I

VISUALLY TRIGGERED EXTENSION, VISUALLY GUIDED REACHING AND OCULAR PURSUIT WHEN TESTED UNDER PHOTOPIC OR SCOTOPIC (*BRACKETS*) ILLUMINATION

[a]Could only be tested if kittens extended their paws as they approached the surface. [b]All kittens followed the moving hand with their eyes if it made a noise. Dashes indicate that this item was not tested.

Kitten	Exposure	Extension	Reaching[a]	Ocular pursuit[b]
1	Complete darkness	no *(no)*	- -	no *(no)*
2		no -	- -	no -
3		no -	- -	no -
4	Floor of dots	no *(no)*	- -	no *(no)*
5		no *(no)*	- -	no *(no)*
6	Square on floor	no *(yes)*	- *(no)*	yes *(yes)*
7		no *(yes)*	- *(no)*	no *(no)*
8		no -	- -	no -
9		no -	- -	no -
10		no -	- -	no -
11		no -	- -	no -
12	Scotopic illumination	no *(yes)*	- *(yes)*	yes *(yes)*
13		no *(yes)*	- *(yes)*	yes *(yes)*

The experimenter was free to test the kittens as often as he wanted, to decide whether extension and pursuit were present or absent. On the reaching task and on the visual cliff, 8 or more 'correct' responses (out of 10 trials) was considered to indicate that the kittens were able to perform the task. Correct responses consisted of hitting a prong — rather than an equally large empty space — and descending to the visually shallow — rather than deep — side of the cliff, respectively.

For the last test, the kittens were mildly food deprived (they were given continuous access to dry food and water, but received eggs and tinned cat-food only during and immediately after testing). A container with a small portion of raw egg or tinned food was placed in one of the 4 corners of the table, and the kitten was released in the centre. We measured the time it took the kitten to find the food at each corner of the table (time resolution 1 s; maximum 150 s; corners in unpredictable order).

Immediately after the behavioural tests, the kittens were given 4 h of additional exposure to photopic illumination in their normal living quarters (the time needed for testing each kitten was subtracted from these 4 h). On the next day, the kittens were tested again, and exposed to another 4 h of photopic illumination; and so on. The reason for repeated testing was that the original exposure may have allowed aspects of behaviour to develop that are essential but not sufficient for performing the task (see the way in which visual experience during locomotion influences the development of visually guided reaching [8]). Monitoring improvements or acquisition of the various aspects of visually guided behaviour may reveal such effects.

The kittens that had been exposed to dots of light responded no differently from those kept in the dark on any of the tests. The kittens exposed to scotopic illumination and those exposed to streaks of light did respond differently from those kept in the dark on some tasks: they showed extension under scotopic illumination (when tested; Table I) and found the food in a corner of the table considerably faster than kittens kept in the dark (Figs. 1 and 2). None of the kittens consistently chose the shallow side of the visual cliff (whereas one additional kitten that had received 49 h of photopic stimulation did do so).

There were some differences between the performance of kittens exposed to scotopic illumination and those exposed to streaks of light. The latter did not develop visually guided reaching (for which vision of the paw is essential [8]) and most of them did not follow a silent moving object with their eyes (Table I). Moreover, on the first testing session, when tested under scotopic illumination, kittens that had previously been exposed to scotopic illumination found the food considerably faster than those previously exposed to streaks of light. This was not so when the kittens were tested under photopic illumination.

Both the dots and the square of light form a visual plane (the floor) which undergoes systematic deformations as the kitten walks around. The fact that the isolated dots of light had no detectable effect on the development of visually guided behaviour, support the hypothesis that such behaviour is guided by surface properties that are extracted from the optic flow on the basis of changes in the orientations of contours. Exposure to a square of light was sufficient for developing visually guided extension under scotopic illumination, and clearly somehow helped the kittens learn to find the food.

Kittens reared under scotopic illumination were better at visually guided reaching than those only exposed to a square of light. Visually guided reaching is known to require prior vision of the paw. They also appeared to be better at ocular pursuit, suggesting that experience with visible moving objects may be required to develop ocular pursuit. These last differences show that although the presence of oriented contours may be essential for developing visually guided behaviour, some basic types of behaviour require additional specific experience.

The present study shows that the development of some aspects of visually guided behaviour require changes in contour orientation. This is presumably related to the development of the primary visual cortex. It does not necessarily mean that all visually guided behaviour is based on changes in contour orientation. We suggest that environmentally guided visual development evolved for aligning the receptive fields of cortical cells for the two eyes (and specific disparities) for binocular depth perception. The plasticity is essential, because the distance between the eyes, as well as the size of the eyes themselves, is constantly changing during development. Animals with limited binocular vision, such as rabbits, show little cortical plasticity [13, 14]. The analysis of optic flow via cells with small receptive fields aligned for the two eyes (as is the case in the primary visual cortex) requires experience to develop. However, optic flow analysis based on global velocity fields may also exist, but not require specific visual experience to develop.

A question that remains to be answered is whether changes in the orientation of a single streak of light are sufficient, or whether variations in the angle formed by two such streaks are essential. Another issue that may be worth examining is related to the fact that the streaks provided more light due to their larger surface (at the same luminance). To examine whether the spatial extent of the stimulation is an important factor, one could, for instance, expose kittens to environments with lines of different lengths.

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1 Blakemore, C. and Cooper, G.F., Development of the brain depends on the visual environment, Nature, 228 (1970) 477–478.

2 Blakemore, C. and Zumbroich, T.J., Stimulus selectivity and functional organization in the lateral suprasylvian visual cortex of the cat, J. Physiol., 389 (1987) 569–603.

3 Brenner, E. and Rauschecker, J.P., Centrifugal motion bias in the cat's lateral suprasylvian visual cortex is independent of early flow field exposure, J. Physiol., 423 (1990) 641–660.

4 Doorn, A.J. van and Koenderink, J.J., Detectability of velocity gradients in moving random-dot patterns, Vision Res., 23 (1983) 799–804.

5 Gibson, J.J., The Ecological Approach to Visual Perception, Houghton Mifflin, Boston, 1979.

6 Hein, A. and Diamond, R.M., Independence of the cat's scotopic and photopic systems in acquiring control of visually guided behavior, J. Comp. Physiol. Psychol., 76 (1971) 31–38.

7 Hein, A. and Diamond, R.M., Contrasting development of visually triggered and guided movements in kittens with respect to interocular and interlimb equivalence, J. Comp. Physiol. Psychol., 76 (1971) 219–224.

8 Hein, A. and Diamond, R.M., Locomotory space as a prerequisite for acquiring visually guided reaching in kittens, J. Comp. Physiol. Psychol., 81 (1972) 394–398.

9 Hein, A. and Held, R., Dissociation of the visual placing response into elicited and guided components, Science, 158 (1967) 390–392.

10 Hein, A., Gower, E.C. and Held, R., Exposure requirements for developing the triggered component of the visual-placing response, J. Comp. Physiol. Psychol., 73 (1970) 188–192.

11 Held, R. and Hein, A., Movement-produced stimulation in the development of visually guided behavior, J. Comp. Physiol. Psychol., 56 (1963) 872–876.

12 Koenderink, J.J., Optic flow, Vision Res., 26 (1986) 161–180.

13 Mize, R.R. and Murphy, E.H., Selective visual experience fails to modify receptive field properties of rabbit striate cortex neurons, Science, 180 (1973) 320–323.

14 Murphy, E.H., Effects of pattern deprivation on visual cortical cells in the rabbit: a reevaluation, J. Neurophysiol., 53 (1985) 1535–1550.

15 Price, D.J., Zumbroich, T.J. and Blakemore, C., Development of stimulus selectivity and functional organization in the suprasylvian visual cortex of the cat, Proc. R. Soc. Lond. B, 233 (1988) 123–163.

16 Rauschecker, J.P., von Grünau, M.W. and Poulin, C., Centrifugal organization of direction preferences in the cat's lateral suprasylvian visual cortex and its relation to flow field processing, J. Neurosci., 7 (1987) 943–958.

17 Van Sluyters, R.C. and Blakemore, C., Experimental creation of unusual neuronal properties in visual cortex of kitten, Nature, 246 (1973) 506–508.