

REVERSAL OF THE BEHAVIOURAL EFFECTS OF MONOCULAR DEPRIVATION IN THE KITTEN

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SUMMARY

1. Eighteen kittens were monocularly deprived of vision until the age of 5, 6 or 7 weeks. Their eyes were then reverse-sutured, and they were allowed to survive for 3–63 days, before physiological recording from area 17.

2. At the time the reverse-suture was performed, and immediately before the recording session, each kitten was tested separately in the two eyes to elicit five simple behavioural responses: optokinetic nystagmus, visual startle reaction, visually-guided paw placing, visual following and negotiation of a 'visual cliff'.

3. Following the opening of their initially deprived eye, all kittens appeared behaviourally blind when forced to use that eye; their performance through the initially open eye was then perfect on all tests. After the period of reversed lid-suture, however, their performance when using the initially deprived eye had improved, while that through the initially open eye deteriorated. This complementary improvement and deterioration was most rapid in kittens reverse-sutured at the age of 5 weeks, and less rapid when reverse-suturing was delayed until the age of 6 or 7 weeks.

4. Most of the kittens showed gross abnormalities of interocular alignment, and exhibited marked exotropia or esotropia.

5. The results of these tests were well correlated with the changes seen in cortical ocular dominance in the same animals.

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INTRODUCTION

The goal of neurobiology is to link the activity of the elements of the nervous system with the behaviour of organisms. Since Hubel & Wiesel (1962, 1968) described the response properties of cat and monkey visual cortical neurones, investigations of the human visual system have drawn on their findings to produce evidence that neurones of the kind they described are critically involved in human pattern vision (e.g. Andrews, 1965; Campbell & Kulikowski, 1966; Blakemore & Campbell, 1969). There is also evidence that these neurones are susceptible to the effects of early visual experience in a similar fashion to those in kittens and monkeys (Mitchell, Freeman, Millodot & Hægerstrom, 1973; Von Noorden, 1973; Movshon, Chambers & Blakemore, 1972; Mitchell & Ware, 1974).

It is impossible to control the early visual experience of human subjects with the precision possible in animal experiments; human studies must depend on an analysis of the visual sequelae of early optical and oculomotor disorders. The monkey is clearly the next best choice for behavioural studies of the effects of early experience (see Weiskrantz, 1972), and has been used to some degree for such investigations (Von Noorden, Dowling & Ferguson, 1970; Von Noorden & Dowling, 1970; Von Noorden, 1973). But most of our knowledge of the physiological aspects of mammalian visual development is based on studies of the cat, a notoriously difficult animal from which to obtain behavioural data in rigorously controlled experimental situations. The cat can, however, readily be used for behavioural testing of a less formal kind. Cats and kittens reared in constant contact with humans are usually friendly and can be handled with ease, and can be induced to perform simple visual tasks in play situations. This makes them not unsatisfactory animals in which to examine time-varying effects through relatively brief testing sessions.

Wiesel & Hubel (1963) performed some informal behavioural observations on monocularly deprived kittens, and described an obvious and profound visual deficit in those kittens when they were forced to use their deprived eye:

'As an animal walked about investigating its surroundings the gait was broad-based and hesitant. . . The kittens bumped into large obstacles such as table legs, and even collided with walls, which they tended to follow using their whiskers as a guide. When put onto a table, the animals walked off into the air, several times falling awkwardly onto the floor. When an object was moved before the eye there was no hint that it was perceived, and no attempt was made to follow it. As soon as the cover was taken off of the left eye, the kitten would behave normally, jump gracefully from the table, skilfully avoiding objects in its way. We concluded that there was a profound, perhaps complete, impairment of vision in the deprived eye of these animals.'

Wiesel & Hubel (1965) made similar behavioural observations of monocularly deprived kittens given longer periods of vision through the deprived eye, with the experienced eye either open or closed. They noted some slight improvement in the visual abilities of these animals when using their deprived eyes, and observed some alerting and following responses to moving objects. The extent of recovery was, however, extremely limited, even after 18 months of binocular vision, or forced vision through the deprived eye. The small amounts of behavioural recovery they observed were not accompanied by any significant recovery of physiological function in the cortex.

Dews & Wiesel (1970) performed a more formal investigation of the residual behavioural capacities of the deprived eye of monocularly sutured kittens. They confirmed the earlier observations of Wiesel & Hubel (1965) on the limited recovery following extended monocular deprivation, but they found that shorter periods of deprivation caused less marked, though equally permanent effects. The behavioural recovery observed in animals deprived monocularly to the age of five weeks was excellent – the only residual deficit was in visual acuity performance and reliability of responding – despite the limited recovery of function shown by physiological recordings in the cortex of the same animals.

Other workers have since reported that, after a period of recovery, monocularly deprived kittens are capable of learning some pattern discriminations, though they are impaired in both speed and reliability of performance compared to normal cats (Ganz & Fitch, 1968; Rizzolatti & Tradardi, 1971; Chow & Stewart, 1972; Ganz, Hirsch & Tieman, 1972).

Dews & Wiesel (1970) and Blakemore & Van Sluyters (1974) both reported excellent recovery of behavioural ability in reverse-sutured kittens. Dews & Wiesel reported that one kitten, reverse-sutured for some months at the age of 7 weeks, performed well when using either eye, but was slightly superior when using its initially *deprived* eye. Blakemore & Van Sluyters, in a series of informal behavioural observations of their experimental kittens, found considerable improvement in visual behavioural capability mediated by the initially deprived eye, even in animals initially deprived for most of the sensitive period.

The present investigation extends these observations on behavioural recovery in reverse-sutured kittens, and provides comparisons with the physiological changes in the visual cortex that accompany reversed deprivation and were discussed in the preceding paper (Movshon, 1976).

METHODS

Eighteen kittens from the series described in the preceding paper (Movshon, 1976), reverse-sutured at the age of 5, 6 or 7 weeks, were each tested on a battery of simple behavioural tasks after the left (second-deprived) eye had been opened just before physiological recording. Many of the kittens were tested on some or all of these tasks at the time the reversal of lid suture was performed. The lids of the sutured eye were parted under halothane anaesthesia, and anaesthetized topically with amethocaine; the kittens were then allowed between 20 and 30 min (during which they received no visual experience) to recover from the halothane. At the end of this period they appeared lively and alert, and normally offered no evidence of discomfort due either to the unfamiliar surroundings of the experimental laboratory or the recently opened eyelids. All of the kittens showed normal orienting and following responses to auditory stimuli, and normal tactile placing responses when they were lowered with their eyes covered until the backs of their forepaws touched the edge of a bench or table-top. Left unattended, most of them explored their new surroundings with apparent interest, though some were more reticent, and tended to stay close to the experimenter as he moved about the laboratory.

Each kitten was tested through the two eyes separately, and with both eyes open, for the following visually elicited behaviours.

Optokinetic nystagmus. A large pattern of alternating black and white stripes (each approximately 2-5° across) was moved slowly in front of the kitten, and its eyes closely observed for the characteristic pattern of smooth following eye movements in the direction of stimulus movement interspersed with fast phases in the opposite direction. Both horizontal and vertical nystagmus was tested.

Visual startle reactions. A large object (normally the experimenter's hand) was brought rapidly toward the kitten, stopping 2-3 in. from the eye being tested, and the kitten observed for reflex withdrawal of the head and eye-blinking reactions. Considerable care was taken to avoid touching the vibrissae during this test, and, if they were unusually long, they were cut.

Visual cliff. An attempt was made to induce the kitten to step out on to a transparent surface covering a drop, a simplified version of the apparatus of Gibson & Walk (1960). The kittens were also observed during free movement on bench-tops, to assess the skill with which they avoided and negotiated the edges.

Visual following. An object was moved in front of the kitten and its ability to follow the object with its head and eyes using visual cues was tested; care was taken to make no sound during testing. The most effective object for eliciting following movements was the experimenter's hand held a few inches away while wiggling the fingers; in some older kittens of more playful disposition, a pencil moved along the edge of a bench top evoked more prolonged responses and apparent visual attention.

Visual triggered placing. The kitten was lowered toward the edge of a table or bench which was dark against a light background, while the back end of its body was supported. If it extended its forepaw when the edge came within reach, this was taken as evidence for the presence of the 'triggered' component of visually guided placing. In some kittens, the 'guided' component of visual placing was also tested, using a prongboard apparatus similar to that described by Hein & Held (1967).

The performance of each eye on each of these tests was judged either to be present, present but abnormally weak or unreliable, or altogether absent.

RESULTS

Visually elicited behaviour

At the time of reverse-suturing, at the age of 5, 6 or 7 weeks, all the kittens tested through the initially open eye performed well on all the behavioural tests. They moved about freely and easily, and appeared normal in all respects. This is in good agreement with the results of Norton (1974), who found that kittens possess a normal complement of visually guided behaviours, including some of those mentioned above, at the age of 5 weeks or so. It was initially my intention to make similar behavioural observations on the series of kittens reverse-sutured at the age of 4 weeks (see Movshon, 1976), but the three youngest animals in that series were difficult to manage and did not give reliable performance on some of the tests, and that portion of the project was therefore abandoned.

Immediately following the reversal of lid suture, all animals showed the profound behavioural deficits described by Wiesel & Hubel (1963), appearing virtually blind in all respects. The only evidence of visual capability which could be obtained from some of these animals was a weak and rapidly habituating optokinetic nystagmus.

Fig. 1 illustrates the results of the behavioural tests on each kitten. The results for each eye are shown separately; binocular vision conferred no advantage on any of the kittens, i.e. performance with both eyes open was as good as that obtained with the better of the two eyes alone. The results of each behavioural test were classed as normal (filled symbols), weak (open symbols) or absent (blank spaces). The results for the two eyes in each series of animals show a complementary pattern of shifting behavioural ability. Shortly after reverse-suturing, animals at all ages retained reasonable behavioural capabilities through their initially experienced left eyes, and exhibited slight recovery of function in their initially deprived right eyes. The capacities of their left eyes deteriorated with increasing periods of reversed deprivation; the performance on the visual cliff, and the placing and following reactions were most susceptible to this deterioration, while the startle reaction and optokinetic nystagmus tests were performed well even after longer periods of reversed suture.

The rate at which control of visual behaviour by the left eye improved and control by the right eye deteriorated depended systematically upon the age of the animal at reverse-suturing. After only 6 days, the performance of the right eye in a kitten reverse-sutured at the age of 5 weeks appeared completely normal; that of the left eye had severely deteriorated. After reverse-suture at the age of 6 weeks, performance through the right eye was not normal on these tests until 24 days after reversal, although the performance of the left eye deteriorated rapidly. And after

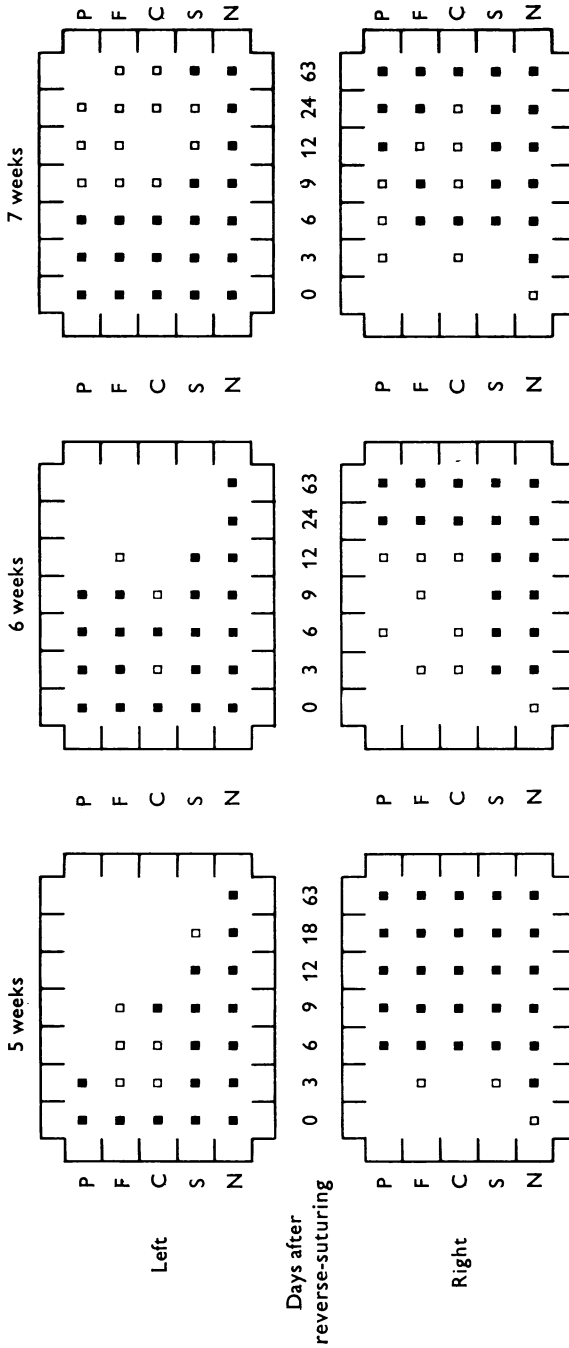


Fig. 1. The visual behavioural capabilities of reverse-sutured kittens. Each box represents the performance using one eye of kittens of the three series reverse-sutured at the ages indicated. Each row of boxes represents the performance through one eye: the initially open left eye in the top row and the initially-deprived right eye in the bottom row. The performance of each kitten through each eye on five behavioural tasks is indicated: a filled symbol signifies normal performance, an open symbol indicates sub-normal performance, and a blank space signifies that the behaviour was totally absent. The five behaviours are indicated by letters: P, visually triggered placing; F, visually triggered following; C, visual cliff; S, visual startle reaction; and N, optokinetic nystagmus. The testing procedures are described in the text.

reverse-suturing at 7 weeks of age, the behavioural capacities of the left eye survived unimpaired for about a week, while those of the right eye did not achieve normality until 9 weeks after reverse-suturing.

In all cases, the first behaviours to disappear in the left eye and the last to appear in the right were visual placing, negotiation of the visual cliff, and visual following reactions; the apparently less demanding tests of startle reaction and optokinetic nystagmus persisted longer and appeared earlier in the left and right eyes respectively; most kittens showed some nystagmus through both eyes.

The upper part of Fig. 2 plots the results of Fig. 1 in graphical form. A 'behaviour score' was calculated for each eye of each animal, by giving two points for a normally present behaviour, one point for a behaviour that was present but weak, and no points for an absent behaviour. The range for each eye could be from 1-10 points. The curves show the progress of the degeneration and recovery of visual capacity in the two eyes in the three series of animals. In general, the longer the second suture was delayed, the slower was the behavioural recovery in the initially deprived eye and the behavioural deterioration in the initially experienced eye.

The lower part of Fig. 2 compares the behavioural results of each kitten with the results of the physiological recordings taken immediately following behavioural testing in each animal, and discussed in the preceding paper (Movshon, 1976). A 'behavioural reversal index' was calculated from the behaviour scores obtained through each eye by simply subtracting the score through the right, initially deprived eye from that through the left, initially experienced eye. The smooth curves represent the physiological results shown in Fig. 3 of Movshon (1976), plotting the reversal index (right-hand ordinate) against the number of days after reverse-suturing.

The agreement between the physiological and behavioural estimates of reversal of eye dominance for the 5-week reversal series is strikingly good (bottom left); the difference in behavioural capability between the two eyes reflects the proportion of cortical cells dominated by each. The agreement is reasonable for the 6-week reversal series (bottom centre), but the kittens from the 7-week reversal series clearly performed better with their initially deprived eyes, relatively speaking, than did the younger kittens. The kitten reverse-sutured for 6 days at the age of 7 weeks could, for example, perform virtually perfectly on the tests when using its right eye, despite the fact that that eye dominated fewer than 25% of cortical neurones. The differences among the three series of animals were generally in the extent to which performance deteriorated in the initially open left eye; the increase in the behavioural capability of the right eye for animals in all three ages was roughly similar.

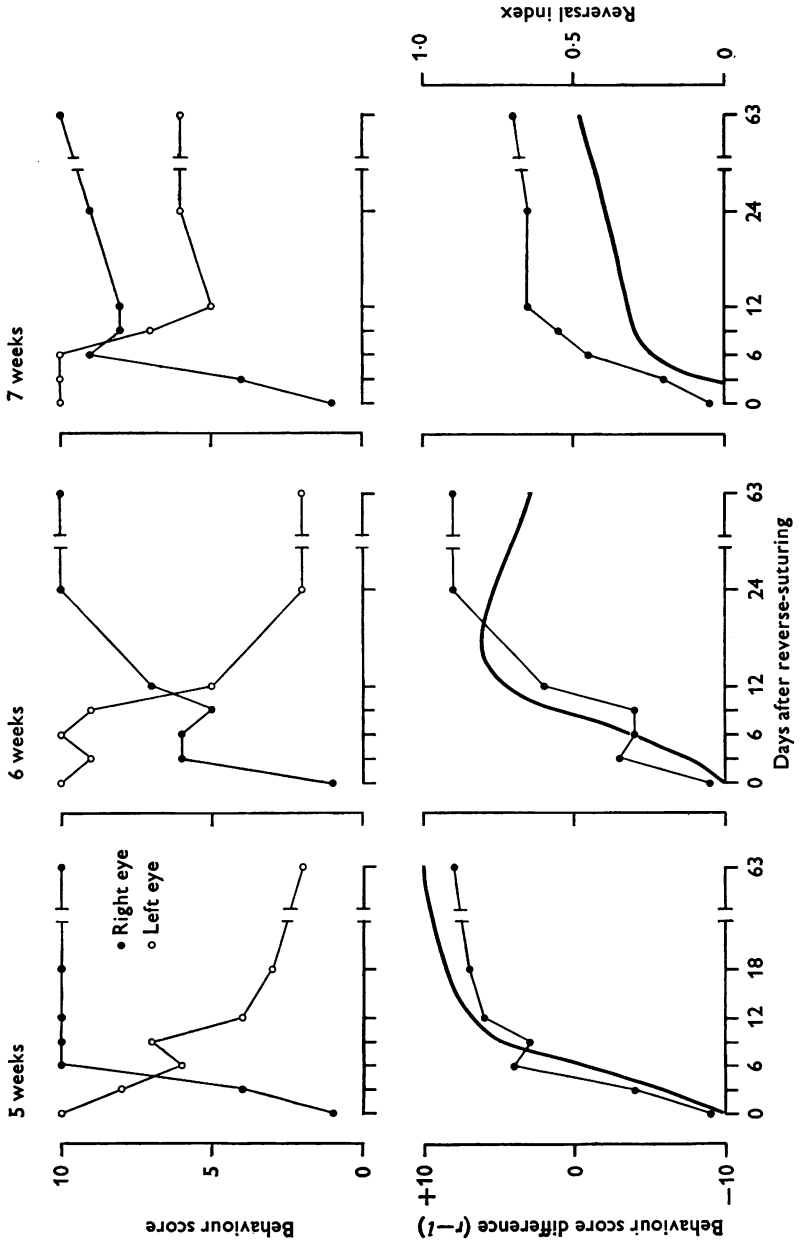


Fig. 2. For legend see facing page.

Interocular alignment

It was noted above that the performance of reverse-sutured kittens using both eyes was no better than it was when the better of the two eyes was used alone. Although none of the tests I employed was aimed at examining, or could be expected to reveal much about binocular functioning, there is another reason why two eyes might be expected to be little better (and perhaps even worse) than one for these animals: most of them possessed a marked strabismus, which was visible on casual observation.

Monocular deprivation and alternating monocular occlusion have been previously reported to derange the normal course of interocular alignment in cats (Sherman, 1972; Blake, Crawford & Hirsch, 1974). The optic axes of the eyes of young kittens are widely diverged, and gradually align over the first 6–8 weeks of life. It is not, however, clear that the eyes are functionally misaligned during the first weeks of life, since artificial strabismus between the ages of 2 and 4 weeks produces a similar loss in binocular interaction to that seen in older animals (R. C. Van Sluyters, personal communication, 1975). It may be that the *visual* axes are aligned much earlier, but coincide much less closely with the *optic* axes than later in life (Olsen & Freeman, 1976).

Fig. 3 plots the relative visual directions of the two visual axes in twenty-three reverse sutured kittens (filled symbols and histograms) and fifteen normal adult cats (open symbols and histograms) determined from the plotted positions of the *areae centrales* on the tangent screen after the animals were paralysed for recording. Each point represents the visual direction of the right visual axis with respect to the left, which is at the origin. The data for normal cats are in agreement with previous reports (Hubel & Wiesel, 1962; Barlow, Blakemore & Pettigrew, 1967) that the eyes diverge slightly after paralysis. The results for reverse-sutured kittens are quite different: the visual axes were very widely scattered with respect

Fig. 2. The results of Fig. 1 are plotted graphically in the upper row of graphs, and compared with the physiological data from the preceding paper (Movshon, 1976) in the lower row. The behaviour score used as an ordinate in the upper graphs is simply calculated from the results of each animal on the five behavioural tests: two points are given for normal performance, one point for subnormal performance and no points for r performance.

The differences between the behaviour scores for the two eyes are used as a behavioural reversal index in the lower row of graphs (points), and compared with the smooth curves, which are fitted by eye to the data on physiological reversal index in the same kittens. The physiological reversal index is simply the proportion of visually responsive cortical neurones dominated by the initially deprived right eye.

to each other; only three of the twenty-three pairs of eyes were aligned within the normal range. In the horizontal direction, the scatter was more-or-less equal convergent and divergent with respect to the normal range; vertically, there was a rather mystifying tendency for the visual axis of the right eye to be below that of the left. The right eye was, of course, the initially deprived eye in all cases, but the significance of this observation is obscure.

Reversal of lid-suture then, causes a marked squint to develop, similar to that caused by monocular deprivation or alternating monocular occlusion.

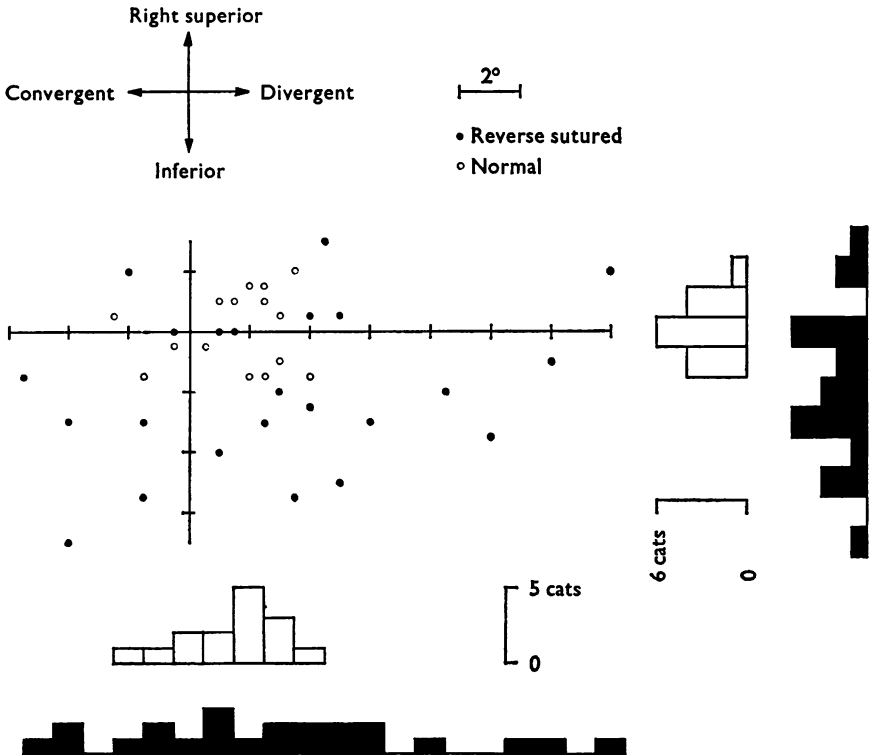


Fig. 3. A comparison of the alignment of the visual axes of fifteen normal cats (open symbols and histograms) with those of twenty-three reverse-sutured kittens (filled symbols and histograms). The positions of the visual axes were determined from the positions of the *areae centrales* plotted on a tangent screen 57 or 114 cm in front of the animals, and are corrected for an interpupillary distance of 4 cm in adults and 3.5 cm in kittens. The points represent the positions of the right visual axes; those of the left eyes have been superimposed at the origin.

DISCUSSION

Although the correlation between visual behavioural capacity and visual cortical neurophysiology shown in Fig. 2 is gratifying, it must be interpreted with some caution. Held (1968, 1970) has discussed the evidence from a number of studies which suggests that it is possible to produce deficits in visual behaviour as gross as those seen in deprived kittens without restricting the visual stimulation necessary for the development of normal sensory processes, merely by preventing an animal from using visual feed-back from motor activity to develop a reliable and functional mapping between sensory and motor systems (Held & Hein, 1963). Furthermore, it is possible to produce reliable control of behaviour by one eye but not the other in situations where each eye should drive roughly the same number of cortical neurones (Hein, Held & Gower, 1970). Ganz & Fitch (1968) concluded from their behavioural studies of monocularly deprived kittens that, in addition to its undoubted effects on visual perception, monocular deprivation also causes remediable deficits in visual-motor coordination; the slight restitution of function seen after opening the deprived eye was held to be due to the development of a sensory-motor link, involving what rudiments of sensory apparatus remained (see Held, 1970). It is therefore necessary to consider the extent to which the development or rearrangement of sensorimotor mapping could account for the results discussed above.

Several features of the recovery of visual function in the initially deprived eye of reverse-sutured kittens are reminiscent of those described during a period of normal sensorimotor activity following deprivation of such activity (Held & Hein, 1963; Hein *et al.* 1970), although those changes were reported to take hours rather than days. The crucial point about those experiments, however, is that rapid and complete recovery takes place when the animal can be presumed to have a normal sensory apparatus at its disposal. In the case of monocular deprivation, the very limited recovery of behavioural ability following prolonged deprivation may reflect a similar phenomenon (Ganz & Fitch, 1968), but monocularly deprived kittens never achieve remotely normal visual behaviour unless there is some physiological evidence that the deprived eye has come to dominate some proportion of cortical neurones (Dews & Wiesel, 1970; Blakemore & Van Sluyters, 1974). Moreover, Spear & Ganz (1975) have recently shown that the recovery of behavioural ability seen after a period of normal vision in monocularly deprived cats depends on the visual cortex: a visual cortical ablation abolishes the recovery. In my experiments, the kittens could never perform reliably on the more

demanding tasks (placing, following or the visual cliff) unless the eye they were using dominated a reasonable proportion of cortical neurones.

The phenomena of sensorimotor adaptation are not uniquely obtained in young animals, and there is ample evidence that similar effects can be produced in adult animals (e.g. Held & Bossom, 1961), but the recovery from the effects of monocular deprivation following reverse-suturing depends critically upon the age of the animal (Dews & Wiesel, 1970; Blakemore & Van Sluyters, 1974). It therefore seems safe to conclude that, although a sensorimotor 'remapping' process must, of course, take place during behavioural recovery from the effects of monocular deprivation during a period of reversed eyelid suture, the sensorimotor factors do not limit that recovery – visually guided behaviour requires, first and foremost, a functioning visual system. The correlation between the properties of visual cortical neurones and the visual behaviour observed in these kittens strongly suggests that these same neurones are the links in the chain between sensory input and motor output that limit visual behaviour in this situation.

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