

# Direction discrimination learning in normal and visually deprived cats and the effects of lateral suprasylvian lesions

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Abstract. We used 5 binocularly deprived cats (BD cats), 4 control cats reared also in the laboratory (C cats) and 4 cats reared in a normal environment (N cats). The cats were trained to discriminate an upward or downward-moving light spot *versus* a stationary spot (detection task) and then an upward *versus* a downward spot (direction task). The N and C cats learned slowly. The learning was slower than in previously studied discriminations of stationary stimuli. However, all N and C cats mastered the detection task and except one C cat the direction task. In contrast, 4 BD cats failed in the detection task and all in the direction task. This result is consistent with single-cell recording data showing impairment of direction analysis in the visual system in BD cats. After completing the training the upper part of the middle suprasylvian sulcus was removed unilaterally in 7 cats and bilaterally in 6 cats. Surprisingly, the unilateral lesions were more effective: the clear-cut retention deficits were found in 5 cats lesioned unilaterally, whereas only in one cat lesioned bilaterally.

**Key words:** visual deprivation, cat, motion discrimination, suprasylvian lesion

#### INTRODUCTION

Discrimination learning of stationary visual stimuli in cats with different visual experience in the early period of life has been intensively studied in our laboratory. We use three categories of animals: (1) Cats deprived binocularly with double linen masks during first 6 months of life (BD cats). (2) Control litter-mates reared also in the laboratory, but with open eyes (C cats). Although our C cats are reared together with BD cats in large boxes, they are certainly in impoverished environment and, moreover, are limited in utilizing sensory stimuli in learning. (3) Cats free-reared in a normal, rural environment during the first months of life (N cats).

We have used various stimuli in discrimination learning: cards of different brightness (Zabłocka and Żernicki 1991), gratings of different orientation (Zabłocka and Żernicki 1996), different figures, usually a cross and a disc (Zabłocka 1975, Zabłocka and Dobrzecka 1986, Zabłocka and Żernicki 1988, 1990) and different objects, usually a three-dimensional cross and a ball (Zabłocka et al. 1975, Zabłocka and Żernicki 1978, Żernicki and Zabłocka 1996). In other laboratories, the effects of visual deprivation was studied on grating (Riesen 1965, Ganz et al. 1972, Van Hof-Van Duin 1979), figure (Ganz et al. 1972) and capital letter (Riesen 1965) discriminations. In short, BD cats are impaired in difficult tasks: when N and C cats learn slowly, the BD cats learn much more slowly and are often not able to meet criterion performance at all (see Żernicki 1991). However, all groups of cats learn easy when discrimination test is simple

Less is known on the effects of visual deprivation on motion discrimination learning. Riesen and Aarons (1959) found that figure movement detection requires longer training in BD cats than in C cats. Furthermore, Pasternak and Leinen (1986) and Pasternak (1987) studied grating motion discrimination learning in cats deprived of motion experience by rearing in a stroboscopically illuminated environment. They determined thresholds for stimulus parameters and found that discriminations of grating direction and speed are impaired in strobe-reared cats.

In a pilot study Żernicki and Zabłocka (1993) compared direction discrimination learning in N, C and BD cats. The stimuli were vertical and horizontal light spots oscillations. However, the task appeared very difficult for all cats and so it was difficult to analyze differences between groups. Nevertheless, the results revealed a significant impairment of learning in the BD group as compared with the N group.

To make the task easier, three methodical changes were introduced in the present study: (1) Direction discrimination was preceded by a detection task. (2) The light spots did not oscillate but moved continuously in opposite directions. Thus, the stimuli were presumably more different than previously. (3) The trajectory of movements was increased. Thus the stimuli were presumably more distinguishable.

In addition, we investigated the effects of lesions of the lateral suprasylvian cortex on preoperatively learned discrimination. The majority of neurons in this cortical area are directionally selective (for review see Spear 1991) and this area controls ocular fixation (Yin and Greenwood 1992, Żernicki and Stasiak 1994, 1996). The lesions were either unilateral or bilateral. This was prompted by the observation (Żernicki and Stasiak 1996) that unilateral lateral suprasylvian lesions can be more harmful than bilateral: an unilateral lesion produced a contralateral visual neglect, which could be ameliorated by removal of the remaining contralateral area.

Available data on the effects of lesions of the lateral suprasylvian cortex on retention of direction discrimination are limited to visually non-deprived cats. Pasternak et al. (1989) found no effect on discrimination performance of grating direction but Rudolph and Pasternak (1996) found a deficit in visually more complex discrimination tasks after bilateral lesions. On the other hand, Krüger et al. (1993) found, surprisingly, an improved performance of figure direction discrimination after bilateral lesions.

It was difficult to predict whether the suprasylvian lesions would be less or more harmful in BD than in N and C cats. On the one hand, numbers of direction-selective neurons are severely diminished in the suprasylvian cortex of BD cats (Spear at al. 1983) and so its role in direction discrimination learning might be diminished as well. On the other hand, since diminution of directionselective neurons occurs also in other visual areas of BD cats (see Discussion), the role of the lateral suprasylvian cortex might be increased. Indeed, Baumann and Spear (1977) reported suprasylvian compensation in cats with lesions of visual cortical areas 17, 18 and 19. It was also found (Zabłocka et al. 1980, Zabłocka and Żernicki 1996) that the superior colliculi, an important target of projection from lateral suprasylvian cortex (for references see Żernicki and Stasiak 1994), have an increased role in BD cats: collicular lesions impaired object and grating discriminations much more in BD cats than in N and C cats.

#### **METHODS**

#### **Subjects**

Thirteen cats were used. Five BD cats were binocularly deprived of pattern visual experience by means of double linen masks fitted on their heads. The masks were put on before eyelid opening and were taken off at the age of 6 months. The average reduction of retinal illumination produced by these masks is comparable to that produced by lid suturing (Zernicki 1991). Two other groups consisted of four C cats, litter mates of BD cats and raised with open eyes together with BD cats in large cages, and four N cats brought to the laboratory when they were 4 months of age. The details of the deprivation technique and rearing conditions used in our laboratory have been described elsewhere (Żernicki 1991). When training started the cats were 7 to 10 months of age.

## **Apparatus**

The two-choice discrimination apparatus consisted of a start compartment and a choice compartment separated by two guillotine doors, opaque and translucent (Fig. 1). The distance between the translucent door and two translucent gates acting as screens was 75 cm. Gates were 12 cm high and wide in stages I and II of training, and 37 cm high and 24 cm wide in stages III to VIII (Table I), and were 5 cm apart.

#### Stimuli

Stimuli were generated on a 14 inch Super VGA monitor screen in stages I and II and on a 23-inch TV screen in stages III to VIII and were viewed through the translucent gates. The stationary stimulus was a light square spot (one of typical stimuli used in stationary discrimination tasks in our laboratory) located in the middle of the bottom of the gate. The size of the spot was 3 x 3 cm which corresponded to 2.3° x 2.3° of visual angle at the moment of cat's release from the start compartment. The moving stimulus was this spot moving downward or upward at 7 cm/s across the middle of a gate. This speed thus corresponded to 5.4°/s at the cat's start and to about 70°/s when the cat was near a gate. When the spot disappeared at the bottom or at the top of a gate, it simultaneously appeared at the opposite side. The extent of excursion was 12 cm in stages I and II and 27 cm in stages III to VIII. Thus, each movement lasted 1.7 s in stages I and II and 5.3 s in stages III to VIII. The positive stimulus was the downward moving spot in six cats (N2, N3, C3, C4, BD4, BD5) and the upward moving spot in seven cats (N1, N4, C1, C2, BD1, BD2, BD3). The stationary spot and the blank gate were negative. The spot luminance was 16 cd/m<sup>2</sup> and that of the background 4 cd/m<sup>2</sup>.

#### **Procedure**

During the first few sessions, the cats learned to push the gates and take the food. Then the proper training,

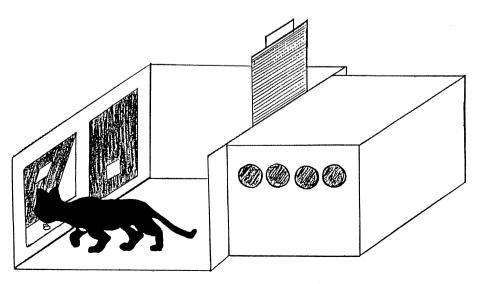


Fig. 1. The two-choice apparatus for discrimination learning. Both guillotine doors between the start compartment and the choice compartment are open but only the opaque door is seen (the translucent door is opened below the apparatus). The left lateral wall of the choice compartment is not shown. The gates are large as used in training stages III to VIII. The light spots move vertically in opposite directions as in stages V and VIII. The cat is pushing the gate with the positive stimulus and gets the meat.

TABLE I

Median numbers of sessions and errors in normal (N), control (C) and binocularly deprived (BD) cats. In successful cats the sessions and errors to criterion (including criterion sessions) and in unsuccessful cats errors during 25 sessions in stage I and during 50 sessions in stages II to VIII

	Stage number and task	Stimuli	Length of trajectory (cm)	Group	Number of cats <sup>a</sup>	Sessions	Errors	
							Initial	Repetitive
I.	Motion	upward or downward spot	12	N	4 (2)	25	128	99
	detection	versus stationary spot		C	4 (4)	25	150	115
				BD	4 (4)	25	189	150
II.	Stimulus	upward or downward spot	12	N	2	12	38	9
	detection	versus blank		C	4	21	79	41
				BD	4(1)	23	125	80
III.	Stimulus	upward or downward spot	27	N	2	17	38	13
	detection	versus blank		C	4	5	7	2
				BD	5	7	13	3
IV.	Motion	upward or downward spot	27	N	4	19	65	23
	detection	versus stationary spot		C	4	23	91	37
				BD	5 (3)	46	230	104
V.	Direction	upward	27 N	N	4(2)	?	?	?
	discrimination	versus downward spot		C	4(1)	21	61	11
		_		BD	2(2)	50	365	143
VI.	Postoperative	upward or downward spot	27	N	0			
	stimulus	versus blank		C	0			
	detection			BD	3	12	19	2
VII.	Postoperative	upward or downward spot	27	N	2	10	16	7
	motion	versus stationary spot		C	1	12	39	1
	detection			BD	5 (2)	13	128	27
VIII.	Postoperative	upward	27	N	4	9	19	3
	direction	versus downward spot		C	4(1)	6	9	0
	discrimination	<del>-</del>		BD	3 (3)	50	354	122

<sup>&</sup>lt;sup>a</sup> In parentheses numbers of cats not reaching the criterion

5 days per week, started. Each session consisted of 16 food-rewarded trials. Before each trial a piece of raw meat was located behind the gate with a positive stimulus. The left/right position of the stimuli was programmed by the computer according to the Gellermann (1933) sequences. After the experimenter opened the opaque door the cat could see the gates with the stimuli. One second later the experimenter opened the translucent door and the cat run forward and depressed one of the gates with its paw or nose. The light stimuli were terminated 3 s after pushing a gate with the positive stimulus (i.e., about end of eating) or immediately after an

error. After eating the meat or after making an error the cat either returned to the start compartment spontaneously or was pushed back by the experimenter. After an error the location of the meat remained unchanged and a rerun followed. The first error in a trial was labeled an initial error, whereas those of the reruns were called repetitive errors. The cats were allowed two repetitive errors. The third rerun was passive, i.e., the cat was pushed by hand to the gate with the positive stimulus.

We distinguished eight stages in training (Table I). However, in some cats some stages were omitted: a cat was not given a stage when it had mastered a preceding more

difficult stage or it had failed a preceding more easy stage. After a suprasylvian lesion (see below) training started in each cat with the last task mastered preoperatively.

During each stage the cats were trained to a sharp criterion of 10% or less of initial errors for 80 trials during 5 consecutive sessions. In cats not reaching the criterion, the training was terminated after 25 sessions in stage I and after 50 sessions in stages II to VIII.

#### Surgery and histology

After completing the training, the cortex of the upper parts of both banks of the middle suprasylvian gyrus was removed by aspiration under pentobarbital (Nembutal) anesthesia. Left lesions were made in 7 cats (N2, N3, C1, C2, BD1, BD2, BD5) and bilateral in 6 cats (N1, N4, C3, C4, BD3, BD4). The animals were killed 5 to 7 months after the surgery. Under overdose of pentobarbital, they were perfused by 0.9% saline followed by 10% formalin. After being embedded in paraffin, the brains were sectioned at 10 µm and stained with Nissl and Klüver-Barrera techniques.

#### RESULTS

## Movement detection training: stages I to IV

In stage I the cats were trained to detect a vertical movement of the spot: the stimuli were an upward or downward spot versus a stationary spot. The majority of cats learned poorly and so the training was terminated already after 25 sessions (Fig. 2 and Table I).

To make the task easier the cats were trained to detect a moving spot in stage II (the second gate was blank). This stage was omitted in cats N1 and N2 that were successful in stage I. One cat (BD4) failed to reach the criterion during 50 sessions in this stage. Other cats mastered the task but learned slowly.

A further attempt to make training easier was an enlargement of the trajectory of movement from 12 to 37 cm in stage III. A new cat (BD5) was added in this stage. All cats mastered the task and except one N cat (N4) and two BD cats (BD3 and BD5) they rapidly reached criterion performance.

In stage IV the cats were retrained in the motion detection task. All N and C cats mastered the task. Learning by the BD cats was much worse. Cats BD3, BD4 and BD5 failed in meeting the criterion performance and cats BD1 and BD2 reached it slowly. Differences in initial errors and in repetitive errors between the BD and N groups and between the BD and C groups were significant (Kruskal-Wallis nonparametric ANOVA test, P<0.02).

## Direction discrimination training: stage V

In stage V the cats were trained to discriminate between the upward and downward movement of the spot. Three BD cats that had failed in stage IV were not trained. Unfortunately, the data for three N cats (N2, N3, N4) were not reliable. In the period of time when these cats were trained there were ongoing and noisy repairs being made in the animal house. Although the repairs were made in the afternoons and the training in the mornings, these cats showed neurotic symptoms during training: they were hyperactive and frequently marked the apparatus. Cats BD1 and BD2 were also trained at this time but did not show such symptoms. We know (see Żernicki 1991) that BD cats are less sensitive to accidental stimuli and presumably also to noise than N cats. Training had been completed on the other cats before the repair period.

The remaining N cat (N1) and three C cats (C1, C3, C4) learned the task promptly, whereas cat C2 and both

#### **TABLE II**

Numbers of initial errors to criterion (including criterion sessions) in the first postoperative stages in normal (N), control (C) and binocularly deprived (BD) cats. The first six cats showed clear-cut retention deficits (see text)

Cat	Lesion <sup>a</sup>	Errors	Stage Number
BD1	un	128	VII
BD2	un	92	VII
N2	un	63	VII
C2	un	39	VII
BD3	bil	32	VI
N3	un	25	VIII
BD5	un	19	VI
N1	bil	12	VIII
C1	un	12	VIII
N4	bil	6	VII
C4	bil	6	VIII
C3	bil	5	VIII
BD4	bil	4	VI

<sup>&</sup>lt;sup>a</sup> Abbreviations: un, unilateral; bil, bilateral

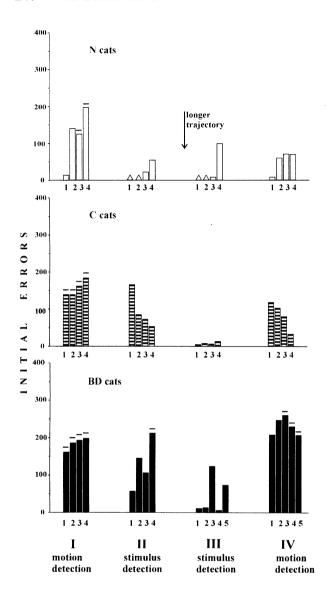


Fig. 2. Numbers of initial errors in normal (N), control (C) and binocularly deprived (BD) cats in stages I to IV. The bars denote errors to criterion (including criterion sessions), or errors during 25 sessions in stage I and during 50 sessions in stages II to IV in unsuccessful cats (dashes above the bars). The arrow indicates increase of trajectory of movement. The Arabic numbers below the bars denote the cats and the Roman ones the stages. The symbol  $\Delta$  indicates that a stage was omitted.

BD cats failed in reaching the criterion performance (Fig. 3 and Table I).

#### Postoperative training: stages VI to VIII

Unilateral or bilateral lesions of the lateral suprasylvian cortex were made following completion of training.

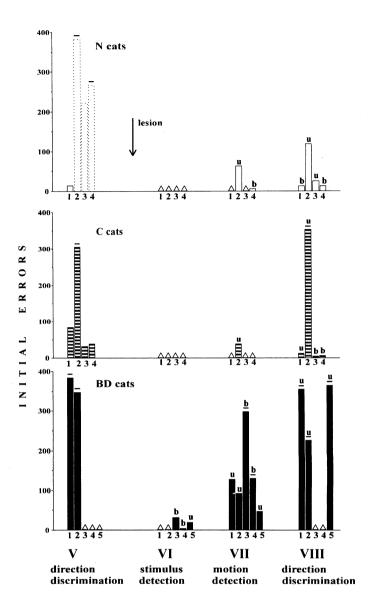


Fig. 3. Numbers of initial errors in normal (N), control (C) and binocularly deprived (BD) cats in stages V to VIII. The bars denote errors to criterion (including criterion sessions), or errors during 50 sessions in unsuccessful cats (dashes above the bars). Bars in dotted lines indicate errors in cats N2, N3 and N4 in stage V (these cats showed neurotic symptoms in this stage). The arrow represents suprasylvian lesion. The letters u and b indicate unilaterally and bilaterally lesioned cats, respectively. Other denotations as in Fig. 2.

The reconstruction of lesions showed that they were similar in all cats (Fig. 4). They included upper parts of four lateral suprasylvian visual areas: posteromedial, posterolateral, anteromedial and anterolateral, i.e., PMLS, PLLS, AMLS and ALLS areas (see Palmer et al. 1978). The lower parts of these areas were not removed due to an exaggerated care to avoid damage to the optical

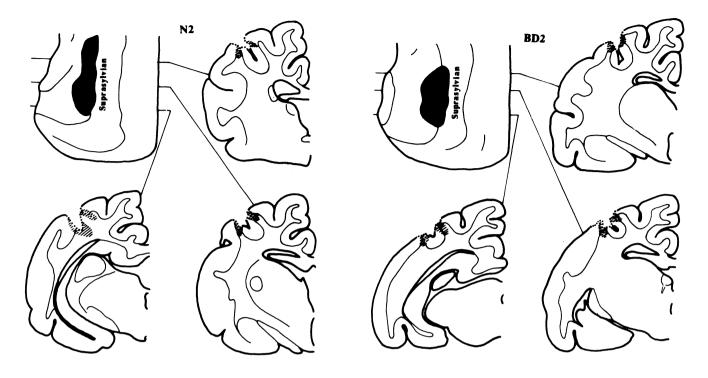


Fig. 4. The reconstruction of typical lesions (cats N2 and BD2). Solid lines indicate the extent of the lesion, dashed lines indicate the area of degeneration of fibers and loss of cells, and dotted lines indicate the extent of cell atrophy.

radiation. In all cases the crown of the suprasylvian and ectosylvian cortex, adjacent to the middle suprasylvian sulcus, was also removed.

During the second week after surgery the cats were tested in a typical perimetry apparatus described in detail by Sherman (1973). Briefly, they learned to fixate a piece of meat held in forceps and to respond to a swab of cotton-wool introduced at forceps at different guide lines during fixation of the meat. Neither unilaterally or bilaterally lesioned cats showed deficit in this test.

Discrimination retraining started two weeks after surgery. In each cat it was started with the last task that had been mastered preoperatively. We accepted arbitrarily that the postoperative performance was clearly impaired in the cats that rereached the criterion performance after minimum 24 initial errors, i.e., after 3 times more errors than allowed in preoperative 5 criterion sessions.

In stage VI, cat BD5 (operated unilaterally) and cats BD3 and BD4 (operated bilaterally) were given stimulus detection task (mastered preoperatively in stage III). Only cat BD3 required clear-cut retraining (Fig. 3 and Tables I and II).

In stage VII, cats N2, C2, BD1 and BD2 (operated unilaterally) and cat N4 (operated bilaterally) were given their first postoperative training. All cats with unilateral lesions required retraining.

Cats BD3, BD4 and BD5 continued their training in stage VII. Cats BD3 and BD4 failed in reaching the criterion performance, whereas surprisingly cat BD5 (unsuccessful in stage IV) reached the criterion.

In stage VIII, cats N3 and C1 (operated unilaterally) and cats N1, C3 and C4 (operated bilaterally) were given their first postoperative training. Only cat N3 required retraining.

Cats N2, N4, C2, BD1, BD2 and BD5 continued their training in stage VIII. Cats N2 and N4 were successful, whereas the others failed.

Altogether, six cats required a noticeable retraining in the first postoperative stage. Five of them (N2, N3, C2, BD1, BD2) had been operated unilaterally and only one (BD3) bilaterally (Table II). Such retraining was necessary in two N cats (N2, N3), one C cat (C2) and three BD cats (BD1, BD2, BD3).

#### **Reaction times**

The reaction time was measured from lifting the translucent door by the experimenter to the pushing one of the gates by a cat. The reaction times for the first runs in trials were similar in different groups and stages. In detection tasks the median reaction times in seconds for N, C and BD groups, respectively, were 1.7, 1.6 and 1.8 in stage one; 1.5, 1.4 and 1.5 in stage IV; and 1.8, 1.6 and 2.0 in stage VII. In direction task in stage VIII the reaction times were 1.7, 1.5 and 1.8. Differences between groups were insignificant (Kruskal-Wallis nonparamteric ANOVA test).

#### **DISCUSSION**

#### Slow learning in N and C cats

In the present study the N and C cats were more efficient in motion discrimination learning than in the pilot study (Żernicki and Zabłocka 1993). All methodical changes (see Introduction) were probably effective, but the increase of trajectory of movement seemed to be particularly beneficial (see stages I and IV in Fig. 2).

Nevertheless, the N and C cats still learned slowly. The learning was clearly slower than that for presumably comparably similar stimuli in brightness, grating, figure and object discriminations studied in our laboratory (see Introduction). Berkley et al. (1978) also found in cats that the detection learning of an oscillating light spot requires longer training than brightness discrimination. That motion discrimination is slow was also reported in rats (Hawley and Munn 1935), rabbits (Van Hof et al. 1983) and pigeons (Hodos et al. 1975).

One can assume that discrimination training can be difficult perceptually or associatively or both. In the first case, it is difficult for an animal to distinguish discriminated stimuli and so to elaborate for them hypothetical separate perceptual assemblies. In the latter, it is difficult to elaborate associations between these assemblies and a drive center and a center for an instrumental response.

First, the perceptual factor will be discussed. Our stimuli were certainly not very similar and were intense and so in these aspects easy to distinguish. However, the problem of their velocity, low at the cat's start, should be considered. On the one hand, in the cat the following reflex shows considerable adequacy when the velocity of a stimulus is from 5 to 30°/s (Dreher and Żernicki 1969, Michalski et al. 1977). Moreover, Berkley et al. (1978) found that in cats motion detection learning is slow even when the spot's velocity is 200°/s. On the other hand, these authors showed that in cats the threshold for detection of spot motion was from 1°/s to 6°/s and Vandenbussche et al. (1986) found that in cats learning is best when dis-

criminated velocities are between 25 and 60°/s. In addition, our current study on direction discrimination of random dot patterns indicates that C cats learn more rapidly when velocity of stimuli is 20°/s than 7°/s. Thus, it is possible that our N and C cats would distinguish better the stimuli of higher velocity, but it is rather unlikely that velocity factor would be fully responsible for their slow learning.

Thus, the associative factor should be considered. Interestingly, the training was not more rapid when the positive stimulus moved downward (cats N2, N3, C3, C4, BD4, BD5), i.e. when it was directed toward the reward, and so the task could be associatively easier. However, another factor might be important. Movement discriminations are always trained in an apparatus known to be suitable for discrimination of stationary stimuli. In such apparatus a moving stimulus always signals a stationary reward. Using a moving reward would make movement discrimination training certainly more natural and possibly easier.

In conclusion, the relatively low velocity of stimuli (perceptual factor) and the possibly difficult association of a moving stimulus with the stationary reward (associative factor) might jointly slow down learning in N and C cats.

As in the pilot study (Żernicki and Zabłocka 1993), the C cats did not show any clear deficit as compared with N cats. Thus, impoverished sensory environment and limited utilization of sensory stimuli did not appear essentially to impair a mechanism of motion discrimination in C cats. This is consistent with good discrimination learning of stationary stimuli in C cats (for reviews see Żernicki 1991, 1993). Interestingly, however, C cats show clear-cut deficits in other tests, in particular, they are dramatically impaired in delayed response learning (Ławicka1989, Stasiak and Żernicki 1991).

## Impairment of learning in BD cats

Our results show that early visual deprivation impairs motion discrimination learning. In other words, a mechanism for such learning is not fully developed in BD cats. The present result is consistent with the previous data on discrimination learning (Riesen and Aarons 1959, Żernicki and Zabłocka 1993) and with data showing deficits in contrast training for direction discrimination in strobereared cats (Pasternak and Leinen 1986, Pasternak 1987)

Numerous data on discrimination of stationary stimuli (see Introduction) strongly suggest that it is impaired in

BD cats when not easy even for N and C cats. Available data suggest that the same may be true for motion discrimination. Our tasks were indeed difficult for N and C cats, and in strobe-reared cats, Pasternak and Leinen (1986) and Pasternak (1987) found a deficit for direction and speed of grating discriminations only when of low contrast, i.e. when the tasks were difficult perceptually.

Single-cell recordings indicate that a system for direction analysis is severely impaired in BD cats. Rearing with sutured eyelids (Wickelgren-Gordon Hoffmann and Sherman 1975, Watkins et al. 1978, Spear et al. 1983), in masks (Dec et al. 1976, Michalski et al. 1983), in darkness (Flandrin and Jeannerod 1975, Cynader et al. 1976) and in stroboscopically illuminated environment (Olson and Pettigrew 1974, Cynader and Chernenko 1976, Flandrin et al. 1976, Kennedy and Orban 1983, Pasternak et al. 1985, Spear et al. 1985) are all effective. The direction selectivity impairment of cell responses is severely affected in visual area 17 (Olson and Pettigrew 1974, Cynader and Chernenko 1976, Cynader et al. 1976, Watkins et al. 1978, Kennedy and Orban 1983, Michalski et al. 1983, Pasternak 1985). Some impairment was also found in visual area 18 (Kennedy and Orban 1983), in the lateral suprasylvian visual cortex (Spear et al. 1983, Spear et al. 1985) and in the superior colliculi (Wickelgren-Gordon 1972, Flandrin and Jeannerod 1975, Hoffmann and Sherman 1975, Dec et al. 1976, Flandrin et al. 1976). Such extensive impairment may certainly affect perception itself and consequently the perceptual learning in BD cats.

In addition, Kossut et al. (1978) found that the ocular following reflex is less adequate in BD cats. This may contribute to the impairment of motion discrimination learning in these animals.

#### The effects of lesions

Our results suggest that unilateral suprasylvian lesions are more effective for producing retention deficit. This is consistent with recent data (Żernicki and Stasiak 1996) that in cats unilateral suprasylvian lesions are more effective than bilateral for producing visual neglect (the effect possibly due to a process of disinhibition occurring in the superior colliculi). However, those observations were made in acute experiments pretrigeminal preparations), whereas in the present study the cats were normal in perimetry when tested one week after surgery. Thus, the visual neglect after lateral suprasylvian lesions seems to be only transient. In fact, Spear et al. (1983) found no deficit in the perimetry 4 weeks after suprasylvian lesions and Hardy and Stein (1988) 1-2 weeks after surgery. However, interestingly Hardy and Stein found a deficit when the cats were required not only to orient to the stimulus but also run to it.

Lesion effects certainly can depend on visual stimuli used in discrimination training. Pasternak et al. (1989) found no deficit in postoperative retention in grating motion detection and grating direction discrimination after lesions of the medial bank of the middle suprasylvian sulcus in cats. Moreover, Krüger et al. (1993) found in cats that performance of figure direction discrimination was even improved after large suprasylvian lesions, the effect possibly simply due to a postoperative training. On the other hand, Pasternak et al. (1989) found that speed discrimination is impaired in suprasylvian cats. Furthermore, Krüger et al. (1993) found postoperative impairment in direction discrimination when figures moved against structural background or vice versa the structural background moved against stationary figures. Using reversible inactivation of middle suprasylvian cortex, Lomber et al. (1996) confirmed this result for stationary figures moving against structural background. These results suggest that suprasylvian cortex is important for perceptually complex discrimination tasks.

It is probable that larger lesions, including regions representing central vision in the lateral suprasylvian cortex (see Palmer et al. 1978), would be more effective. Krüger's et al. (1993) results suggest indeed that the extent of the lateral suprasylvian lesions is important for affecting direction discrimination. On the other hand, Hardy and Stein (1988) found that even very small suprasylvian lesions can affect the ocular fixation reflex.

Surprisingly our results did not show any clear-cut differences in the retention deficits between N, C and BD cats.

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#### REFERENCES

Baumann T. P., Spear P. D. (1977) Role of the lateral suprasylvian visual area in behavioral recovery from effects of visual cortex damage in cats. Brain Res. 138: 445-468.

- Berkley M. A., Warmath D. S., Tunkl J. E. (1978) Movement discrimination capacities in the cat. J. Comp. Physiol. Psychol. 92: 463-473.
- Cynader M., Berman N., Hein A. (1976) Recovery of function in cat visual cortex following prolonged visual deprivation. Exp. Brain Res. 25: 139-156.
- Cynader M., Chernenko G. (1976) Abolition of direction selectivity in the visual, cortex of the cat. Science 193: 504-505.
- Dec K., Sarna M., Tarnecki R., Żernicki B. (1976) Effects of binocular deprivation of pattern vision on single unit responses in the cat superior colliculus. Acta Biol. Exp. 36: 687-692.
- Dreher B., Żernicki B. (1969) Visual fixation reflex: behavioral properties and neural mechanism. Acta Neurobiol. Exp. 29: 359-383.
- Flandrin J. M., Jeannerod M. (1975) Superior colliculus: environmental influences on the development of directional responses in the kitten. Brain Res. 89: 348-352.
- Flandrin J. M., Kennedy H., Amblard B. (1976) Effects of stroboscopic rearing on the binocularity and directionality of cat superior colliculus neurons. Brain Res. 101: 576-581.
- Ganz L., Hirsch H. V. B., Tieman S. B. (1972) The nature of perceptual deficits in visually deprived cats. Brain Res. 44: 547-568.
- Gellermann L. W. (1933) Chance orders of alternating stimuli in visual discrimination experiments. J. Genet. Psychol. 42: 206-228.
- Hardy S.C., Stein B. E. (1988) Small lateral suprasylvian cortex lesions produce visual neglect and decreased visual activity in the superior colliculus. J. Comp. Neurol. 273: 527-542.
- Hawley J. M., Munn N. L. (1935) Visual discrimination of movement by white rats. J. Comp. Psychol. 16: 137-142.
- Hodos W., Smith L., Bonbright Jr. J.C. (1975) Detection of the velocity of movement of visual stimuli by pigeons. J. Exp. Anal. Behav. 25: 143-156.
- Hoffmann K.-P., Sherman S. M. (1975) Effect of early binocular deprivation on visual input to cat superior colliculus. J. Neurophysiol. 38: 1049-1059.
- Kennedy H., Orban G. A. (1983) Response properties of visual cortical neurons in cats reared in stroboscopic illumination. J. Neurophysiol. 49: 686-704.
- Kossut M., Michalski A., Żernicki B. (1978) The ocular following reflex in cats deprived of pattern vision from birth. Brain Res. 141: 77-87.
- Krüger K., Kiefer W., Groh A., Dinse H. R., Von Seelen W. (1993) The role of the lateral suprasylvian visual cortex of the cat in object-background interactions: permanent deficits following lesions. Exp. Brain Res. 97: 40-60.
- Ławicka W. (1989) Delayed response to light stimuli in binocularly deprived cats. Acta Neurobiol. Exp. 49: 73-92.
- Lomber S. G., Payne B. R., Cornwell P., Long K. L. (1996) Perceptual and cognitive visual functions of parietal and temporal cortices in the cat. Cereb. Cortex 6: 673-695.

- Michalski A., Kossut M., Turlejski K., Chmielowska J. (1983) Responses of area 17 neurons in cats binocularly deprived by rearing in hood. Acta Neurobiol. Exp. 43: 263-272.
- Michalski A., Kossut M., Żernicki B. (1977) The ocular following reflex elicited from the retinal periphery in the cat. Vision Res. 17: 731-736.
- Olson C. R., Pettigrew J. D. (1974) Single units in visual cortex of kittens reared in stroboscopic illumination. Brain Res. 70: 189-204.
- Palmer L. A., Rosenquist A. C., Tusa R. J. (1978) The retinotopic organization of lateral suprasylvian visual areas in the cat. J. Comp. Neurol. 177: 237-256.
- Pasternak T. (1987) Discrimination of differences in speed and flicker rate depends on directionally selective mechanisms. Vision Res. 27: 1881-1890.
- Pasternak T., Horn K. M., Maunsell J. H. R. (1989) Deficits in speed discrimination following lesions of the lateral suprasylvian cortex in the cat. Visual Neurosci. 3: 365-375.
- Pasternak T., Leinen L. J. (1986) Pattern and motion vision in cats with selective loss of cortical directional selectivity. J.Neurosci. 6: 938-945.
- Pasternak T., Schumer R. A., Gizzi M. S., Movshon J. A. (1985) Abolition of visual cortical direction selectivity affects visual behavior in cats. Exp. Brain Res. 61: 214-217.
- Riesen A. H. (1965) Effects of early deprivation of photic stimulation. In: The biosocial basis of mental retardation (Eds. S. F. Osler and R. E. Cooke). Johns Hopkins Press, Baltimore p. 61-85.
- Riesen A. H., Aarons L. (1959) Visual movement and intensity discrimination in cats after early deprivation of pattern vision. J. Comp. Physiol. Psychol. 52: 142-149.
- Rudolph K. K., Pasternak t. (1996) Lesions in cat lateral suprasylvian cortex affect the perception of complex motion. Cereb. Cortex 6: 814-822
- Sherman S. M. (1973) Visual field defects in monocularly and binocularly deprived cats. Brain Res. 49: 25-45.
- Spear P.D. (1991) Functions of extrastriate visual cortex in non-primate species. In: Vision and visual dysfunction. The neural basis of visual function (Ed. A. Levental). Vol. 4. Macmillan, London, p. 339-370.
- Spear P. D., Miller S., Ohman L. (1983) Effects of lateral suprasylvian visual cortex lesions on visual localization, discrimination, and attention in cats. Behav. Brain Res. 10: 339-359.
- Spear P. D., Tong L., McCall M. A., Pasternak T. (1985) Developmentally induced loss of direction-selective neurons in the cat's lateral suprasylvian visual cortex. Dev. Brain Res. 20: 281-285.
- Spear P. D., Tong I., Sawyer C. (1983) Effects of binocular deprivation on responses of cells in cats lateral suprasylvian cortex. J. Neurophysiol. 49: 366-382.
- Stasiak M., Żernicki B. (1991) Delayed response learning to visual stimulus in cats. Acta Neurobiol. Exp. 62: 738-855.

- Vandenbussche E., Orban G. A., Maes H. (1986). Velocity discrimination in the cat. Vision Res. 26: 1835-1849.
- Van Hof M. W., Chow K. L., Van Der Mark F. (1983). Movement discrimination in the rabbit. Behav. Brain Res. 8: 411-
- Van Hof-Van Duin J. (1979) Development of visuomotor behaviour in normal and light-deprived cat. In: Visual handicap in children. Clinics in developmental medicine (Eds. V. Smith and J. Keen). Vol. 73. William Heinemann Medical Books, London, p. 1112-1123.
- Watkins D. W., Wilson J. R., Sherman M. (1978). Receptivefield properties of neurons in binocular and moncular segments of striate cortex in cats raised with binocular lid suture. J. Neurophysiol. 41: 322-337.
- Wickelgren-Gordon B. (1972) Some effects of visual deprivation on the cat superior colliculus. Invest. Ophthalmol. 11: 460-467.
- Yin T. C. T., Greenwood M. (1992) Visuomotor interactions in responses of neurons in the middle and lateral suprasylvian cortices of the behaving cat. Exp. Brain Res. 88: 15-32.
- Zabłocka T. (1975) Go-no go differentiation to visual stimuli in cats with different early visual experiences. Acta Neurobiol. Exp. 35: 399-402.
- Zabłocka T., Dobrzecka, C. (1986) Permanent deficit of interocular transfer in binocularly deprived cats. Acta Neurobiol. Exp. 46: 281-292.
- Zabłocka T., Konorski J., Żernicki B. (1975) Visual discrimination learning in cats with different early visual experiences. Acta Neurobiol. Exp. 35: 389-398.
- Zabłocka T. Żernicki B. (1978) Object discrimination learning in cats deprived on pattern vision from birth. Acta Neurobiol. Exp. 38: 63-70.
- Zabłocka T., Żernicki B. (1988) Binocularly deprived cats are normal in visual discrimination learning in a simple apparatus. Acta Neurobiol. Exp. 48: 215-221.

- Zabłocka T., Żernicki B. (1990) Partition between stimuli slows down greatly discrimination learning in binocularly deprived cats. Behav. Brain Res. 36: 13-19.
- Zabłocka T., Żernicki B. (1991) Brightness discrimination learning in cats is influenced by early visual deprivation. Behav. Brain Res. 44: 221-224.
- Zabłocka T., Żernicki B.(1996) Discrimination learning of grating orientation in visually deprived cats and the role of the superior colliculi. Behav. Neurosci. 110: 621-625.
- Zabłocka T., Żernicki B., Kosmal, A. (1980) Loss of cbject discrimination after ablation of the superior colliculus-pretectum in binocularly deprived cats. Behav. Brain Res. 1:
- Żernicki B. (1991) Visual discrimination learning in binocularly deprived cats: 20 years of studies in the Nencki Institute. Brain Res. Rev. 16: 1-13.
- Żernicki B. (1993) Learning deficits in lab-reared cats. Acta Neurobiol. Exp. 53: 231-236.
- Zernicki B., Stasiak M. (1994) The contralateral impairment of the orienting ocular-following reflex after lesions of the lateral suprasylvian cortex in cats. Acta Neurobiol. Exp. 54: 405-409.
- Żernicki B., Stasiak M. (1996) Visual neglect in pretrigeminal cats with lateral suprasylvian lesions. Arch. Ital. Biol. 134: 241-248.
- Żernicki B., Zabłocka T. (1993) Discrimination learning of the vertical and horizontal light spot oscillations in normal and visually deprived cats. Acta Neurobiol. Exp. 53: 563-567.
- Żernicki B. Zabłocka T. (1996) Object discrimination learning and object -pattern discrimination transfer in visually deprived cats. Behav. Brain Res. 82: 79-83

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