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THE IMPORTANCE OF THE RESPONSE FOR DISCRIMINATION LEARNING AND INTEROCULAR TRANSFER IN VISUALLY DEPRIVED CATS

by

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of the requirements for the degree of
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CHAPTER I

INTRODUCTION

In recent years, the amount of research investigating the effects of early experience on adult behavior has increased greatly. The impetus for this research has been generally ascribed to the writings of Freud (1938) and to those of Hebb (1949). For those experiments in visual perception, in particular, Hebb's influence is unquestionably outstanding. The paradigm for this type of research is a manipulation of experience early in the life of the organism followed by a test in adulthood for the effects of this early condition on some specified behavior. King (1958) has pointed out the methodological considerations of this type of research.

Many investigators have suggested that early experience is not only important, but also more important than similar experience occurring later in life. To account for this phenomenon, various mechanisms have been proposed including: (a) primacy and perseverance of early learning (Beach & Jaynes, 1954; Thompson & Schaefer, 1961); (b) ease of producing changes in the young organism (Thompson & Schaefer, 1961); (c) critical periods of development (Beach, 1954; Beach & Jaynes, 1954; Thompson & Schaefer, 1961); and (d) intense drives in

infancy which greatly reinforce responses (Beach & Jaynes, 1954). In addition, several explanations have been offered for the deleterious effects of early deprivation. Maadi and Fiske (1961) suggested that early restriction precludes the occurrence of critical experiences. Riesen (1961b) identified these critical experiences as the concurrence of two types of events necessary for the development of adult perceptual abilities: (a) sensory-sensory, (b) sensory-motor, (c) motor-sensory, and (d) motor-motor. It has also been suggested that deprivation keeps arousal at a low level so that possibilities for learning are reduced (Maadi & Fiske, 1961; Thompson, 1955).

One method of studying the effects of early experience is that of early deprivation. This method represents an attempt to determine what, if any, experience is needed for the normal development of particular adult behaviors. When such deprivation experiments involve the visual system, the early deprivation often consists of rearing the experimental animals in darkness, usually with interpolated sessions of light stimulation. Sometimes, chronic diffuse-light stimulation is used. The deprivation period generally begins at or shortly after birth

and continues throughout the duration of the experiment, typically into early adulthood.

But the deprivation method does not provide a pure analysis of the effects of normal early experience *per se*. Deprivation, when begun at birth, not only imposes an unusual type of early experience on the organism, but it also prevents specific types of usual early experience. The effects of specific early experiences are confounded, therefore, with the absence of certain types of early experience. This being the case, experiments using the early deprivation technique have usually had to settle for simply separating behaviors into the categories of innate or learned. In those investigations in which adult performance is retarded as a function of the early visual deprivation, it is usually concluded that the behavior in question is learned in some way through early visual experience. If no adult retardation occurs, the behavior under study is usually interpreted as being innate in so far as visual support is involved.

For example, Hebb (1949) claimed that pattern perception must be learned. He argued that "phase sequences" --learned, central nervous system traces--must be built up slowly through visual experience before pattern or shape

discrimination can occur in its adult form. Experiments in which visually deprived animals are slower than normal controls in learning a pattern discrimination problem have been regarded as a confirmation of this hypothesis (e.g., Chow & Nissen, 1955).

Such experimental findings, however, could also be explained on the basis of other kinds of effects of visual deprivation. For example, it is possible that the visual deprivation produces peripheral neurological and/or ophthalmological changes to the receptor apparatus which visually handicap the experimental animals. "While it might be convenient for psychological theory for sensory deprivation to produce changes limited to central neural structures, it is not convenient, perhaps, for the nervous system itself to make such a distinction" (Weiskrantz, 1958, p. 1050). This peripheral hypothesis can be refuted if visually deprived animals which have developed the peripheral changes in question are able nevertheless to learn a particular discrimination as rapidly as normal controls.

A third hypothesis is that visual deprivation may preclude the normal development of optic reflexes, reflex visuo-motor coordination, or visual mediation of the motor aspect of the learned discriminatory response. The role

of such motoric factors can be evaluated by testing perceptually deprived animals on perceptual tasks that vary in terms of response requirements.

Although these three hypotheses are not mutualy exclusive, it is possible that any one of them could explain fully the behavioral differences between the deprived animals and the normal controls. If either of the latter two possibilities is responsible for the behavioral deficiency of deprived animals, their sensory, perceptual processes could well be intact and, thus, presumably innate.

A start in evaluating these three hypotheses can be made by presenting data from various studies concerned with early visual deprivation in animals. First, findings concerned with peripheral change and optic and visuomotor reflexes will be discussed. These findings will serve as a brief review of such specific effects of visual deprivation and, more importantly, will serve as a context within which to evaluate finally the results of studies concerned more generally with the larger question of the effect of visual deprivation on the ability to master tasks of visual discrimination.

Effects of Visual Deprivation on the Peripheral Visual System

Intraocular Abnormalities

Ophthalmoscopic investigations have uncovered intraocular abnormalities in various species as a result of visual deprivation. The anomalies appear to be more severe in "higher" animals, varying from partial "opacity of the fluid media of the eyes" in birds (Siegel, 1953a), to abnormal development of the pigment in the stroma of the iris in chickens (Tucker, 1957), to paling of the optic disc in chimpanzees (Chow & Nissen, 1955; Riesen, 1960). Surprisingly, rats (McAllister, 1955; Nealy & Edwards, 1960) and cats (Riesen, 1960; Riesen & Aarons, 1959) are not reported to manifest such gross ophthalmoscopic changes as a function of dark-rearing.

These anomalies have resulted from various types of visual deprivation: rearing in total darkness, in darkness with interpolated sessions of diffuse- or patterned-light stimulation, and with chronic, diffuse-light stimulation. It does appear that with chimpanzees, however, the severity of intraocular abnormalities was related to the duration and the severity of the visual deprivation (Chow & Nissen, 1955; Riesen, 1960).

Cytochemical Changes

In several species, dark-rearing caused a reduction of ribonucleic acid (RNA) in the peripheral visual system. Such a reduction was observed in the retinal ganglion cells of rats (Riesen, 1960) and chimpanzees (Riesen, 1960) and in the receptor, bipolar, and retinal ganglion cells of cats (Rasch, Riesen, & Chow, 1959; Riesen, 1960). This RNA diminution occurred in cats even when periods of light stimulation were administered during the dark-rearing (Riesen, 1960).

In addition, the retinal cells of dark-reared cats had a reduced nucleolar volume and an irregular dispersion of Nissl substance (Rasch et al., 1959).

Neuronal Atrophy

Improper neural development in the visual system has also been observed in visually deprived animals. For example, thinning of the inner plexiform layer of the retina was produced in dark-reared cats (Rasch et al., 1959; Riesen, 1960; Weiskrantz, 1958). Its occurrence was not precluded by interpolated sessions of patterned-light stimulation (Weiskrantz, 1958).

Neuronal atrophy caused by visual deprivation appears to be more drastic in "higher" animals. Chimpanzees, dark-reared for long time periods, suffered atrophy of the

retinal ganglion cells, correlated atrophy of the optic nerve, and transneuronal damage in the lateral geniculate nucleus (Chow, Riesen, & Newell, 1957).

Effects of Visual Deprivation on Optic Reflexes and Visuo-Motor Coordination

Spontaneous Nystagmus

Animals reared from birth in darkness or with chronic, diffuse-light stimulation often develop a nystagmic condition. This has been observed in chickens (Tucker, 1957), in cats (Riesen & Aarons, 1959; Riesen & Mellinger, 1956), in chimpanzees (Chow & Nissen, 1955; Riesen, 1958), and in postoperative, human patients who had suffered from congenital cataracts (Senden, 1960). Even when permitted intermittent periods of patterned-light stimulation, dark-reared cats (Riesen & Aarons, 1959) and Chimpanzees (Chow & Nissen, 1955) sometimes became nystagmic. If only one eye of a cat is visually deprived from birth, the normal eye (when exposed by itself) will often not be nystagmic; but, frequently, when both eyes are subsequently exposed to patterned-light stimulation, nystagmus is seen in both the normal and the deprived eye (Riesen, 1961a).

Heterotropia, Inability to Fixate Objects, and Absence of Eyeblink Response

Cats reared in total darkness sometimes displayed heterotropia (Riesen & Aarons, 1959), did not blink their eyes in response to a rapidly approaching object (Baxter, 1959), and were handicapped in fixating or visually pursuing objects (Baxter, 1959). If the dark-rearing lasted two months or more, the cats, even though given patterned-light stimulation for a month in a laboratory situation, still failed to display an eyeblink response or adequately fixate or visually pursue objects (Baxter, 1959; Riesen & Mellinger, 1956).

Dark-reared chimpanzees presented a syndrome similar to that reported for cats. Raised in total darkness or in darkness but given interpolated sessions of diffuse- or patterned-light stimulation while restrained, they developed heterotropia and failed to show an eyeblink response (Chow & Nissen, 1955; Riesen, 1958). However, one chimpanzee, dark-reared but given intermittent periods of patterned-light stimulation while free-moving, did not develop heterotropia (Riesen, 1958). In addition, chimpanzees reared in total darkness or in darkness with intermittent sessions of diffuse-light stimulation were unable to fixate or visually pursue objects (Riesen, 1958).

Visuo-motor Coordination

Animals reared in total darkness or with chronic, diffuse-light stimulation are usually handicapped in visually mediating their motor activity (Riesen, Kurke, & Mellinger, 1953; Senden, 1960; Siegel, 1953a; Tucker, 1957). These effects varied from a lack of pecking precision in chickens (Tucker, 1957) to running into barriers (Riesen et al., 1953) and being unable to step down from a 6 in. high platform (Baxter, 1959) in cats.

It is interesting to note that "Under monocular exposure the unexposed eye does not share the improvements accruing to the exposed eye" (Riesen & Mellinger, 1956, p. 519). Studies with visually deprived cats indicate that they improve gradually in visuo-motor coordination after being allowed pattern vision. It also appears that ample opportunity for motor activity is needed for this acquisition of visuo-motor coordination. Cats reared in darkness demonstrated abnormal visual placing response after only five hours of unrestricted movement in the presence of patterned-light stimulation (Riesen, 1961c). But cats which were first dark-reared and then caged for 30 days in a lighted laboratory were unable (at the end of the 30 days) to perform various tests of visuo-motor coordination (Baxter, 1959).

Discriminatory Ability in Visually Deprived Animals

This part of the review will be limited to those investigations of visual deprivation that have studied pattern discrimination, movement discrimination, or the interocular transfer of pattern discriminations, since these three topics are most relevant to the experimental part of the present work.

In each of the sections to follow, the reported research will be separated into two groups: (a) Those studies in which visually deprived animals were reported to perform as well as normal controls, and (b) Those studies in which visual deprivation resulted in a clear behavioral deficit. For each of the three behavioral categories, an attempt will be made to assess the relevance of the three hypotheses suggested above as to how visual deprivation leads to deficient performance on perceptual tasks.

Pattern Discrimination

Pattern discrimination learning as rapid as that of normal controls has been observed in several species visually deprived from birth. Chickens, reared with one eye receiving normal stimulation and the other eye exposed only to diffuse-light stimulation, normally learned a pattern discrimination problem with the diffuse-light

stimulated eye (Tucker, 1957). Rats raised in total darkness were not retarded in mastering a simple, pattern discrimination task (Woodruff, 1955). Cats (Riesen & Mellinger, 1956) as well as chimpanzees (Riesen, 1958), dark-reared but allowed short daily sessions of binocular, patterned-light stimulation, learned pattern discriminations under the condition of binocular viewing as quickly as did normal controls.

Conversely, studies using a variety of rearing and training situations have reported visually deprived animals to be retarded in the learning of pattern discriminations. Chickens (Tucker, 1957), rats, on a complex discrimination (Woodruff, 1955), and chimpanzees (Riesen, 1958), reared in total darkness, were slower than normals in learning pattern discriminations. Such retardation was also observed following rearing with chronic, diffuse-light stimulation in chickens (Tucker, 1957), birds (Siegel, 1953a), chimpanzees (Riesen, 1958), and human congenital, cataract patients (Pokrovsky, 1953; Senden, 1960). Finally, cats (Riesen et al., 1953; Riesen & Mellinger, 1956) and chimpanzees (Chow & Nissen, 1955), dark-reared but allowed intermittent sessions of patterned-light stimulation to one eye and diffuse-light stimulation to the other eye,

were slow to master pattern discrimination problems with the patterned-light eye.

There seems to be some reason to believe that the peripheral changes (discussed previously) that have been observed to be associated with visual deprivation are not sufficient to account for this retardation in pattern discrimination learning. Several species, in which these changes can be assumed to have occurred, performed as well as normal controls. For example, cats (Riesen & Mellinger, 1956) which, on the basis of other studies (Rasch et al., 1959: Weiskrantz, 1958), can be presumed to have undergone retinal RNA depletion and thinning of the inner plexiform layer of the retina were not retarded in learning a pattern discrimination task.

The third hypothesis is not, however, easy to reject. Several studies suggest that the abnormal development of optic reflexes and visuo-motor coordination by the visually deprived animals may have retarded their performance in the learning situations. That is, some of the visually deprived animals performed better than other deprived animals which were more handicapped in this respect. For example, a dark-reared chimpanzee, allowed intermittent patterned-light stimulation while freemoving, had fewer

abnormalities of optic reflexes than a chimpanzee permitted such stimulation while restrained (Riesen, 1958). The former animal was not retarded in learning a pattern discrimination problem, but the latter was. This same analysis, although not quite so compelling, applies to visuo-motor coordination in chickens (Tucker, 1957).

Of course, without a direct demonstration of the importance of optic reflexes and visuo-motor coordination in such experiments, the first hypothesis (that previous visual experience is required to build the sensory capacity for normal pattern discrimination) cannot be rejected. Woodruff's (1955) finding that dark-reared rats performed as well as normal controls on a simple, but not on a complex, pattern discrimination can perhaps be construed as a confirmation of this Hebbian hypothesis. On the other hand, it is possible that the dark-reared rats in t is study (Woodruff, 1955) had developed abnormal optic reflexes. If this were true, their ability to discriminate complex patterns might have been more severely impaired than their ability to discriminate simpler patterns. For example, a nystagmic condition might not interfere with distinguishing vertical and horizontal striations but might make it difficult to differentiate crosses and

circles. Moreover, it is true that this hypothesis is weakened by the normal performance on a pattern discrimination task by chickens with an eye exposed only to diffuse-light stimulation prior to training (Tucker, 1957).

It should be added that possible species differences in the effects of visual deprivation may be a confounding factor in such attempts to explain various behavioral processes by citing comparative data.

Movement Discrimination

Only one study exists in which visual movement discrimination was examined as a function of visual deprivation (Riesen & Aarons, 1959). The results can be succinctly summarized. Cats, dark-reared but allowed daily sessions of binocular, patterned-light stimulation while freemoving, mastered the movement discrimination problem as rapidly as normal controls. Conversely, cats dark-reared and exposed daily, while restrained, to either diffuse- or patterned-light stimulation were unable to learn the movement discrimination at all.

Obviously, the second hypothesis concerned with peripheral visual damage cannot be invoked to explain the differences. If peripheral changes did occur (which can probably be assumed), they should have affected equally

the restrained and freemoving cats which received patterned-light stimulation. But since the performance of the two groups of animals differed, this hypothesis can be rejected.

On the other hand, an explanation in terms of differences in visuo-motor coordination cannot be rejected. The cats which received patterned-light stimulation while freemoving had the opportunity to develop normal visuo-motor coordination. The cats which were restrained while getting their light experience, however, had no such opportunity. Since the training situation required such coordination, this difference in visuo-motor skill might have accounted for the observed behavioral difference. Included in this analysis is the possibility that while moving about during the training, the previously "restrained" cats were unable to distinguish externally produced from self-induced visual movement. That is, their motor activity produced a movement of the visual image across the retina (which they had not had a chance to experience previous to training), and they may have been unable to distinguish this induced movement from objective, visual movement. Certainly, such a confusion would make it difficult to discriminate objective movement of a

visual stimulus.

The hypothesis suggested by Riesen and Aarons (1959), that visual experience correlated with appropriate somesthetic and proprioceptive stimulation is a prerequisite for discriminating visual movement, is jeopardized by the foregoing analysis. The more parsimonious explanation, in terms of self-induced, visual movement, must be rejected before Riesen and Aarons' hypothesis, by itself, can be accepted.

Interocular Transfer of Pattern Discrimination

There are several studies in which visually deprived animals achieved successful interocular transfer. Chickens (Tucker, 1957), reared with one eye receiving normal patterned-light and the other only diffuse-light stimulation, demonstrated good transfer regardless of which eye was trained and which eye was tested. (Tucker reported that the chickens trained with the patterned-light eye did not display immediate transfer. The data, though, seem to argue otherwise. Their mean transfer score was 86%, and 6 of the 10 chickens in this group surpassed the training criterion of 90% correct choice.) Furthermore, cats (Riesen & Mellinger, 1956) and chimpanzees (Chow & Nissen, 1955), dark-reared but allowed alternating periods

of monocular stimulation with patterned light, displayed immediate interocular transfer of a pattern discrimination.

Conversely, a number of investigations with visually deprived animals did not find immediate interocular transfer. Chickens (Tucker, 1957), raised in total darkness or with chronic, binocular stimulation with diffuse light, and birds (Siegel, 1953b), reared with chronic, binocular stimulation with diffuse light, failed to show immediate interocular transfer of a pattern discrimination. Also, cats (Riesen et al., 1953; Riesen & Mellinger, 1956) and chimpanzees (Chow & Nissen, 1955), dark-reared but permitted interpolated sessions of monocular, patterned-light stimulation, when trained with the patterned-light eye, did not immediately transfer pattern discriminations to the deprived eye.

The second hypothesis, that peripheral neurological and ophthalmological changes suffered by the visually deprived animals prevented interocular transfer is untenable. These changes can be assumed to have been equally distributed among animals that did and did not achieve transfer. For example, those changes should have occurred both in those cats given alternating monocular patterned-light stimulation and in those given such stimulation only to

one eye (Riesen & Mellinger, 1956). The former achieved successful interocular transfer, however, while the latter did not.

The third hypothesis, that the abnormal development of optic reflexes and visuo-motor coordination may have prevented the interocular transfer of pattern discrimination, appears to have merit. The studies in which successful transfer occurred in deprived animals appear to be those in which the eye tested for transfer was least afflicted with optic reflex and visuo-motor coordination anomalies. For example, cats (Riesen & Mellinger, 1956), dark-reared but exposed to daily periods of monocular, pattern vision alternated between the two eyes, had the opportunity to build up good visuo-motor coordination with either eye and displayed immediate transfer. But those cats (Riesen et al., 1953; Riesen & Mellinger, 1956) which experienced sessions of only monocular, pattern vision had no opportunity to develop visuo-motor coordination with the deprived eye subsequently used in transfer tests. They showed fairly severe visuo-motor incoordination, which disrupted their test behavior with the transfer eye, and failed to achieve interocular transfer. This analysis also applies to findings with chickens

(Tucker, 1957) and birds (Siegel, 1953b), but it seems to be inapplicable to those with chimpanzees (Chow & Nissen, 1955). Chimpanzees, reared in darkness and given intermittent periods of monocular, patterned-light stimulation, failed to achieve interocular transfer of a pattern discrimination with the deprived eye as the test eye (Chow & Nissen, 1955). But since one of these chimpanzees had been trained earlier on a different pattern discrimination with the deprived eye and, thus, had built up visuo-motor coordination appropriate to the task mediated by this eye, the failure to achieve interocular transfer could not have resulted from inadequate visuo-motor coordination. Abnormal optic reflexes also could not have prevented successful interocular transfer in these chimpanzees. One chimpanzee, dark-reared but exposed to daily sessions of binocular, patterned-light stimulation, showed immediate transfer of a pattern discrimination in spite of the presence of a severe nystagmus and the absence of the eye-blink response in its test eye. Therefore, either the analysis is incorrect, or the species differences regarding effects of dark-rearing, which do exist, account for the variant results.

The first hypothesis, that previous visual experience

is required to assure the interocular equivalence of a learned pattern discrimination, has been qualified by a number of experiments. Hebb's (1949) early suggestion that prior binocular experience with visual patterns is a prerequisite for transfer has not received experimental support (Chow & Nissen, 1955; McCleary & Longfellow, 1961; Riesen & Mellinger, 1956; Tucker, 1957). Moreover, it does not seem necessary for both eyes to have had monocular, patterned-light stimulation, at least in chickens (Tucker, 1957). It would seem difficult at the present time to make a comprehensive statement of what, if any previous visual experience is required for the interocular transfer of a pattern discrimination.

In summary it is clear that Hebb's emphasis of the importance of early experience for the normal development of central sensory processes stimulated an impressive series of perceptual studies. Thirteen years later, however, it is still not certain in what specific manner this early visual experience contributes to adult perceptual ability. In large part, Hebb's suggestions have been tested by visually depriving newborn experimental animals and behaviorally measuring their visual discriminatory ability at maturity. Except when various types of partial

deprivation have been employed, clear behavioral deficits have been reported with high regularity. But, along with Hebb's original rationale for his hypothesis, two alternative mechanisms have received necessary consideration as possibly accounting for some part of the deficiency at perceptual tasks noted in visually deprived animals: (a) Degenerative changes in the peripheral, visual system, and (b) Inadequate development of optic reflexes and visuo-motor coordination.

The present experimental work is concerned with the latter hypothesis as it might apply to pattern discrimination, movement discrimination, and interocular transfer in visually deprived animals. Underlying the following experimental studies is the question of whether the use of a discriminatory response, not requiring complex visuo-motor coordination, would permit efficient perceptual performance even following visual deprivation. More specifically, the discriminatory response employed is a simple, conditioned leg-flexion. This response is not only motorically simple, but it does not require visual guidance on the part of the experimental subject.

CHAPTER II

EXPERIMENT I

THE IMPORTANCE OF THE RESPONSE FOR INTEROCULAR TRANSFER IN VISUALLY DEPRIVED CATS

There has been some apparent experimental support for Hebb's (1949) suggestion that prior binocular experience with visual patterns is necessary for successful interocular transfer of a learned pattern discrimination. For example, Tucker (1957), working with chickens, demonstrated that raising experimental subjects in total darkness or with binocular experience limited to only diffuse light prohibited the occurrence of such interocular transfer. Similarly, ring doves limited to binocular diffuse-light stimulation also failed to show interocular transfer (Siegel, 1953b). Dark-reared cats (Riesen et al., 1953; Riesen & Mellinger, 1956) and dark-reared chimpanzees (Chow & Nissen, 1955), in which one eye had been allowed periods of normal pattern vision while the other eye had only diffuse-light experience, also failed to show transfer when the pattern-deprived eye was used as the test eye. So it is clear that various kinds of early perceptual deprivation can indeed interfere with an adult

animal's ability to demonstrate the capacity for interocular transfer.

On the other hand, there is now ample experimental evidence that prior binocular experience is not itself essential for the development of the ability to transfer. In fish (McCleary & Longfellow, 1961) and chickens (Tucker, 1957), in which there had been no prior chance for binocular pattern vision, immediate transfer of a learned pattern discrimination has been reported. Further, interocular transfer of a pattern discrimination has also been demonstrated in cats (Riesen & Mellinger, 1956) and chimpanzees (Chow & Nissen, 1955) who had previously been allowed only monocular pattern vision, alternated between the two eyes.

Since prior binocular experience is not necessary for transfer, the question still remains as to why the more severe forms of perceptual deprivation (total dark-rearing or previously limiting the test eye to experience with diffuse light only) have consistently led to an absence of interocular transfer along with other apparent perceptual deficiencies. The present work attempts to investigate this problem and is based on a suggestion previously made by McCleary (1960). The suggestion was

that animals deprived of all experience with pattern vision could have their alleged perceptual deficiency based on some inability to visually mediate the complex type of discriminatory response that has customarily been employed in the perceptual testing of such deprived animals. Accordingly, the present study of perceptually deprived animals, concerned with pattern discrimination and interocular transfer, employs a simple, discriminatory response --conditioned leg-flexion--that does not require visual guidance.

Method

Subjects

The experimental group for the present study consisted of five kittens from two litters born in the laboratory at the University of Michigan. The litters (A & B) numbered five and four kittens respectively at birth. Two kittens of litter A died of distemper during rearing, and two kittens of litter B were used in Experiment II. The kittens from litter A were Siamese, while those from litter B were domestic.

The control group consisted of four domestic cats

which were either young or full-grown adults. They were brought into the laboratory shortly before training began for them.

All animals were maintained on a diet of commercial cat food. In addition, the animals in the experimental group were given evaporated milk until the onset of pretraining.

Apparatus and Stimuli

The training apparatus is shown in Figure 1. The animals were trained in an oilcloth hammock which was attached to a metal frame. The hammock was constructed so that the thoracic and abdominal regions of the cat rested on a broad band of material. Its legs hung down on either side of this band and were secured with strips of cotton gauze. Its tail fitted through a short slit in the posterior extension of the hammock and could be tied with a gauze strip if the animal thrashed it excessively. The cat's head protruded through an opening in the wood frontpiece and was fixed in place by a sliding panel. A standing paneled screen with a blue-black cloth draped over it was placed in front of the hammock so that it occupied most of the S's visual field.

Tied above the joint of the right, rear leg was a

string which was attached at the other end to a plastic rod. The plastic rod was screwed down at the other end to a wooden base which in turn was secured to a heavy metal base. When the animal flexed this leg, the plastic rod struck an overhanging microswitch, completing a circuit of four 1.5-v. dry cells in series and a 6- to 8-v. light bulb mounted on the metal frame. The microswitch was mounted on a wood block which in turn was secured by screws to the heavy metal base.

A Cunningham incontinence clamp, attached just above the foot pad of the cat's right, rear leg, served as a shock clamp. On both inner surfaces of the clamp there was a layer of foam rubber with an attached zinc electrode, 0.4 in. in diameter. Electrode jelly, EKG Sol, was applied to the electrodes. The shock was produced by four 1.5-v. dry cells in series and varied by an inductorium.

While in the hammock, one or both of Ss' eyes were covered with hemispherical contact lenses[1] made of opaque black Vinylite. The lenses adhered closely to the corneal surface and completely covered the exposed eyeball. Ophthaine, an ophthalmic anesthetic solution, was always

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[1] The author is indebted to Dr. Austin M. Riesen (The University of Chicago) who supplied the contact lenses.

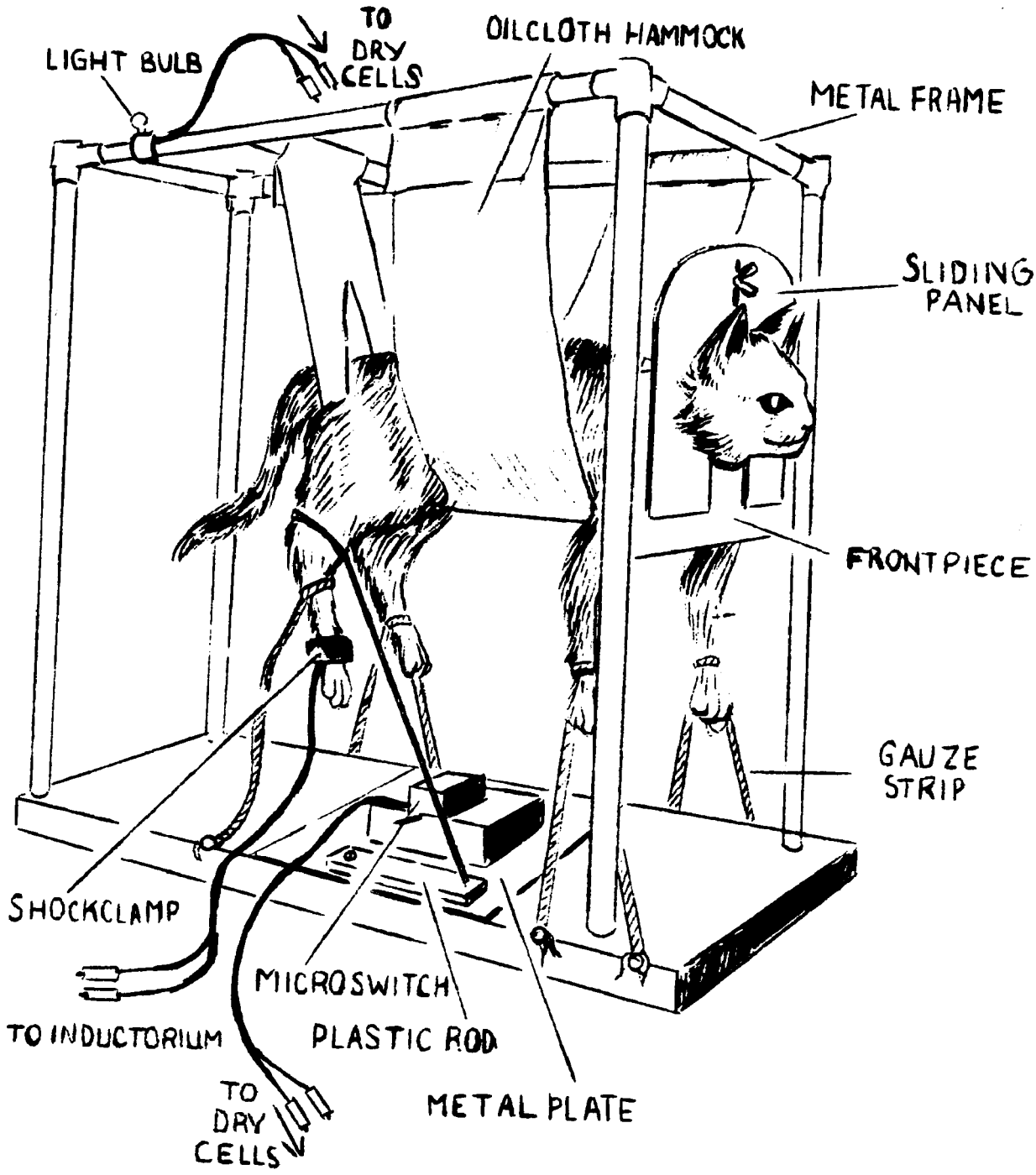


Fig. 1. Apparatus used for restraining cat during avoidance conditioning and interocular transfer tests. (See text for description.)

squirted into the eye before a contact lens was introduced. A small rubber suction cup facilitated insertion and removal of the lenses. The lenses were 0.02 in. thick and had an inner diameter of 0.68 in.

The stimuli were a cross and a circle. They were three-dimensional wooden forms and were painted silver. The arms of the cross were 3.0 in. long and 0.5 in. wide. The circle had an outer diameter of 2.7 in. and an inner diameter of 2.2 in. Both forms were 0.5 in. thick. The two stimuli were equal in area and, therefore, also in brightness. Each stimulus was mounted on the end of a thin, black wand 26 in. long.

Procedure

Rearing conditions. The kittens in the experimental group were moved into a darkroom a few days after their birth and before their eyes had opened. The two litters from which the experimental group was selected were housed with their mothers in large cages measuring 3 ft. by 3ft. by 3 ft. Each cage had a shelf along its rear wall so that ample space was provided for the animals' activity. The kittens of litter A were weaned when nine weeks old, while those of litter B were eight weeks old when weaned. When seven weeks old, the experimental Ss began receiving

binocular, visual experience for 1 hr. per day. White cotton hoods, which admitted diffuse light, were fitted onto their heads while they were in the darkroom. They were then placed in a large box in a lighted laboratory and allowed to romp. The box was specifically illuminated from 1 ft. above by a 100-w. bulb. The control animals lived in individual cages measuring 2 ft. by 2 ft. by 2 ft. They experienced the normal light-dark cycle of the laboratory.

These rearing conditions were maintained for the duration of the experiment.

Pretraining. The kittens of litter A were 35 weeks of age at the beginning of pretraining, while those of litter B were 30 weeks of age. Both the control and the experimental Ss began receiving their entire daily food ration in the experimental apparatus at intervals of 22 to 24 hrs. rather than in their home cages. Moreover, evaporated milk was deleted from the diet of the Ss in the experimental group. These feeding conditions were maintained until the termination of the experiment.

All Ss were adapted to the apparatus over a period of five days. On the first day, they were placed in the hammock, and their legs were tied fast with gauze strips.

An opaque contact lens was inserted into one eye of the control Ss so that their vision was monocular. Opaque contact lenses were inserted into both eyes of the experimental Ss, however, so that vision was prevented but feeding permitted. The shock clamp and the string attached to the plastic rod were gradually added during the five days of pretraining.

The purpose of the pretraining was to reduce the Ss' struggling in the experimental apparatus. In all cases, this was relatively successful although most Ss were restless periodically.

Tests for reflexes. On the first day of training, experimental and control Ss were tested briefly for eyelid closure in response to corneal contact and for eyelid closure in response to a pencil moved rapidly towards the eye. Both of these tests were monocular since the animals' vision in one eye was occluded by an opaque contact lens. At the termination of the experiment, the experimental and control Ss were given binocular tests for visual placing (extension of front paws onto a surface towards which the animal is being lowered). In addition, their locometery behavior on a floor surface littered with objects was observed.

Training. Monocular training on the form discrimination began on the day after the last day of pretraining. Daily sessions of 20 trials each were given at intervals of 22 to 24 hrs. Since the training was administered in a lighted laboratory, the experimental animals were light-adapted with diffuse-light stimulation for 20 min. immediately prior to each session. Extending the stimulus wands, E presented the stimuli approximately 12 in. in front of Ss. A 10 sec. stimulus interval was used. Periodically, Ss were fed a few mouthfuls at the end of the positive stimulus interval. At the outset of training, the animals were fed after every other positive stimulus presentation; but as training progressed, feedings were reduced to after every third presentation. If Ss failed to make a leg-flexion avoidance response to the negative stimulus, E delivered a brief pulse of shock at the end of the stimulus interval. The criterion for this response was a leg-flexion sufficient to make the plastic rod strike the microswitch and, thus, illuminate the light bulb. Whenever a reinforcement, either positive or negative, was delivered, the appropriate stimulus was presented for an additional second or two so that the stimulus and reinforcement events overlapped.

Both order of stimulus presentation and shock level were flexible. (The unstable and highly emotional behavior caused by shocking restrained cats necessitated this accomodation of the procedure to individual Ss.) The shock level was adjusted so that it would elicit a definite flexion response but not cause undue pain or distress. This level varied among Ss and even for the same S over time. The sequence of stimuli was adjusted to S's performance. For example, if avoidance responses were being emitted indiscriminately to both positive and negative stimulus presentations, the proportion of positive stimulus presentations was increased. In any session of 20 trials, therefore, the number of positive and negative stimulus presentations was not necessarily equal. The criterion of learning was set arbitrarily at two consecutive sessions of 85% correct performance or better. For both of these criterion sessions, there were 10 positive and 10 negative stimulus presentations. During the second of these two sessions and for all subsequent sessions, the stimuli were presented in random order, with the restriction of equal numbers of positive and negative stimulus presentations.

Interocular transfer tests. On the day following

achievement of criterion, Ss were first given five reinforced trials (two positive and three negative) with the training eye. The contact lens was then switched to the other eye, and 20 unreinforced trials were given to the transfer eye. The criterion for transfer was set at 75% correct or better. The criterion for interocular transfer was set at a lower level than that for training because the first two days of the transfer trials were run under the condition of extinction.

If Ss did not achieve criterion, they were again tested for interocular transfer on the following day; but a different procedure was used: the animals were given 20 reinforced trials with the training eye in a morning session and 20 unreinforced trials with the transfer eye in an afternoon session 4 hrs. later. (For the afternoon session, food was given before, but not during, the trials.) This temporal separation of training and transfer trials was instituted to control for any irritation caused by the rapid switching from one eye to the other of the contact lens on the first day of testing, which might have prevented the demonstration of interocular transfer.

If Ss again did not achieve criterion, they were

given a third transfer test on the following day. Once more there were morning and afternoon sessions, but on this day the trials in the afternoon with the transfer eye, as well as those in the morning with the training eye, were reinforced. This change in procedure was instituted in order to create optimal conditions for transfer at this point.

Results

Tests for Reflexes

All experimental Ss had normal corneal reflexes. Conversely, no experimental S displayed eyelid closure in response to a pencil moved rapidly towards the eye. This reflex was present in the control Ss.

Visual placing by the experimental Ss was not immediately evident at the termination of the experiment. The experimental animals displayed fear and "froze" during much of the time they were allowed to locomote on a floor surface. Nevertheless, it was still possible to observe that their behavior manifested poor visuo-motor coordination. When they did move about, they bumped into walls and objects. In attempting to step up onto raised surfaces,

they often initiated their efforts prematurely by as much as 12 in. Generally, they seemed to guide their locomotion by tactile, rather, than by visual cues.

Form Discrimination

The training data for all Ss are presented in Table 1. The experimental Ss required many more trials than the control Ss to master the form discrimination problem. There was no overlap in the two distributions of scores. The experimental Ss required a mean of 348 trials to achieve criterion, while the control Ss averaged 180 trials to criterion. As computed by the nonparametric, one-tailed randomization test (Siegel, 1956), $p=.008$ that this difference was due to chance.

Because of the flexible training procedure and the resultant possibilities for experimenter bias, conclusions concerning rate of training are somewhat equivocal. It should be pointed out, however, that the ratios of positive to negative trials for the experimental and control groups (Table 2) were not significantly different ($p=.444$; two-tailed randomization test; Siegel, 1956). It is possible, therefore, that the results on the learning of the form discrimination task are not vitiated by an experimenter bias.

The experimental animals seemed to have difficulty in fixating the stimuli on the early trials of the training. As training progressed this difficulty in fixation appeared to be overcome. Such difficulties in visual fixation have been reported before in visually deprived cats (Baxter, 1959; Riesen & Mellinger, 1956) and, presumably, are dependent on deficiencies in oculo-motor control and balance. In one experimental S (A-3, discussed below) there was sufficient oculo-motor imbalance to lead to nystagmus that was grossly evident.

Interocular Transfer

All Ss demonstrated good interocular transfer of the form discrimination (Table 1). Two of the experimental Ss and three of the control Ss displayed immediate transfer on the first day. The range of transfer scores on the first test day of the experimental group (50% to 95% correct response) and that of the control group on the same day (65% to 95% correct response) overlapped. Furthermore, the performance of the control group and of the experimental group on the first test day were not significantly different ($p = .095$; one-tailed, randomization test; Siegel, 1956).

No animal failed to transfer the form discrimination

interocularly, although one experimental S (A-3) required three days of tests before achieving criterion. Since this animal suffered from gross, spontaneous nystagmus in its transfer eye, there is some suggestion that the nystagmic condition might have impeded transfer in this animal. No systematic observations for the detection of

Table 1

Training and Interocular Transfer Data on a Pattern Discrimination Problem

Cat	Positive Stimulus	Training Eye	Trials to Meet Training Criterion[a]	Per Cent Correct Response on Interocular Transfer Test		
				1	2	3
Experimental Group						
A-1	Circle	R	320	70	90	
A-2	Cross	R	220	95		
A-3	Cross	R	360	50	60	95
B-3	Circle	L	480	50	85	
B-4	Cross	L	360	95		
Control Group						
1	Circle	R	200	65	80	
2	Cross	R	120	75		
3	Cross	L	200	95		
4	Circle	L	200	75		

[a]Two consecutive sessions of 20 trials each at 85 per cent correct performance or better. The number of trials in this column does not include the 40 trials during which criterion was achieved.

nystagmus were made in the other cats, and, therefore, no definite conclusion regarding the possible influence of nystagmus in this particular animal's performance can be made.

Table 2

Ratios of Positive to Negative Trials on a Pattern Discrimination Problem

Experimental Group		Control Group	
Cat	Ratio	Cat	Ratio
A-1	.75	1	.70
A-2	.82	2	.82
A-3	.95	3	.92
B-3	.74	4	.83
B-4	1.05		

CHAPTER III

EXPERIMENT II

THE IMPORTANCE OF THE RESPONSE FOR DISCRIMINATION OF VISUAL MOVEMENT IN VISUALLY DEPRIVED CATS

It has been suggested that previous, normal somesthetic and motor experience correlated with visual experience is needed to learn a problem of visual movement discrimination (Riesen & Aarons, 1959). In fact, dark-reared cats exposed intermittently to binocular, diffuse- or patterned-light stimulation while restrained (and, thus, denied normal somesthetic and motor experience while in the light) failed to learn such a discrimination problem; but dark-reared cats given periods of binocular, patterned-light stimulation while freemoving quickly learned this same discrimination task (Riesen & Aarons, 1959). The cats were required to perform a visually guided and motorically complex type of discriminatory response.

The present study is based on a suggestion concerning the importance of the discriminatory response previously made by McCleary (1960). It is possible that the behavioral deficiency noted above resulted from an inability to visually mediate the complex discriminatory response

rather than from an inability to discriminate visual movement. Moreover, because the discriminatory response employed by Riesen and Aarons (1959) required locomotion by the cats, both externally produced and self-induced visual movement were present in the experimental situation. Since only the animals which were restrained during their visual experience had no opportunity to perceive self-induced visual movement, their inability to learn the discrimination problem may have been due also to an inability to distinguish externally produced and self-induced visual movement.

Accordingly, the present study of perceptually deprived animals, concerned with visual movement discrimination and interocular transfer, uses a simple, discriminatory response--conditioned leg-flexion--which requires neither visual guidance nor locomotion by the subjects.

Method

Subjects

The experimental group for the present study consisted of four kittens from two litters born in the laboratory at the University of Michigan. Both litters (B and

C) numbered four kittens at birth. Two kittens of litter B were used in Experiment I, and two kittens of litter C were not used. All of the experimental animals were domestic cats.

The control group consisted of four domestic cats which were either young or full-grown adults. They were brought into the laboratory shortly before their training began.

All animals were maintained on a diet of commercial cat food. In addition, the animals of the experimental group were given evaporated milk until the onset of pre-training.

Apparatus and Stimuli

Except for one change, the training apparatus was identical to that used in Experiment I (see Figure 1). The animals were suspended in the hammock, and the same devices were used for delivery of shock and measurement of leg flexion. Opaque black Vinylite contact lenses were again used to occlude vision. The change in the apparatus was the addition to the frontpiece of a shelf to which were attached movable side panels (see Figure 2 for a similar device). The lower jaw of the cat rested on the shelf. The side panels could be moved into contact

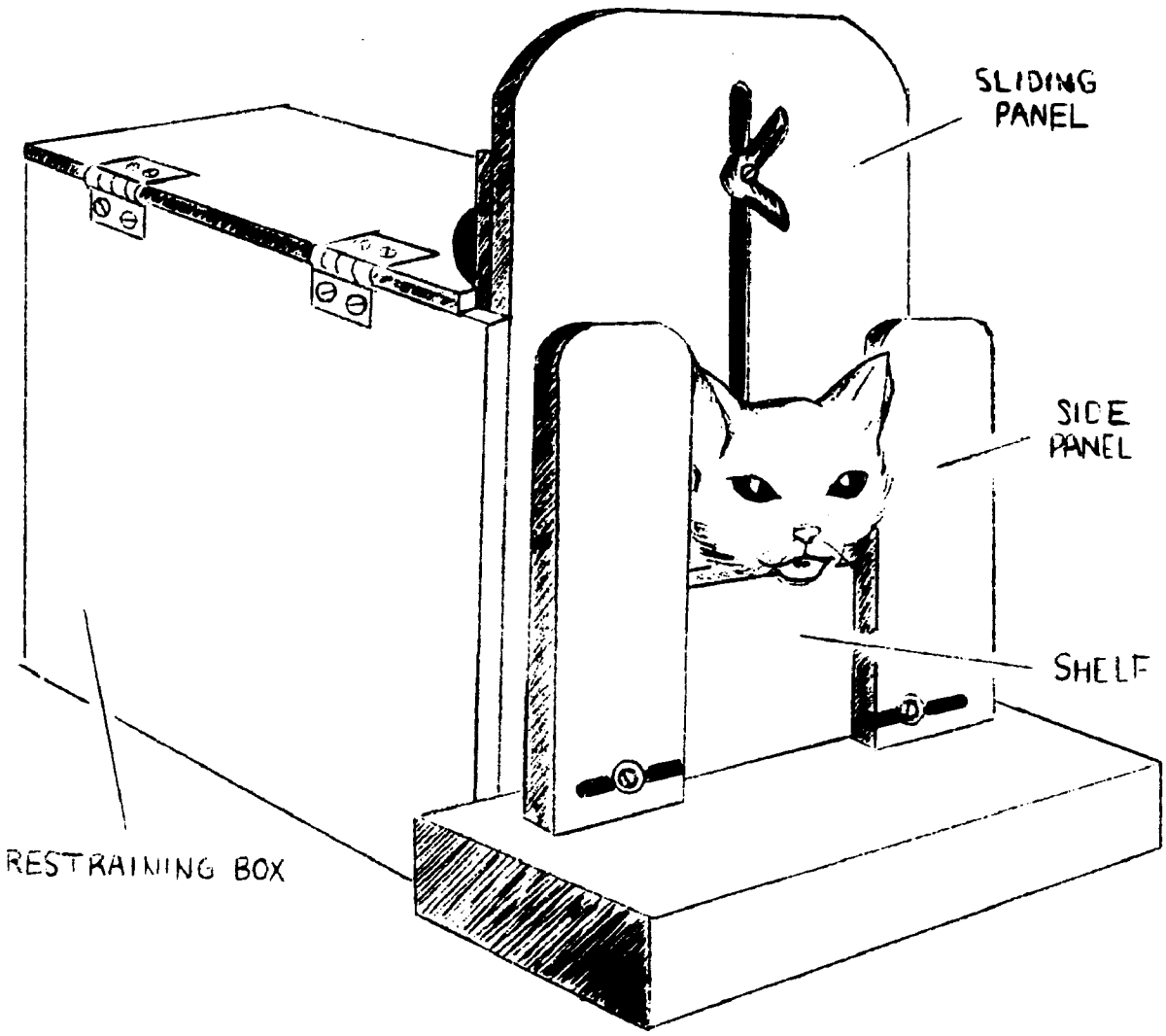


Fig. 2. Box used to restrain experimental animals during their daily periods of visual experience.

with the sides of the cat's head. In this way, head movements were restricted, although not completely eliminated.

One stimulus, the cross of Experiment I, was used.

Procedure

Rearing conditions. The kittens in the experimental group were treated in a similar fashion to the experimental Ss of Experiment I. They were moved with their mothers into a darkroom a few days after their birth and before their eyes had opened. All kittens were weaned when eight weeks old. When seven weeks old, the experimental Ss began receiving binocular, visual experience for 1 hr. per day. Fitted with black cotton hoods over their heads, they were brought into a lighted laboratory from the darkroom. They were then placed individually in rectangular boxes (Figure 2) and their hoods were removed. Each box had a hinged top and a frontpiece through which the kitten's head protruded. A sliding panel prevented their retracting their heads. Placed in front of the box was a shelf with attached side panels which limited head movements. In this way, the experimental Ss were exposed to daily sessions of binocular, patterned-light stimulation while restrained. The control animals lived in individual

cages measuring 2 ft. by 2 ft. by 2 ft. They experienced the normal light-dark cycle of the laboratory.

These rearing conditions were maintained for the duration of the experiment.

Pretraining. The kittens of litter B were 30 weeks of age at the beginning of pretraining, while those of litter C were 29 weeks of age. With one exception, pretraining proceeded exactly as in Experiment I. That is, the Ss were restrained and fed in the hammock, and, over a period of five days, experienced the addition of the shock clamp and the string attached to the plastic rod. The procedural change was that the experimental, as well as the control, Ss had vision in only one eye occluded by a contact lens.

Training. Monocular training on the movement discrimination problem began on the day after the last day of pretraining. Training was identical to that of Experiment I except for two differences. First, the experimental Ss were light-adapted while in the restraining box with patterned-light stimulation immediately prior to each session. Secondly, although the stimulus, a cross, was again extended by E to approximately 12 in. in front of Ss and for a 10 sec. interval, it was presented in one

of two ways: either stationary or rotating counterclockwise at a speed of 0.5 cps. For half of the Ss the rotating stimulus was the positive stimulus, while the stationary stimulus was the positive stimulus for the remaining Ss. The criterion of learning, 85% correct performance or better, was the same as that used in Experiment I.

Interocular transfer test. On the day following achievement of criterion, Ss were first given 20 reinforced trials with the training eye in a morning session. In an afternoon session 4 hrs. later, they were given 20 unreinforced trials with the transfer eye. During both of these sessions, the stimuli were presented in random order, with the restriction of equal numbers of positive and negative stimulus presentations. The criterion for transfer was set at 75% correct performance or better.

Tests for reflexes. Immediately following the test for interocular transfer, all Ss were tested binocularly for the visual placing response. In addition, their locomotory behavior on a floor surface littered with objects was observed.

Results

Movement Discrimination

The training data for all Ss are presented in Table 3. The experimental Ss actually required fewer trials to achieve criterion than did the control Ss. The experimental Ss had a mean of 75 trials to criterion, while the control Ss had a mean of 150 trials. This difference was not significant ($p=.229$), however, as computed by the two-tailed, randomization test (Siegel, 1956).

Again, conclusions on rates of learning are somewhat equivocal because of the flexible training procedure and the resultant possibility of experimenter bias. It is important to note, though, that the ratios of positive to negative trials for the experimental and control groups (Table 4) did not differ significantly ($p=.600$; two-tailed, randomization test: Siegel, 1956). It may be, therefore, that the rates of training on the movement discrimination problem are not confounded by an experimenter bias.

Interocular Transfer

All Ss demonstrated immediate interocular transfer (Table 3). Although the experimental Ss were slightly superior also on the transfer test, the difference was

Table 3

Training and Interocular Transfer Data on a Movement Discrimination Problem

Cat	Positive Stimulus	Training Eye	Trials to Meet Training Criterion[a]	Per Cent Correct Response on Interocular Transfer Test
		Experimental Group		
B-1	Stationary	R	80	100
B-2	Moving	L	40	95
C-1	Moving	L	160	90
C-2	Stationary	R	60	90
		Control Group		
1	Stationary	R	160	95
2	Moving	L	40	95
3	Moving	L	360	85
4	Stationary	R	40	85

[a]Two consecutive sessions of 20 trials each at 85 per cent correct performance or better. The number of trials in this column does not include the 40 trials during which criterion was achieved.

not significant ($p=.371$; two-tailed, randomization test; Siegel, 1956).

Tests for Reflexes

While visual placing was immediately present in the control Ss, this was not the case with the experimental Ss. When put on a floor surface, they did not move about very much. What locomotion they did attempt, however,

demonstrated visuo-motor incoordination. They frequently collided with walls and objects.

Table 4

Ratios of Positive to Negative Trials on a Movement Discrimination Problem

Experimental Group		Control Group	
Cat	Ratio	Cat	Ratio
B-1	.97	1	.92
B-2	.90	2	.95
C-1	1.13	3	1.09
C-2	.96	4	.86

CHAPTER IV

DISCUSSION AND SUMMARY

The data of Experiments I and II on optic reflexes and visuo-motor coordination demonstrate that the dark-reared kittens were handicapped as a result of the visual deprivation. They did not blink their eyes in response to a rapidly approaching pencil. They did not manifest the visual placing response and had difficulty in visually mediating their locomotion. These observations are in accord with those generally reported for dark-reared cats (Baxter, 1959; Riesen, 1961b; Riesen & Aarons, 1959; Riesen et al., 1953; Riesen & Mellinger, 1956).

The presence of this visuo-motor incoordination makes apparent the necessity of using a response measure not dependent on such coordination, when studying sensory capacities in the dark-reared cat. Either an autonomic response or a motor response not visually guided should be employed.

The results on the form discrimination problem of Experiment I show that the experimental Ss required more trials than the control Ss to be trained to criterion.

These results are consonant with those with visually-deprived chickens (Tucker, 1957), ring doves (Siegel, 1953a), rats (Woodruff, 1955), cats (Riesen et al., 1953; Riesen & Mellinger, 1956), chimpanzees (Chow & Nissen, 1955; Riesen, 1958), and humans (Pokrovsky, 1953; Senden, 1960). Unlike the dark-reared cats in previous studies of pattern discrimination (Riesen et al., 1953; Riesen & Mellinger, 1956), the experimental Ss in the present study experienced no pattern vision--and thus had no opportunity for pattern discrimination learning--previous to their training.

Before the results can be understood, several explanations must be disposed of as inadequate. First, the visuo-motor incoordination of the experimental Ss cannot account for the difference in the rates of training between them and the control Ss. Contrary to other studies with dark-reared cats (Riesen et al., 1953; Riesen & Mellinger, 1956), a simple, nonvisually-mediated response, which was felt to be independent of visuo-motor coordination, was used. The poor visuo-motor coordination observed probably did not interfere, therefore, with the performance of the discriminatory response by the experimental Ss.

Secondly, this difference probably did not result from the various peripheral neurological changes (Rasch et al., 1959; Riesen, 1960; Weiskrantz, 1958) observed in dark-reared cats. This statement is supported by the rapid mastery of a pattern discrimination problem by cats (Riesen & Mellinger, 1956), dark-reared and allowed daily sessions of binocular, patterned-light stimulation, which probably suffered similar damage. Of course, the experimental Ss in this study received daily sessions of diffuse- rather than patterned-light stimulation. This difference is probably not crucial, though, since Weiskrantz (1958) reported no difference in the thinning of the inner plexiform layer of the retina between eyes exposed to sessions of diffuse- or patterned-light stimulation.

A third possible explanation cannot be ruled out on the basis of present evidence. The experimental Ss might have been handicapped by various visual anomalies usually produced by dark-rearing. These include heterotropia and absence of fixation (Riesen & Aarons, 1959) and spontaneous nystagmus (Riesen & Aarons, 1959; Riesen & Mellinger, 1956). Since the stimuli were presented and maintained in the Ss' central field of vision in this experiment, both heterotropia and absence of fixation can probably

be discounted as critical factors. It is possible, however, that the animals were handicapped by spontaneous nystagmus. Unfortunately, systematic observations on its occurrence were not made, although it was quite apparent in one experimental animal.

Another plausible explanation for the retardation in learning of the experimental Ss is that the perception of forms "as distinctive wholes is not immediately given but slowly acquired through learning" (Hebb, 1949, p. 35). This is a central, rather than a peripheral, explanation. Thus, the experimental Ss, deprived of pattern vision prior to their training, had to undergo a relatively slow learning process in order to discriminate the two stimuli. They were then faced with the problem of learning the reinforcement contingencies associated with these stimulus events. Presumably, the control Ss were able to learn the experimental discrimination more rapidly than the dark-reared cats because they were already sophisticated in the ways of discriminating patterns.

Since an explanation of central learning processes has been invoked, it is appropriate to deal with the effect that the daily sessions of diffuse-light stimulation had on the visual cortices of the experimental Ss.

Could these sessions have provided the occassion for visual learning? Clearly, this unarticulated stimulation could not have supported pattern discrimination learning. In addition, it is interesting to note that diffuse-light stimulation evokes clear responses in cats from retinal ganglion and lateral geniculate cells but little or no response at the cortical level (Hubel, 1959; Hubel & Wiesel, 1959).

The major finding of Experiment I is that the experimental, as well as the control, Ss achieved good interocular transfer of the form discrimination problem. This finding disagrees with that of Riesen et al. (1953) in which cats deprived of previous binocular patterned vision were unable to transfer interocularly a pattern discrimination. This empirical disagreement can be explained, probably, by the behavioral method used in that experiment. Riesen et al. (1953) used a modified Yerkes-Watson discrimination apparatus, which requires a discriminatory response greatly dependent on visuo-motor coordination. If the experimental Ss did, in fact, have interocular equivalence for the sensory discrimination but not for the sensory-motor mechanisms requisite to its demonstration, interocular transfer would not have been evident. The following description of the initial behavior in the modified Yerkes-Watson box guided by the deprived, transfer

eye of dark-reared cats which had received intermittently monocular, patterned-light stimulation makes this hypothesis seem plausible: "When running in the apparatus, they bumped into the walls of the box, ran into the partition separating the stimulus doors, and had difficulty finding food on the feeding platform" (Riesen & Mellinger, 1956, p. 518).

If this hypothesis (that sensory discriminations but not sensory-motor coordinations are transferred) is accepted, it explains why cats, dark-reared but exposed to daily periods of monocular, pattern vision alternated between the two eyes, did achieve successful interocular transfer of a pattern discrimination (Riesen & Mellinger, 1956). They had had opportunities to develop good visuo-motor coordination with both eyes separately. It also provides the explanation for the present study. Namely, the experimental Ss, required to perform a discriminatory response which was simple and not visually guided, were not prevented from displaying their interocular equivalence for the sensory discrimination. Indeed, McCleary (1960) demonstrated that successful interocular transfer in fish was not evident if the discriminatory response was motorically too complex.

A brief examination of neuroanatomical and neurophysiological studies may indicate a mechanism for this transfer. The lateral geniculate body, the first major structure in the optic tract, probably does not play a significant role. Crossed and uncrossed fibers of retinal origin enter different cellular laminae (Barris, 1935), while the relative paucity of interlaminar connections in this structure (O'Leary, 1940) would suggest its inability to function as the site of interocular transfer of a form discrimination.

Sectioning of the optic chiasma does not obviate the interocular transfer of a pattern discrimination in cats (Myers, 1955a; Myers, 1955b). This is to be expected, however, since single cell recordings in the visual cortex indicate minimal overlap of projection from the two retinae (Jung, 1961). Moreover, this finding with the optic chiasma (Myers, 1955a; Myers, 1955b) again demonstrated that the lateral geniculate body cannot be the locus of interocular transfer. This is because the chiasma section eliminates bilateral retinal projection to the lateral geniculate bodies. Conversely, transection of both the chiasma and the corpus callosum does prevent the occurence of such transfer in cats (Myers, 1955b; Myers,

1956; Sperry, Stamm, & Miner, 1956). In fact, it appears to be the posterior 20% of the corpus callosum which is crucial for the interocular transfer of a pattern discrimination in cats (Myers, 1955b). Finally, Bianki (1959) found that transection of only the corpus callosum in rabbits prevented the interocular transfer of a learned response to the onset of light.

A further question concerning the mechanism of interocular transfer is whether the transfer occurs at the time of original monocular training or at the time of testing for transfer. A study by Myers (1957) suggests that the latter alternative may be correct. He trained optic chiasma-sectioned cats monocularly on a pattern discrimination task, sectioned their corpus callosums, and then tested for interocular transfer. From the poor transfer test scores, he concluded:

> This outcome is similar to that in which there was, instead of corpus callosum section, ablation of critical cortex from the 'experienced' hemisphere following training...Furthermore the loss of ability to perform the...discrimination with the untrained eye following corpus callosum section indicates that the 'experienced' hemisphere normally actively contributes to correct performance with the 'naive' hemisphere through corpus callosum interaction (p. 92).

It appears that interocular transfer occurs, at least

partially, during testing with the transfer eye.

In summary, the presence of interocular transfer in the experimental group of Experiment I adds further confirmation to previous reports which have shown prior binocular experience to be inessential for transfer. But, more importantly, this present finding suggests strongly that lack of transfer in many previous deprivation studies did not represent a perceptual deficit but, rather, resulted from response difficulties with complex discriminatory tasks.

The major finding of Experiment II concerns the perception of movement by dark-reared cats. Allowed intermittent exposures to binocular patterned-light stimulation while restrained, these cats learned to discriminate visual movement as quickly as the controls. However, the important finding is that the experimental Ss were capable of mastering a movement discrimination problem at all.

Riesen and Aarons (1959) found that dark-reared cats exposed daily to binocular, patterned-light stimulation, while restrained, were unable to learn a visual movement discrimination. They attributed this inability to perceive visual movement to a lack of somesthetic and motor experience correlated with vision. An explanation

other than inability to discriminate visual movement *per se* is possible. The experimental *Ss* which had never perceived visual movement while moving themselves might have been unable to discriminate between objective and subjective, or externally produced and self-induced, visual movement. But since the modified Yerkes-Watson discrimination apparatus was used, they were required to make such a discrimination. Later Riesen (1961b) himself suggested this alternative explanation: "It can be concluded that during locomotion toward the choice-point and to the surface onto which the stimuli were projected, these animals were unable to distinguish self-initiated from externally produced movement across the visual field" (p. 74).

The present experiment represents a confirmation of the above analysis. In fact, cats, dark-reared but given daily periods of patterned-light stimulation while restrained, can learn to discriminate objective, visual movement, *if* they are also restrained during training. The restraint during experimental training eliminates the confounding of self-induced and externally produced movement. As discussed above, it also permits the animal to display abilities otherwise masked by visuo-motor

incoordination.

Several neurophysiological studies permit interesting speculations concerning the above analysis. Cells in the cat's visual cortex are extremely sensitive to the movement and the direction of the movement of a visual stimulus (Hubel, 1959; Hubel & Wiesel, 1959). Such cortical responses are found in the restrained animal (Hubel & Wiesel, 1959). Of course, Hubel and Wiesel's cats, unlike the experimental Ss of the present study, had a history of perceiving visual movement while moving themselves. It might be reasonable to assume, however, that the perception of visual movement depends at least partially, upon the activity of these cells and that this activity is not dependent upon the previous occurence of unrestrained visual experience.

On the other hand, Grüsser and Grüsser-Cornehls (Jung, 1961) and Grüsser, Grüsser-Cornehls, and Saur (Jung, 1961) found vestibulovisual interaction for nearly all of the neurons which they sampled in the visual cortex. It is possible that vestibular modulation of activity in the visual cortex provides a basis for the perception of self-induced, visual movement and for its discrimination from externally produced, visual movement. If it is

further assumed that this is a learned mechanism, the failure of Riesen and Aarons' (1959) experimental Ss, which had not had opportunities to perceive self-induced, visual movement, to master a movement discrimination problem can be explained by their simply not having acquired this learned mechanism.

The final finding of Experiment II concerned the interocular transfer of a visual movement discrimination task. The experimental Ss achieved immediate transfer. This result was fully expected, since the experimental Ss were exposed periodically to binocular, patterned-light stimulation during rearing, a circumstance already demonstrated to be sufficient for the development of normal interocular transfer (Riesen & Aarons, 1959).

Summary

The present study consisted of two experiments designed to examine visual perceptual abilities in the visually deprived cat under test conditions that minimized the motor demands of the discriminatory response.

In Experiment I cats were trained monocularly on a form discrimination problem and then tested for interocular transfer. The experimental Ss were reared in darkness from birth. When seven weeks of age, the

experimental Ss began receiving a daily, 1 hr. session of binocular diffuse-light stimulation, which was maintained until the termination of the experiment. When 30 or 35 weeks of age, the experimental Ss began training--avoidance conditioning with a leg-flexion response--on the discrimination problem. Following mastery of the pattern discrimination task, the Ss were tested for interocular transfer. On the first day of training and on the day following transfer tests, various tests of optic reflexes and visuo-motor coordination were conducted.

The dark-reared cats showed no eyeblink response and displayed poor visuo-motor coordination. The five experimental Ss required more trials ($p=.008$) than the four control Ss to master the form discrimination problem but performed as well ($p=.095$) on interocular transfer. The difference in rates of training on the form discrimination was thought to have resulted either from anomalies of optic reflexes in the experimental Ss or from the slow progression of their initial, perceptual learning. It was proposed that the use of a simple, discriminatory response which was not visually guided had allowed the occurrence of the interocular transfer in the dark-reared cats which otherwise might have been masked by their

visuo-motor incoordination. It was suggested that the corpus callosum probably plays a crucial role in this transfer.

In Experiment II cats were trained monocularly on a visual, movement discrimination problem and then tested for interocular transfer. The experimental Ss were reared in darkness from birth. When seven weeks of age, the experimental Ss began receiving daily, while restrained, 1 hr., binocular exposures to patterned-light stimulation, which was maintained until the termination of the experiment. When 29 or 30 weeks of age, the experimental Ss began training--avoidance conditioning with a leg-flexion response--on the discrimination task. Following mastery of the discrimination problem, the Ss were tested for interocular transfer. Finally, the Ss were tested for visuo-motor coordination.

It was found that the four experimental Ss mastered the visual, movement discrimination at least as rapidly ($p=.229$) as the four control Ss. There was no difference ($p=.371$) between the experimental and control groups on interocular transfer, which was immediate for all Ss. It was concluded that cats which had never locomoted during their visual experience and displayed visuo-motor

incoordination can learn a problem of visual, movement discrimination, if they are restrained during conditioning. This experimental situation eliminates the confounding of self-induced and externally produced (objective) visual movement. Finally, a possible neurophysiological mechanism for this finding was suggested concerning cells in the visual cortex responsive to visual movement.

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