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THE EFFECTS OF EARLY EYELID OPENING ON THE DEVELOPMENT OF
INTERSENSORY RELATIONSHIPS IN THE RAT

City University of New York

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THE EFFECTS OF EARLY EYELID OPENING ON
THE DEVELOPMENT OF INTERSENSORY RELATIONSHIPS IN THE RAT

by

Patricia A. Kenny


A dissertation submitted to the Graduate
Faculty in Psychology in partial fulfill-
ment of the requirements for the degree
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1984

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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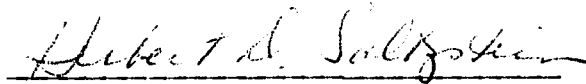
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Abstract

THE EFFECTS OF EARLY EYELID OPENING ON
THE DEVELOPMENT OF INTERSENSORY RELATIONSHIPS IN THE RAT

by

Patricia A. Kenny

Adviser: Dr. Gerald Turkewitz

The present investigation examined a theory of sensory and perceptual development which suggests that limitations on sensory functioning at early stages of development, common to most organisms to varying degrees, are beneficial to development of adaptive abilities, and that removal of those limitations would hinder sensory and/or perceptual development. As limitations on sensory functioning are particularly pronounced for altricial organisms, considerable development occurring postnatally, the effects of removing limitations on visual functioning were examined in the altricial rat pup. Normally, the rat's eyelids remain sealed for approximately two weeks after birth; for these studies, eyelids were opened surgically on Day 7. Using a matched pairs design, experimental and control groups were compared in three experiments. First, to assess the effects of early eyelid opening on an integrated behavioral response, the development of home orientation was examined. Soiled shavings were left in the corner of the home cage which had contained the nest, and shavings were removed from the other three corners. The ability of

the pups to initiate and maintain locomotion toward the home corner, and the tendency to remain there, were tested between Days 6 and 20. The homing pattern of the control pups was similar to that previously reported: a quadratic trend, showing a gradual increase, peaking at Day 14, followed by a gradual decline. The experimental pups' pattern was a linear increase in homing, reaching peak homing levels on Day 20. A second homing study examined the importance of visual cues in the observed continued increase in homing by experimental pups in Study I. Olfactory salience of the home was maintained while visual cues were reduced. The nest shavings, which visually differentiated the home in Study I, were removed for testing in Study II, while an odor-absorbent substrate remained in place. Under these conditions, homing patterns of experimental and control groups did not differ: both were quadratic trends, showing a gradual increase and a gradual decline. These results suggested that the linear increase in the experimental pattern of homing in Study I was due to the visual salience of the nest. In Part II, a visual cliff was used to examine the ontogenetic course of attention to visual vs. tactile cues in normal and early eyelid-opened pups, between Days 12 and 20 and again on Day 30. Control animals descended preferentially to the shallow side only on Day 16, the first test day following complete eyelid opening for most control animals; before

and after Day 16, the number of shallow descents did not differ significantly from the number of deep descents. Experimental animals descended preferentially to the deep side on Day 14, and by Day 20, descended preferentially to the shallow side; on all other test days, the number of shallow descents did not differ significantly from the number of deep descents. These results suggested that interpretation of visual cliff performance in young animals in terms of differential responding to the quantitative or intensity differences in the stimulation produced by the two sides (e.g., motion parallax) may be more parsimonious than an interpretation requiring the appearance and disappearance of depth avoidance. In Part III, pups whose eyelids had been opened early were tested as adults on operant discrimination tasks requiring attention to auditory and visual cues simultaneously. All animals learned the task to criterion, and experimental and control animals did not differ in rate of acquisition or final performance. It was suggested that the tasks may have been too easy and that more difficult tasks might differentiate the two groups as adults.

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Dr. Gerald Turkewitz, my dissertation adviser, has been my primary source of support and advice throughout the long years of graduate school. He seems to blend perfectly a combination of encouragement and criticism - always professional and yet also personal, providing therapy whenever I've requested it. He has always treated me as colleague, rather than student, giving me free rein in most of my pursuits; as a result, I have succeeded at some and failed in others, but have benefited immeasurably from each experience. Perhaps most important, Gerry is a treasured friend, and at last I feel able to simply enjoy that friendship.

I would like to thank my dissertation committee members, Drs. Gordon Barr, Josh Wallman, Christina Williams, and Stephen Brake, for their careful reading and very thoughtful comments and suggestions.

Dr. Robert Thompson was instrumental in this research, as all of it was done in his laboratory. Thank you, Dr. Thompson, for your patience and generosity, and also for the wisdom you've expounded on demand whenever I've requested instruction or clarification on some fine point of methodology. As the head of the program during my formative years, and later as consultant on some rather esoteric matters, you have, to a great extent, aided my progress through the program.

Damary Collado dropped out of heaven one day, offering to help me in running experiments and caring for animals. She has played a very important role in the completion of these studies as a competent and conscientious assistant, and collected much of the data reported here; she has also become a good friend. I am indebted to her.

Thank you, Stewart Riegler, for your technical assistance in designing equipment, and for rescuing me in desperate moments of equipment failure. Thank you, Alan Fried, for performing some of the more unpleasant tasks and for contributing both brain and brawn in the laboratory during my tenure there. Thank you, Suzanne Radano, for our occasional consciousness-raising, confidence-building sessions.

Thank you to my close friends and to my family: you really have been a safety net for me over these arduous years of graduate work. You've kept me sane, clothed, fed, housed, and relatively happy - in the face of great odds.

Patricia A. Kenny
March, 1984

Dedication

To my parents, Helen and William Kenny, for in some very important ways, you have contributed to my success. For as long as I can remember, you have been telling me that I could do anything, that I was capable of and expected to do the best - whatever the best was. Something in me has always believed that, and I am certain it has carried me through difficult times. Your unswerving, unconditional love has buoyed me for the past 29 years. Thank you for doing such a good job of loving me.

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"This one's going out to you, baby."

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INTRODUCTION

This investigation was prompted in part by an earlier theoretical paper (Turkewitz and Kenny, 1982), which discussed the possible adaptive importance of limitations in sensory functioning that attend early stages of development. One aspect of that work suggested that limited sensory functioning serves to reduce sensory input, and that this reduced input may decrease competition from emerging systems at critical ontogenetic stages. Evidence was cited which suggested that when the normally encountered patterns of competition between developing systems were altered (by removing or reducing a source of sensory input), perceptual development and even neural organization were altered. These effects were not limited to the altered sense system, however: the evidence suggests that modifications of sensory experience have profound intermodal, as well as intramodal consequences.

Studies of the development of sensory function have dealt primarily with intramodal phenomena, examining the effects of experience or, more usually, the absence or reduction of experience in a modality on development of function in that modality. These studies have focused primarily on the auditory and visual systems, and have indicated, to varying degrees, the importance of stimulation within a modality for subsequent normal

functioning of and/or perception in that modality (see Tees, 1976, for review).

Studies investigating intermodal aspects of the development of sensory function - the effects of modifying input to one modality on functioning or organization in another modality - are comparatively rare, however. These investigations have focused on different facets of development, including the effects of modifying input to one modality on perceptual, attentional, neurological, and biochemical development in another modality.

Observations, such as the fact that sensory systems do not become functional at the same time in development (Gottlieb, 1971), have spurred interest in possible intermodal relationships during early development, and in "...how sensory systems and their stimulation histories relate to one another" (Tees, 1976, p. 306). The sequence of functional onset is invariant, at least in those birds and mammals thus far studied; development proceeds in a proximal-to-distal direction, i.e., vestibular, tactile, olfactory, auditory, visual (Gottlieb, 1971).

Intermodal Influences on Perceptual and Attentional Development

Turkewitz, Gilbert and Birch (1974) found that reducing input from an earlier developing system led to the precocial utilization of a later developing system. They

clipped the vibrissae of kittens, thereby reducing tactile input; these kittens responded appropriately on a visual cliff at an earlier age than the control kittens, receiving normal tactile input.

Small (1978) interfered with olfactory functioning in neonatal hamsters via transection of the lateral olfactory tract or olfactory bulbectomy. These pups continued to show a thermal preference at an age when such preference has normally declined and been replaced by responsiveness to olfactory stimuli. This finding suggested that the basis for the normal transition from thermal to olfactory mediation of responsiveness is not the independent maturation of the thermal system, but rather the consequence of increasing competition from the olfactory system. That is, since eliminating competition from the olfactory system while leaving the thermal system intact prolonged thermal responsivity, it appears that competition from the emerging olfactory system is required for the normal decline in thermal mediation.

There is some evidence that during normal development in infants and young children, the availability of multimodal input may disrupt rather than enhance functioning. Rose, Gottfried, and Bridger (1978) reported that when six-month-old infants are allowed to simultaneously see and manipulate objects, there is no evidence that they subsequently recognize the object

visually, although such recognition is clearly evidenced when they are given only visual pre-exposure. Renshaw, Wherry, and Newlin (1930) reported that the ability of young children to localize a touched spot on their body surface is interfered with if they are allowed to use vision during localization. The same procedure results in improved localization in older children and adults.

There is fragmentary evidence that visually deprived organisms exhibit compensatory functioning in other senses. For example, sighted and late-blinded rats do not perform as well as rats blinded early in life on a nonspatial auditory learning task (Spigelman and Bryden, 1967). Spigelman and Bryden interpreted the inferior performance in terms of a failure to attend to the relevant auditory cues. Such compensatory functioning has been observed in humans who have been deprived of the use of one or another modality at or around birth. Instances of the highly organized use of auditory information in congenitally blind individuals have been reported, such as a congenitally blind boy being able to ride his bike through the streets of Boston by using auditory cues (Gibson, 1969).

Intermodal Influences on Neurological and Biochemical Development

Although the current investigation does not address these aspects of intersensory effects, an understanding of

them is necessary for elucidating mechanisms that may mediate the observed behavioral and perceptual changes.

Studies indicate that modification of the patterns of competition between sense systems encountered during normal development can markedly influence structural relationships. In a series of experiments, Krech, Rosenzweig, and Bennett (1963) examined the brains of visually deprived rats for anatomical and biochemical changes resulting from such deprivation. They found that dark-raised rats developed heavier somesthetic cortical areas than did control (light-raised) littermates, and that the biochemical activity of nonvisual areas of the cortex was greater than in the control animals. These effects may reflect the influence of absence of competition from the visual system on the organization of other sensory systems. In a somewhat similar vein, Gyllensten, Malmfors, and Noylin (1966) compared changes in the auditory cortex of visually deprived mice with changes in the visual cortex. They reported two primary findings: after two months in the dark, they found hypotrophy of both cortical areas, i.e., a decrease in amount of internuclear material and in the diameter of the nuclei of visual and auditory cortical cells, the decrease being much greater in the visual than in the auditory cortex. After four months, however, this hypotrophy persisted in the visual cortex and was succeeded by hypertrophy, or increased internuclear material and

nuclear diameter of cells in the auditory cortex.

Gyllensten et al. (1966) suggested that the eventual hypertrophy in the auditory cortex might be attributable to the increased use of the auditory mode by the visually deprived animal.

Cynader (1979) investigated intermodal effects on neural organization by dark-rearing cats and recording the responses of cells in the superior colliculus. In the normal cat, cells in the superficial layers of the superior colliculus are driven exclusively by visual stimuli, while cells in the intermediate and deep layers are responsive to somatic and auditory, as well as visual stimuli. As expected, following a period of dark-rearing, Cynader found a loss of directional selectivity in the superficial layers, and a shift of ocular dominance in favor of the contralateral eye; visual responses could be elicited, however, from nearly all cells encountered in these layers. However, in the deeper collicular layers, where multimodal receptivity is normally found, responses to visual stimuli were depressed while responses to auditory and tactile stimuli were not. According to Cynader, in the superficial layers of the colliculus, visual responsivity is maintained in the dark-reared animal due to the absence of competitive input. In the intermediate and deeper layers, however, visual afferents are at a "competitive disadvantage" relative to somatic and auditory inputs, and hence lose

their ability to influence cells in these layers.

Intersensory Relationships During Development

The serial development of sense systems, well-documented for many animals, may occur mainly or totally during the prenatal period (as in many precocial animals), or it may span prenatal and early postnatal life (as in altricial animals) (Gottlieb, 1971). This uneven rate of development and sequential onset of functioning of the sense systems may have consequences for the development of relationships between them. In reviewing possible types of intersensory relationships, Mendelson and Haith (1976) suggest independence between systems as one possibility, although they point out that there is no evidence for such independence in infants. Intersensory independence might, however, characterize various phases of embryogenesis, owing to the uneven rate of development of sense systems (Turkewitz and McGuire, 1978). Because of its consequences for reducing and regulating competition between emerging systems, such independence of sense systems may play an important role in the development of sensory function. Other types of relationships that might characterize emerging sense systems include facilitation: input to one system may be integrated with input from another and facilitate learning or perceptual processing within a

modality, and competition: input to one system may compete with input to another, and one system is dominant over another (Turkewitz and McGuire, 1978). These relationships might be evident on a number of levels - neuroanatomical, biochemical, or behavioral - and they might undergo ontogenetic variation, or modulate ontogenetic changes (Turkewitz and Kenny, 1982).

Transitions in Sensory Mediation of Responding

The timing of onset of function in sense systems may be a factor in determining the nature of intersensory relationships (e.g., sensory dominance hierarchies), and may shape the response systems of the organism, by determining sensory mediation of responding at different developmental stages. For example, home orientation in kittens has been shown to develop in phases: initially, prior to eyelid-opening, orientation to the home is mediated primarily by thermal and olfactory cues. When vision begins to function, there is a transition period during which olfaction and vision jointly mediate home orientation; kittens then gradually develop visual orientation to the home. Soon after the onset of visual functioning, the kittens' center of orientation shifts from the home region to the mother and littermates, and consequently, home orientation declines (Rosenblatt,

Turkewitz, and Schneirla, 1969).

Transitions in the sense systems mediating huddling in the rat have been described (Alberts, 1978; Brunjes and Alberts, 1979), the changes occurring between 10 and 15 days of age. Initially, tactile and thermal properties of siblings initiate and maintain huddling; later, olfactory characteristics become the primary stimuli.

Rosenblatt (1983) has suggested that olfaction plays a pivotal role in early development of many altricial mammals, because it mediates a critical developmental transition. Initially, neonatal responding is mediated by tactile and thermal stimuli; this responding is based on intensity or quantitative characteristics of stimulation (Schneirla, 1965). When olfaction begins to mediate responding, according to Rosenblatt (1983), the organism begins to respond to qualitative characteristics of stimuli, i.e., responding becomes based upon "stimulus meaning".

I am suggesting that, underlying the emergence of olfaction as the sense system responsible for this critical transition, and of even more fundamental importance, is the sequence of functional onset of the sense systems. This sequence, allowing as it does the sequence of response mediation, may be a determining factor in normal behavioral development; alterations in this sequence might result in aberrant development.

Modifying Early Sensory Experience

Studies involving manipulations of the sensory experience of young animals have focused primarily on some sort of deprivation, particularly of the auditory and visual systems (see Zubek, 1969, for review). Another approach has consisted mainly of subjecting the animal to excessive stimulation, e.g., continuous or abnormally bright illumination or light flashes (Paulson, 1965; Heron and Anchel, 1964; Rose and Gruenau, 1971). Because I consider the sequential onset of sensory function to be of critical importance, I have developed an approach to altering early sensory experience that involves neither deprivation nor augmentation of sensation, but a change in time when sensory information becomes available. This investigation is concerned with the effects of prematurely opening the eyelids of rat pups. Eyelid opening normally occurs between 13-15 days of age; for this investigation, eyelids were opened on postnatal Day 7.

Development of the Rat's Visual System Prior to Eyelid Opening

Of obvious concern to the present study is the question of what the rat can see, if anything, prior to the day of normal eyelid opening. Evidence from a variety of

sources indicates that the visual system of the rat is quite well-developed and functional before the eyes normally open.

It has long been known that very young rats (as young as eight-days-old) will respond to light in the same fashion as adults, i.e., they are negatively phototactic (Crozier and Pincus, 1937). To some extent, those findings have gone relatively unnoticed, as evidenced by comments such as "...this stage (birth to 12-14 days) occurs without visual stimulation, even of a diffuse kind through the eyelids" (Lund and Lund, 1972, p.16). Recently, the response of the newborn rat to light prior to normal eyelid opening has been more systematically and thoroughly examined (Routtenberg, Strop, and Jerdan, 1978). As early as Day 6, albino rats have been shown to demonstrate negative phototaxis; elimination of this response by bilateral, but not unilateral, eye enucleation has indicated the importance of retinal pathways in mediating the response. In addition, these data eliminated the possibility that the observed response was actually avoidance of the heat produced by the light source, a possibility that existed in the Crozier and Pincus study (Gottlieb, 1971).

Another line of evidence comes from investigation of the ontogenesis of evoked visual electrocortical responses. In both kittens and rats, the earliest visual evoked

responses (VERs) have been observed prior to eyelid opening: at 2-3 days in kittens and 8-10 days in rats (Rose, 1971). For rats, this early VER is not identical to the adult response, but between 10 and 15 days of age, the wave forms are modified; by 16 days of age, the obtained wave form is similar to that of the adult rat. Rose (1971) points out that this mature wave form is attained very rapidly in the rat, within 5 days after onset, in contrast to the kitten: although onset of VERs is earlier in the kitten, the mature wave form is not attained until 30 days of age.

Finally, some correlative evidence was obtained from an examination of the optic media of the experimental animals from a litter used in a pilot run of the first study. Optometric examination of these animals on postnatal Day 10 indicated that, while their optic media were not as clear as the adult rat's, they were relatively free of opacities; theoretically, at least, these rats were able to receive some patterned visual stimulation (Dr. J. Trachtman, personal communication).

Thus, the evidence indicates that, to a limited extent, the rat's visual system is able to function prior to normal eyelid opening.

In the following three studies, I have examined the effects of early availability of visual stimulation, via

early eyelid opening, on: 1) orientation to the home, or homing; 2) performance on a visual cliff; and 3) acquisition of operant discriminations by these pups as adults, requiring attention to auditory and visual cues.

GENERAL PROCEDURE

For all three studies, the rearing conditions, eyelid opening procedure, and attendant treatment and handling of the pups were identical.

Subjects

Subjects were Long-Evans hooded rats, bred in our laboratory. Cages were checked at least twice daily (morning and evening) for births; the day of birth was considered Day 1. All litters were reared in clear polypropylene cages (38.1 x 33.0 x 17.1 cm), and provided with pine shavings; Purina Rat Chow and water were continuously available. Lights were on from seven AM to seven PM, during which time all testing took place. Litters were culled to eight pups (four male, four female) within 48 hours after birth, and left undisturbed until Day 6, when they were matched for sex and weight, assigned to experimental and control groups, and marked with food coloring (McCormick) or non-toxic markers (Magic Marker) for individual identification.

Procedure

On Day 7, experimental pups and their control littermates were anesthetized in pairs, by placing in a freezer for 20 minutes. The eyelids of the experimental pups were then opened, by stretching the lids and cutting along the margin (which is quite prominent) with a scalpel.

The procedure is very simple, produces little or no bleeding, and requires about one-two minutes per pup. Antibiotic ophthalmic ointment was applied to all pups (in the eyes of experimental, on the lids of control) on Days 7-9. Experimental pups' lids were checked daily, and if they had resealed, were reopened by applying warm water and gently pulling them apart.

At all stages of the procedure, care was taken to equate as closely as possible treatment of the experimental pups with their control littermates. Thus, experimental-control pairs were anesthetized together, control pups were handled as often and in approximately the same way as their experimental littermates, and received warm water and antibiotic applications yoked with those of the experimental pups. There was, however, no attempt made to apply a control surgical procedure, as no comparable one seemed available.

HOMING

Orientation to the nest site, or homing, has been observed in several species, including rat pups (Turkewitz, 1966; Gregory and Pfaff, 1971; Altman and Sudarshan, 1975; Sczerzenie and Hsiao, 1977), kittens (Rosenblatt, Turkewitz, and Schneirla, 1969), and hamster pups (Devor and Schneider, 1974). Most studies examining homing behavior in rat pups have utilized either of two primary measures of orientation to the nest: a simple discrimination of home vs. clean nest material (Gregory and Pfaff, 1971; Sczerzenie and Hsiao, 1977), or the ability to initiate and maintain locomotion toward the nest area when displaced from the nest (Turkewitz, 1966; Johanson, Turkewitz, and Hamburgh, 1980). In this experiment, the homing behavior of rat pups was tested in the home cage in the absence of mother and littermates.

Homing was selected as my measure for several reasons. It is a relatively complex early behavior that follows a fairly consistent developmental pattern in normal pups: a gradual increase, peaking at 14-15 days, followed by a gradual decline (Turkewitz, 1966). Along with, and possibly responsible for this pattern, is a sequence of transitions in the sensory system mediating home orientation: it is initially mediated by thermal and olfactory cues, and the onset of visual functioning may be

related to the decline seen in home orientation. Finally, homing, rather than some arbitrarily selected response or set of responses, represents an adaptive pattern; investigation of developmental processes which may underlie, or at least permit such a pattern, is therefore of considerable importance.

This investigation consisted of two studies: Study I - examining homing in an essentially unmodified situation, i.e., the home retained its visual and olfactory characteristics during testing. Study II examined the role of visual cues in homing: the home retained its usual olfactory characteristics, but characteristics that identified the home visually were reduced.

Study I

Method

Subjects

A total of 36 pups (18 pairs) from five different litters were subjects in Study I. They were culled, matched, and marked, as described under General Procedure, on Day 6.

Procedure

On Day 7, eyelids of experimental pups were opened, as described under General Procedure.

Testing

Home orientation was tested on alternate days, from

Day 6 through Day 20. Prior to testing, the position of the nest in the home cage was noted, and that quadrant of the cage in which the nest was located was designated as "home". For testing, mother and pups were removed from the cage; some of the shavings were removed, and the rest were brushed into the home quadrant. Pups were tested individually, and each had three two-minute trials per test day, each trial starting from a different quadrant: the home, the adjacent corner nearest the home, and the corner diagonally opposite the home. The path of the pup was traced on a facsimile of the cage bottom, divided into four quadrants. The pup was scored as "homing" if it was in the home quadrant at the end of the two-minute trial. In addition, time of exit from the start quadrant, and exits from and entries into the home quadrant were recorded, read from a digital timer (Hunter, Model 1520). These values allowed subsequent determination of time spent in the home, latency to enter the home, and latency to leave the start quadrant.

Results

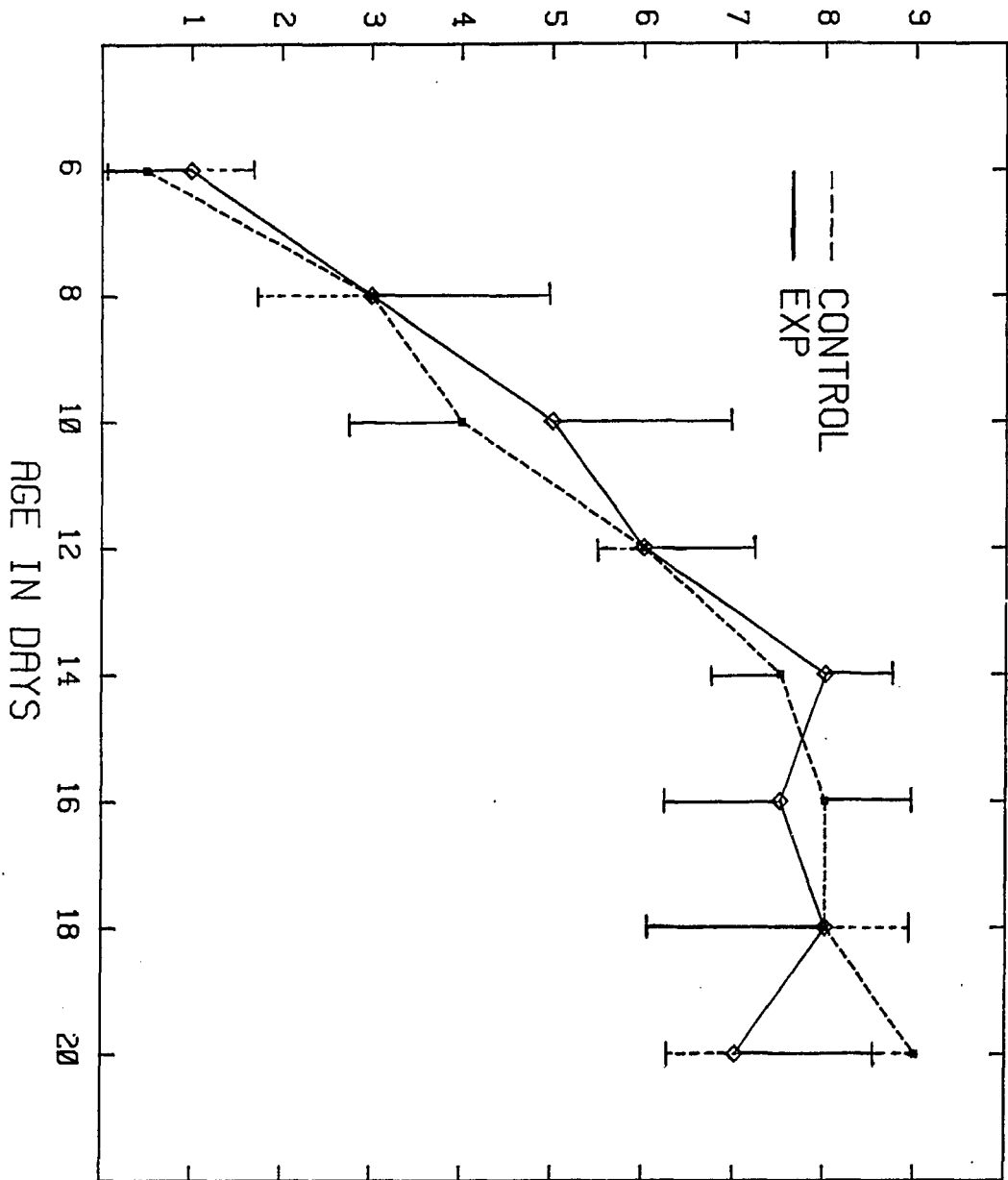
In order to determine whether experimental and control pups were similar in amount of activity during the test period, activity scores, based on the number of quadrants entered during the three trials on a test day, were computed. These data were recorded for 14 pairs of pups

only. On any trial, the maximum number of quadrants a subject could enter was three (excluding the start quadrant); on any day, therefore, the maximum number of quadrants entered by a subject was nine (three trials/day). Figure 1 presents the median activity scores for experimental and control groups as a function of age. For this measure, medians are presented for descriptive purposes, to reduce the effects of many deviant scores; means were used for statistical analysis, however. It is clear that the two groups did not differ on this measure, the number of quadrants entered increasing linearly from Day 6 through Day 20 for both experimental ($F(1,91)=98.4$, $p<.01$) and control ($F(1,91)=128.0$, $p<.01$) animals.

In that homing might be influenced not only by ability to get to the home but by attractiveness of the home as well, data were analyzed to determine whether the two groups spent equivalent amounts of time there. The proportion of each trial spent in the home quadrant was calculated as the ratio of the amount of time spent in the home to the amount of time available or remaining in that trial, once the pup reached the home quadrant. For example, if a pup took 50 seconds to enter the home on a trial starting from the diagonal or adjacent quadrant, 70 seconds remained in that trial; the proportion of that trial spent in the home was considered as the ratio of the amount of time spent in the home to 70 seconds, the time

Figure 1. Medians of activity scores of experimental and control animals as a function of age. Activity score = # of quadrants entered over three trials. Bars indicate semi-interquartile range. Medians and semi-interquartile ranges are presented in the Appendix, Table A.

MEDIAN # OF QUADRANTS ENTERED



remaining in that trial. On trials starting from the home quadrant, the amount of time available to be spent in the home was 120 seconds. The mean proportion of available time spent in the home for three trials was determined for 14 pairs of pups; the means of these values as a function of age are shown in Figure 2. Time spent in the home increased linearly with age for both experimental ($F(1,91)=51.4, p<.01$) and control ($F(1,91)=34.1, p<.01$) groups. The data for the experimental animals also exhibited a cubic component ($F(1,91)=5.86, p<.05$), indicating that the apparent increase in time spent in the home by the experimental animals on Day 20 was significant. A post-hoc analysis of the data for experimental and control animals on Day 20 confirmed this: experimental animals spent more time in the home on Day 20 than control animals ($t(df=13)=2.6, p<.05$; t-test for matched pairs, two-tailed).

In that eyelid opening usually occurs around the age at which the decline in homing exhibited by normal pups typically occurs (Turkewitz, 1966), eyelid opening may be implicated in this decline; the day of eyelid opening for the control pups was therefore noted. Figure 3 shows the day of complete bilateral eyelid opening for the control animals. In nearly every case, eyelid opening (which usually occurs gradually) had begun the day before complete opening occurred, so that patterned visual input became

Figure 2. Mean proportion of time remaining in trial spent in the home (once pup reached home) by experimental and control animals as a function of age (means of three-trial mean for each pup). Bars indicate standard errors. Means and standard errors are presented in the Appendix, Table B.

PROPORTION OF AVAILABLE TIME

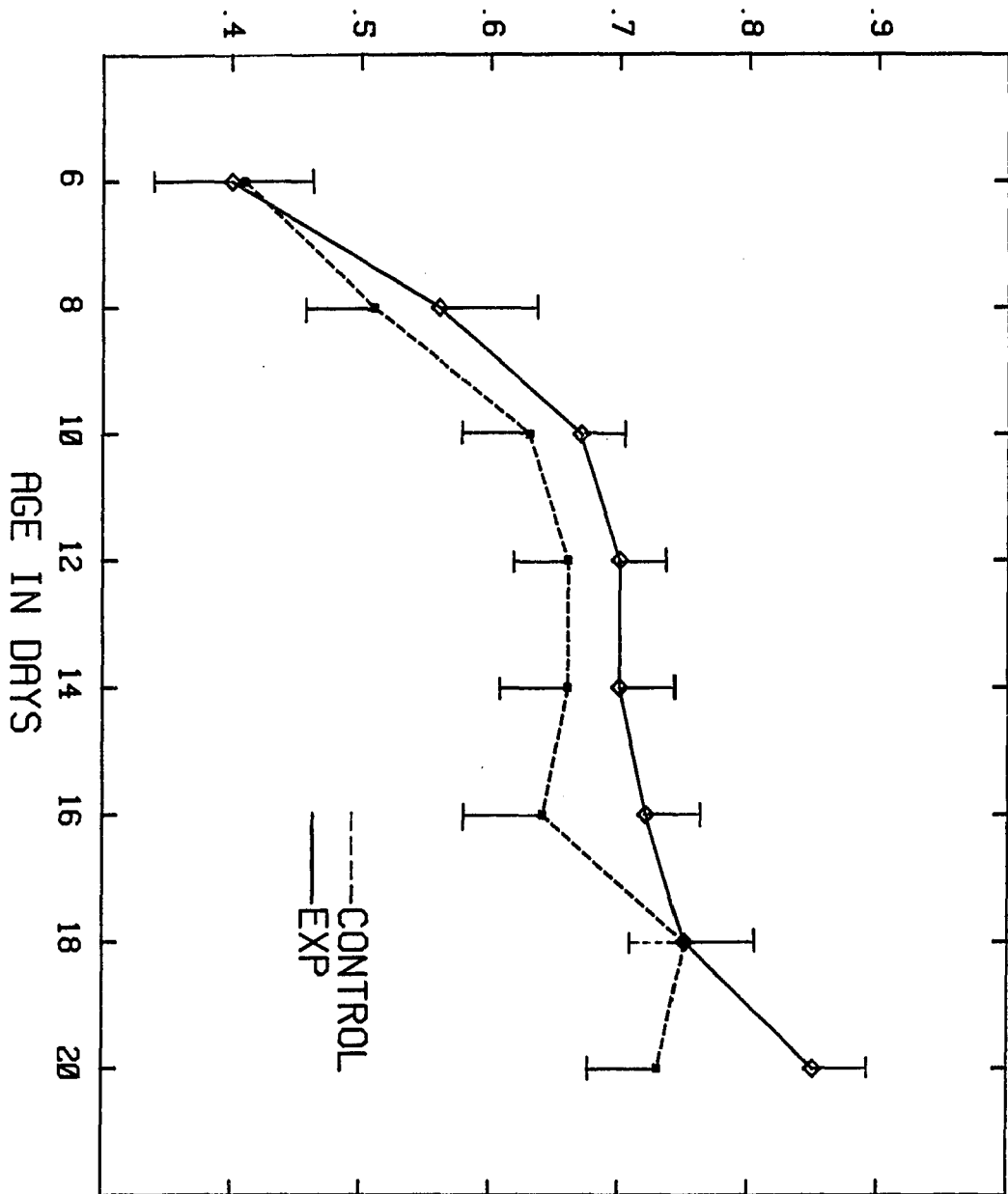
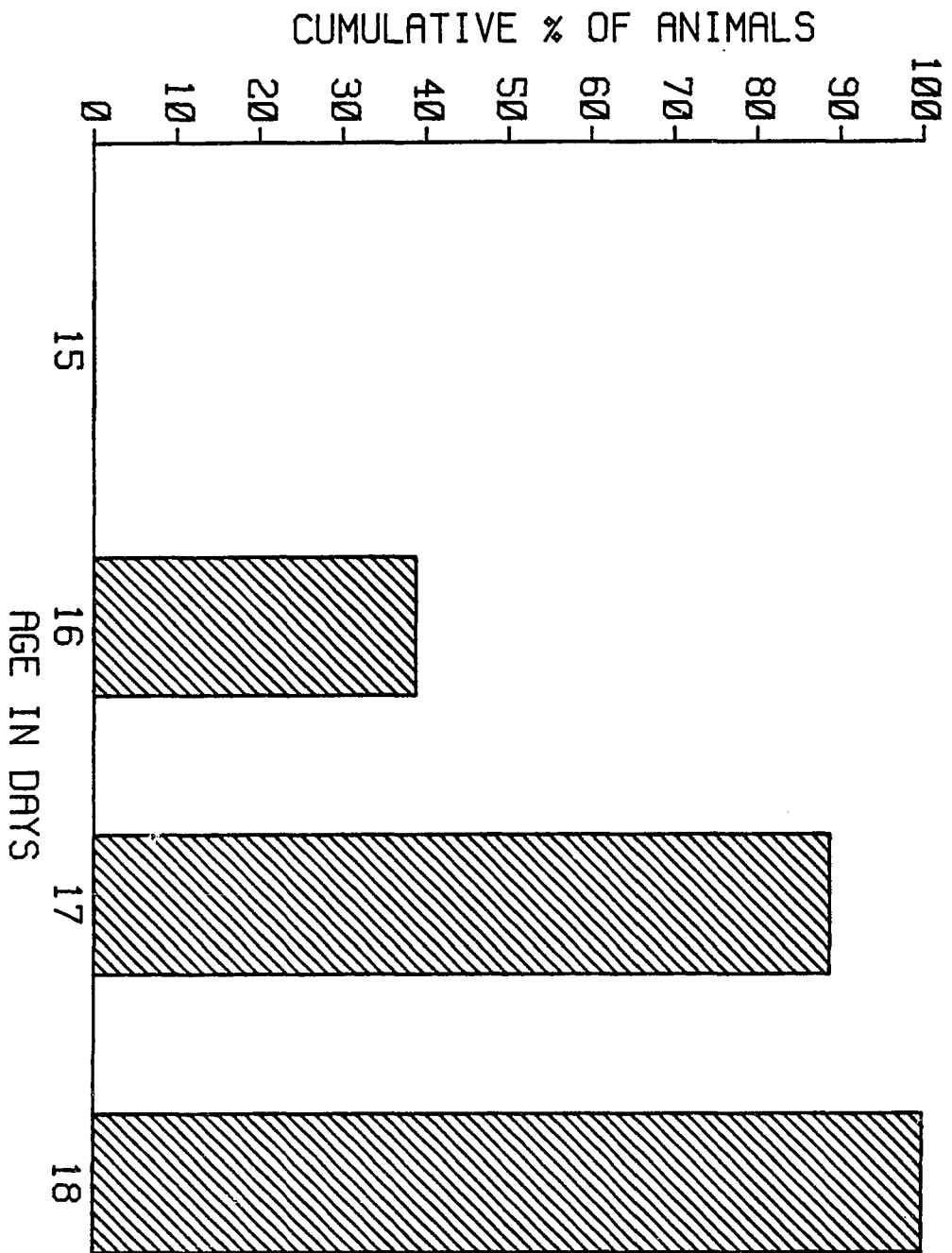


Figure 3. First day of complete bilateral eyelid opening for control animals.



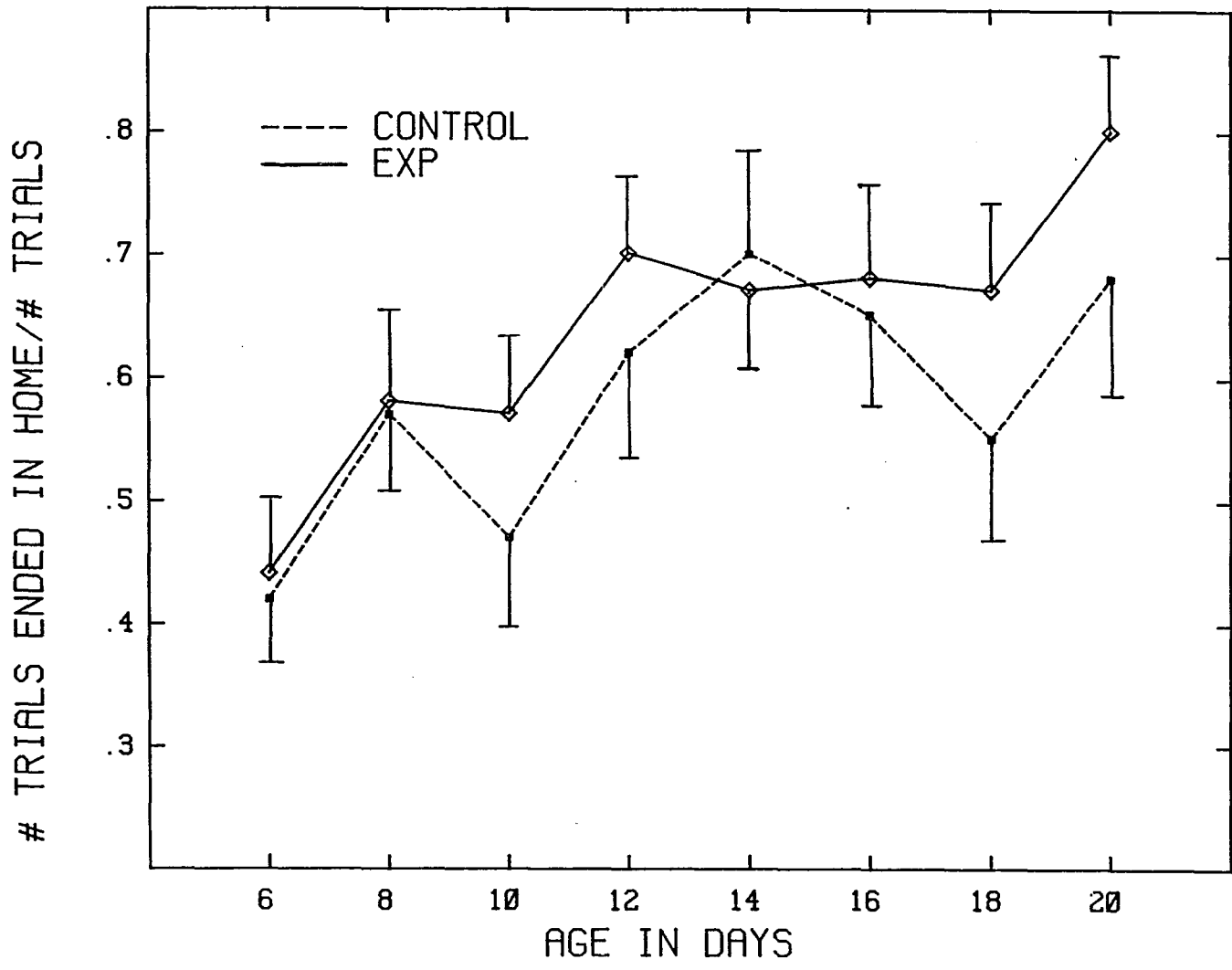
available for nearly all control pups by Day 15 or 16.

Homing Ratio

The principal measure of homing was the homing ratio, computed for 18 pairs of animals on each test day: it is the ratio of the number of trials ended in the home/ the number of trials run (or three each test day). Figure 4 shows mean homing ratios across test days for experimental and control groups. Despite apparent similarities in the curves for the experimental and control groups, further analyses indicated substantial differences between them. The control pattern is similar to that previously reported: a gradual increase, peaking at Day 14, followed by a decline beginning on Day 16. Analyses of the data from this group indicated a significant quadratic trend ($F(1,119)=3.99, p<.05$), with no cubic component, suggesting that the apparent increase on Day 20, which has not been observed in prior studies, is not reliable. For the experimental group, there was a gradual increase in homing from Day 6, which continued until Day 20, at which age experimental animals were homing on 80% of the test trials. For this group, trend analyses indicated a highly significant linear trend ($F(1,119)=16.35, p<.01$), and unlike the case for the control group, no quadratic component.

The data were further analyzed using a more stringent measure of homing: the proportion of animals that homed on

Figure 4. Mean homing ratios for experimental and control animals as a function of age. Homing ratio = # of trials ended in the home/3. Bars indicate standard errors. Means and standard errors are presented in the Appendix, Table C.



all three trials on any given day, seen in Figure 5. This analysis produced results very similar to those obtained using the simple homing ratio: until Day 14, the performance of the two groups was very similar. However, from Day 16 through 20, the proportion of experimental animals showing consistent homing increased in a linear fashion, while that proportion of control animals decreased. Trend analyses were comparable to those obtained using the homing ratio measure: the data from the experimental animals yielded a highly significant linear component ($F(1,119)=11.57, p<.01$), with no quadratic component, while data from the control animals showed a significant quadratic trend ($F(1,119)=4.12, p<.05$).

In that the decline in homing noted for the control animals occurred just after their eyes opened, the data suggested a causal relationship between eyelid opening and the decline in homing. To examine this possibility, I considered the homing measure of the control animals in relation to the individual day of eyelid opening. Figures 6 and 7 present the homing data aligned according to the day of eyelid opening of the control animals. For purposes of comparison, the data from experimental animals were organized according to the age at which the eyes of their matched controls opened. For example, if a control animal's eyes opened on Day 16, Day 15 for both that control pup and its experimental littermate was considered

Figure 5. Proportion of experimental and control animals that homed on all three trials as a function of age (N=18 pairs).

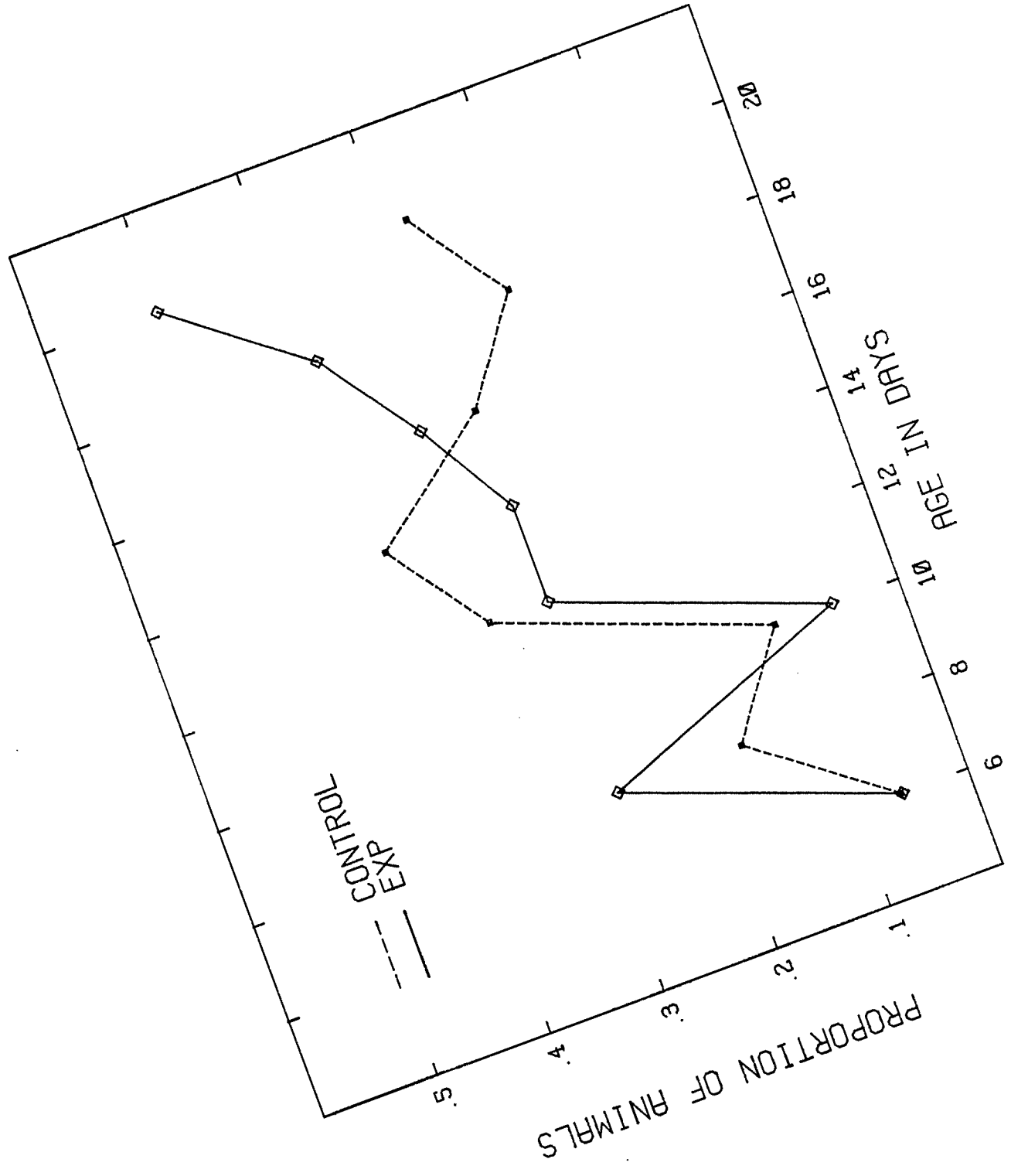


Figure 6. Homing ratios aligned according to the day of eyelid opening of control animals. See text for description.

OF TRIALS ENDED IN HOME/#TRIALS

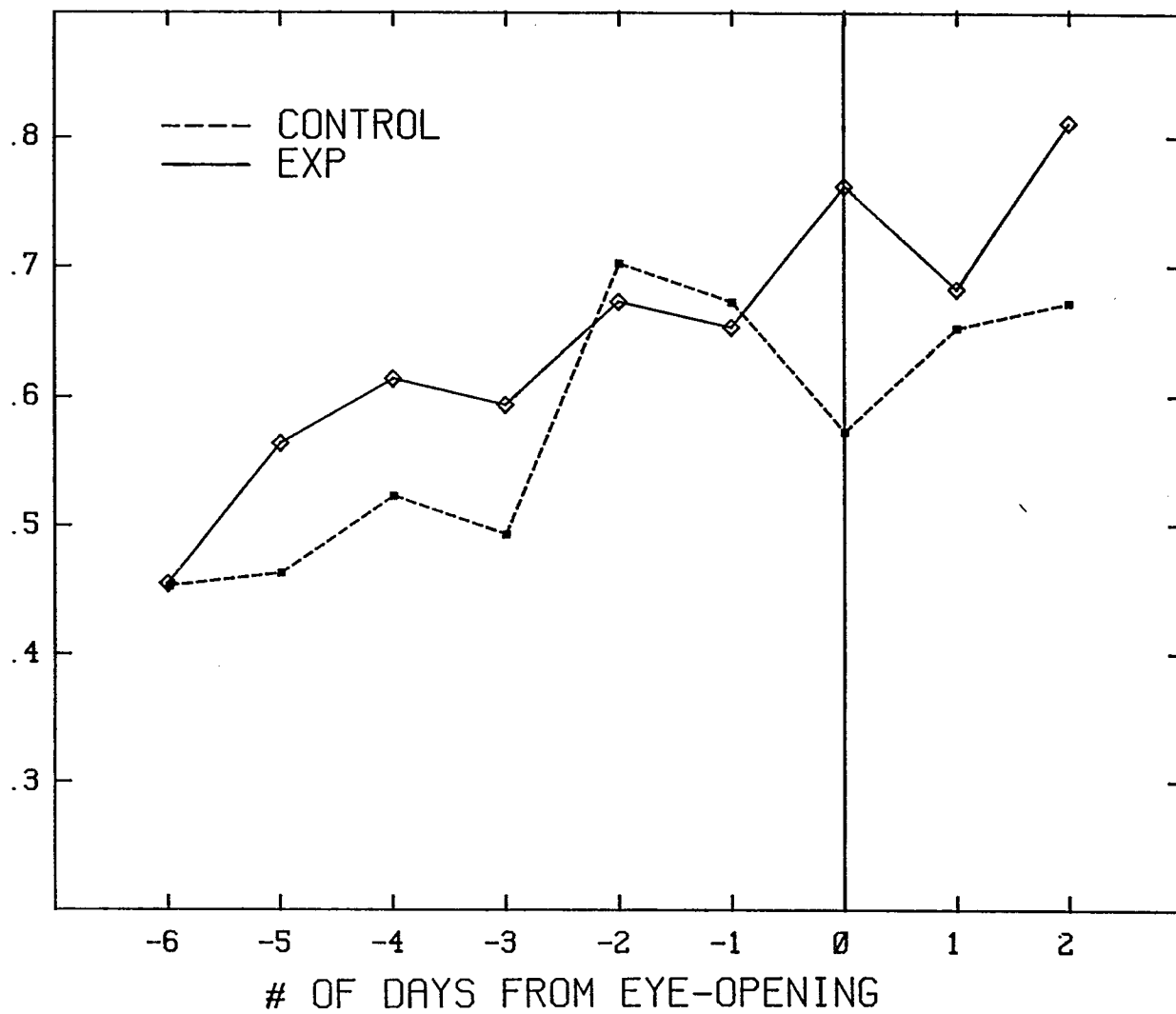
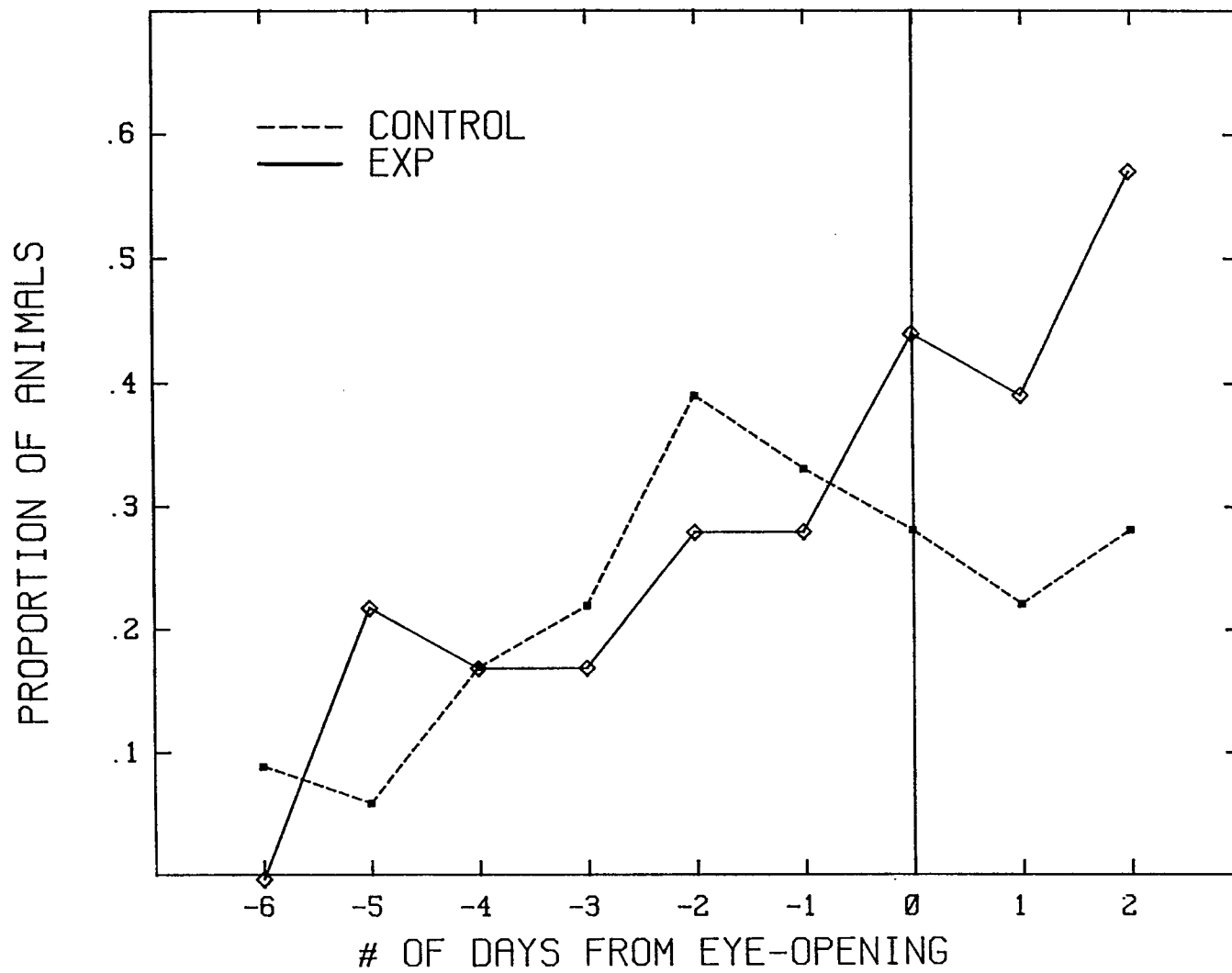


Figure 7. Proportion of animals homing on all three trials aligned according to the day of eyelid opening of control animals. See text for description.



Day -1, etc. Figure 6 shows mean homing ratios for the two groups and Figure 7 shows the proportion of animals homing on all three trials. These realigned data suggest that the initial diverging of the two curves occurs on the day of complete bilateral eyelid opening of the control animals, i.e., on the day that patterned visual input first became available (Day -1).

Discussion

These data suggested that early eyelid opening, with the concomitant premature availability of patterned visual information, alters the normal pattern of homing in rat pups. The principal finding of this study was that the decline typically seen in homing at or around the normal time of eyelid opening does not occur in pups whose eyes have been opened prematurely. There are several possible routes by which this alteration might occur.

In normal rat pups, the increase seen in homing between Days 6-14 may be mediated by development of olfactory sensitivity: pups may become better at using olfactory cues to guide them home. This is an adaptive pattern, as the nest is the primary site for mother-pup interactions (e.g., nursing, licking) during this early litter period (Rosenblatt and Lehrman, 1963). By the end of the second week, however, the nest becomes less and less the center of activity, as the pups increasingly make

excursions outside the nest. Pups begin to approach the mother outside the nest to suckle, and thus the nest's significance as a nurture center begins to dwindle. All of this is coincident with, and may be the cause of, the decline in homing typically seen after Day 14. Another possible explanation (and these are not mutually exclusive) for the observed pattern of homing in normal pups is that the onset of vision acts to "disorganize" the behavior pattern that has been organized around olfactory input. The increase of visual input beginning around Day 16 may act to disorganize this behavior, forcing the animal to another level of behavioral organization. The decline seen in homing of normal animals may result from the diminished importance of the nest, or alternatively, the diminished importance of the nest may result from the decline in homing, mediated by the disruptive effects of the onset of visual stimulation. The finding that the homing curves for the experimental and control groups began to diverge at the point when the control animals' eyes began to open (Figures 6 and 7) suggests that the decline seen in the normal homing pattern may be mediated by the onset of visual stimulation, and its possible disruptive effects.

If normal eyelid opening creates a disruption necessary for the reorganization of the pup's behavior, early eyelid opening, which occurs before there is a pattern to disrupt, may preclude this later disruption.

Nothing happens to interrupt or disturb the pup's organization, and so it persists in its behavioral patterns; this implies continued olfactory mediation. Alternatively, the pups whose eyes have been opened early could be responding to the visual characteristics of the home. The experimental procedure of brushing the shavings into the home quadrant may render the home visually, as well as olfactorily salient. The experimental pups could be responding to these visual characteristics at the very early age of 8 or 10 days; this might alter normal intersensory relationships, and the experimental pups could be more visually oriented than normal pups. This might result in the observed continued increase in the experimental pups' homing, as use of the visual system continued to improve.

The second study was designed to identify some of the factors involved in this continued increase in homing exhibited by the experimental group, or stated alternatively, the failure of the experimental group to exhibit the decline typically seen in homing of normal rat pups.

Study II

In this study, olfactory salience of the home was maintained while visual cues, potentially capable of mediating homing, were reduced. The nest shavings, which

visually differentiated the home from the other quadrants in the first study, were removed for testing in Study II, while an odor-absorbent substrate remained in place.

Method

Subjects

Nineteen pairs of rat pups, culled from five litters, were used. Litters were reared in the same type of cage as in Study I, but a false bottom was inserted. Wood shavings, distributed evenly over the cage bottom, provided an odor-absorbent substrate. To secure the substrate, the shavings were covered with 1/4" steel mesh, fastened to the cage at the corners. Lines were drawn on the mesh to delineate the quadrants. Mothers were provided with the same shavings for building nests.

Procedure

For testing, unlike Study I, all loose shavings were removed from the cage, leaving only the absorbent substrate in place. Data collection differed slightly from Study I: rather than tracing the path of the pup and noting only times of exits from the start quadrant, and entries into and exits from the home quadrant, the path of the pup was not traced. Instead, times of exits from and entries into each quadrant were noted during the two-minute trial (read from the digital timer), making it possible to determine the amount of time spent in each quadrant. While such a method did not permit a qualitative recreation of the pup's

path (as in Study I), it did permit what may be considered a quantitative summary of each trial.

All other procedures were identical to those described for Study I.

Results

Activity scores were computed for both groups, based on a more sensitive measure than that used in Study I. The method of data collection described above permitted determination of the number of crossings into and out of quadrants for each trial. The mean number of crossings for both groups across test days is shown in Figure 8. It can be seen that activity levels of both groups increased linearly with age (control: $F(1,126)=450.2, p<.01$; experimental: $F(1,126)=289.4, p<.01$), declining somewhat for both groups on Day 20.

The day of complete bilateral eyelid opening for animals in the control group was noted (see Figure 9). Since in nearly every case, eyelid opening had begun the day before it was complete, almost all (84.0%) control animals were receiving some patterned visual input by Day 15.

Homing Ratio

Homing ratios were determined for both groups; mean homing ratios across test days are shown in Figure 10. Unlike the findings of Study I, the experimental and

Figure 8. Mean activity scores of experimental and control animals as a function of age. Activity score = # of quadrant crossings over three trials. Bars indicate standard errors. Means and standard errors are presented in the Appendix, Table D.

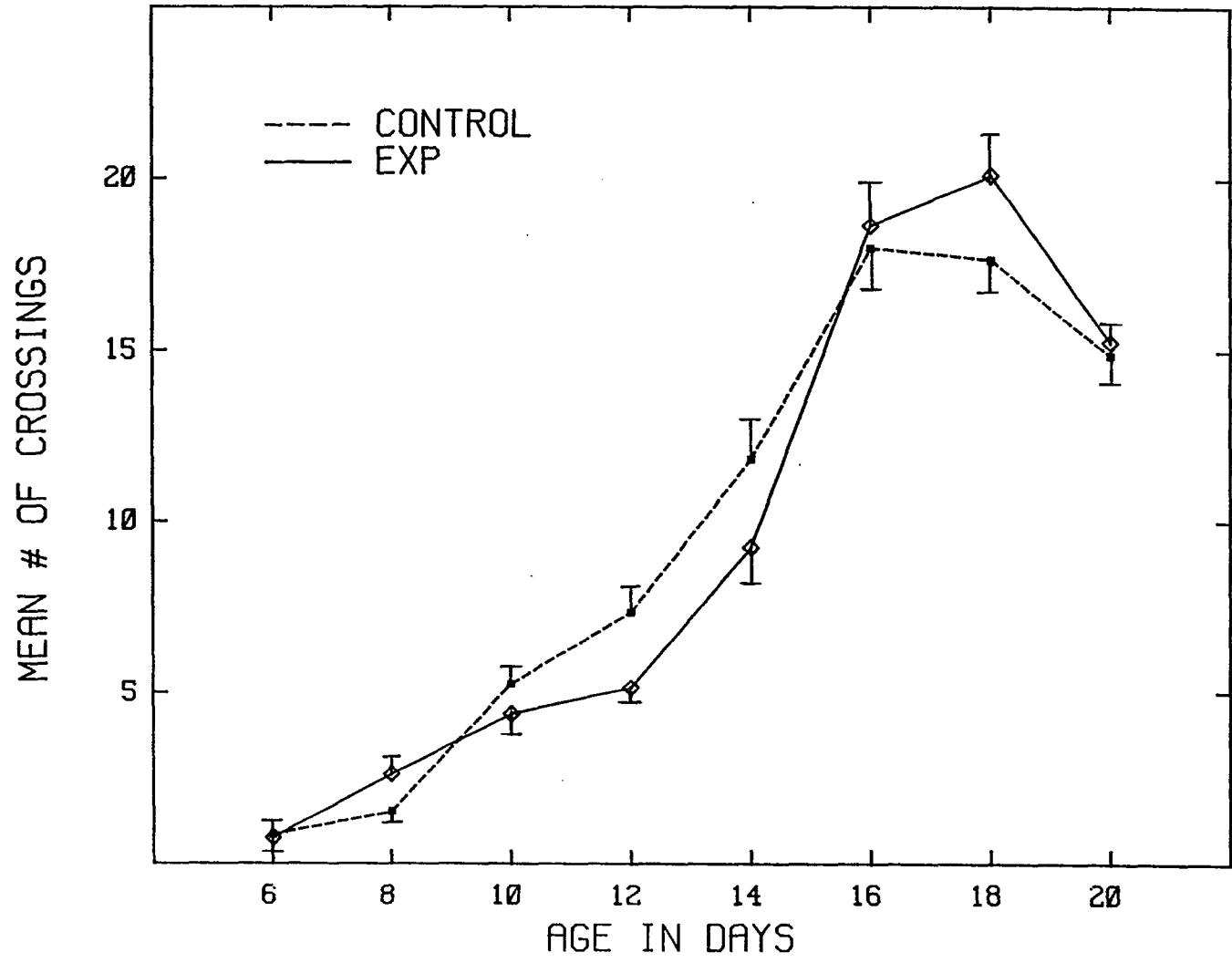
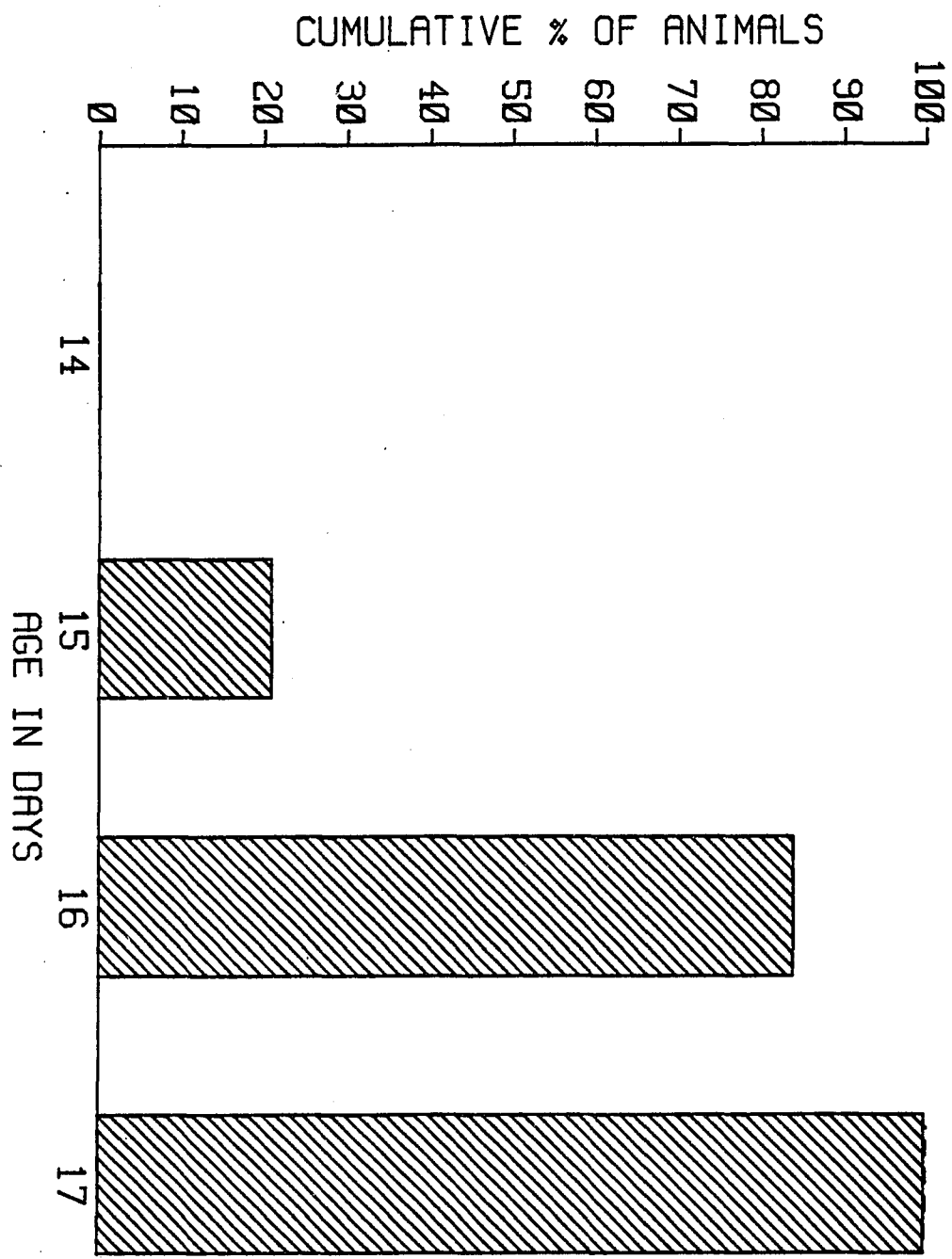


Figure 9. First day of complete bilateral eyelid opening for control animals.



control patterns of homing did not differ: both show a gradual increase and a gradual decline. Trend analysis indicated a significant quadratic trend for both the experimental ($F(1,126)=6.61, p<.01$) and control ($F(1,126)=8.58, p<.01$) animals, unlike the first study, where the data from the experimental animals showed no quadratic component.

Figure 11 contrasts the performance of the experimental groups from Studies I and II. The overall homing levels are lower for Study II, but more striking is the divergence of the homing ratios of the two groups that began on Day 12. The Study I group continued in its linearly increasing homing behavior, while the animals from Study II exhibited a decline in homing, beginning on Day 12, that continued until Day 20.

Discussion

The principal finding of this study was that when visual cues were removed from the testing situation, early eyelid-opened pups showed homing patterns that did not differ from normal pups. These data suggest that the persistence and, in fact, improvement in homing beyond the age of its typical decline in the experimental pups of Study I was related to the visual prominence of the nest site. They further suggest that not only are early eyelid-opened pups sensitive to this premature visual

Figure 10. Mean homing ratios for experimental and control animals as a function of age. Bars indicate standard errors. Means and standard errors are presented in the Appendix, Table E.

TRIALS ENDED IN HOME/# TRIALS

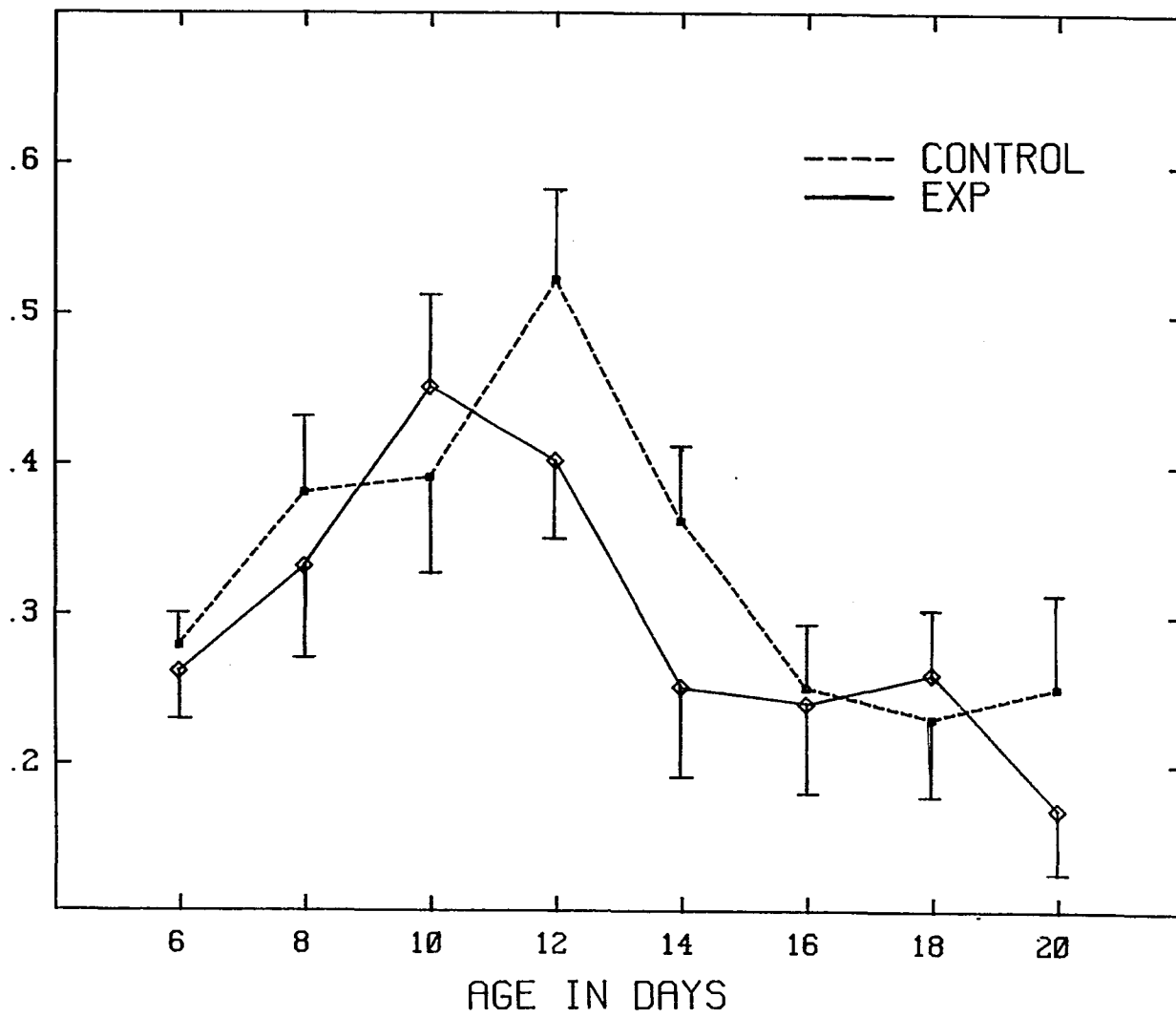
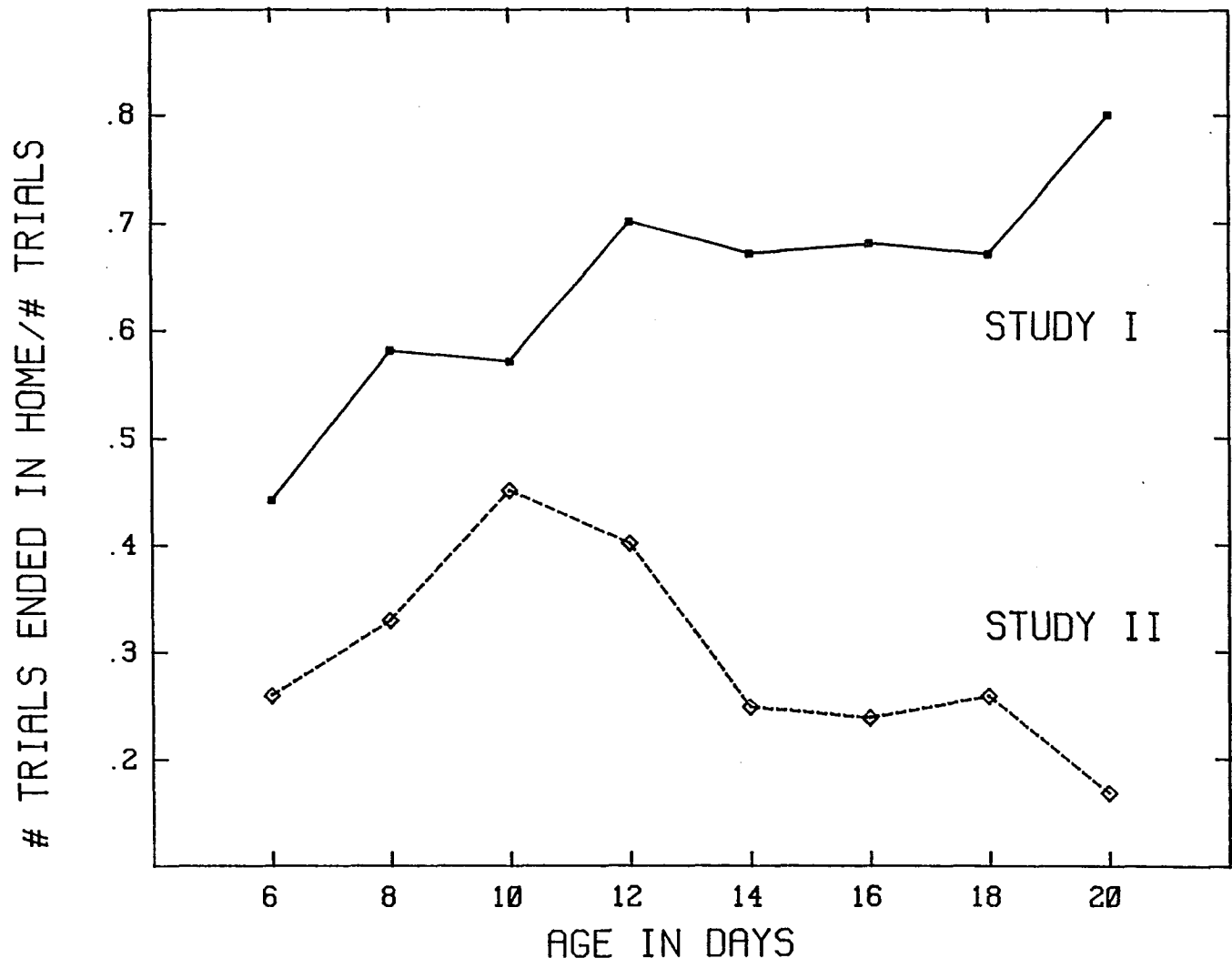


Figure 11. Mean homing ratios of experimental animals from Homing Study I and Study II as a function of age.



stimulation, but also that the premature availability of visual information can alter an integrated response pattern such as homing.

These data provide suggestive evidence of intermodal effects of early eyelid opening, specifically possible effects on attention to or use of olfactory cues. That is, since the experimental pups responded to the visual salience of the nest site (in Study I), they may have been using visual cues to guide them home at the early age of 8 or 10 days. At that time, control pups were presumably using olfactory, and possibly thermal, cues to guide them home. Early eyelid opening may have pre-empted normal attention to and/or use of olfactory cues for homing, i.e., premature visual input may have competed with olfactory input in mediating home orientation. This could be tested by presenting pups with a choice between a nest that is visually identical to their nest, but lacking appropriate olfactory cues, vs. an olfactorily salient nest site that is either lacking visual salience or presents visual cues that conflict with those of their nest.

The overall lower homing levels found in Study II might be attributable to a variety of factors. The unusual nature of the testing situation, which was different from the normal home situation or the test situation of Study I, might have contributed. Homing was probably more difficult in the absence of all nest material, as it is very likely

that the nest material used in Study I during testing rendered the home more olfactorily discriminable. The nest material, therefore, facilitated olfactorily-mediated homing, while at the same time permitted visually-mediated homing.

It is not clear what the consequences of the effects of early eyelid opening might be for adaptive functioning. If pups' eyes opened earlier, the data suggest that they might continue to orient to the home past the time that homing normally declines. That could be deleterious to the pups' development to the extent that it delayed independent functioning, channelled energy unnecessarily into maintenance of the nest, and interfered with pups' exploration of the rest of their environment.

Observations of these animals in the home cage with mother and siblings would provide additional information regarding their behavior in a more natural setting. Mother and siblings would produce visual stimulation at least as salient as that produced by the nesting material, and the early eyelid-opened pup might preferentially orient to those visual cues. Since mother and pups spend progressively less and less time in the nest after the first two weeks of the litter period, such visual orienting might lead to diminished interest in the home in favor of mother and siblings. That is, the results of the first homing study might be limited to a situation where mother

and siblings are absent. In addition, naturalistic observations would elucidate whether or not early eyelid opening adversely affects mother-pup interactions, e.g., if, early in the litter period, early eyelid opening interfered with olfactorily-mediated nipple selection and attachment, or later, if experimental pups were less likely to leave the nest to suckle. Such observations are necessary to determine the significance of these data for the normal development of behavior and adaptive perceptual abilities.

VISUAL CLIFF

The results from the homing study indicated that early eyelid opening modified the normal sensory mediation of a response pattern, causing the pups to respond persistently to visual cues when they were made salient. These findings suggested that this early availability of patterned visual input may have altered the normal hierarchically determined distribution of attention and response to sensory inputs. The second experiment further investigated possible alterations of sensory mediation resulting from the premature availability of patterned visual input, by using the visual cliff. The visual cliff is typically regarded as an apparatus designed to measure visual discrimination abilities, specifically depth discrimination. However, as it presents the animal with the opportunity to respond to tactile and visual aspects of the situation, it may provide a useful framework in which to examine the relationship between vision and touch.

Sensory Hierarchies and the Visual Cliff

Schiffman (1968) reported that rats differ from chicks in their behavior on the visual cliff, regarding the importance of "optical information for support", defined by Walk and Gibson (1961) as "a relatively coarse optical texture of an array surrounding the animal's feet" (p. 41). When placed on a clear sheet of glass providing no optical

support information (as on the deep side of the visual cliff), the chick appears to be visually dominant: even though the "optical void" provides physical support, the chick avoids the deep side. The rat, however, is tactually dominated on the visual cliff, and is indifferent to the absence of optical support when physical support is present. Despite the fact that they are capable of making visual discriminations, rats, when given conflicting tactile and visual cues (such as the visual cliff provides), will respond preferentially to the tactual information: they will not exhibit a preference for either the deep or shallow side (Schiffman, Lore, Passafiume, and Neeb, 1970).

Investigation of the source of the non-visual information utilized by rats indicated the importance of vibrissae (Schiffman et al., 1970). When vibrissae of rats were removed, they showed a preference for the shallow side of the visual cliff, thus demonstrating that visual discrimination ability is present, but that tactual cues are dominant over visual cues for the rat (Schiffman et al., 1970).

Kittens exhibit developmental changes in sensory mediation of responding on the visual cliff. Before postnatal day 29, kittens respond equivalently to the deep and shallow sides of the cliff; shallow preference increases with age, and by day 31, kittens exhibit a

significant preference for the shallow side, indicating a transition from tactile to visual control of responding. This transition can be accelerated, however, by reducing tactile cues: when the vibrissae of kittens are clipped, reducing tactile input, kittens respond in a visually-dominated manner (preferring the shallow side) at an earlier age, day 27 (Turkewitz, Gilbert, and Birch, 1974).

Development of Visual Cliff Behavior in Rats

The vast majority of studies examining visual cliff performance in rats have dealt with the adult rat. Bauer (1973), investigating the developmental course of this behavior, examined the temporal relationship between visual cliff discrimination and eye opening in hooded rat pups. Animals were tested beginning on Day 12 through Day 20, and exhibited a shallow preference on Day 16 - i.e., they responded visually, even though tactual cues were available. Before and after Day 16, the shallow preference declined to a level exhibited by the older rat. Bauer (1973) speculated that rats may be visually oriented around Day 16-17, which corresponds to the period 2-3 days after the beginning of eye opening.

The present study investigated the effects of premature availability of patterned visual input on the developmental course of visual cliff behavior in rat pups.

In addition, using a procedure nearly identical to that of Bauer's (1973), the normal developmental course of visual cliff behavior was examined.

Method

Subjects

A total of 38 naive pups (19 pairs) from five different litters were used. They were culled, matched, and marked, as described under General Procedure, on Day 6.

Apparatus

The apparatus was a Lafayette Instrument Co. visual cliff: a hollow square box (30" x 30" x 24" high), with an inside bipartite glass surface. A patterned board, composed of red and white checks (2-inch square), was inserted directly under one half of the glass surface (shallow side). An identically patterned board was placed on the floor, 18" below the other half of the glass surface (deep side). A centerboard (4" wide x 30" long), raised 1" above the surface, bisected the glass surface.

Lighting was from two overhead fluorescent lamps (15 watts each) covered with vellum to diffuse the light and reduce glare. Positions of the lamps were adjusted to equate the illumination of the shallow and deep sides. Illumination as measured (Gossen Lunasix meter) from the centerboard was approximately seven footcandles on either side.

Procedure

On Day 7, eyelids of experimental pups were opened, as described under General Procedure.

Testing

Animals were tested on the visual cliff on alternate days, beginning Day 12 through Day 20, and again on Day 30. Each subject had three trials/test day, with a maximum trial length of 180 seconds and a 30 second inter-trial interval. A trial ended when either a descent or a fall occurred, or 180 seconds had passed. A response was scored as a descent only when all four paws touched the glass surface and the two front paws had preceded the rear paws. If an animal did not respond within 180 seconds, that trial was scored as "inhibited". If an animal fell from the centerboard (i.e., either two rear paws or two side paws touched the surface first, followed by the other two paws), that trial was scored as a "fall". Latencies to both four-paw and two-paw descents were recorded, read from a digital timer (Hunter, Model 1520). The glass and centerboard surfaces were wiped with a commercial glass cleaner (Glass Plus) after each animal's last trial. The position of the experimenter and the apparatus remained constant throughout testing, while placement of the animal, in the middle of the centerboard and in a line parallel to it, was alternated each trial. For example, on a given test day, placement order was: toward the experimenter

(Trial 1), away from the experimenter (Trial 2), and toward the experimenter (Trial 3). Six different permutations of those two positions in three trials were used for the six test days.

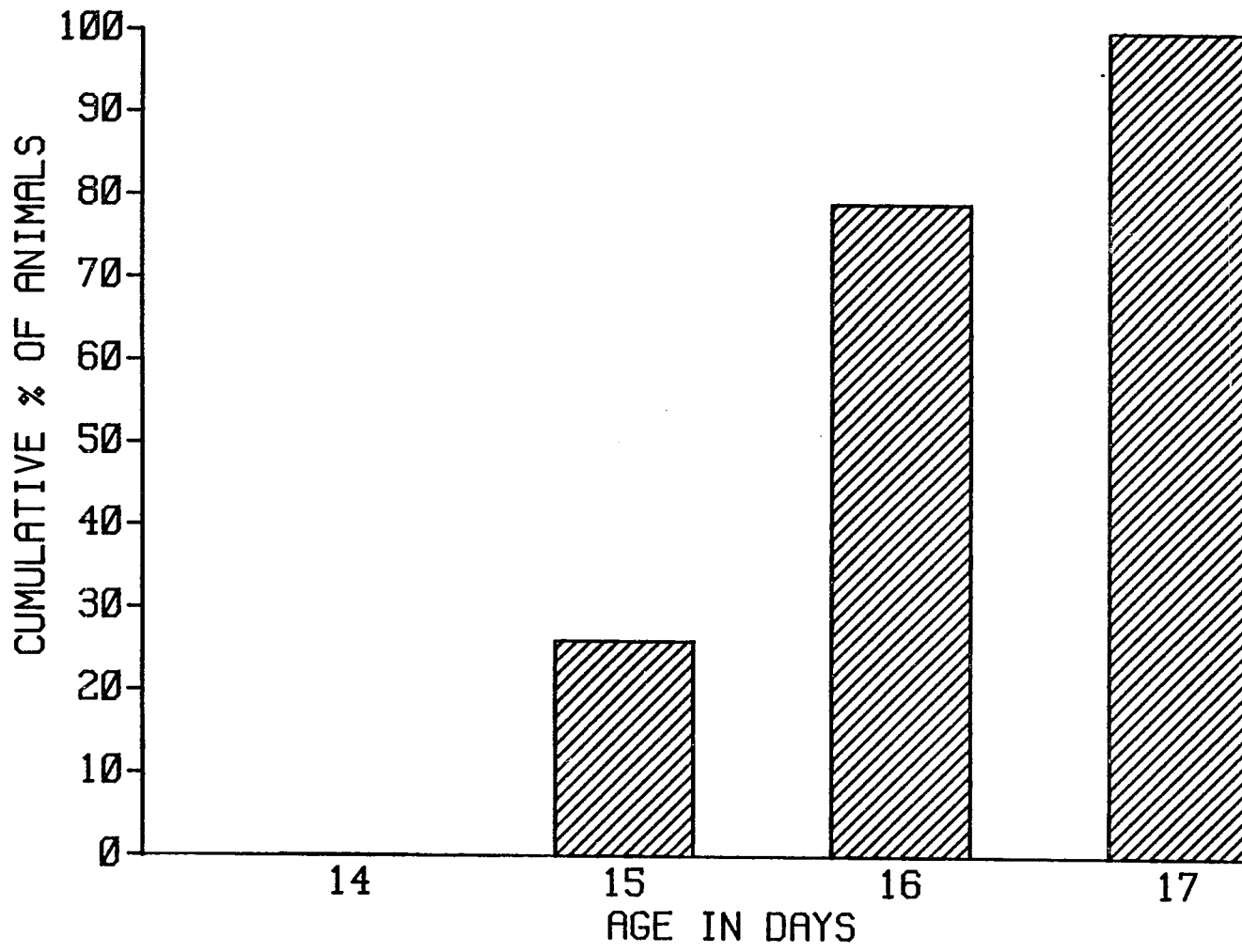
On Day 30, in addition to the three trials, each animal was observed for a three-minute post-test. The animal was placed on the centerboard, facing the experimenter; for three minutes, the animal was permitted to descend to either side, climb back on to the centerboard, descend to the other side, etc. The number of descents to either side and the duration of those descents were recorded.

Results

Day of complete bilateral eye opening for the control group is depicted in Figure 12. The eyes of nearly all control animals (79%) were completely opened by Day 16, and all were completely opened by Day 17. Since eye opening usually begins at least one day prior to complete bilateral opening, all control animals were receiving some patterned visual stimulation by Day 16.

Figure 13 depicts the percentage of descents that were to the shallow side for control and experimental groups across test days. Since these data represent percentage of descents to the shallow side, and not percentage of trials (some trials ended with falls, particularly on Days 12 and

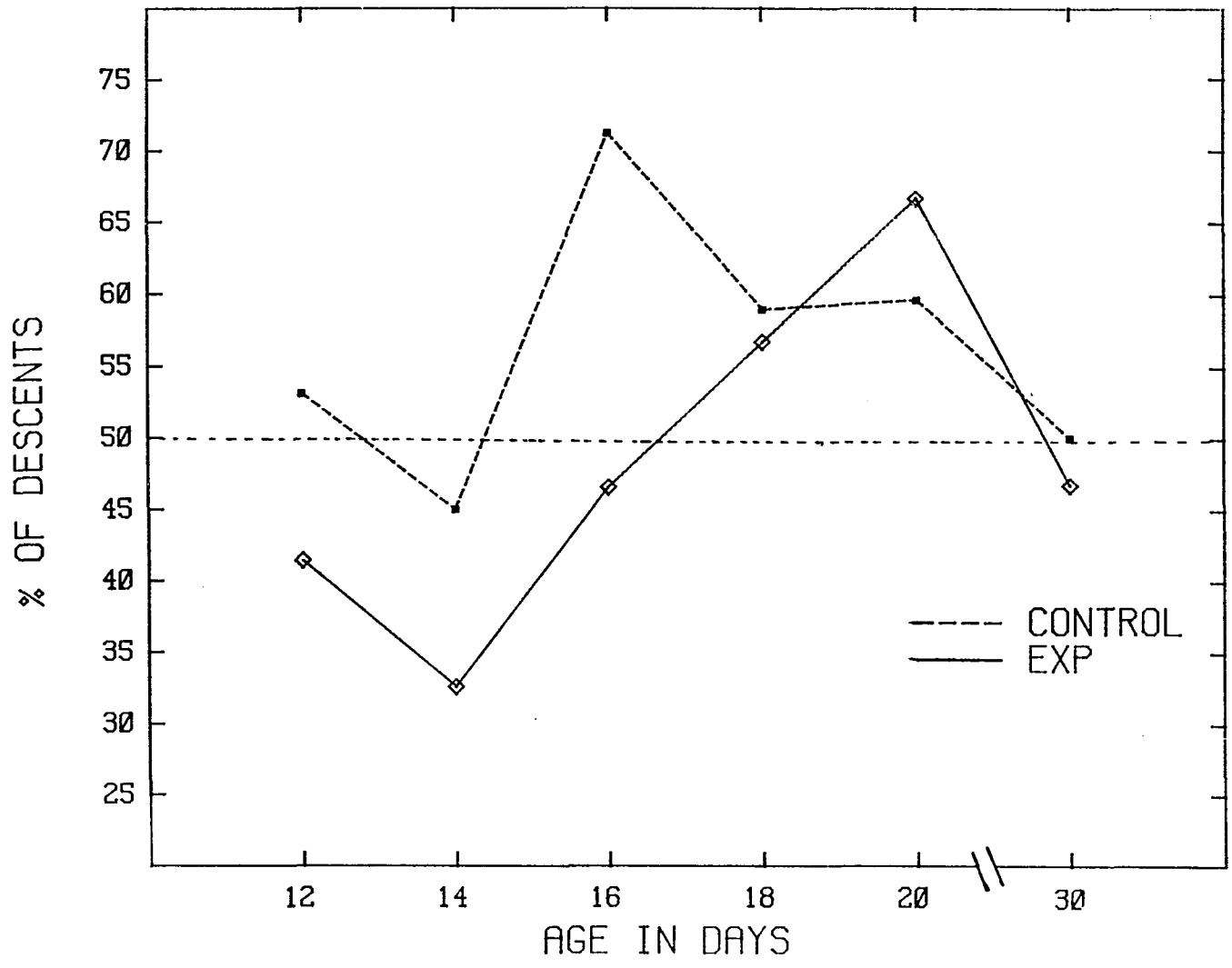
Figure 12. First Day of complete bilateral eyelid opening for control animals.



14), percentage of descents to the deep side is actually the reciprocal function. Thus, on Day 14, when 32.6% of the experimental group's descents were to the shallow side, 67.4% of their descents were to the deep side. The pattern of descents by control animals is notably similar to that previously reported by Bauer (1973). Analyses of the data from this group indicated a significant quadratic trend ($F(1,90)=4.28, p<.05$), with maximum descents to the shallow side occurring on Day 16, and decreasing thereafter. The only day on which animals in this group exhibited a shallow preference was Day 16 ($t(df=18)=3.07, p<.01$; t-test for matched pairs, two-tailed): on all other test days, the number of shallow descents did not differ significantly from the number of deep descents (the next largest t-value, on Day 20, was 1.39, $p>.05$).

The pattern of shallow descents by animals in the experimental group was quite different. Although data from these animals also exhibit a significant quadratic trend ($F(1,90)=6.50, p<.05$), the maximum number of shallow descents did not occur until Day 20, at which time the animals in this group exhibited a significant shallow preference ($t(df=18)=2.82, p<.01$; t-test for matched pairs, two-tailed). Even more strikingly, the significant quadratic trend obtained with this group was in part based on the animals' tendency to descend on the deep side on Day 14. This tendency was reflected in a significantly higher

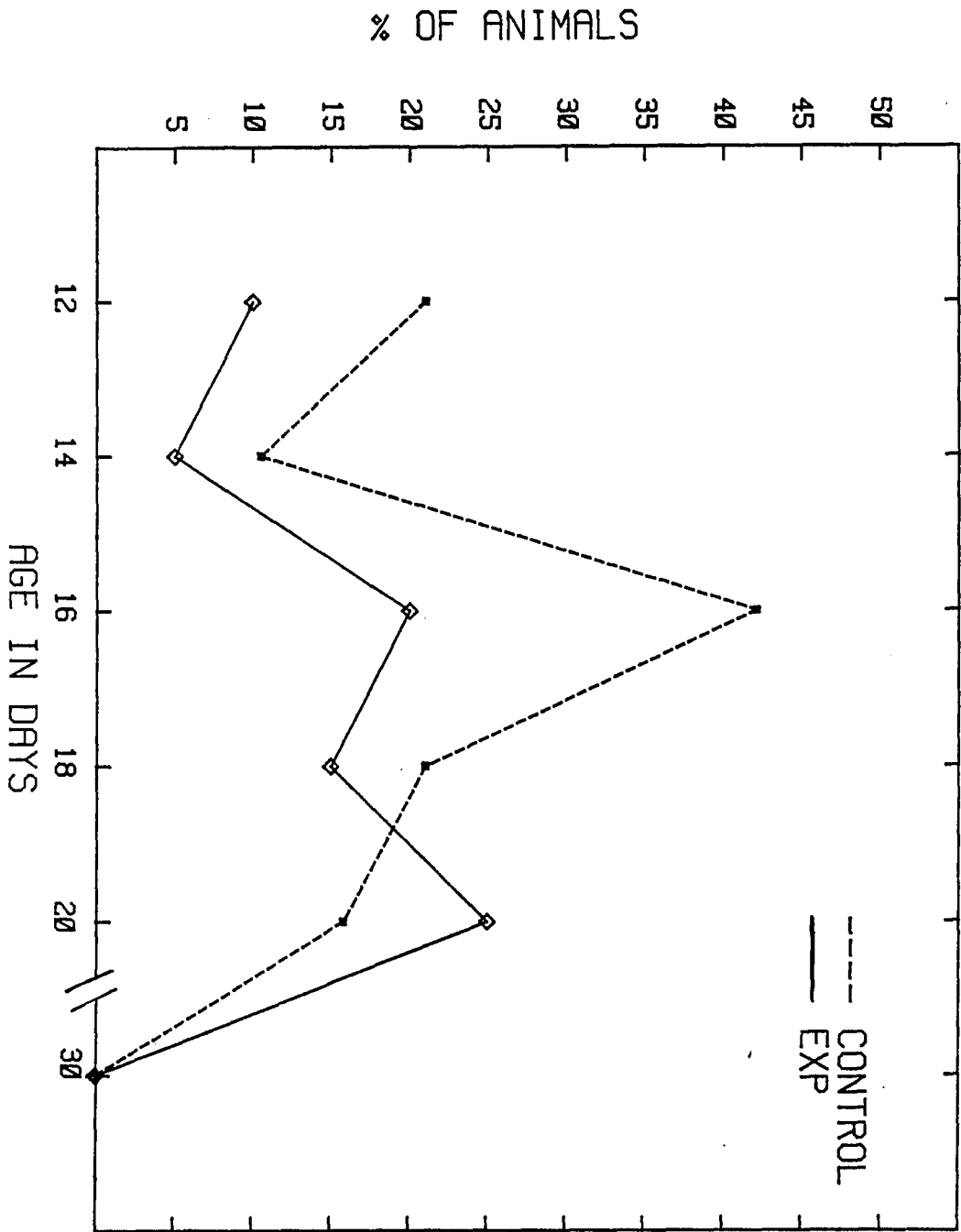
Figure 13. Per cent of descents to the shallow side of the visual cliff for experimental and control animals, as a function of age.



number of descents to the deep than to the shallow side ($t(df=18)=2.76$, $p<.01$; t-test for matched pairs, two-tailed). At no age other than Days 14 and 20 did animals from this group differ with regard to the number of their shallow or deep descents. Thus, unlike the control animals whose response pattern shifted from no-preference, to shallow preference on Day 16, and back to no-preference, the experimental animals' response preference was initially to the deep side, then shifted to the shallow side on Day 20, and then to no-preference.

As an additional and more stringent measure of shallow preference, the percentage of animals whose descents were all to the shallow side on all three trials was examined. Figure 14 shows the percentage of animals who descended consistently to the shallow side on each test day. For the control animals, the pattern of consistent shallow preference corresponded well to the pattern of shallow descents shown in Figure 12. The day on which the highest percentage (42.1%) of control animals descended consistently to the shallow side occurred on Day 16, the only day the control group showed a significant shallow preference. The highest percentage (26.0%) of experimental animals descending consistently to the shallow side occurred on Day 20, thus agreeing with the only day the experimental group showed a significant shallow preference. These data, however, are less clearly peaked than the data

Figure 14. Per cent of experimental and control animals whose descents were all to the shallow side as a function of age (N=19 pairs).



from the control group, and considerably fewer experimental animals descended consistently to the shallow side on Day 20, compared to consistent shallow descents by control animals on Day 16.

Figure 15 depicts a measure of consistent deep preference: the percentage of experimental and control animals whose descents were all to the deep side on each test day. For both groups, the percentage of animals descending consistently to the deep side was greatest on Days 12 and 14 and decreased on subsequent test days. Although the percentage of experimental animals descending consistently to the deep side was greater than that percentage of control animals on Days 12 and 14, neither difference was significant (Day 12: $\chi^2(df=1)=1.16$, $p>.05$; Day 14: $\chi^2(df=1)=.54$, $p>.05$).

The consistent shallow vs. deep preferences of the control group are contrasted in Figure 16, which presents the percentage of control animals whose descents were all to the shallow or deep sides on each test day. It can be seen that the two curves first diverged on Day 16, when the percentage of control animals consistently descending to the shallow side increased to its highest point (42.1%) and the percentage descending consistently to the deep side dropped to 5.3%. The percentage of animals descending consistently to the shallow side began to decrease by Day 18, and by Day 30, no control animals descended

Figure 15. Per cent of experimental and control animals whose descents were all to the deep side as a function of age (N=19 pairs).

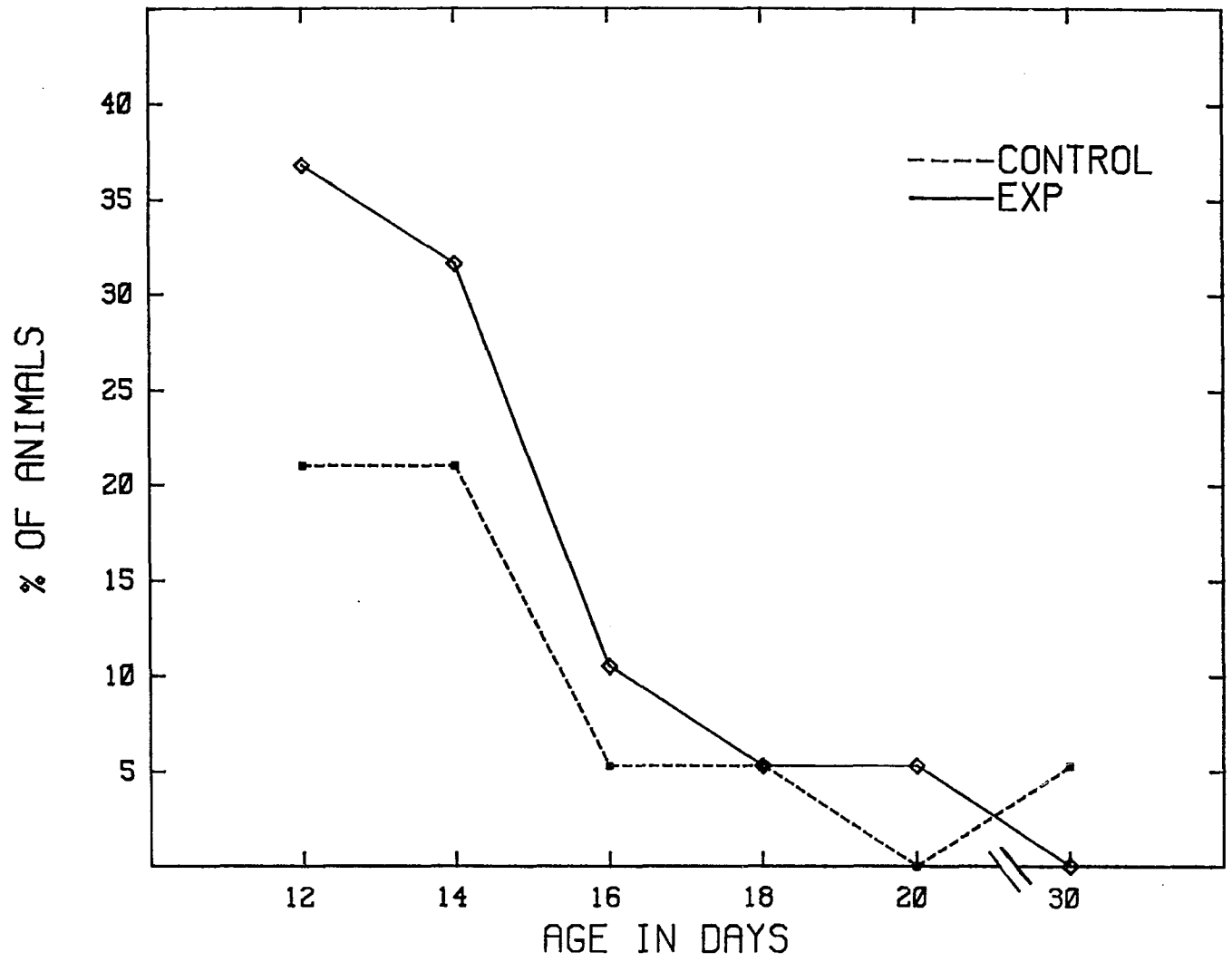
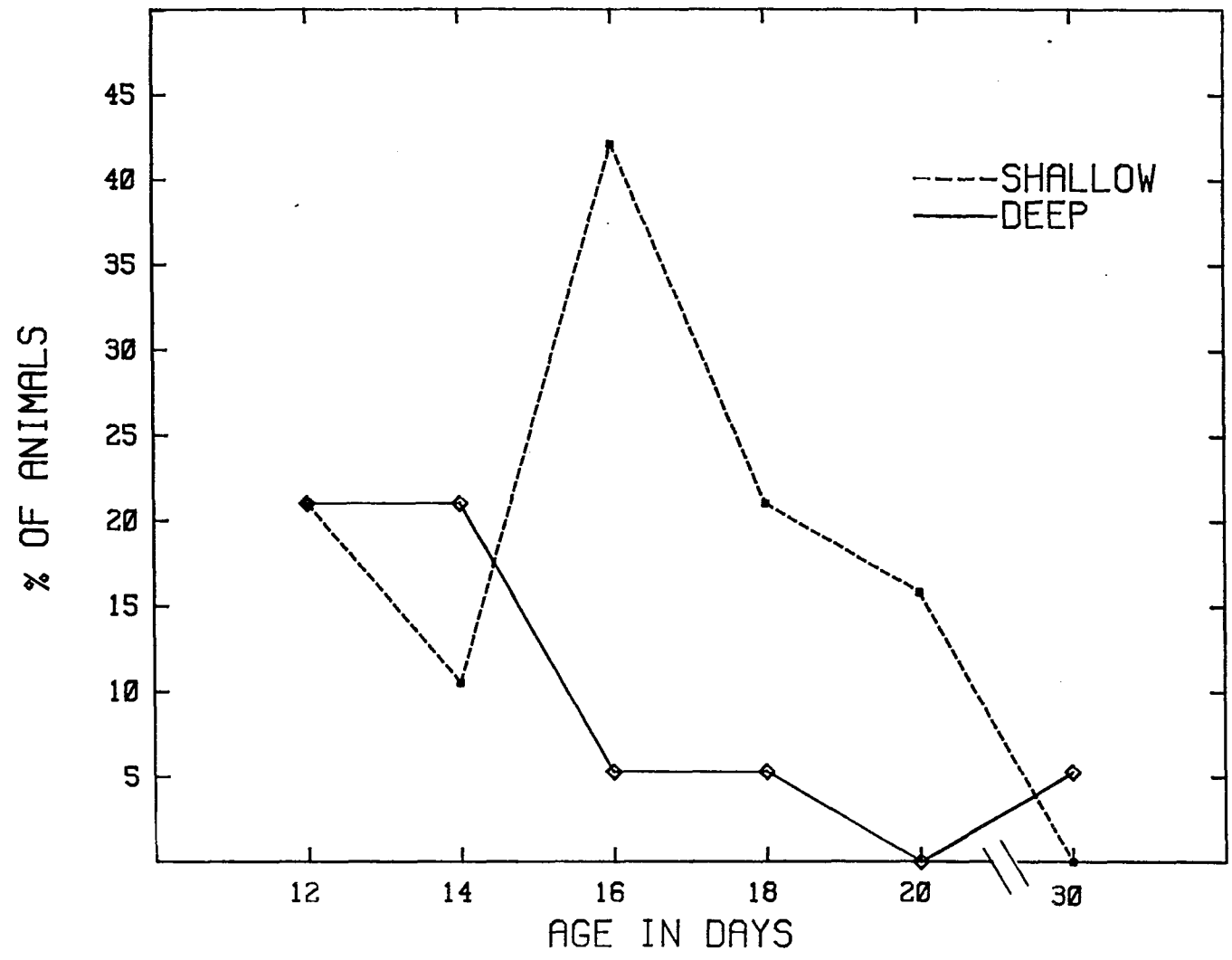


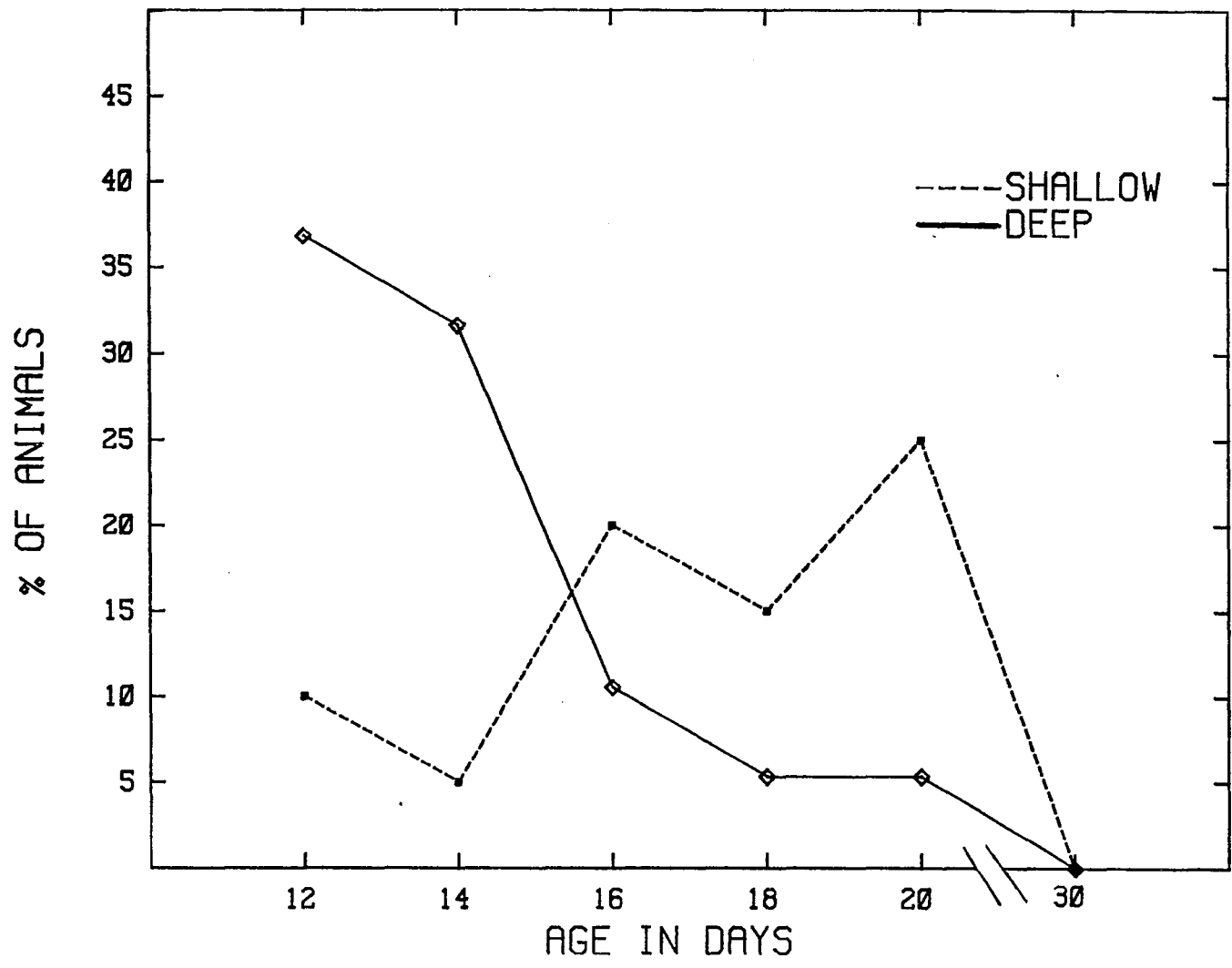
Figure 16. Per cent of control animals whose descents were all to the shallow or deep side as a function of age (N=19).



consistently to the shallow side. These data are thus in agreement with the pattern of control responding depicted in Figure 13: an initial lack of consistent preference for either side on Days 12 and 14, a sharp increase in consistent preference for the shallow side (with a concomitant decrease in consistent deep preference) on Day 16 - the first day of complete bilateral eyelid opening for most of the control animals, followed by a decline in consistent shallow preference beginning on Day 18, and finally reaching a stage of no consistent preference for either side by Day 30.

The consistent shallow vs. deep preferences of the experimental group are seen in Figure 17, which depicts the percentage of experimental animals whose descents were all to the shallow or deep sides across test days. In contrast to this comparison for the control group (Figure 16), the two curves were initially divergent, the percentage of experimental animals descending consistently to the deep side being greater than the percentage consistently descending to the shallow side on both Days 12 (36.8% vs. 10.5%) and 14 (31.6% vs. 5.3%), although neither of these differences was significant when compared to control data (Day 12: chi-square(df=2)=1.52, $p > .05$; Day 14: chi-square(df=2)=1.08, $p > .05$). These data suggest a pattern of descent preferences similar to that seen in Figure 13: initially (Days 12 and 14), more experimental animals

Figure 17. Per cent of experimental animals whose descents were all to the shallow or deep side as a function of age (N=19).



consistently preferred the deep side than preferred the shallow side (although the consistent shallow vs. consistent deep comparison was not significant); the consistent deep preference subsequently declined while the consistent shallow preference increased, reaching a peak on Day 20 (26%). Finally, by Day 30, no experimental animals consistently preferred either the deep or shallow sides.

Discussion

The data for the control group were in close agreement with those previously reported (Bauer, 1973): as in Bauer's (1973) study, control subjects preferred the shallow side, or avoided the deep side, to a significant extent only on Day 16, and showed no preference on the other test days. The essentially random descent pattern exhibited by the control animals on test days other than Day 16 suggested mediation by non-visual, i.e., tactile cues. Thus, other than their performance on Day 16, the control pups exhibited descent patterns that suggested that in the presence of both tactile and visual input, the animals responded to the tactile stimuli.

The apparently tactually-mediated resonding of control pups on Days 12 and 14 was not surprising, as no control animal's eyes were opened completely by Day 14 (Fig.11). Visual information was thus limited on Days 12 and 14 to that which was transmitted through sealed lids, or, at

most, partially opened lids.

The appearance on Day 16 of a shallow preference, or depth avoidance, by the control group, both in terms of overall shallow descents (Fig. 13) and the number of animals consistently descending on the shallow side (Fig. 14), is not easily interpretable in terms of a preference based on responsiveness to shallow and/or deep, as such. However, the fact that this shallow preference behavior declined and then disappeared by Day 30 makes it unlikely that the Day 16 behavior of the control pups indicated ability to discriminate depth and subsequently avoid it. Such an interpretation requires that, immediately after eye-opening, rat pups are capable of depth discrimination and subsequent depth avoidance. According to this interpretation, they then either lose the ability to discriminate depth and hence don't avoid it (Bauer, 1973), or continue to discriminate depth but ignore it in favor of tactile information. As Bauer (1973) found no difference in descent patterns between naive animals and those tested repeatedly, it does not seem likely that the behavior of these animals on the visual cliff can be attributed to learning.

Although it is possible that in older rats or in different organisms, systematic preferences for descents to the shallow side may represent depth avoidance, one need not interpret the preferential shallow descending on Day 16

by the control animals as evidence of discrimination and avoidance of depth, per se. A more likely interpretation, and one more parsimonious in terms of inferred mechanisms, is that the differential responding to the shallow vs. deep sides is based on quantitative, rather than qualitative differences in the stimulation produced by the two sides (Schneirla, 1959,1965). The two sides of the visual cliff apparatus differ quantitatively, as well as qualitatively, in the visual stimulation each provides, and it may be on this basis that the infant rat responds. Motion parallax differs on the two sides, and it has repeatedly been shown to be an important cue in visual cliff behavior (Walk and Gibson, 1961; Gibson and Walk, 1960; Walk and Waters, 1974). In addition, the optical textures of the two sides differ, the texture that is farther away appearing coarser than the nearer texture; this has been found to influence the preferences of chicks and rats (Walk and Waters, 1974).

There are, therefore, visual cues available to the newborn animal on the visual cliff that might determine descent preferences, that do not require inference of any higher-order perceptual processes such as depth perception and avoidance. For example, Campos, Langer, and Krowitz (1970) examined the visual cliff responses of prelocomotor infants by placing them on either the shallow or deep side and monitoring their cardiac rate. Contrary to the author's expectations, infants placed on the deep side

exhibited cardiac deceleration, a response indicating orienting or attending to a novel stimulus array, and not cardiac acceleration, associated with a fear or startle response. These findings suggest that, at early stages of development, lower level, non-perceptual processes may determine differential responding on the visual cliff.

Interpreting the descent preferences of the control animals as being mediated by quantitative differences between the two sides of the cliff does not preclude the possibility of ontogenetic changes in attention and/or responsiveness to visual stimuli: i.e., the control animals may, in fact, be more visually oriented on Day 16 than on days before and after, at least in a situation such as that presented by the visual cliff. Thus, on Days 12 and 14, prior to complete eyelid opening, the animal's responsiveness was mediated by tactile stimuli, the intensity equivalent on the two sides. On Day 16, when the majority of control animals' eyes are completely open for the first time, visual cues may be temporarily prepotent over tactile cues, and responses may be mediated by visual information. The differences in visual stimulation produced by the two sides may render visual cues even more salient. The significant preference for the shallow side exhibited by the control animals on Day 16 may be just that: a preference for, or approach toward, the shallow side; it need not be viewed as the result of depth

perception and depth avoidance (which implies an innate fear of falling).

This interpretation suggests that the term "shallow side" may be inappropriate when discussing newborn animals, because it attributes to the newborn higher level perceptual functioning than is necessary. That is, while the young animal may respond to the shallow side in a manner that suggests a discrimination made on the basis of shallow vs. deep differences, the response may be governed by a discrimination based on quantitative differences in the stimulation produced by the two sides. For the present, however, the word "shallow" will be used (for lack of a better single-word expression), without implying such a designation by the newborn rat.

The subsequent decline in shallow preference on Days 18, 20, and 30 by animals in the control group can be similarly interpreted. These animals may become progressively less visually oriented after the initial day of eyelid opening, and the effective intensity of the sides again becomes equivalent, as the animal responds to tactile cues.

The preferential descending to the deep side by the animals from the experimental group on Day 14 is clearly visually-mediated, since tactile cues were identical on the two sides. These data, in conjunction with the data from the control animals, make interpretation in terms of

quantitative or intensity-based responsiveness, rather than appearance and disappearance of depth avoidance, even more compelling. The alternative interpretation, that preferential descending to the shallow side indicates depth avoidance, implies another highly unlikely possibility - that preferential descending to the deep side = shallow avoidance, or at least depth preference. The preferential descending to the deep side on Day 14 indicated that the experimental animals were able to use visual information at that age, and did so in the presence of conflicting tactile information. Their response to the visual cues, however, was quite different from that of their control littermates on Day 16, when most of the control animals' eyes were open. For the experimental group, the intensity of the deep side on Day 14 elicited an approach response, while at no age was that the case for the control group.

Of particular interest is the shift in descent preference by the experimental animals: on Day 14, they descended preferentially to the deep side, while by Day 20, they were descending preferentially to the shallow side. Unlike the control animals, it does not seem to be the case that the experimental animals were most visually oriented on the day they showed a shallow preference (Day 20); their behavior seems to have been equally visually oriented on Day 14. Their response to visual cues, however, was reversed by Day 20.

These data address two primary questions regarding visual cliff performance: first, the normal course of development of behavior on the visual cliff was investigated. The appearance of a shallow descent preference on Day 16, and no preference on days before and after, were discussed in terms of ontogenetic changes in effective intensity; it was suggested that the rat pup may be more visually oriented on Day 16, the first day of complete bilateral eyelid opening for the majority of subjects in this study. The data indicate that, considering the subsequent decline in such preference, the shallow preference observed on Day 16 is not likely to be due to depth discrimination and avoidance.

The second primary finding was that early availability of patterned visual input clearly altered the normal descent pattern on the visual cliff. This alteration was due in part to changes in the sequence of transitions in sensory mediation of visual cliff responding: premature mediation by visual cues at a time when responding was determined by tactile cues for the control group (Day 14), and visually oriented responding after the control animals were again responding to tactile cues (Day 20).

In addition to changes in the sequence of sensory mediation transitions, early eyelid opening led to differential use of the available visual information by the experimental animals. While the visually-mediated response

of the control animals, appearing only on Day 16, was an approach to the shallow side, the initial visually-mediated response of the experimental group (Day 14) was an approach to the deep side, a preference never shown by the control animals.

MULTIMODAL DISCRIMINATION

Except for the auditory and visual systems, all other systems are functional at or around the time of birth in the rat. Tactile and vestibular sensitivity have been demonstrated in the prenatal rat (Gottlieb, 1971), thermal sensitivity is present in the rat at birth (Alberts and Brunjes, 1978), and olfaction seems to function within hours of birth, indicated by the role it plays in early suckling (Teicher and Blass, 1977). It is possible, therefore, that early eyelid-opened pups may differ primarily with regard to the relationships between the latest-developing modalities, audition and vision. Since the other sensory systems have been exposed to considerable stimulation prior to Day 7 (the day of eyelid opening), there has been opportunity for organization of inputs and mediation of behavior by these modalities. Organization in these earlier-developing systems may be more stable and less easily affected by early availability of patterned visual stimulation.

The first two studies, of the effects of premature eyelid opening on homing and behavior on the visual cliff, examined one aspect of intersensory relationships, namely the nature of the stimulus to which pups are primarily responsive under conditions in which multimodal inputs are available. Those results indicated that transitions occur

in the sense system that predominantly mediates an infant rat's behavior. Homing is initially mediated by olfactory cues, and the onset of vision may be responsible for the normal decline in homing. On the visual cliff, prior to normal eyelid opening, responding is mediated by tactile cues; this is followed by a period of visual mediation, and finally tactile mediation. These transitions might be considered changes in the sense system that is dominant in directing an animal's attention and/or influencing its perceptions. Sensory dominance might affect pups' responsiveness in a variety of ways. If attending to one modality precludes attention to others, then in the presence of multimodal inputs, a pup may ignore inputs from a non-dominant sense system. This may be beneficial if the task or situation at hand requires attention to one modality and exclusion of other modalities' inputs, as would be the case if the pup were required to attend to olfactory cues only, to the exclusion of visual, auditory, or tactile cues. This system would inhibit potentially disruptive effects on learning from simultaneous multimodal stimulation. It would be detrimental, however, if a task required attention to multimodal stimulation simultaneously: for example, if the solution to a problem necessitated attention to both auditory and visual stimuli. In that case, attending to only one modality's inputs would obviously hinder performance.

Sequential Control of Behavior

In the normal rat, the sequential onset of sensory system functioning (Gottlieb, 1971) may at least contribute to the sequential changes in sensory control of behavior. These have been described (Schneirla, 1965; Birch, 1962) as developmental shifts in dominance: from proximal receptor systems (e.g., tactile, olfactory), to dominance by distal receptor systems (e.g., visual, auditory). These sequential processes may be advantageous for the animal to the extent that they reduce competition between inputs from various modalities (Turkewitz and Kenny, 1982). Prior to onset of auditory and visual functioning, for example, behavior might be more easily organized around inputs from earlier-developing modalities than would be the case if the animal had to contend with inputs from all senses, simultaneously. Following organization at some level, the introduction of input from a later-developing modality would be less likely to disrupt behavior, but rather would be assimilated into the existing framework.

Intersensory Integration vs. Attention to Multimodal Inputs

A variety of interactions among sensory systems are possible, some of which have already been discussed; intersensory interactions have been loosely categorized as

types of intersensory integration, although not all aspects of these interactions involve integration of sensory stimulation.

Intersensory integration includes what has been called cooperation between the senses (Ryan, 1940), and there are different types of cooperative functions. One type is intersensory equivalence: the ability to recognize the same stimulus in different modalities, e.g., recognizing that the sound of mother's voice and the sight of mother's face, presented separately, specify the same stimulus - mother. This ability requires cross-modal transfer of information. Another type of cooperative function involves the use of multimodal inputs, where multimodal inputs are used to specify a given stimulus and contribute to the perception of a unified whole. Intersensory equivalence is considered the more sophisticated process of the two, because it requires that the organism detect and respond to similarities and differences across modalities.

Turkewitz and Kenny (1982) previously hypothesized that early eyelid opening would adversely affect intersensory integration, specifically the second type of cooperative function - integration and processing of multimodal inputs to specify a unified whole. The increase in competition between developing systems produced by the premature availability of visual stimulation might hinder the pups' ability to integrate new information into their

existing framework. As a result, the pup might fail to adequately integrate multimodal inputs, and this deficiency might continue into adulthood.

A third type of multimodal process does not involve intersensory transfer or integration of information, but attention to multimodal inputs simultaneously. An example of a task requiring attention to simultaneous multimodal inputs is a conditional discrimination, where an animal must respond to a light one way in the presence of a tone, and another way in the absence of a tone. It is this third type of intersensory process that is examined in this study.

The normal rat may develop an attentional and/or perceptual processing strategy that reflects the sequential utilization of sense systems, and favors attention to unimodal stimulation, rather than simultaneous multimodal stimulation. That is, since as a pup, the rat did not have to contend with inputs from all modalities simultaneously (due to limited functioning in various sense systems), this may contribute to an adult strategy that preferentially attends to unimodal stimulus inputs, to the exclusion of other modalities' inputs.

Conversely, the pup whose eyelids have been prematurely opened has had more opportunity for experience with multimodal inputs, and has had to contend with simultaneous stimulation from the well-developed thermal

and olfactory systems, plus the newly-developing auditory system, plus the prematurely developing visual system. It may not have had the opportunity for sequential attention or processing of multimodal stimuli that the normal pup has had. This history may contribute to an adult strategy that permits attention to simultaneous multimodal inputs.

The third experiment was designed to test this possibility: that as adults, pups whose eyes have been opened prematurely will perform better than their control littermates as adults on a task that requires attention to simultaneous multimodal inputs, specifically, auditory and visual stimuli. There were three stages of training, all requiring acquisition of an operant discrimination: 1) a simple visual discrimination, 2) a simple auditory discrimination, and 3) a complex auditory-visual discrimination - the multimodal condition. Stages one and two of training were included to determine whether experimental and control pups were comparable in their ability to attend to and discriminate auditory and visual cues. In stage 3, the animal had to discriminate a multimodal stimulus compound (auditory-plus-visual) from a simple unimodal stimulus (auditory or visual). If the experimental animals are more likely to attend to simultaneous multimodal inputs, then they should perform better than the control animals in the complex auditory-visual discrimination. Stage 3 also permitted

examination of the relative discriminability of the unimodal auditory vs. unimodal visual stimulus from the multimodal compound for experimental and control groups, i.e., whether either group was more likely to make errors when the auditory stimulus was the unimodal cue vs. when the visual stimulus was the unimodal cue.

Performances on three discrimination tasks were compared. In the simple visual discrimination, subjects were trained to approach and press one of two levers; which lever was correct on any trial was signalled by a visual stimulus. In the simple auditory discrimination, an auditory stimulus signalled which was the correct lever. The third discrimination task required the animal to attend to both auditory and visual stimuli. In this complex auditory-visual discrimination, the correct lever was identified by an auditory-plus-visual stimulus compound. Simultaneously, the animal was presented with a unimodal stimulus, associated with the incorrect lever; the unimodal stimulus was either the auditory or visual stimulus presented alone.

Method

Subjects

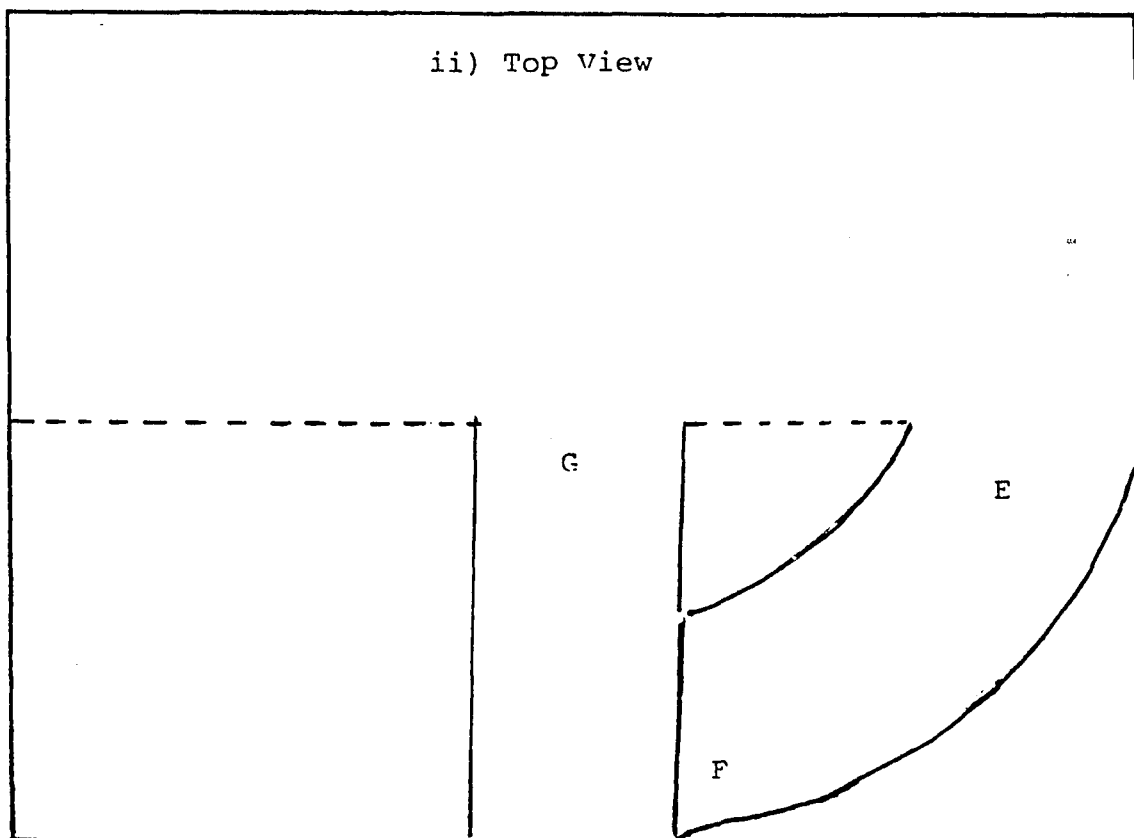
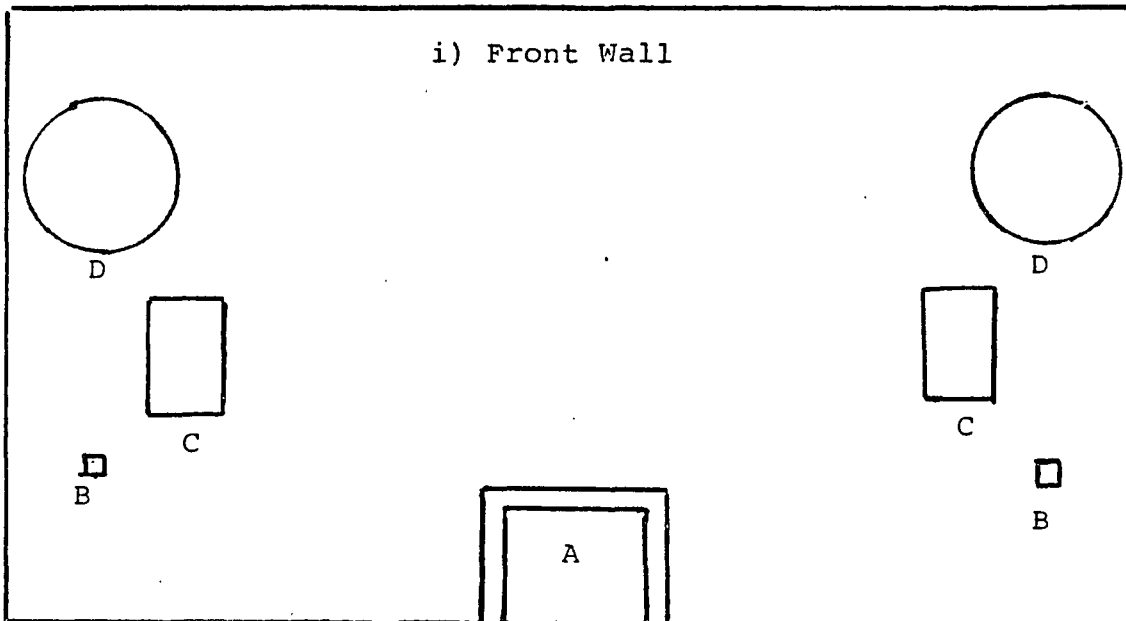
Fourteen males (six control, eight experimental) were selected from the pool of subjects from Homing Studies I and II; selection was determined by current space avail-

ability in the vivarium. They were separated from their litters on Day 22, and reared singly in standard suspended stainless steel cages (9-1/2" L x 7" W x 7" H), housed in a small windowless vivarium. Subjects were provided with ad lib. water and Purina Rat Chow, and were handled only for weighing, approximately once/week. Lights were on from seven AM to seven PM; all testing took place during those hours. When subjects reached 100-110 days of age, they were food-deprived until they had reached 80% of their ad lib. weight, at which point magazine training began.

Apparatus

A rectangular chamber was constructed of 1/4" steel mesh (14-1/2" L x 11" W x 8" H), reinforced with 1/8" rods along the sides (see Fig.18). In the center of the front wall (the longest wall) was a food hopper (A); food pellets (45 mg., Noyes Co.) were delivered via a tube from a pellet dispenser (Gerbrands) located outside the chamber. On either side of the hopper, 1" from the right and left sides, were mounted omnidirectional levers (Gerbrands) (B). The lights providing the visual stimuli were mounted on the outside of the front wall, the right light above and slightly to the left of the right lever, the left light above and slightly to the right of the left lever (C). Each light consisted of a small bayonet-based lamp (#47, 7.3 volt) mounted in a plastic reflector, and covered by a 1" x 1-1/2" piece of translucent plexiglass. This assembly

Figure 18. Schematic diagram of experimental chamber built for operant discrimination training. See text for description.



was mounted on the outside of the front wall, the plexiglass flush with the mesh and facing inward. When the lamp was on, the effect produced was a glowing rectangle, 1" x 1-1/2".

Directly above the levers on either side, speakers, produced by separating the earpieces of a pair of headphones (Grason-Stadler), were mounted on the outside of the chamber, facing inward (D). The white noise stimulus was produced by a Grason-Stadler noise generator (Model 901B), located outside the chamber. The output of the noise generator went through an interface (Interfacer 80, Alpha Product Co.), which, via switch openings and closures, pulsed the noise on and off at a rate of approximately 500 msec on-250 msec off.

To monitor the animal's activity at the food hopper, a photocell was attached outside the hopper; a small, bayonet-based lamp (#47), mounted outside the hopper, was directed at the photocell. This hopper light also provided the chamber's only illumination during testing, other than the visual stimuli; it remained on for the duration of a session.

On the right side of the chamber was a narrow (3" wide) passageway (E), leading to the back; a top-hinged door hung at the end of the passageway (F). When the animal passed through the doorway, it closed a switch, made a 90-degree right turn, and emerged with its head in the

middle (G) of the chamber (the observing response). The switch closure turned on the stimulus(i) with the animal facing the front, a position in which there was at least a 60-degree angle between head and speakers, maximizing localizability of the auditory stimulus.

The entire experimental chamber was placed in a sound-attenuating chamber (Industrial Acoustics Company). A computer (Radio Shack TRS80, Model III), with connected interface, was located outside the chambers; programs were written to control all stages of training.

Magazine Training Program

The magazine training program timed inter-pellet intervals (IPIs) and directed pellet delivery via an output relay on the interface. An input line on the interface monitored voltage changes from the photocell, and if a voltage increase was detected during an IPI, the program reset timing of that interval to zero.

Observing Response and Lever-Press Shaping

Observing response and lever-press shaping were controlled by the experimenter, who directed the computer to deliver reinforcement for progressively closer approximations of desired responses.

Operant Discrimination Programs

For the three discrimination task conditions, a session began when the hopper light was turned on; the

animal then determined the onset of the stimulus(i) by opening the swinging door, thus closing a switch. Presentation of stimuli on the right or left was determined by a Fellows series (Fellows, 1967) that was written into the program. The Fellows series allowed equal distributions of right and left presentations, with a maximum run length of three presentations to any one side. When a lever press occurred, the stimulus was terminated. If the lever press (right or left) matched the value from the Fellows series currently in effect, the response was correct. If correct, reinforcement was delivered and the appropriate variables incremented (the number of trials completed and the number of responses correct on the right or left levers). After the animal had been to the hopper (monitored via the photocell), if the number of trials was < 300, another trial began with reading of the next value of the Fellows series and waiting for the observing response switch closure. If the lever response was incorrect, the appropriate variables were incremented (number of trials completed and number of responses incorrect on the right or left levers), and if the number of trials was < 300, another trial began. After an incorrect response, the Fellows series value previously in effect remained in effect, and the next trial began with waiting for the observing response switch closure. When the number of trials completed = 300, the hopper light was turned off,

the data printed on the screen, ending that session.

Data Collection

In addition to counting the number of responses correct and incorrect, the distributions of correct and incorrect responses on the right vs. left levers were recorded. For the complex auditory-visual discrimination, in addition to the above-mentioned divisions, data were also categorized according to the type of unimodal stimulus, i.e., auditory vs. visual. For this condition, therefore, there were eight subdivisions in collection of the data: number of correct responses on the right vs. left and number of incorrect responses on the right vs. left when light was the unimodal stimulus, and the same four categories for trials with sound as the unimodal stimulus.

Procedure

Upon reaching 80% ad lib. weight, each subject had two sessions of magazine training in the chamber (the levers and swinging door were removed for this phase). Pellets were delivered on a variable time three-minute schedule; timing of the IPIs began when the animal removed its head from the hopper. Insertion of the head prior to the completion of any IPI reset timing to the beginning of that interval. From this point on, all training took place on consecutive days. On the third day, the animal was shaped to enter the passageway and go through the doorway - the observing response; lever-pressing was then shaped.

Training of the first discrimination task began immediately after.

Each subject learned three discrimination tasks, in the following sequence: simple visual discrimination, simple auditory discrimination, complex auditory-visual discrimination. Training in each condition continued until the subject reached a criterion level of at least 80% correct on a minimum of 150 trials, for two consecutive sessions. Upon reaching criterion in one condition, each animal progressed to the next. In addition, after learning the complex auditory-visual discrimination to criterion level, each animal was run for one additional session of that condition.

In all three conditions, each session ended after completion of 300 trials or passage of three hours, whichever happened first. A correction procedure was used for each condition, and went into effect after an incorrect response: on the next trial, the relevant stimulus was on the same side as in the previous trial, and remained so until the animal made a correct response, i.e., switched levers. After a correct response, presentation of the stimulus on the right or left again became determined by the Fellows series.

Simple Visual Discrimination

The animal started a trial with an observing response, turning on the light above one of the levers. A correct

lever press, i.e., pressing the lever under the light that was on, was reinforced with a food pellet, turned off the signal, and ended that trial. The next trial began with another observing response. Presentation of the stimulus on the right or left side was determined by a Fellows series.

Simple Auditory Discrimination

This was procedurally identical to the visual discrimination, but an observing response initiated the auditory stimulus. The pulsed noise continued until a lever press occurred. All other contingencies and the patterning of right-left stimulus presentations were as described for the visual discrimination.

Complex Auditory-Visual Discrimination

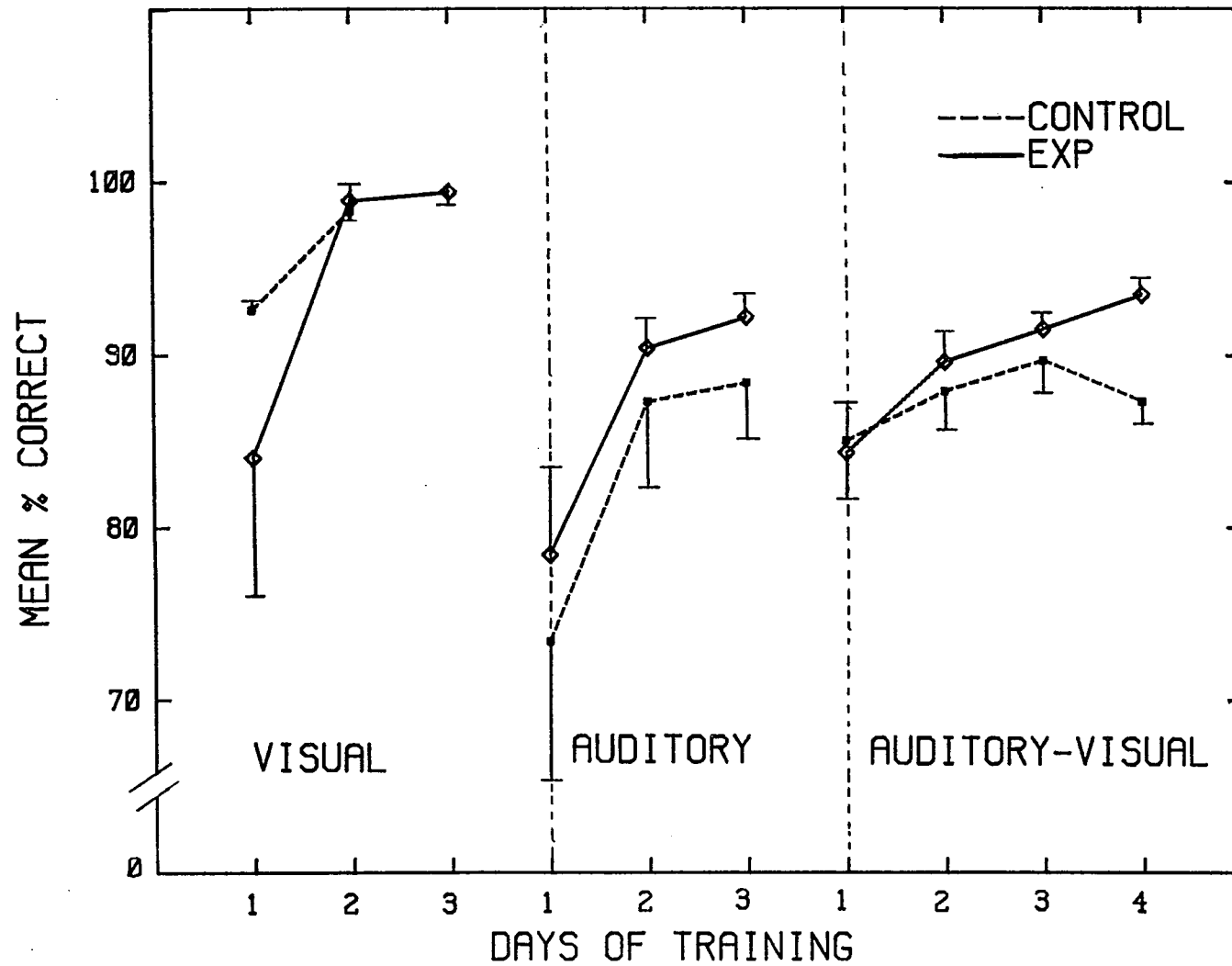
An observing response turned on a stimulus compound on one side, produced by the simultaneous presentation of the auditory and visual stimuli, and a simple stimulus on the other side, either the auditory or visual stimulus. The correct response was a lever press on the side with the multimodal stimulus compound; conversely, the animal responded incorrectly when it pressed the lever on the side with either the auditory or visual stimulus presented alone. As in the other conditions, stimulus presentations on the right or left were determined by a Fellows series, but for this condition, two series were used, values from one series alternating with values from the other series.

The computer read two values to determine each presentation of stimuli: one value determined whether "correct" (i.e., the auditory-visual stimulus compound) was on the right or left, and the other determined which stimulus (the auditory or visual) was on the "incorrect" side, i.e., whether the auditory or visual stimulus was the unimodal stimulus for that trial. These series were arranged so that approximately 50% of the time the left was the correct lever and 50% of the time, the right was correct. Similarly, presentation of the auditory vs. visual stimulus alone was distributed approximately evenly: 50% of the time, the auditory stimulus was presented singly, and 50% of the time the visual stimulus was presented singly.

Results

The mean percentage of correct responses on each day of training in the three conditions for experimental and control groups is shown in Figure 19. The three discriminations were learned by both groups, and within a condition, the pattern of acquisition did not differ significantly for the two groups. In the visual condition, all animals in both groups reached criterion level in two sessions, except for two experimental animals, who required three sessions. Although the mean per cent correct responses of the control animals on Day 1 of visual training was 92.6 vs. 34.0 % for the experimental animals,

Figure 19. Mean per cent correct responses for experimental and control animals as a function of days of training in visual, auditory, and auditory-visual discrimination tasks. While N=6 control, 8 experimental animals, all animals did not require the same amount of training to reach criterion. Thus, for the visual condition, the Day 3 point represents two experimental animals; in the auditory condition, five experimental and three control animals required three days of training; and in the auditory-visual condition, two experimental and two control animals required four days of training. Bars indicate standard errors. See Appendix, Table F, for means and standard errors.



this difference was not significant ($t(df=12)=.94, p>.05$), and the means of the two groups on Day 2 were nearly identical (experimental = 98.9%, control = 98.3%).

In the auditory condition, all animals in both groups learned the task to criterion within three sessions; three experimental and three control animals required only two sessions. None of the differences in scores between the two groups were significant. For the auditory-visual condition, six experimental and four control animals learned the task to criterion level within two sessions. The remaining two experimental and two control animals reached criterion level within three sessions. Again, no differences in either percent correct or days to criterion between the two groups were significant.

To determine whether the two groups differed in their transition from one condition to the next, the data were also analyzed for differences between conditions. There was a significant drop in performance when animals began auditory training, compared to their performance on the last day of training in the visual condition: to 78.4% correct (from 98.9%) for the experimental group ($t(df=7)=4.83, p<.01$), and 73.4% correct (from 98.3%) for the control animals ($t(df=5)=3.46, p<.02$). Every animal in both groups made more errors on the first day of auditory training than on the final day of visual training.

There was also a decrease in mean percentage correct

between the last day of auditory training and the first day of auditory-visual training. While the difference for the experimental animals only approached significance ($t(df=7)=2.26, p<.10$), the scores of the control animals decreased significantly on the first day of auditory-visual training as compared to the final day of auditory training ($t(df=5)=9.0, p<.01$). Thus, when the control animals were first required to choose the lever associated with the multimodal stimulus compound, and not the lever associated with either type of unimodal simple stimulus, they did significantly worse than they had in the simple auditory session which immediately preceded.

It is not apparent from the figure that the comparison of control data on the last day of auditory training vs. the first day of auditory-visual training should yield a significant difference, while the comparison of experimental data on those days did not produce a significant difference. This discrepancy was due to the inclusion of the data from two experimental animals, whose difference scores were extremely deviant, and lay well outside the range delimited by two standard errors of the mean. When the data from these animals were omitted, the standard error term was nearly halved (3.13 vs. 1.84), but the mean difference was reduced by more than half (7.08 vs. 2.77). The resulting t-value was even smaller and farther from reaching significance ($t(df=5)=1.5, p>.10$). Thus,

whether or not these data were included, the decrease in scores from the last day of auditory training to the first day of auditory-visual training was not significant for the experimental animals, but was significant for the control animals.

There were two types of errors made during auditory-visual training: 1) choosing the lever associated with the simple auditory stimulus, and 2) choosing the lever associated with the simple visual stimulus. The distributions of these two types of errors were very similar for the two groups, and so these data were combined for analysis. On all days of training, more errors were made on those trials when the simple visual stimulus was associated with the incorrect lever than when the simple auditory stimulus designated the incorrect lever; however, the proportion each contributed changed as training progressed. On Day 1, 60% of the errors were made on trials when the incorrect lever was associated with the simple visual stimulus, while by Day 3, errors made on those trials accounted for 83% of the total. This increase was not due to an increase in the number of errors made on trials when the visual stimulus was associated with the incorrect lever (that number remained relatively constant across days), but to a decrease in errors made when the auditory stimulus was associated with the incorrect lever. By Day 3, the mean number of errors made by all animals in

both groups on trials when the auditory stimulus signalled the incorrect lever was 4.3, vs. a mean of 21.6 for trials when the visual stimulus was associated with the incorrect lever ($t(df=13)=8.07, p<.01$).

Both groups of animals exhibited a preference for the left lever, strongest in the first phase (visual), and most of the errors were the result of this position preference. The correction procedure maintained equal distribution of reinforcement on the right and left levers, however; the animal was never reinforced for perseverating on the left lever, and this preference declined as training progressed.

Discussion

Experimental and control animals were remarkably similar in their performances on the three discrimination tasks: in fact, at no point did the two groups differ significantly from each other. While the comparison of primary interest, that of the performance of the two groups in the multimodal condition, did not yield a significant difference, there was a suggestion of that difference in the intragroup comparison. In the transition from the simple auditory condition to the multimodal condition, the performance of the control animals declined significantly, while there was no significant difference in the same comparison for the experimental animals. These results tend to support the view that premature eyelid opening

facilitates attention to multimodal stimuli: the control animals exhibited more difficulty with the multimodal task as compared to the simple discrimination task. However, in view of the absence of any significant difference in the intergroup comparison of performances in the multimodal condition, the data offer only weak support for this position.

Given the findings of reliable effects of early eyelid opening during early stages of development, there are several possible explanations for the absence of differences between experimental and control animals as adults on the multimodal task. Whatever the effects of early eyelid opening, they may be restricted to early stages of development, and may abate by adulthood; that would not reduce the significance of such effects, however. In addition, the fact that terminal behaviors may be similar does not necessarily indicate that intermediate behaviors were similar; the developmental paths taken to reach similar ends may be quite different.

The impoverished environments of these animals (the small, bare, stainless steel cage) may have contributed to the similarities between the two groups. Being reared in an enriched environment might encourage the maintenance and development of differences that exist between the two groups as pups.

The two groups may, in fact, differ as adults in their

use of multimodal cues, but the methods used may not be the ideal ones for investigating those differences. The prior experience with the simple auditory and visual stimuli in the first two stages of training may have equalized the two groups as they began the multimodal task. Starting animals in the third stage, with no prior experience, might serve to emphasize any differences between them in their attention to multimodal cues.

Finally, the somewhat arbitrary nature of the tasks may have contributed to the absence of any differences between the two groups. Perhaps rats ordinarily use auditory and visual cues so infrequently that the locus of effects of the experimental manipulation lies elsewhere. Also likely is the possibility that the tasks were too easy, and that utilizing difficult tasks that taxed the rat's abilities might serve to differentiate the two groups.

At this point, the lack of effect should not be considered a strong indication that further investigation is unwarranted. Comparison of these animals on tasks requiring actual intersensory integration or transfer of multimodal information might uncover differences not brought to light by this study, and indicate more persistent effects of the premature availability of visual input.

CONCLUSIONS

These investigations were a preliminary attempt at gathering evidence for a theory of development that takes a position somewhat at odds with a prevailing view of development, that "earlier is better" and "the more the better". One aspect of that theory states that, rather than viewing differences between adults and infants as deficiencies in the infant, it may be more meaningful "...to view the somatic and behavioral capacities of the developing organism as uniquely adapted to that organism's current stage of development" (Turkewitz and Kenny, 1982, p. 358). Part of the somatic capacities of the developing organism are limitations on functioning of sensory systems, and according to this view, removal of those limitations on functioning should be maladaptive for the organism.

Early eyelid opening clearly removes a normally-occurring limitation on sensory functioning: it permits - potentially, at least - patterned visual stimulation at a prematurely early age. Precisely what the experimental pups can see upon early eyelid opening remains, to a large extent, to be systematically examined. But the findings make it abundantly clear that they do use this prematurely available visual information. Following early eyelid opening, pups attend to visual cues prior to the normal day of eyelid opening, and they respond to visual cues in a

manner different from their control littermates, once their eyes have opened.

In the homing study, for example, premature eyelid opening led to prolonged and increased home orientation, past the age at which it normally declines. The fact that reducing visual cues associated with the nest resulted in homing behavior that did not differ from normal, indicated the importance and utilization of visual cues by the experimental animals. In the study of visual cliff behavior, experimental animals responded in a visually-mediated manner at 14 days of age; this response, however, was preferential descending to the deep side. There was a shift in preference by the experimental animals, and by Day 20, their visually-mediated response was preferential descending to the shallow side. The control animals' behavior was quite different: on Day 14, their responses were tactually-mediated and indicated no preference; on Day 16, they responded in a visually-mediated manner, but unlike the initial visually-mediated response of the experimental animals, they descended preferentially to the shallow side. On subsequent days, the control animals showed no descent preference, indicating tactile mediation.

What is not clear or obvious is whether the premature utilization of visual information would be adaptive or maladaptive in the rat's normal environment. How might prolonged orientation to the home, found in the first study

for the experimental pups, be considered maladaptive? As already pointed out, following the first two weeks of the litter period, the home becomes less and less the center of activity: the pups leave the nest more and more, and approach the mother outside the nest to suckle. One can at least speculate that continuing to return to the nest when littermates and mother are not likely to be found there would deprive the pup of whatever experience is provided by excursions and encounters outside of the home, and delay the onset of independent functioning.

The behavior of the experimental animals on the visual cliff is particularly interesting in view of the behavior of their control littermates. The results strongly suggest that normal rat pups are more visually oriented on Day 16 than on days before and after, at least in a situation such as that presented by the visual cliff. The fact that Day 16 was the first day of complete bilateral eyelid opening for the majority of control animals in that study suggests a causal relationship between eyelid opening and visually-oriented behavior. The onset of availability of patterned visual stimulation for the normal rat may result in something analogous to what Piaget has called disequilibrium. Although his emphasis was primarily with regard to cognitive development, disequilibrium may be a useful concept in understanding perceptual development. Prior to normal eyelid opening, the pup's behavior may be

organized around the existing sensory inputs, primarily tactile, thermal, and olfactory. Eyelid opening permits the emergence of competition from the visual system, and this may result in the disruption of a stabilized organization, providing the basis for a subsequently more advanced reorganization of function. The attention to and utilization of visual cues by the control animals may be a symptom of this disruption. With time, the availability of visual information may become less disruptive and the information more readily assimilated (or ignored), as the pup ceases to be visually dominated.

Early eyelid opening clearly altered the normal pattern of sensory mediation on the visual cliff, and those effects might be attributable, in part, to the fact that the emergence of competition from the visual system occurred too early. The behavioral organization of the experimental pups on Day 7 may have been less stable than that of the control animals on their day of eyelid opening; they may not yet have fully assimilated and integrated the existing sensory inputs. If that were true, the emergence of visual competition on Day 7 would occur at a time when disruption might not be beneficial to the organism. Competition from the visual system at that premature stage might not pave the way for a more advanced reorganization, but might simply be disruptive to organization. The evidence indicates that early eyelid opening interfered

with normal organization and utilization of sensory information; it suggests that these effects were mediated, in part, by interference with the normal disruptive effects of eyelid opening.

The results of the third study, the multimodal discrimination indicated that early eyelid opening did not adversely affect the development or use of vision by experimental animals, as they learned the visual discrimination as readily and as well as control animals. This might be considered post hoc evidence that the differences found between the two groups as pups were not the result of malfunctioning of the visual system, but rather reflected perceptual or attentional differences.

Evolutionary Implications

In discussing the evolutionary adaptiveness of structures or functions, it is all too easy to resort to the ploy: what occurs naturally must be adaptive; therefore, what deviates from the normal must be maladaptive. The importance and validity of the results of these investigations do not rest, however, on how well they do or do not fit into an evolutionary scheme. They have indicated that a change in the normal sequence of functional onset of sensory systems can modify behavioral development. More specifically, the data have indicated that the removal of a normally-occurring limitation on

sensory functioning led to aberrant behavioral development. These results provide at least suggestive evidence for the potential selective advantage to the regular sequence of functional onset of the sensory systems, although such a sequence "...may be the result of constraints having to do with the development of other aspects of structure or function..." (Turkewitz and Kenny, 1982, p.360). The invariance of this sequence, which has been described as "...the most conservative feature of the evolution of embryonic behavior in vertebrates..." (Gottlieb, 1968, p.166), in such a wide variety of species, may suggest its adaptive importance.

These results, and the theory which prompted them, suggest several directions for further research. Observing these animals as pups in a more natural setting - in the home cage with mother and littermates - would provide information about their interactions in and out of the home. Since suckling is a very early-developing response that is not based on visual cues, it would be interesting to investigate whether or not early eyelid-opened pups would attach and suckle as effectively as normal pups. Neuroanatomical and neurophysiological studies of these animals could determine what, if any, structural or electrophysiological changes occur as a result of early availability of patterned visual information. Also suggested is the reverse manipulation - keeping pups'

eyelids closed past the normal day of opening.

While the results are not conclusive and are open to alternative interpretations, they provide a basis for launching what promises to be a very fruitful area of study.

APPENDIX

Table A
 Median Activity Scores of Pups From
 Homing Study I
 (Median \pm Semi-Interquartile Range)

Age (days)	Control (N=14)	Experimental (N=14)
6	.5 \pm 1.0	1.0 \pm 1.0
8	3.0 \pm 1.25	3.0 \pm 2.0
10	4.0 \pm 1.25	5.0 \pm 2.0
12	6.0 \pm .5	6.0 \pm 1.25
14	7.5 \pm .75	8.0 \pm .75
16	8.0 \pm 1.0	7.5 \pm 1.25
18	8.0 \pm 1.0	8.0 \pm 2.0
20	9.0 \pm 2.75	7.0 \pm 1.5

Table B

Mean Proportion of Available Time*
Spent in the Home (once pup reached home) By
Pups from Homing Study I (Means of 3-trial means)
(Mean \pm Standard Error)

Age (Days)	Control (N = 14)	Experimental (N = 14)
6	.41 \pm .05	.40 \pm .06
8	.51 \pm .05	.56 \pm .07
10	.63 \pm .05	.67 \pm .03
12	.66 \pm .04	.70 \pm .04
14	.66 \pm .05	.70 \pm .04
16	.64 \pm .06	.72 \pm .04
18	.75 \pm .04	.75 \pm .05
20	.73 \pm .05	.85 \pm .04

*seconds

Table C
 Mean Homing Ratios of Pups From
 Homing Study I
 (Mean \pm Standard Error)

Age (Days)	Control (N=18)	Experimental (N=18)
6	.42 \pm .05	.44 \pm .06
8	.57 \pm .06	.58 \pm .07
10	.47 \pm .07	.57 \pm .06
12	.62 \pm .08	.70 \pm .06
14	.70 \pm .08	.67 \pm .06
16	.65 \pm .07	.68 \pm .07
18	.55 \pm .08	.67 \pm .07
20	.68 \pm .09	.80 \pm .06

Table D
 Mean Activity Scores of Pups From
 Homing Study II
 (Means \pm Standard Errors)

Age (Days)	Control (N=19)	Experimental (N=19)
6	.86 \pm .35	.79 \pm .22
8	1.54 \pm .32	2.64 \pm .49
10	5.26 \pm .54	4.40 \pm .58
12	7.34 \pm .70	5.15 \pm .38
14	11.82 \pm 1.13	9.24 \pm 1.04
16	17.97 \pm 1.16	18.64 \pm 1.28
18	17.64 \pm .89	20.11 \pm 1.30
20	14.87 \pm .80	15.26 \pm .56

Table E
 Mean Homing Ratios of Pups From
 Homing Study II
 (Mean \pm Standard Error)

Age (Days)	Control (N=19)	Experimental (N=19)
6	.28 \pm .02	.26 \pm .03
8	.38 \pm .05	.33 \pm .06
10	.39 \pm .06	.45 \pm .06
12	.52 \pm .06	.40 \pm .05
14	.36 \pm .05	.25 \pm .06
16	.25 \pm .04	.24 \pm .06
18	.23 \pm .05	.26 \pm .04
20	.25 \pm .06	.17 \pm .04

Table F

Mean Per Cent Correct Responses of Animals in the
Multimodal Discrimination Study, on Each Day of Training
in the Visual, Auditory, and Auditory-Visual Conditions
(Means \pm Standard Errors)

VISUAL

Day	Control (N=6)	Exper. (N=8)
1	92.6 \pm .42	84.0 \pm 7.8
2	98.3 \pm .42	98.9 \pm .38
3	—	99.4 \pm .32 (N=2)

AUDITORY

Day	Control (N=6)	Exper. (N=8)
1	73.4 \pm 7.4	78.4 \pm 3.8
2	87.3 \pm 5.0	90.4 \pm 1.8
3	88.4 \pm 3.1 (N=3)	92.2 \pm 1.2 (N=5)

AUDITORY-VISUAL

Day	Control (N=6)	Exper. (N=8)
1	85.0 \pm 2.2	84.3 \pm 2.4
2	87.9 \pm 2.1	89.6 \pm 1.5
3	89.7 \pm 1.8	91.5 \pm 0.8
4	87.3 \pm 1.2 (N=2)	93.5 \pm 1.1 (N=2)

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