in response to alternating gratings can be useful to distinguish peripheral from central diseases of the visual neural pathway. Our findings supply a pathophysiological interpretation for recently reported clinical findings on impairment of pattern reversal ERG in patients with retinal degeneration, optic neuritis, and amblyopia.7-11

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Key words: ERG, flash stimulus, pattern stimulus, ganglion cells, occlusion, retinal artery, retrobulbar optic neuritis

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Development of binocular depth perception in kittens. BRIAN TIMNEY.

By means of the jumping stand technique, binocular and monocular depth thresholds were measured in kittens 4 weeks to 4 months old. Binocularly, performance improved very rapidly during the fifth and sixth weeks, coinciding with the maturation of cortical disparity-specific neurons. Discriminations made monocularly took longer to learn and thresholds were consistently poor. The results demonstrate that kittens can use binocular cues for depth at a very early age.

Under most circumstances, judgments about the relative distance of nearby objects are far more accurate if a person can use both eyes rather than one. The primary cue contributing to this binocular superiority is retinal disparity, and a great deal is known about stereoscopic depth perception in adults. However, it is only recently that data about its origin and development have begun to accumulate. I have been studying this problem in kittens using a behavioral technique and find evidence for binocular superiority at least by the end of the fifth week of age. These data coincide with physiological evidence showing that binocular neurons develop their disparity specificity over the first few weeks of life. The results suggest that these disparity-specific cortical neurons, which are thought to underlie stereopsis, are functional from a very early age.

Most previous studies of depth perception in young animals have used the visual cliff technique developed by Walk and his colleagues, who have shown that kittens begin to discriminate the deep from the shallow side reliably by the end of the first month. The visual cliff technique relies on the natural tendency of animals to avoid stepping over a sharp drop, and it has proven invaluable in demonstrating that very young animals are able to discriminate large differences in depth. However, the procedure seems inappropriate for obtaining accurate threshold measurements, perhaps because the threshold for caution with respect to a cliff is greater than that for recognizing that a slight difference in height is present.

The present study capitalized on the kitten’s tendency to descend to the closer appearing of two surfaces, rewarding such responses with a small amount of food and punishing attempts to go to an apparently more distant surface with a loud (>95 dB) high-frequency (4.5 kHz) tone. The procedure is a modification of the jumping stand technique used by Mitchell et al. for measuring visual
The apparatus has been described in detail elsewhere\(^1\) and is illustrated in Fig. 1. The kittens descended onto the apparatus from a jumping platform of variable height (not shown). When training first began, this platform was situated almost flush with the landing surface so that the kittens could simply step down to either side of the centerboard. As the animals became older and more agile, the platform was raised until the jumping height was between 70 and 80 cm. It might be noted here that by the age of 30 days kittens are becoming quite skilled at getting around and any limitations in performance almost certainly are not because of their inability to perform the task.

Initially, the opaque mask of the apparatus was removed to provide the maximum number of cues. The stimuli placed on each arm of the seesaw consisted of a set of dots, varying in size from 8 to 20 mm, which were distributed randomly over the surface. The number of dots per unit area was approximately 25%. The kittens were trained to go toward the closer arm, which was placed 20 cm higher than the other arm. They were prevented from falling by the presence of the transparent Plexiglass cover. The side of the closer arm was switched randomly over trials. Once a kitten had mastered this problem to a criterion of 27 correct out of 30 consecutive trials, the mask was replaced to reduce the number of possible depth cues. The kittens were retrained if necessary, and the threshold measurements were begun. Thresholds were obtained with a modified staircase procedure, in which the separation was decreased if the kitten achieved criterion (4 out of 5 correct) and increased if the kitten failed to meet criterion. Threshold was taken as the smallest separation at which a kitten performed consistently with a minimum of 70% correct when trials were summed over a session. Testing was conducted both binocularly and monocularly, the latter conducted when the kittens wore an opaque occluder over one eye. In the present study, five kittens were tested, although they were not all tested through the full age range.

With the jumping stand it is possible to begin training kittens younger than 4 weeks, and we were able to obtain thresholds on normal kittens by about 30 to 35 days. Prior to this age the kittens typically were very distressed and paid little attention to the task. Once they had learned the discrimination they performed willingly when tested binocularly. However, when one eye was occluded with an opaque contact lens, performance deteriorated markedly. Most kittens no longer seemed to know what was required of them. Sev-
eral additional sessions were often necessary before it was possible to obtain a monocular depth threshold. It is unlikely that the poorer monocular performance was a result simply of the kittens' reactions to the lens; they paid little attention to it after it was inserted. Furthermore, other kittens that had been monocularly deprived by lid suture or made strabismic at the time of natural eye opening generally took much longer to learn the discrimination with the mask present than normal cats, suggesting that level of performance is controlled by the ability to use binocular cues.

The developmental functions for monocular and binocular thresholds also differed markedly (Fig. 2). To make a meaningful comparison between monocular and binocular performance, all thresholds were expressed in units of retinal disparity. In the binocular case, disparity was calculated in the conventional manner, taking into account interocular separation, viewing distance, and the separation of the targets. When the kittens were tested monocularly, threshold separations were converted to the angular retinal disparity that would have been present if both eyes had been open. No functional significance should be attached to these units, they simply provide a common measure. Binocularly, thresholds improved very rapidly up to the age of about 6 weeks. At this age the best kittens were able to discriminate a separation of 3 cm from a viewing distance of 40 cm, which is equivalent to about 20 min of retinal disparity. After the sixth week there was a gradual improvement toward adult levels. The normal adult cat is able to resolve a separation of 2 cm or less from a viewing distance of 70 cm, which represents a disparity of 5 to 10 min. Although there was some variability among animals, the best of them reached asymptotic values by about 80 days.

When tested monocularly, the kittens performed consistently worse than when they could use both eyes. As mentioned above, they took longer to learn the task initially, and even when they had learned it they required much greater separations to be able to discriminate between the two landing surfaces. Asymptotic threshold values were achieved also by about 80 days. At this age most kittens were able to resolve a separation of 10 cm from a distance of 50 cm, which is equivalent to about 30 min of retinal disparity. It may be seen from Fig. 2 that final monocular thresholds are worse by a factor of 5 or 6 compared with binocular thresholds.

It is possible that the very rapid improvement in binocular performance is because of the animals learning better the task required of them. However, the fact that they performed well with large separations and poorly when the separations were decreased suggests that they were aware of what to do but had reached the limits of their ability to discriminate depth.

The most striking feature of the present data is the very early age at which kittens are able to utilize binocular cues in discriminating depth compared with their use of monocular cues. It is difficult to quantify the magnitude of this difference, since we were unable to obtain satisfactory monocular thresholds when the kittens were very young. However, their behavior under the two viewing conditions was quite different. For the

![](image_url)
most part, with both eyes open they descended to the closer surface quite spontaneously; with one eye covered the task seemed unfamiliar to them and they had to be trained to go to the appropriate side. Also, when the height of the jumping platform was changed, the first few jumps of the kittens typically were very awkward when they were forced to use one eye.

The superiority of binocular thresholds, even in animals as young as 34 days, suggests that stereoscopic vision is present in very young kittens. Evidence for the mechanisms that would permit such an ability has been provided by Pettigrew. He reported that after the fifth week, the proportion of binocular neurons tuned for retinal disparity begin to approach adult levels. His data correlate well with the present finding of a rapid improvement in binocular performance during the fifth and sixth weeks. Taken together, the present results and those of Pettigrew provide strong support for the view that disparity-specific neurons underlie stereoscopic depth perception and that these neurons are able to mediate behavior as soon as they are physiologically mature.

Recent studies by Held et al. have suggested that similar developmental changes may take place in human infants. These authors found a very rapid improvement in stereacuity occurring over a period of just a few weeks. Their data, as well as those from the present study, suggest that the mechanisms for stereoscopic depth perception develop independently of those responsible for spatial resolution, which seem to develop with a much different time course.

I thank John Orphan for constructing the apparatus and Betty Kay Williams, Carla Schneider, and Cathy Fuller for help in testing the kittens.

From the Department of Psychology, University of Western Ontario, London, Canada. This research was supported by grant A7062 from NSERC Canada and MA 7125 from MRC Canada. Submitted for publication April 20, 1981. Reprint requests: Brian Timney, Department of Psychology, University of Western Ontario, London, Canada N6A 5C2.

Key words: stereopsis, kittens, visual development, depth discrimination

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