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Development of Visual Responsiveness in *Macaca nemestrina* Monkeys

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A battery of tests for assessing visual responsiveness was administered to 69 *Macaca nemestrina* monkeys ranging in age from 2 days to 6 months. Age changes were found on all of the tests. None of the responses could be consistently elicited at birth. Tests involving simple sensory capacities and orienting motor responses generally appeared first. Tasks requiring more complicated sensory processing or motor responses emerged at progressively older ages. By 5 weeks after birth normal monkeys ordinarily responded positive on all of the tests. The battery appears to be a convenient and effective screening tool for assessing whether a young monkey has normal vision. Age norms are presented in terms of the percent of animals at each age expected to respond positive on each test. These results are also compared to the development of analogous responses in human infants.

Macaque monkeys are becoming the species of choice to use as animal models for studying many forms of abnormal visual development (for a review see Boothe, 1981). Experiments with monkey models are usually, of necessity, restricted to small numbers of animals, and therefore it would be important to establish that an infant monkey has normal vision before assigning it to an experimental treatment group. In addition, it is often desirable to be able to quickly and efficiently assess the visual capabilities of a young monkey to determine whether a given treatment has produced a visual deficit. Casual observation of behavior can be misleading in this regard, and more rigorous testing methods often require either too much time to be practical or specialized equipment that may not be readily available.

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We have developed a battery of behavioral tests to assess the visual responsiveness of young monkeys. This battery has been used in our laboratory to assess the behavioral effects of dark rearing on monkeys (Regal, Boothe, Teller, & Sackett, 1976) and more recently to assess vision in naturally strabismic monkeys (Kiorpes & Boothe, 1981). Many of the tests are similar to those used to assess visuomotor behavior in normal and deprived cats (Norton, 1974; Van Hof-Van Duin, 1976). We have found this battery to be an effective and efficient method for quickly assessing whether a young monkey responds normally to visual stimuli.

These tests can be administered over a range of ages starting as early as 1 or 2 days after birth and, if the infants are used to being handled by humans, continuing up until 6–8 months. We have discovered that performance on these tests varies with age. Neonates fail to respond consistently on any of the tests, but there is a rapid postnatal development of these visual functions during the first month.

In this article we describe the postnatal development of responses to our battery of tests in infant pigtail monkeys (*Macaca nemestrina*) and present age norms for this species. While preparing this article, it came to our attention that a similar battery of tests has been developed independently for assessing visual responsiveness in young rhesus (*Macaca mulatta*) monkeys (Mendelson, 1982).

Method

Subjects

Data were obtained from 69 presumed normal *Macaca nemestrina* monkeys ranging in age from 2 days to 6 months. About 10 animals were tested at each age. Fourteen of the infants were tested at more than one age so that our results are a mixture of cross-sectional and longitudinal data. All infants were born at the Regional Primate Research Center and raised in the Infant Primate Nursery Facility at the University of Washington according to standard laboratory protocol (Ruppenthal, 1979).

Materials

These tests can be conducted with just a few props easily obtained or constructed: (a) A small hand-held light source (we used a penlight flashlight); (b) a small brightly colored object that can be moved about in front of the infant, such as a ball point pen or a small rubber toy; (c) a grating pattern of high-contrast, fat, black and white stripes (we constructed this by placing parallel strips of 2 cm black tape on a white piece of 30 cm × 60 cm cardboard); and (d) a soft, blunt object (we used a rolled up cloth diaper).

These tests are conducted in a room containing a table or a countertop. One of the tests requires testing behind glass. On this test we held the infant behind a window or a piece of plexiglas.

One person holds the monkey while a second person administers each test and makes a judgment as to whether the monkey's response is (a) positive, indicating that the monkey appeared to respond appropriately to the test; (b) negative, indicating that the monkey did not appear to respond visually; or (c) no test, indicating that no judgment could be made.

The person administering the test is instructed to make a forced-choice judgment between negative and positive whenever possible. However, there are two sets of conditions in which the experimenter is allowed to make a no-test judgment. First, the animal sometimes becomes too agitated or rambunctious to allow meaningful judgments about visual responsiveness. When this happens, the experimenter is allowed to score a no test rather than scoring the response as negative.

Second, it is sometimes impossible to elicit a particular required motor response even with nonvisual stimuli. We did not score such failures to respond as negative. In any instance where a monkey does not respond to one of our tests, the experimenter then attempts to determine whether the motor component of the response can be elicited by sound or tactile cues. If the required motor response cannot be elicited under these conditions, the test is scored no test rather than negative. More specific criteria to be used for making these judgments on the specific tests are described below. The specific tests administered and scored are:

1. *Visual tracking of a light.* The room is darkened and the monkey allowed a few seconds to adapt to the dark. Then the small light source is slowly moved from side to side in front of the monkey's face. Head and eye movements are examined and a judgment is made as to whether the monkey tracks the moving light.
2. *Visual tracking of a large object.* The experimenter positions himself or herself directly in front of the monkey and tries to establish eye contact. The experimenter then moves his own head and torso slowly from side to side and makes a judgment as to whether the monkey tracks these movements.
3. *Visual tracking of a small object.* The small brightly colored object is held in front of the monkey just beyond arm's reach. The small object is then slowly moved from side to side and a judgment is made as to whether tracking head or eye movements can be elicited.
4. *Reaching response.* The same small object as used for Test 3 is also used for this test. The small object is positioned within arm's reach and moved about in order to see if a reaching response can be elicited. The reaching movement does not have to be accurate to be scored positive as long as the experimenter makes a judgment that the monkey is attempting to reach out and grab the object. If the experimenter cannot get the monkey to respond, the object is touched to the monkey's nose. If the monkey does not respond even to a tactile stimulus, a no test is scored.
5. *Optokinetic nystagmus (OKN).* The grating is slowly moved back and forth across the monkey's field of view. The experimenter watches the monkey's eye movements in order to see if nystagmus can be elicited.
6. *Visual placing.* The same grating as is used for the OKN measurements is laid on top of the table so that the tabletop has high contrast contours. Then the monkey is held above the table with its head lower than the rest of its body. The monkey is slowly lowered toward the top of the table. The experimenter notes whether the animal reaches out and places its hands on the table as it approaches the tabletop. Occasionally an animal responds to being lowered even when no tabletop is present. In such cases the animal is lowered several times with no tabletop to try to habituate this response. A positive response is recorded only if the animal responds when lowered towards the tabletop but does not respond to being lowered when no table is present.

   If an animal does not respond, it is lowered to the table and its nose allowed to bump into the top of the table. If the nose bump does not elicit tactile placing, a no test is scored, but if it does, a negative is scored.
7. *Avoidance of impending collision.* The soft blunt object is slowly moved toward the monkey's nose. If the monkey does not move its head to avoid the impending collision, the object is bumped into its nose. Several repeated trials are given. If the animal grimaces or turns its head to avoid being bumped, the test is scored positive. If the animal just becomes generally agitated, but does not make specific responses correlated with the approach of the object, the response is scored negative.
8. *Blink response.* The experimenter jabs a finger toward the monkey's eyes in order to determine whether an eye blink can be elicited. This response must be dem-

onstrated behind glass—to eliminate air flow as a cue—before being scored as positive.

Results

Examination of the responses of individual monkey infants across the battery of tests reveals that the average 1-week-old infant responded positive on only 1.5 tests. Out of 12 infants tested during the first week, 4 responded positive on 3 tests, 2 on 2 tests, 2 on 1 test, and 4 failed to respond positive on any of these tests. On the other hand an individual animal over 1 month of age seldom fails on more than one or two tests in the battery. At intermediate ages there is a gradual increase in the number of positive items.

The order in which the positive responses emerge does not appear to be random, but instead follows an orderly progression. The responses most likely to be present near birth are visual tracking of a light and visual tracking of a large object. The responses most likely to appear next are the OKN response, visual placing, and visual tracking of a small object. Finally, at progressively later ages, the blink, reaching, and avoidance responses begin to appear.

Age norms for these test items have been determined by grouping the results from all of our infants into weekly age categories. For each age group we determined the proportion of responses on each test that were positive rather than negative. We ignored responses that had been scored as no test. The results are summarized in Figure 1.

The same progression in the order of appearance of the various responses as demonstrated in the grouped data is evident in our longitudinally tested monkey infants. To demonstrate this, we rank-ordered the eight test items for each longitudinally tested infant in terms of the order in which the items appeared for that infant. (In cases where two or more items both appeared at the same testing, they were assigned an equal mean rank.) Then we calculated the mean rank, across infants, for each test item. These mean ranks along with their standard deviations are shown in Table 1. They demonstrate an orderly progression in the same sequence as shown by the grouped data in Figure 1.

These results demonstrate that visual responsiveness develops over the first 5 weeks postnatal in this species. In this study during the first week after birth, there were only three tests on which at least half of the infants responded positive—tracking a light, tracking a large object, and OKN eye movements. Less than 25% of the infants responded positive on any of the other tests during the first week. By the third week after birth, about half of the infants tracked a small object and showed a visual placing response. More than half of the infants responded positive to all tests during the fourth postnatal week. All of the tests produced positive responses from more than 75% of the infants over 1 month of age, and several tests consistently resulted in 100% positive responses.

Table 1
Mean and Standard Deviation Rank Order of Appearance of Each of the Eight Test Items Calculated Across Monkey Infants Tested Longitudinally

Test item	*M*	*SD*
Visual track (large)	3.0	1.6
Visual track (light)	3.4	1.8
OKN	4.3	1.9
Visual place	4.3	1.7
Visual track (small)	4.5	1.5
Blink response	5.2	1.9
Reach response	5.5	2.0
Avoidance response	5.8	1.5

Note. OKN = optokinetic nystagmus.

Discussion

The development of visual responsiveness in pigtail macaques proceeds over the first postnatal month. The normative data presented demonstrate that positive performance on several tests of visual responsiveness, although easily elicited in older pigtail macaque monkeys, cannot be elicited at birth. This result is not surprising in light of previous findings that basic visual functions such as acuity (Teller, Regal, Videen, & Pulos, 1978) and contrast sensitivity (Boothe, Williams, Kiorpes, & Teller, 1980), as well as a wide variety of perceptual-motor behaviors (Boothe & Sackett, 1975), are not mature at birth. These results are also consistent with the protracted postnatal devel-

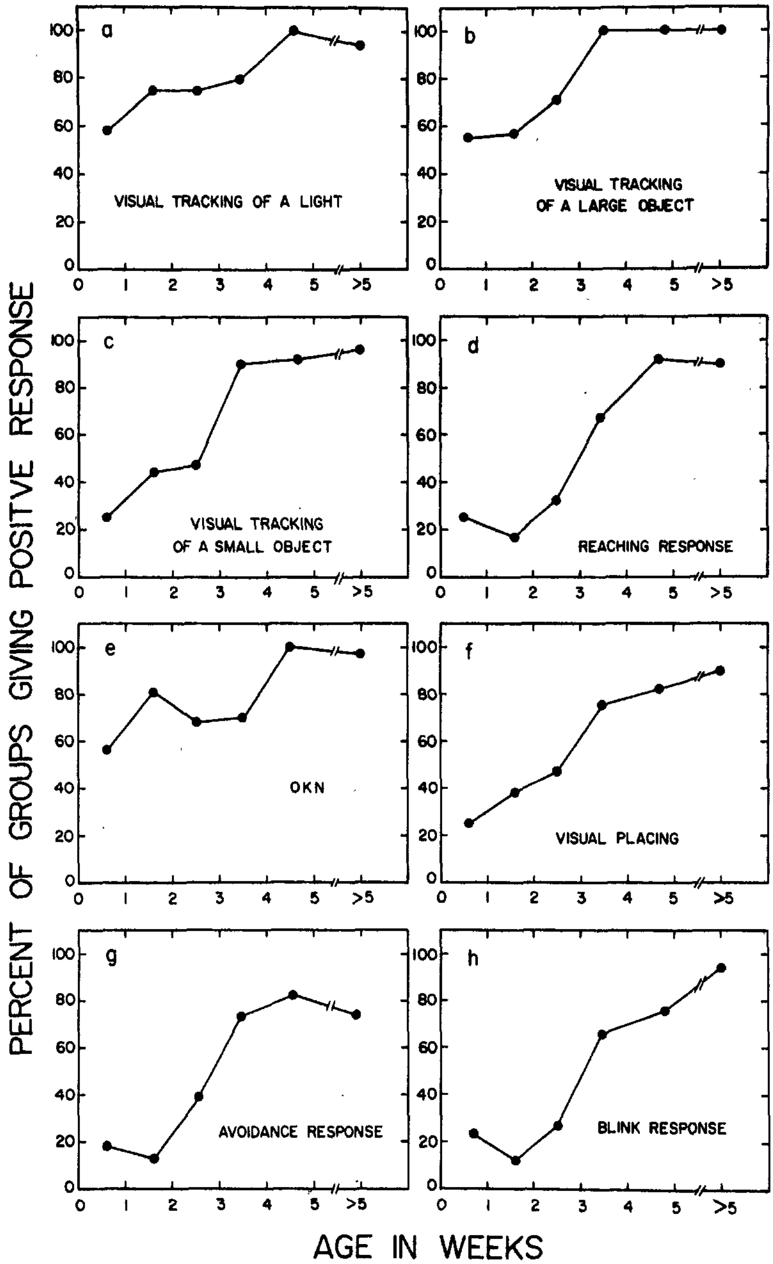

Figure 1. Proportion of infants who responded positive rather than negative at each age on each test. (The results have been grouped according to age in weeks as follows: Results obtained the day of birth through the 6th day after birth were grouped together as Week 1; results from the 7th through the 13th day after birth were grouped together as Week 2; etc.)

opment of the monkey central visual system as measured physiologically and anatomically (e.g., Blakemore & Vital-Durand, 1981; Boothe, Greenough, Lund, & Wrege, 1979; LeVay, Wiesel, & Hubel, 1980).

Monkeys older than 1 month normally respond positive on most of these tests. Therefore the tests can be administered as a screening tool to demonstrate that an animal over this age shows normal visual responsiveness. Advantages of this battery of tests as a screening device include the following: (a) The tests require no specialized equipment except for a few props that can be easily obtained or built. (b) Persons with little or no specialized training in behavioral testing methods can be easily taught to administer the tests. (c) The entire battery of tests can be administered to a monkey in just a few minutes. (d) Most important, we have found that these tests differentiate visually normal from abnormal monkeys much better than casual observation of the animal's behavior (Regal et al., 1976). When used with monkeys younger than 1 month of age, the responses to the battery of tests must be evaluated with reference to the age norms shown in Figure 1.

The results of this study demonstrate that there is an orderly progression in the postnatal development of visual responsiveness. The same progression was found for individual infants tested longitudinally as was found for the pooled group data. The tests in our battery that give positive responses earliest (tracking a light, tracking a large object, and OKN) are those involving simple sensory and motor components. None of these responses require that the visual system resolve fine spatial detail. The motor responses in these tasks involve only orienting or tracking eye and/or head movements.

Tasks requiring other motor responses (avoidance, eyeblink, placing), finer spatial resolution (tracking a small object), or both (reaching towards a small object) do not emerge until progressively later in development. Mendelson (1982) used a similar battery of tests on *Macaca mulatta* monkeys and found a similar progression, with orienting responses being elicited earliest and visually guided reaching emerging last. Similar progressions for the development of analogous responses have also been found in kittens (Norton, 1974; Van Hof-Van Duin, 1976).

On the basis of comparisons of the time course of acuity development in the two species, it has been suggested that visual development in months in humans is similar to development in weeks for macaque monkeys (Boothe, 1981; Teller & Boothe, 1979). There are not enough parallel studies using similar methods and equipment to allow careful age comparisons between the two species on visual responsiveness. However, the overall sequence of development appears to be similar in the two species. Responses that are present earliest in monkeys also appear to be present early in humans. Visual tracking of relatively large objects is present within the first month (Greenman, 1963), and an OKN response appears by the second month (Atkinson, 1977). A consistent blink response can be elicited from human infants by the third month (Pettersen, Yonas, & Fisch, 1980; White, 1971). There is disagreement about the time courses for the appearances of visual placing, avoidance, and reaching responses in human infants, but it is generally agreed that these responses are all present by 6 to 8 months after birth (see Bower, 1975; Yonas & Pick, 1975).

The similarities in the sequence of development of visual responsiveness provide additional evidence that the macaque monkey is a good model with which to study various aspects of human visual development. Studies that are invasive or otherwise not feasible with human infants can be conducted with this model. Thus important information can be obtained regarding the underlying mechanisms involved in the development of visual perception.

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