Behavioral assessment of visual acuity in mice and rats

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Abstract

We have developed a simple computer-based discrimination task that enables the quick determination of visual acuities in rodents. A grating is displayed randomly on one of two monitors at the wide end of a trapezoidal-shaped tank containing shallow water. Animals are trained to swim toward the screens, and at a fixed distance, choose the screen displaying the grating and escape to a submerged platform hidden below it. Both mice and rats learn the task quickly. Performance falls below 70% when the spatial frequency is increased beyond 0.5 cycles in most C57BU6 mice, and around 1.0 cycles per degree (cpd) in Long–Evans rats. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Studies of the neural basis of mammalian vision have concentrated largely on frontal-eyed carnivore and primate models. Although many of the cellular mechanisms controlling the development of visual function (Shatz, 1990; Hendry & Carder, 1992; Daw, Reid, Wang & Flavin, 1995; Bear, 1996; Cellerino & Maffei, 1996; Cruikshank & Weinberger, 1996; Fregnac, 1996) and the etiology of visual system disorders (von Noorden, 1978; Murphy & Mitchell, 1987; Milleret, 1994) have been elucidated using these models, little progress has been made toward an understanding of the genetic basis of vision. Currently mice, and to a growing extent rats, offer advantages over other mammalian systems for investigating the molecular basis of brain function: the development of transgenic and knockout techniques have enabled the direct control over the genetic makeup of animals and as such, have provided a novel opportunity to study the relationship between brain structure and function.

Many mutant and knockout mouse lines have been created in order to investigate the molecular basis of

learning and memory (Chen & Tonegawa, 1997; Gingrich & Roder, 1998; Picciotto & Wickman, 1998; Silva, Giese, Fedorov, Frankland, & Kogan, 1998), and diseases of the nervous system (Aguzzi, Brandner, Marino & Steinbach, 1996; Bates & Davies, 1997; Campbell, Stalder, Chiang, Bellinger, Heyser, Steffensen et al., 1997; Price & Sisodia, 1998; Zhao & Schwartz, 1998). However this technology has not been applied as widely to other problems in neurobiology. In particular, much of our knowledge of the rules governing the developmental plasticity of the brain has been generated using the visual system as a model, but few experiments have applied transgenic and gene targeting techniques to murine models of visual plasticity (Gordon, Cioffi, Silva & Stryker, 1996; Hensch, Gordon, Brandon, McKnight, Idzerda & Stryker, 1998). One reason for this may be the difficulty in assessing the visual capabilities of mice and rats. It is possible to estimate the visual capabilities of murine rodents electrophysiologically, with visually-evoked potentials, or anatomically by determining the sampling grain of the retina (Hughes, 1977; Martin, 1986); however these methods alone cannot accurately quantify visual function. Due to their invasive nature they also preclude longitudinal measurements of normal visual development as well as investigations of the time course of functional recovery following manipulations. Indeed,

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behavioral techniques, coupled with established psycho-physical procedures, offer one of the best ways to obtain a quantification of visual function and circumvent these problems. Operant visual tasks were originally developed for rats (Lashley, 1930); however, these methods are quite time consuming and have not been widely applied in mice. In addition, these techniques have not been successfully used in sub-adult animals where manipulations of the visual input can radically affect the structure and function of the visual system (Drager, 1978; Carmignoto & Vicini, 1992; Fagiolini, Pizzorusso, Berardi, Domenici & Maffei, 1994; Gordon & Stryker, 1996).

We have designed a computer-based, two-alternative, forced-choice visual discrimination task for assessing the spatial acuity of murine rodents as young as 40 days of age, using standard psychophysical techniques. With this method, it is possible to assess basic visual function, including visual acuity for gratings; however,
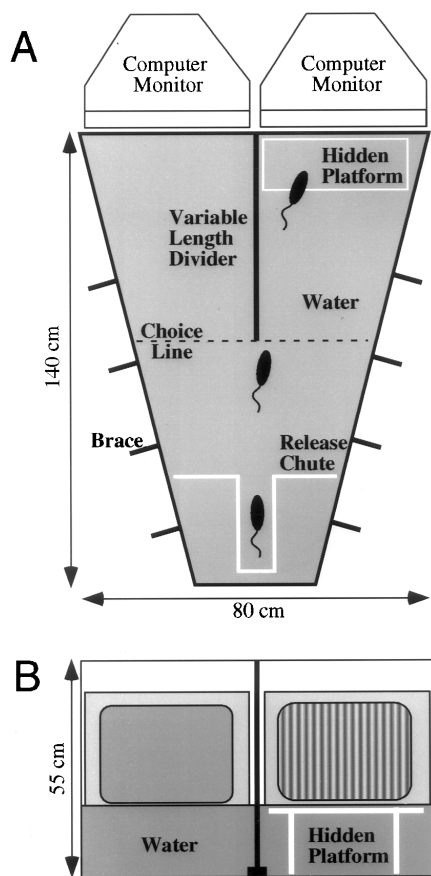

Fig. 1. Schematic diagram and components of the visual water box. (A) View from above showing the major components including pool, midline divider, platform, starting chute and two monitors. The pool is filled with clean water (gray), and the braces are needed to resist its weight. Following release from the chute, animals choose to swim on the side of the pool displaying the grating in order to find the hidden platform and escape from the water. (B) Front view showing monitor screens, submerged platform and midline divider. See text for details.

the method could also be modified to examine other visual capabilities such as motion detection, functional recovery following visual deprivation or damage to the visual system, or to assess visual contributions to cognitive tasks. A preliminary description of the apparatus and a report of these data in mice has been published earlier in abstract form (Douglas & Prusky, 1998).

2. Method

The method for assessing visual function in this report combines the working principles of a Thompson box (Thompson & Bryant, 1955), itself a modification of Yerkes box, with a Morris water maze (Morris, Garrud, Rawlins & O'Keefe, 1982). Mice and rats are instinctive swimmers and the task exploits their natural inclination to escape from water to a solid substrate, the position of which is predicted by a visual cue.

2.1. Visual water box

The basic apparatus consists of a trapezoidal-shaped pool with two computer-controlled monitors placed side-by-side at one end (Fig. 1). The pool and monitors sit on a solid table (183 cm long × 82 cm wide × 73 cm high) that has a drain hole (10 cm in diameter) in one end. The table is buttressed in the center with an extra leg to support the weight of the tank when filled with water. The pool is made of 6 mm clear Plexiglas and comprises a rectangular floor (140 cm long × 80 cm wide) and 55 cm (high) walls. The pool is wider at one end (80 cm) than the other (25 cm) and the two long walls and narrow end are finished on the inside with flat black paint to reduce reflections. The two long walls are supported on their outside with triangular braces (12 × 12 × 12 cm³). Midline dividers (40 cm high) of different length sit in guides and extend from the end wall between the monitors into the pool, bisecting it along its long axis. The dividers are painted flat black on both sides to make them opaque and reduce reflections within the pool. The length of the divider sets the choice point and effective spatial frequency: it is the closest an animal can get to the monitors without entering one of the two arms. A portable escape platform (37 cm long × 13 cm wide × 14 cm high) is placed below one of the monitors and a release chute (35 cm long × 7 cm wide × 20 cm high for mice; 35 cm long × 15 cm wide × 40 cm high for rats), the front surface of which is painted flat black, is centered at the narrow end of the pool. The pool is filled with tepid (22°C) water to a depth of 15 cm. Screen reflections on the surface of the water render the platform invisible from water level.

2.2. Computer hardware

Visual stimuli are displayed on two identical 17 in. computer monitors (Acer, AcerView 76ie) that face into the wide end of the pool. The bottoms of the screens are at water level. The black levels and contrast of the monitors are equated and the mean luminance is set at 43 cd/m^2. The monitors are driven by Twin Turbo 128 PCI video cards (IXMicro) over 2 m extension cables. The video cards are operated by a Power Macintosh compatible computer (Starmax 160/4000; Motorola).

2.3. Computer software

A custom computer program, Vista© (CerebralMechanics), is used to control the computer hardware and organize the experiments. The gamma response is measured for each monitor and is used subsequently to linearize all output to the screens. Vertically-oriented sine-wave gratings are produced by filling graphics memory with a linear ramp and loading the hardware color look-uptable with a sine-wave of the required amplitude and frequency. A homogeneous gray stimulus is generated in the same way, except the contrast is set to zero. The spatial frequencies made available are restricted to those with full cycles to ensure there is no difference in mean luminance between the screens. Vista© also manages the randomization of the stimuli, grouping of animals, and displays and saves the data sets. Data are entered into the program on a trial-by-trial basis through pushbuttons interfaced to the computer and software through an Apple Desktop Bus Input/Output device (ADB I/O, BeeHive Technologies).

2.4. Visual water task

The rationale of the task described here is to use an animal's ability to associate a sine-wave grating with escape from water, as an index of its acuity. Animals must first be conditioned to distinguish a low spatial frequency sine-wave grating from homogeneous gray with high reliability before the limit of this ability can be assessed at higher spatial frequencies. There are three phases to the task: pretraining shaping; task training; and acuity testing.

In a pretraining phase, animals are shaped gradually to locate a platform hidden below a screen displaying a low spatial frequency grating. A divider (46 cm) is placed in the pool, a grating with a large period (∼ 0.12 cycles per degree (cpd)) is displayed on one of the screens, and the platform is positioned directly below the grating. On the first trial, animals are removed from their holding cage and released, facing the screen, into the pool a few centimeters from the platform. Upon being released, most animals swim directly forward and touch the platform, then climb upon it. They are al-

lowed to remain on the platform for a few seconds and are subsequently removed and returned to their holding cage. On the next trial, the location of the grating and the platform are switched to the opposite side and another trial is run. After this routine is repeated a few times, the release distance from the platform is gradually increased until animals can reliably swim to the platform from the opposite end of the pool.

In the training phase, animals are conditioned to distinguish between a low spatial frequency sine-wave grating (∼ 0.12 cpd) and homogeneous gray. A release chute is positioned in the pool to center the swimming path of the animals and remove any placing biases by the experimenter. The alternating pattern of the grating and platform position is replaced, first with a LRLL-RLRR sequence, and then with a pseudorandom pattern where no more than three trials are allowed on one side (Gellerman, 1933). On all trials, animals are required to swim until they find the platform. If an animal breaks the plane perpendicular to the end of the divider on the side of the tank with the monitor displaying gray, the trial is recorded as an error, and after finding the platform, the animal is immediately required to run another trial- If an animal makes three incorrect choices in a row, it is reshaped to learn the task. After animals have achieved near-perfect (80% +) performance over 20–40 trials on a pseudorandom schedule in the training phase, the testing of visual acuity can begin. The length of the central barrier affects how punitive the task is, as after an incorrect response, the animal must swim around it to get to the escape platform.

For the testing phase we use a method of limits procedure to minimize the number of incorrect responses by the animals: small incremental changes in the spatial frequency of the stimulus are made between successive blocks of trials until the ability of animals to distinguish a grating from gray falls to chance. A pseudorandom display schedule is again used to determine on a trial-by-trial basis which monitor will display the test grating. An animal is placed in the release chute and is allowed to find the platform under the grating. If the animal makes a correct choice, the spatial frequency of the stimulus is increased by adding one cycle on the screen, and another trial is executed. This procedure continues for the low spatial frequencies until an error is made, thus minimizing the time spent far from threshold. Once an error occurs, additional trials are run until four correct responses are made in sequence, or seven correct choices are made in a block of ten trials. After trials covering approximately half of the animal's projected threshold are completed, the minimum number of trials is increased to three, and then again increased to four around three-quarters of the projected threshold. Errors at the higher spatial frequencies are followed by the same criterion testing as

described above. This method of consecutive testing utilizes about 15 different spatial frequencies for mice and about 30 for rats.

Mice are usually tested in groups of five to six in a session of ten interleaved trials, with each session lasting 45–60 min and no more than three sessions are performed in a single day. Rats are also tested in groups; however, each of the three sessions could have a few more trials (up to 15) than with the mice. A preliminary threshold is attained for both mice and rats when they fail to achieve 70% accuracy at a spatial frequency. In order to ensure the accuracy of this estimate, spatial frequencies around the threshold are retested until a clear pattern of performance is generated. The highest spatial frequency achieved consistently is recorded as the acuity threshold. In some circumstances, the data around the estimate are averaged and a frequency-of-seeing curve is constructed. Typically, a final threshold estimate is generated in 2 or 3 days with about 60 trials for mice, and 150 trials for rats.

At any phase of the procedure, but particularly during training, animals can adopt a spatial bias in their responses. These biases are easy to detect because Vista© provides graphic feedback of the ongoing performance of the animals. We observe three such response patterns including a side bias, where animals repeatedly swim to one side, alternations, where animals alternate between left and right responses, and a win-stay, lose-shift response, where animals swim to the side where they found the platform last. These behavioral patterns are not compatible with accurate measurements of visual acuity; however, they can usually be extinguished. In our hands, the most effective way to change the behavior is to introduce a bias in the order of presentation of the gratings. For example, if an animal develops a left side bias, it is often removed by presenting twice as many trials with the grating on the right as the left, i.e. RRLRRLRRL. Then, as soon as the animal starts responding to the visual stimuli instead of following a spatial pattern, a pseudorandom pattern is reinstated (Mitchell, Griffin & Timney, 1977). Response biases can also occur when animals reach their acuity threshold during testing. Mice, in particular, often resort to a side bias when they make several errors in a row. In this case, it is necessary to first remove the bias at a much lower spatial frequency before animals can be retested. Rats do not normally develop such a strategy at threshold and it is usually only necessary to reduce the spatial frequency to a point where they responded with near-perfect accuracy before retesting their threshold.

Excessive retraining or prolonged testing, especially for mice, do not guarantee accurate results, because animals can get hypothermic and tired. We allow our mice to rest on a heating pad between trials; however,

if animals appear visibly cold or tired, the best strategy is to let them rest before continuing with the experiment.

3. Results

Our findings demonstrate that mice and rats can be trained in the visual water task and their acuities for gratings can be assessed quantitatively. In addition, we demonstrate that stable, reliable measurements can be made over a prolonged length of time.

In the pretraining phase, both mice and rats learned quickly to associate swimming to the platform with escape from the water. Usually two or three sessions, separated by at least an hour, were required to complete the shaping. On some occasions, the sessions were run over 2 successive days. Although the pretraining phase was necessary to shape the animal's behavior to locate the platform, pretraining also provided experience in water for animals, such as ours, that were naive swimmers.

The training phase usually commenced the day after pretraining was completed and generally two to four sessions of 10–15 trials were needed before the animals reached criterion. All rats and mice eventually learned the task. Fig. 2 shows the typical pattern of acquiring the visual water task for a mouse (A) and a rat (B) during training. The spatial frequency of the stimulus was set at 0.12 cpd and the divider was 46 cm in length. The filled squares along the top of the graph represent correct responses and the open squares at the bottom represent incorrect responses. The average percent-correct for blocks of ten trials is plotted against trial number. The dotted line indicates the 70% performance criterion. On the first trial block, both animals performed at or near chance; however, after two to three more blocks of training, performance improved to near-perfect.

Fig. 3 illustrates the typical pattern of performance of a mouse (A) and a rat (B) during testing. The average performance (% correct) at a spatial frequency is plotted against trial number. Gray bars indicate spatial frequency and the dotted line indicates the 70% performance criterion. Accurate performance in the mouse was maintained until 0.47 cpd. When the stimulus was increased to 0.51 cpd, the animal required ten trials to demonstrate 70% accuracy; however, it made four errors at 0.56 cpd. When the last two spatial frequencies were retested, the animal made three correct choices in a row at 0.51 cpd but again failed to reach criterion at 0.56 cpd.

A similar pattern of behavior was present in the rat; however, near flawless performance was maintained through 26 spatial frequencies before a block of ten trials at 0.92 cpd was required to confirm performance
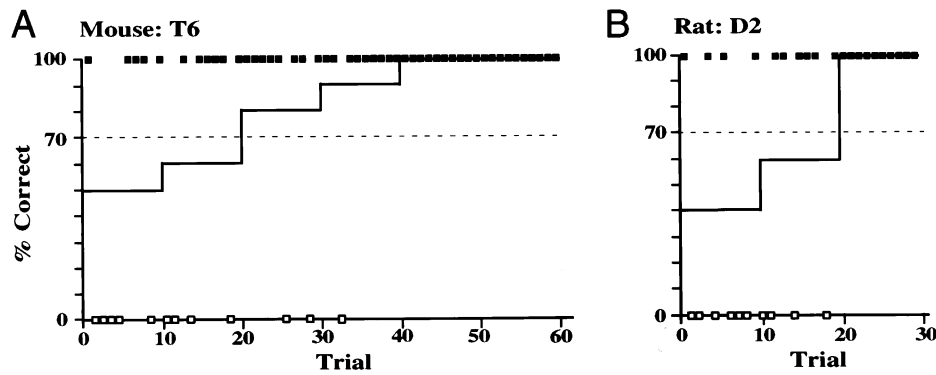
Fig. 2. Acquisition of the visual water task for a mouse (A) and a rat (B) when being trained with 0. 12 cpd grating. The average performance in blocks of ten trials is shown for one animal of each species by the solid lines, and the 70% criterion by the dotted line. Filled squares are correct responses and open squares indicate incorrect responses. Both rats and mice learned the task quickly and eventually performed at or near perfect levels.
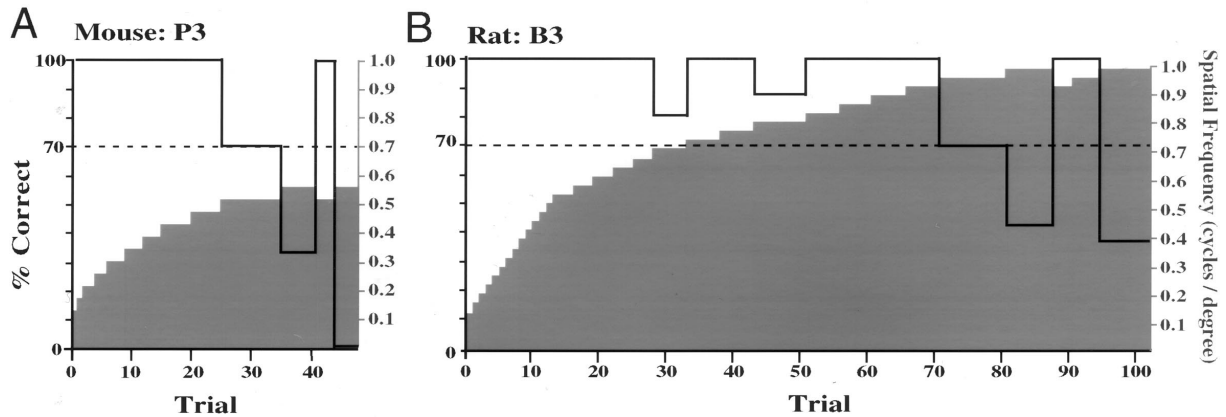

Fig. 3. Measurement of visual acuity in a mouse (A) and a rat (B). In the testing phase the spatial frequency of the grating (gray bars) was gradually increased. When average performance (solid lines) fell below criterion (dotted line), the spatial frequency was reduced and the last few frequencies were retested.

at or above 70%. At the next spatial frequency tested, 0.95 cpd, the animal made four errors in the first five trials. Spatial frequencies around 0.92 cpd (0.89–0.95) were then retested, and confirmed that the animal could see spatial frequencies up to, but not beyond 0.92 cpd.

Recording the last spatial frequency where 70% accuracy was achieved is an expeditious method of estimating the acuity of our animals, but the practice may slightly underestimate their visual capabilities. In some animals we averaged their performance around threshold to generate a frequency-of-seeing (FOS) curve. Fig. 4 illustrates FOS curves for a mouse (left) and a rat (right), where numerous trials around the estimated threshold were performed. In both cases the six highest spatial frequencies tested were used to generate the curves. The threshold values predicted from FOS curves for both the mouse (0.53 cpd) and the rat (0.94 cpd) were slightly higher than the estimate gener-
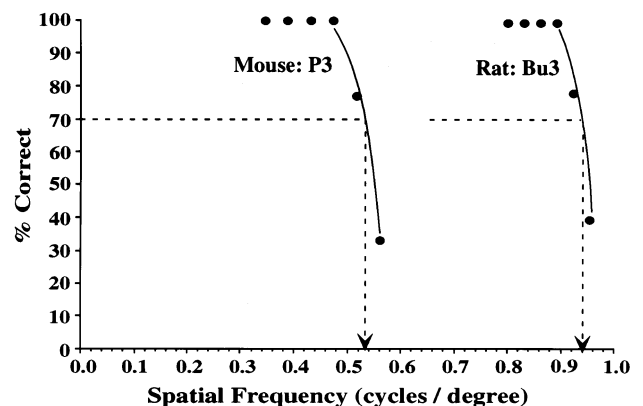

Fig. 4. Frequency-of-seeing curves for a mouse (left) and a rat (right). Each of the points is the average performance at a spatial frequency. Only the highest six spatial frequencies tested are shown. A curve was fit to the data by eye and the intersection with the 70% criterion was used as an acuity estimate.
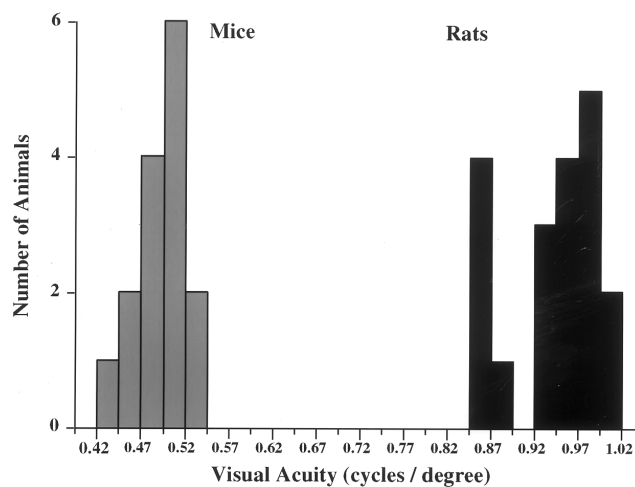
Fig. 5. Distribution of acuities for mice (left) and rats (right). Acuities were clustered within a narrow range for each species, and the average acuity of rats was approximately twice that of mice.

ated by recording the last spatial frequency where performance was above 70% (mouse — 0.51 cpd; rat — 0.92 cpd). Note, however, that the curves in both cases are steep, indicating that when animals neared their acuity threshold, their performance declined rapidly. Because most animals did not require extensive retesting around their threshold, using the spatial frequency where 70% performance was last achieved is a reliable and effective method of quantifying the visual acuity of our animals, even though it may slightly underestimate their acuity.

In many animals, behavioral changes occurred as the spatial frequency of the stimulus was increased. At low spatial frequencies animals swam directly toward the grating after they were released. As the spatial frequencies were increased and approached threshold, animals took more time to make their choices. The increase in latency for mice near threshold was most often the result of swimming across the pool several times near the choice line while apparently inspecting the screens carefully before making their choices. Rats, however, would often swim to the end of the divider, grasp the end with their paws, and then look at each screen several times before making their choice.

There was consistency in the acuity of animals within a species. Fig. 5 illustrates the range of acuities measured for 15 mice (A) and 19 rats (B). The number of animals (Y axis) is plotted against the highest spatial frequency where performance exceeded 70% accuracy. The threshold values for mice extended from 0.42 to 0.54 cpd with an overall mean of 0.49 cpd. The average acuity of rats (0.94 cpd) was approximately twice that of mice, with threshold estimates ranging from 0.84 to 1.0 cpd.

The longitudinal stability of the acuity estimates were studied in a group of six mice. The mean acuity mea-

sured at P129 and P235 was not significantly different from than that obtained initially at P89. Indeed the animals appeared to retain knowledge of the task for months, and experience with only a few trials at low spatial frequencies was necessary to reacquaint the animals with the task before they were retested.

4. Discussion

The behavioral task described here yielded consistent and reliable acuity measures for both mice (0.49 cpd) and rats (0.95 cpd). Although a number of operant behavioral tasks have been used to evaluate the visual acuity of animals such as cats (Mitchen et al., 1977), horses (Timney & Keil, 1992), gerbils (Baker & Emerson, 1983; Wilkinson, 1984) and rats (Seymoure & Juraska, 1997), the visual water task appears to be more efficient for measuring acuity in rats. A recent study of mice by Gianfranceschi, Fiorentini and Maffei (1999) used food as a reinforcement in a behavioral paradigm similar to the one employed here. However, their animals required many more trials to learn the task and they did not report on the success of training and testing animals younger than adults. The increased ease and speed with which acuity measures could be obtained in mice with our task is significant, given their increasing use in biomedical research.

In general, the acuity measures obtained here for both rats and mice were comparable to those obtained in other studies. Although the optics of the eye only limit the maximum acuity of rats to 2.5 cpd (Artal, Herreros de Tejada, Munoz Tedo & Green, 1998), acuity estimates in this species using electrophysiological methods have ranged from 1.0 cpd (Dean, 1981) to 1.2 cpd (Silveira, Heywood & Cowey, 1987). A recent behavioral study also found acuities of between 1.0 and 1.6 cpd in hooded rats (Seymoure & Juraska, 1997). There are less data available for mice, but our estimate of 0.49 is close to the 0.5–0.6 cpd estimate obtained by Gianfranceschi et al. (1999) with a behavioral task similar to that described here, close to the 0.5 cpd estimate from an optokinctic investigation by Sinex, Burdette and Pearlman (1979), but lower than the 0.65 cpd estimate from a visual evoked potential study by Pizzorusso, Poraciatti, Strettoi and Maffei (1997). Although it is possible that the lower threshold estimates reported here are due to inherent limitations of the task, our animals closely inspected the display when the spatial frequency was near threshold and often swam laterally in front of the choice point, or put a paw up on the end of the barrier and paused before making a choice. Moreover, when testing was repeated, their performance declined around the same frequency. These observations suggest that reduced performance

near threshold was not due to motivational or attentional factors.

It is also possible that differences in acuity measures across different behavioral studies are the result of differences in stimulus properties such as luminance and contrast. However, our computer-generated gratings had a higher contrast (97%) and overall luminance (43 cd/m^2) than the printed patterns of Seymoure and Juraska (1997) and Gianfranceschi et al. (1999), which should have contributed to higher, not lower, acuity estimates. Also, the use of sine wave gratings in our study should not have produced lower measures of acuity than those obtained with square waves. Other factors like the larger display size and greater involvement of the upper visual fields in the present study also seem unlikely explanations of the discrepancies.

One possible reason for our estimates being lower is that our use of a 70% criterion underestimated the acuity threshold. In fact, we did observe slightly higher acuities calculated from FOS curves than the estimates based on the last frequency that met the criterion, but the differences were small. It may be that the slopes of our curves were artificially steep because we have not detected a shift in the animal's behavior to a non-visual strategy after making several errors. If so, then our underestimation would be somewhat larger. Interestingly, the FOS curves reported by Gianfranceschi et al. (1999) are much shallower.

One problem with any visual behavioral study in freely moving animals is that the viewing distance cannot be controlled precisely. Thus, our acuity values might be underestimated because we calculated the spatial frequency as if the gratings were viewed from the end of the barrier. In fact, the actual distance at which many animals made their decisions may have been a few centimeters further away. In addition, if the animals were making their decisions near the midline of the pool they would have been viewing the screens at an angle. This may also have produced an underestimation of the spatial acuity.

Among the foremost advantages of the visual water task over other behavioral techniques is the speed with which the evaluation of visual capabilities can be made. Once trained, acuity estimates can be obtained from a large number of animals in 2–3 days. Lashley (1930) developed a task to measure visual discriminations in rats that utilized a jumping stand in a two-choice paradigm. This task has the advantage that the distance from which animals make their discriminations is rather easily monitored and from which estimates of the visual angle can be calculated. To our knowledge, however, this task has not been used with computer-generated stimuli to successfully measure visual acuity in rats, nor has it been adapted for use with mice. In any case, the time required to train and test the visual acuity of rodents in such a task takes a substantial amount of time (Seymoure & Juraska, 1997). Additional drawbacks with the jumping stand are that animals are food deprived to motivate their performance, and the manual production, placement and randomization of sine-wave stimuli is an arduous task. A Thompson box or a Y-maze could also be adapted to measure the visual acuity of rodents (e.g. Gianfranceschi et al., 1999), though they would suffer from the same problems as the Lashley jumping stand: a substantial period of time is required for animals to be trained, and some form of deprivation is required to motivate their performance.

The visual water task can enable longitudinal measurements of changes in visual function that may accompany manipulations of early visual input, following damage to the visual system, or after genetic or pharmacological manipulations. We have successfully used this task to measure visual acuity in each eye of mice at P40 monocularly and binocularly-deprived (Prusky & Douglas, 1998) during a physiologically defined critical period ending at P32 (Gordon & Stryker, 1996). Similar work in progress in rats has also confirmed that estimates of visual acuity can be made in animals as young as 40 days of age and the acuity of each eye can be made separately with the aid of visual occluders.

Many rodent behavioral tasks rely on the visual competence of animals in order to measure unrelated behavioral functions. For example, the Morris water task (Morris et al., 1982) and the radial arm maze (Becker, Walker & Olton, 1980) have been used to measure the spatial abilities of rats and mice. In their most common configurations, both tasks rely on visual cues to guide spatial exploration. In the Morris water task, it is common to assess visual competence by placing a large cue on a platform, and assessing whether animals can swim directly to the cue when placed in the water. Although this procedure measures visual function, it does not measure visual acuity; the ability to see closely adjacent objects and borders as distinct. One application of the visual water task could be to quantitatively assess the role of visual acuity in tasks, like these, that depend on vision in order to measure other behavioral functions. When we have undertaken such experiments in our lab (Prusky, West & Douglas, 2000), we have found that the added benefit of training animals first in the Morris water maze habituates them to swimming in water and reduces even further the length of time to train animals in the visual water task.

An unexploited feature of using a computer to quantitatively control the stimulus display is that animals can be trained to discriminate between any visual stimuli, and the limits of those abilities can be investigated with psychophysical methods similar to those described here. It may be necessary to vary the experimental procedures and tailor a task to specific criteria, but almost any visual discrimination should be possible.

5. Conclusions

The visual water task employs the natural inclination of rodents to escape from water to enable the quantification of visual discriminations. If a flexible method of training and testing is adopted, this technique provides accurate and reliable measures of different visual capabilities, including the quantitative assessment of grating acuities. This behavioral method is a non-invasive way of measuring many different visual capabilities relatively quickly, and therefore complements anatomical and electrophysiological methods of assessing visual thresholds. Because animals can be trained on this task as juveniles and retested often, it may be the method of choice for measuring visual function in experiments aimed at elucidating the mechanisms underlying developmental plasticity in the rodent visual system.

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