

SPATIAL CONTRAST SENSITIVITY OF THE TREE SHREW*

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Abstract—Spatial contrast sensitivity functions (CSFs) were measured for 3 tree shrews. Our two-alternative forced-choice discrimination paradigm required the animals to discriminate a vertical sine-wave luminance grating from a homogenous field of the same size (16°) and mean luminance (35 cd/m^2). Spatial frequencies tested ranged from 0.1 to 2.0 c/deg and grating contrast was varied trial-by-trial using a modified staircase technique. Small between-subject variations in the shape of the CSFs appeared to be correlated with our estimates of refractive error for each animal. In general, the CSFs were of the typical band-pass type with peak sensitivity occurring at approximately 0.7 c/deg. Estimates of grating acuity derived from the CSFs ranged from 1.2 to 2.4 c/deg and are within the limitations set by the eye size and retinal anatomy of the tree shrew.

Tree shrew Contrast sensitivity Spatial vision Grating acuity Animal psychophysics

INTRODUCTION

Tree shrews are diurnal mammals from Southeast Asia which are quite similar to North American gray squirrels in their habits and appearance. They possess a well-developed visual system, a feature which led in part to their taxonomic classification as prosimian primates (LeGros Clark, 1934, 1959; Simpson, 1945). Because their primate status has been frequently disputed (see Lockett, 1980, for review), tree shrews have been the subject of many neuroanatomical investigations. A considerable number of these have studied their visual system (see Campbell, 1980, for review). Such studies revealed a large, well-developed striate cortex that receives an almost exclusively thalamic input from a lateral geniculate nucleus with six clearly delineated layers (Snyder and Diamond, 1968; Diamond *et al.*, 1970; Harting *et al.*, 1973; Casagrande and Harting, 1975; Hubel, 1975). These features may well have foreshadowed the great expansion of the retino-geniculate-striate system that is one of the defining characteristics of the primate visual system. However, unlike primates, the tree shrew retina is composed almost exclusively of cones and contains no foveate specialization. This may be reflective of their transitional taxonomic status.

In contrast to the neuroanatomical line of inquiry, there have been relatively few behavioral investigations of the visual capacities of the tree shrew.

Several studies have measured grating acuity (Ordy and Samorajski, 1968; Schafer, 1969; Ware *et al.*, 1972; Ward and Masterton, 1970), but the acuity estimates obtained span quite a wide range, from 1.2 c/deg (Ward and Masterton, 1970) to 15–30 c/deg (Ordy and Samorajski, 1968). Furthermore, no measurements have been made of the more comprehensive index of visual resolution, the contrast sensitivity function (CSF). The goals of the present study were to measure the spatial CSF of the tree shrew, as well as to contribute to a clarification of the discrepancy over its visual acuity.

METHODS

Subjects

Three normal adult tree shrews (*Tupaia belangeri*), two males and one female, raised from birth in our breeding colony, were selected for study. Prior to training, these animals were housed in pairs in large wire cages in our colony room, which is maintained on a 14 hr light/10 hr dark cycle. Just before training was initiated, each animal was separated and placed in its own cage in the same room. All three animals were six months old (i.e. adults) when training began.

Slit-lamp refraction was performed at 30 cm while the animals were anesthetized (Ketamine HCl) and their pupils dilated (Mydriacyl). Measured values were adjusted using Glickstein and Millodot's (1970) correction for retinoscopic measurement of small eyes, assuming an axial length of 7.1 mm. The resulting estimates of refractive error showed one animal (TS 11) to be -1 D , another (TS 13) to be $+2 \text{ D}$, and the third (TS 10) to be -7 D . For each animal, measurements of the left and right eyes were within

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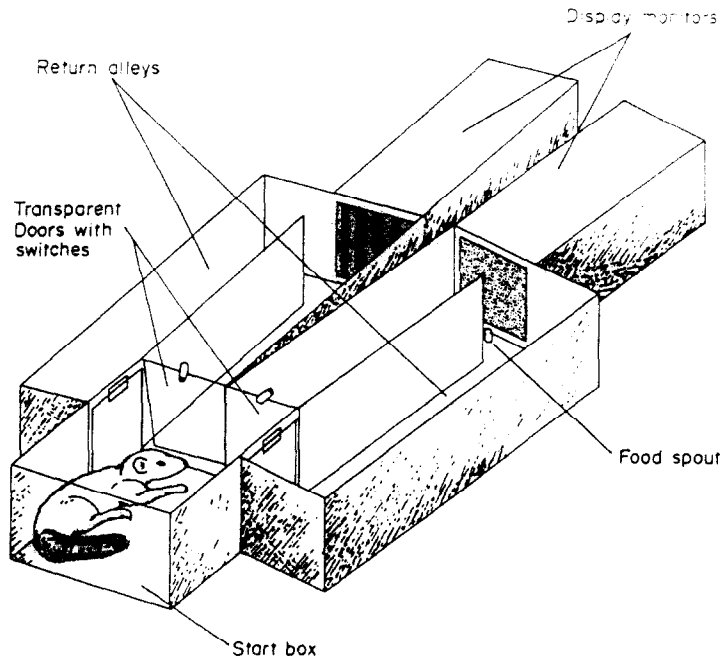


Fig. 1. Sketch of behavioral testing apparatus. At the start of each trial, the animal views the display monitors through transparent doors. His response is to pass through the doors and run toward the stimulus. Mercury switches mounted on the doors register the response and activate door locks (not shown). When the animal chooses the alley with the grating stimulus, he is rewarded with a small amount of puréed food delivered through the food spout. His return to the start box, by way of the return alleys, activates a microswitch beneath the start box floor and begins the next trial.

1 D agreement. No optical correction was made during the experiment. Each animal was maintained at approximately 85% of its normal body weight throughout the experiment.

Apparatus

Stimuli were generated on two Tektronix 608 display monitors, using standard techniques. On any one trial, a vertical sine-wave luminance grating was presented on one monitor, while a spatially homogeneous field of the same mean luminance was simultaneously displayed on the other screen. Frame rates for the *X*- and *Y*-axes were 1 and 500 kHz, respectively, while variation of the frequency and amplitude of the signal modulating the *Z*-axis allowed the spatial frequency and the modulation contrast of the grating to be controlled independently. Grating contrast, as defined by the standard Michelson formula ($L_{\max} - L_{\min} / L_{\max} + L_{\min}$), was measured using a Photovolt Photometer (Model 520 M). It was found to vary linearly with voltage over a range of 0.03–0.85 when a mean luminance was maintained at approximately 35 c/m^2 (SEI Photometer). A photocell was used before each session to insure that stimulus conditions remained constant throughout the experiment.

The display screens, measuring 12.5 cm in width by 10.0 cm in height, were positioned at the ends of the arms of a modified Y-maze, shown in Fig. 1. The distance from the stimulus to the transparent door

(from where the animal must make his choice) was 45.5 cm, resulting in a stimulus field subtending approximately 15.7° of visual arc horizontally and 12.5° vertically. No surround was used, although the testing apparatus was constantly illuminated by a diffuse light source at approximately $4 \text{ c}/\text{m}^2$ (Litemate 3, Photo Research). This level of ambient light is well within the photopic range of the duplex human eye (Boynton, 1966), and was presumed to be of sufficient intensity to maintain photopic levels in the essentially all-cone retina of the tree shrew. Both the maze and the monitors were interfaced with a TRS-80 micro-computer system, which controlled the stimulus presentation, recorded the response, and performed preliminary data analysis.

Procedure

Sessions were run at approximately the same time each day, which corresponded to the peak activity time for this species (Sprankel, 1961; Vandenberg, 1963). Each trial began with the animal's entry into the start box of the maze (a microswitch was located under the start box floor) and was controlled and recorded by the microcomputer system. The animal viewed both stimuli through the transparent plexi-glass doors. Its task was to choose that alley in which the grating was present (i.e. two-alternative forced choice). A mercury switch, mounted on top of each door, was used to record the animal's choice and to activate door "locks" (solenoids located under the

floor) which prevented the animal from retracing its steps. If the choice was correct a small amount of pureed food was delivered to the animal via a food spout from a dispensing system located beneath the maze. If the animal's choice was incorrect, the display lights were dimmed and no food was delivered. The animal's return to the start box by way of the return alleys (equipped with one-way doors) started the next trial. Stimulus position was controlled by the computer, using a pseudorandomized schedule.

Training was begun using a light-dark discrimination. After this task was mastered, high contrast grating stimuli were introduced. When the animals were performing consistently well on this task (i.e. greater than 90% correct over several 50- to 100-trial sessions) for a wide range of spatial frequencies, testing was begun.

Daily testing sessions consisted of 50–100 trials. Each testing session started with 5–10 practice trials in which high contrast (0.85) gratings were presented. The spatial frequency of the grating stimulus was held constant during each session, but contrast was changed for each trial dependent upon the animal's performance on the previous trial. A modified staircase/method-of-limits procedure was used. Briefly, this consisted on a one-up/one-down staircase rule, except that stimulus contrast was increased substantially following two consecutive errors. It was necessary to implement this procedure to combat the frequent adoption of a position bias by the animal following a series of trials at contrast levels near its sensory threshold. The modified procedure insured that the animal never went more than two trials without either receiving a reinforcement or being presented with a considerably easier task. This schedule served to maximize stimulus presentations near threshold while simultaneously maintaining a high level of stimulus control.

RESULTS

For each animal, a set of frequency-of-seeing curves was constructed for spatial frequency values ranging from 0.1 to 2.0 c/deg. This was accomplished by plotting the percentage of correct responses at each contrast level tested for each spatial frequency. The mean number of trials per frequency-of-seeing curve was 270. Threshold was defined as that grating contrast which resulted in the animal performing at a level halfway between maximum (96–100% depending on the animal) and chance performance (50%).

Contrast sensitivity functions (CSFs) were obtained for each animal by plotting the reciprocal of the threshold contrast (i.e. sensitivity), which was calculated for each spatial frequency tested. As shown in Fig. 2, the curve for TS13 showed a peak at approximately 0.7 c/deg, a low frequency roll-off and an extrapolated high-frequency cut-off (or visual acuity estimate) of approximately 2.4 c/deg. The CSF

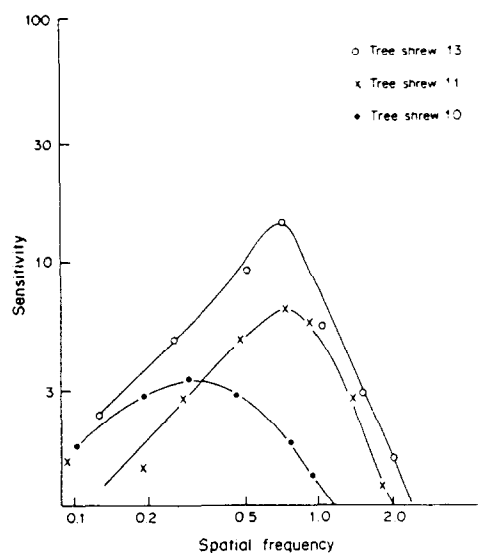


Fig. 2. Individual contrast sensitivity functions for three tree shrews. Contrast sensitivity (the reciprocal of contrast threshold) is plotted against spatial frequency for the tree shrews. Smooth curves were drawn through the points by eye.

for TS11 also peaked at approximately 0.7 c/deg, but showed considerably lower sensitivity at each spatial frequency tested. Its estimated acuity was slightly less than 2.0 c/deg. The CSF of TS10 showed a peak at approximately 0.3 c/deg, and its performance at higher spatial frequencies, with an estimated acuity value of 1.25 c/deg, was much poorer than the other animals. At low spatial frequencies, however, this animal's performance was similar to that of TS13, and exceeded that of TS11.

DISCUSSION

Our behavioral measurements of spatial contrast sensitivity in the tree shrew revealed the typical band-pass type of contrast sensitivity function (CSF). The small variations in the shape of our curves and their position relative to the sensitivity scale appeared to be correlated with our estimates of refractive error for each animal. That is, the tree shrew (TS13) that was most sensitive to contrast modulation and had the highest high-frequency cut-off (2.4 c/deg) was estimated to have a refractive error of approximately -1.0 D. Another animal (TS11) was slightly less sensitive than TS13 yet it displayed a CSF that was similar in its shape, its peak frequency (0.7 c/deg), and in its high frequency cut-off value (2.0 c/deg). This second animal was also estimated to have only a moderate refractive error (i.e. $+2.0$ D). On the other hand, the third tree shrew (TS10) was estimated to have a substantial refractive error of -7.0 D. The CSF of this animal displayed quite a low peak sensitivity, which was shifted more than an octave toward the lower spatial frequencies. Its high-

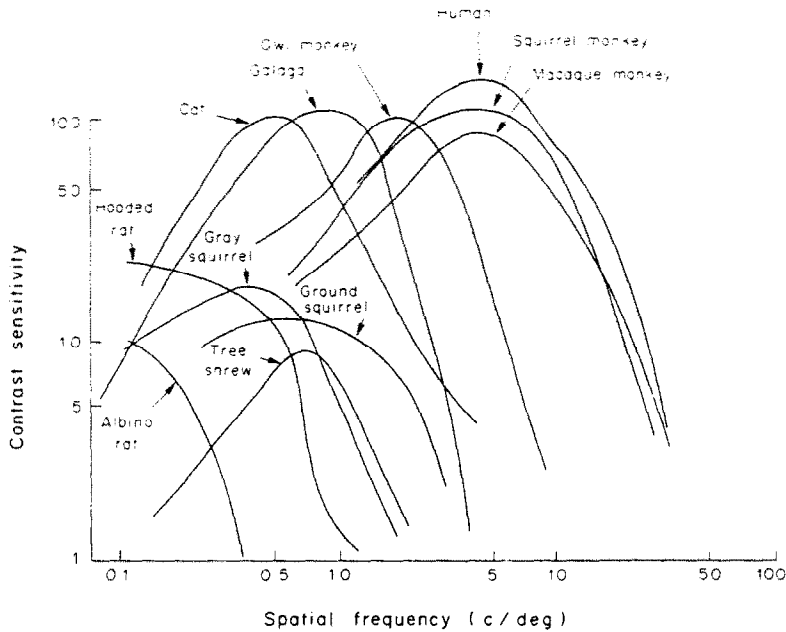


Fig. 3. Behaviorally determined spatial contrast sensitivity functions for a variety of mammalian species. Curves were drawn by eye through data points (omitted for clarity) obtained in the independent studies listed below: albino rat (*Rattus norvegicus*), Birch and Jacobs (1979); cat (*Felis domesticus*), Blake *et al.* (1974), Bisti and Maffei (1974); galago (*Galago crassicaudatus*), Langston *et al.* (1981); gray squirrel (*Sciurus griseus*), Jacobs *et al.* (1982); ground squirrel (*Spermophilus beecheyi*), Jacobs *et al.* (1980); hooded rat (*Rattus norvegicus*), Birch and Jacobs (1979); human, DeValois *et al.* (1974); macaque (*Macaca nemestrina* and *Macaca fascicularis*), DeValois *et al.* (1974); owl monkey (*Aotus trivirgatus*), Jacobs (1977); squirrel monkey (*Saimiri sciureus*), Merigan (1976); tree shrew (*Tupaia belangeri*), present study.

frequency cut-off value was also approximately 1 log unit lower. The low-frequency roll-off was about the same for each animal, however, so it does not appear that the CSF for TS10 is merely shifted relative to the CSFs of the other tree shrews. Rather, its shape resembles that predicted by Fiorentini and Maffei (1976) for an emmetropic eye viewing a grating stimulus through a blurring lens. We calculated the depth-of-focus for our best subjects, using Green *et al.*'s (1980) formula, and obtained values of ± 0.8 and ± 1.0 D for TS13 and TS11 respectively. Thus, given our viewing distance of 0.5 m and the near-focused optical system of the tree shrew (Schafer, 1969), the minimal refractive error of these two animals should have had little effect on their spatial vision. However, our estimate of a -7 D refractive error for TS10 far exceeds the tree shrew depth-of-focus as computed for the other two animals and should, therefore, produce a perceptible blurring of the stimulus. We believe that this animal's poor performance at the higher spatial frequencies may be due largely to these optical factors.

The point where the CSF crosses the abscissa (i.e. the high frequency cut-off value) may be taken as an estimate of visual acuity. For our subjects, acuity estimates ranged from 2.0 to 2.4 c/deg (for TS11 and TS13) to 1.1 c/deg (for TS10). Previous behavioral studies by Ward and Masterton (1970) and Ware *et al.* (1972) obtained values of 1.2 and 1.7 c/deg, respectively. These estimates fall within the range re-

ported in the present study. Higher estimates of tree shrew visual acuity have been reported by Schafer (1969) and Ordy and Samorajski (1968). Schafer's estimate of an acuity of 4.7 c/deg may have been influenced by the higher luminance level (127 c/m^2) of his stimuli. Furthermore, his criteria for determining threshold are not clear and may have differed from the methods used in the present study. Ordy and Samorajski's estimate of an acuity of 15–30 c/deg was also obtained using stimuli of high luminance, although their criteria for threshold (80% correct) were slightly more stringent than ours. Nonetheless, the anatomical structure of the tree shrew retina makes it highly unlikely that the tree shrew visual system could be capable of such fine visual resolution. As Schafer points out, such an acuity value would require a receptor diameter of only $1 \mu\text{m}$, and the cones in the tree shrew eye have been measured to be more on the order of $4 \mu\text{m}$ in diameter (Samorajski *et al.*, 1966). Moreover, if one assumes that it is ganglion cell density and not receptor diameter that is the limiting factor of visual resolution (for discussion, see Berkley, 1976), then it is more clear that even 15 c/deg is an overestimate of tree shrew acuity. For example, it is possible to use Shannon's sampling theorem (Shannon and Weaver, 1949) to calculate the theoretical minimum resolvable grating spatial frequency (see Hughes, 1977, for discussion). Based on a peak ganglion cell density in the tree shrew retina of $20,000/\text{mm}^2$ (DeBruyn and Casagrande, personal

communication), tree shrew visual acuity should be no higher than 5.0 c/deg.* Our estimates of tree shrew acuity, as well as those of Schafer (1969), Ward and Masterton (1970), and Ware *et al.* (1972) are well within this theoretical limit. We believe the variation between behavioral studies may be due to the different stimulus parameters used (e.g. size, luminance, viewing distance), but, quite conceivably, these differences may reflect individual variation within the normal tree shrew population.

The relationship of the tree shrew spatial CSF to behaviorally-obtained CSFs for other mammals is shown in Fig. 3. Overall, the tree shrew appears rather insensitive to spatial stimuli when compared to the other species.† However differences in eye size and retinal anatomy appear to have a profound effect. Whereas the group of animals with high-peaked CSFs (i.e. the monkeys, cat, galago and human) all have relatively large eyes (e.g. > 14 mm in diameter) and well-developed foveal or area centralis regions, the group with lower-peaked CSFs (i.e. rats, squirrels and tree shrew) have relatively small eyes (e.g. < 11 mm in diameter) and less well-developed retinal centralization. Furthermore, within each group the CSFs of those species with a high percentage of cone receptors (i.e. human, squirrel monkey, macaque, squirrels and tree shrew) predict a much higher visual acuity than the curves of those species with mostly rod receptors (i.e. owl monkey, galago, cat, and rats). Interestingly, those animals with a very small proportion of rod receptors (e.g. tree shrew and ground squirrel) are the least sensitive to spatial contrast modulation. Despite these differences in the position of the various CSFs relative to the sensitivity and spatial frequency axes, and also despite variation in the stimulus parameters and testing procedures used to generate these functions, Uhlich *et al.* (1981) noted that when the CSF curves are transformed by normalizing contrast sensitivity and expressing spatial frequency as octave distance from the peak, a single function can adequately characterize all CSFs. When transformed in this manner, our tree shrew data from each of the three subjects also fit this U-shaped function.

In conclusion, the spatial contrast sensitivity functions which we measured in the tree shrew are consistent with the limitations set by the eye size and retinal anatomy of this animal. Although its spatial resolution appears to be quite limited, good temporal resolution has been found in tree shrews using behav-

ioral and electroretinographic methods (Schafer, 1969; Tigges *et al.*, 1967). Interestingly, similar low-spatial/high-temporal resolution abilities have been noted for gray squirrels and ground squirrels (Jacobs *et al.*, 1980, 1982; Tansley, 1965; Yolton, 1975). These squirrel species also resemble tree shrews in their eye size, cone-dominated retinas and diurnal habits.

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*To account for an acuity of 15 c/deg, the tree shrew eye either would need to have a diameter of 24 mm, or its ganglion cells would need to be 33 layers thick.

†To rule out the possibility that our testing apparatus or procedure may have produced spuriously low estimates of contrast sensitivity, two human subjects were tested using identical stimuli and viewing conditions. Results were in agreement with previously published CSFs for humans (Campbell and Robson, 1968; Campbell and Maffei, 1974).

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