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Short communication

The effects of time, luminance, and high contrast targets: Revisiting grating acuity in the domestic cat

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ABSTRACT

Based on optical clarity and retinal cone density, the cat has a potential acuity of 20–30 cycles per degree (cpd), yet most behavioral studies estimate feline acuity between 3 and 9 cpd. Those studies, however, were limited by restrictive experimental conditions that may have inadvertently lowered the estimated grating acuity. Two domestic cats previously trained on a two-choice visual discrimination task were retrained on a grating detection/discrimination task with unlimited time, high luminance, high contrast targets, and adequate space to prevent poor accommodation from affecting the results. Initially, vertical gratings of increasing cpd were tested until failure. Then, horizontal gratings of increasing cpd were tested until failure. Finally, the finest horizontal grating resolved was confirmed with a third test requiring 24 correct out of 36 consecutive trials, yielding a binomial probability less than 0.02 of non-random occurrence. M1, a 7-year-old male gray tabby with +2.00 OU refraction, tested for a grating detection acuity of 15 cpd for both vertical and horizontal gratings (binomial probability = 0.009). F1, a 2-year-old female gray tabby with +0.25 OU refraction, tested for a grating orientation discrimination acuity of 20 cpd for both vertical and horizontal gratings (binomial probability = 0.004). These results demonstrate that a young cat with good focus is capable of discriminating 20 cpd, in close agreement with the physiologic maximum. Uncorrected focusing errors appear to degrade visual performance. Optimum experimental conditions resulted in better grating acuity measurements than previously reported, emphasizing the importance of environmental factors in feline behavioral testing.

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Despite the fact that the cat's visual system was the first to be extensively described (Barlow, 1982; Hubel and Wiesel, 1962; Wurtz, 2009), behavioral experiments lag behind electrophysiological studies because cats are, at best, reluctant experimental subjects. Based on optical clarity, the cat's eye is capable of resolving gratings as fine as 20–30 cycles per degree (cpd), depending on pupil dilation (Robson and Enroth-Cugell, 1978). Based on the retinal cone density of 1.7 min of arc, compared to human cone density of 1.0 min of arc, the cat's retina has the potential for approximately 18 cpd (Blake, 1988; Steinberg et al., 1973), marginally worse than the maximum optical clarity. Most behavioral studies, however, estimate feline vision between 3 and 9 cpd (Berkley and Watkins, 1973; Blake et al., 1974; Bonds, 1974; Hall and Mitchell, 1991; Harris, 1978; Jacobson et al., 1976; Jarvis and Wathes, 2007; Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983). This loss of acuity is thought to result because retinal cones are pooled together into smaller numbers of retinal ganglion cells, constraining the retinal sampling rate and decreasing the overall acuity (Hughes, 1975, 1981; Stone, 1965).

Five broad categories of experiments have been used to estimate the cats' grating acuity: recording electrical potentials within the brain in response to targets (Berkley and Watkins, 1973; Harris, 1978); behavioral experiments selecting targets with a nose press (Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983); behavioral experiments avoiding electrical shocks linked to visual targets (Blake et al., 1974; Jacobson et al., 1976); behavioral experiments jumping to visual targets (Hall and Mitchell, 1991); and calculating the cat's optical modulation transfer function (Bonds, 1974; Jarvis and Wathes, 2007). All of these studies have one or more of the following important limitations. The first limitation is the lack of adequately illuminated, high contrast targets (Blake et al., 1974; Pasternak and Merigan, 1981; Pasternak et al., 1983). To stimulate feline photopic cones, a minimum illumination of 64 cd/m^2 should be used (Hammond and Mouat, 1985), and 80–320 cd/m^2

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and 100% contrast (black on white) is considered optimal for human testing (Sheedy et al., 1984). The second limitation is the exclusive use of near targets (Berkley and Watkins, 1973; Blake et al., 1974; Hall and Mitchell, 1991; Harris, 1978; Jacobson et al., 1976; Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983). Cats have a limited ability to accommodate near visual targets (Bloom and Berkley, 1977), and 50% of that accommodation should be held in reserve to achieve best vision (Ostrin and Glasser, 2004). Therefore, the closest target should ideally be greater than 80 cm from the eyes, instead of the 25 cm–80 cm used in these studies (Berkley and Watkins, 1973; Blake et al., 1974; Bonds, 1974; Hall and Mitchell, 1991; Harris, 1978; Jacobson et al., 1976; Jarvis and Wathes, 2007; Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983). The third limitation is that most of these studies failed to check the refraction (Blake et al., 1974; Bonds, 1974; Hall and Mitchell, 1991; Jacobson et al., 1976; Loop et al., 1981). Refraction must be taken into account because poor focus reduces the optical clarity of the eye, diminishing the potential maximum visual acuity (Bonds, 1974; Konrade et al., 2012; Rose et al., 1974). The fourth limitation is the rapid presentation of visual trials in an enclosed, potentially stressful environment (Berkley and Watkins, 1973; Blake et al., 1974; Hall and Mitchell, 1991; Harris, 1978; Jacobson et al., 1976; Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983). Best visual acuity results are achieved by giving the subjects adequate time to view and process the targets prior to making a choice. Cats are not working animals by nature, so giving them dozens of trials per day can lead to loss of motivation and concentration, producing suboptimal results. In addition, stress, either from the closed environments or from electrical shocks for incorrect choices (Blake et al., 1974; Jacobson et al., 1976), can produce pupillary dilation, blurring the vision (Hall and Mitchell, 1991). The fifth limitation is the use of food restriction to encourage a fast and steady work rate within the test environment (Blake et al., 1974; Jacobson et al., 1976; Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983). While maintaining cats at 80–85% of their normal weight might motivate them to worker harder for food rewards, it is unlikely that hunger promotes better performance on tests that require fine visual discrimination and target selection.

Therefore, to address those limitations and maximize the behavioral measurement of feline grating acuity, we modified experimental conditions to limit the number of trials per day and provide unlimited time within each trial to view the targets. We used high contrast gratings at relatively long viewing distances with sufficient lighting to ensure photopic viewing. Finally, we did not enforce dietary restrictions, but instead rewarded successful testing with a food treat to motivate further participation in the study.

The experimental subjects were two (one male and one female) spayed or neutered gray tabby mixed breed domestic cats with no known medical or ophthalmic problem. Prior to testing, the refraction was measured in each cat with streak retinoscopy through the undilated pupil (Konrade et al., 2012; Murphy et al., 1992). This study strictly adhered to the guidelines within the ISAE Ethical Treatment for Animals (Sherwin et al., 2003) and EU directive 2010/63/EU for animal experiments. Throughout the study, the cats were maintained on their regular diet, without restrictions to food, activity, or treats. In addition, vision testing was conducted upon demand. Throughout the day, the cats were free to roam within a two-story home. They signaled readiness for testing by waiting outside the testing room in anticipation of performing for their treat. This "on demand" testing limited the trials to 3–6 per day, usually spaced by hours, throughout the testing period.

Trials were conducted in a windowless, 3.1 m by 3.4 m uniform white room with light beige carpeting illuminated by two 13-W compact fluorescent bulbs (60 W incandescent equivalent), generating 140 cd/m^2 measured luminance. The testing room was partially diagonally divided by a 61 cm tall by 183 cm long, thin wooden panel placed at a 45-degree angle against the far corner directly across from the room entrance. The end of the panel closest to the door represented the choice point, the minimum distance that the cats could view both targets prior to making a choice.

The gratings were presented on two iPad 2 tablets (Apple®, Cupertino, CA) with a pixel density of 52 pixels per cm. Both tablets were set to maximum brightness, generating a luminance of 410 cd/m^2 for white and 0.43 cd/m^2 for black (contrast ratio 99.9%) (Soneira, 2011). The tablets were covered with identical black rubber and plastic stand cases and were positioned in landscape mode tilted 15° from vertical. To prevent a difference in luminance or other physical attributes from biasing the choices, the tablets did not change from side to side and only the images were changed on each screen.

The gratings were created as Tagged Image File Format (TIFF) files in Adobe Photoshop® (Adobe®, San Jose, CA) with identical black stripes spaced symmetrically on a white background to maintain whole number pixel dimensions according to the calculations shown in Table 1. Initially, the negative target was selected to be a blank, uniformly white TIFF image with decreased brightness to match the luminescence, but it proved difficult to consistently match the luminance of the white image on one tablet with the luminance of the gratings on the other tablet. The negative target was then chosen to be a 1-pixel width grating, below the maximum theoretical resolution of the feline retina. The 1-pixel width grating contained exactly the same numbers of black and white pixels as the larger grating patterns, matching the overall screen luminance, but the iPad 2's screen displayed it with apparent banding that artificially created the appearance of a larger grating. Subsequently, a 2-pixel width grating was used as the negative target, but presented in an orthogonal orientation to the positive target (i.e. a horizontal 2-pixel width grating was used as the negative target for vertical gratings). A 2-pixel width grating is near the maximum possible theoretical acuity (Table 1), but the orthogonal presentation allows the cats to make the proper visual target choice even if they could resolve the 2-pixel grating. A prior study has shown that there is no difference in results between grating detection and grating discrimination tasks (Hall and Mitchell, 1991). The 2-pixel width grating also contained the same number of black and white pixels as the larger grating patterns to match the overall screen luminance with both tablets set to maximum brightness and, at the testing distances used, had a maximum cpd less than the Nyquist limit of the retinal cone array (Williams and Coleta, 1987), preventing aliasing (Blake, 1988; Levitan and Buchsbaum, 1996) from causing an overestimation of grating discrimination.

Each trial consisted of a two-choice discrimination task using pseudo-random Fellows sequences (Fellows, 1967). Before each

Table 1
Conversion of iPad 2 pixel widths to cycles per degree.

Cycles per degree	Pixel width	Distance (mm)
30.0	2	1325
24.0	2	1060
20.0	2	880
15.0	3	992
12.0	4	1058
8.6	5	945
6.0	7	925
4.0	10	882

The iPad 2's screen has a resolution of 5.2 pixels/mm and demonstrated banding with 1-pixel width black lines. The millimeter distances from the choice point are calculated for the desired cycles per degree by constraining the minimum viewing distance to greater than 800 mm and the minimum stroke width to whole numbers 2 pixels or larger. As an example, the distance D for 20.0 cycles per degree (1.5 min stroke width) using 2-pixel width strokes is calculated as follows: $D = 2$ pixels/(5.2 pixels/mm $\times$ TAN(1.5 min/60 min/degree)) $= 880$ mm.

trial, identical treats were hidden from view in plastic containers behind each tablet placed a pre-specified distance (Table 1) behind the choice point on either side of the dividing panel. The best work rate was obtained with a few pieces of dry, solid cat treat (Friskies® Party Mix Beachside Crunch, Nestle Purina, St. Louis, MO) intermixed with a few pieces of beef jerky, and that combination was used throughout the study. The container behind the negative target had a lid that was perforated with small holes to allow scent to escape but no access, preventing scent from playing a role in the selection process, while the container behind the positive target had a lid with a large, central opening to allow access. Once the targets and treats were in place at the proper distance, the cats were admitted individually into the testing area. A human observer stayed in the room near the entrance, out of view when the cats faced the visual targets, during each trial. This individual took great care to avoid any verbal or nonverbal cues, only providing stereotypic encouragement such as “Go get your treat”.

There was no time pressure, but the cats were removed from the room without a treat if they demonstrated a lack of interest in the task (e.g. laying on the ground, grooming, exploring the room, etc.) and no result was recorded for that trial. If the cat passed the choice point headed towards the positive target, the trial was recorded as a success; the cat received positive encouragement and was allowed to eat the treat. If the cat passed the choice point headed towards the negative target, the trial was recorded as a failure; the cat was removed from the room without any positive feedback or treat.

Because the cats were already trained in two-choice visual discrimination tasks, they immediately began grating testing without additional specific training for this task. The grating testing was divided into three phases. The first phase was conducted with the vertical gratings defined as the positive targets and the 2-pixel width horizontal grating defined as the negative target. Beginning with the 4 cpd grating (10-pixel stroke width), each vertical grating was considered successfully resolved if the cat accurately chose it at a binomial probability of non-random occurrence at the 0.01 level: 7 consecutive correct choices, 9 correct out of 10 trials, 11 correct out of 13 trials, 13 correct out of 16 trials, or 16 correct out of 20 trials. Subsequent positive gratings of increasing cpd were presented until failure, defined as two Fellows sequences with a 50% or worse success rate.

The second phase used horizontal gratings as the positive target compared with the 2 pixel-width vertical grating as the negative target. For this phase, trials began with horizontal gratings one step lower in cpd than the best vertical grating achieved in the first phase (Table 1). The same success and failure criteria were used.

The final phase was the confirmation phase. Trials were conducted using the highest successful horizontal cpd grating, the last grating resolved, compared with the 2 pixel-width vertical negative grating. To confirm success, each cat needed to correctly identify at least 24 out of 36 consecutive trials, achieving a binomial probability of non-random occurrence at the 0.02 level or better. This final acuity represents a conservative estimate of the best grating acuity because the cats made their decision a variable distance away from the choice point, the end of the dividing panel, and thus saw the target a longer distance than was used for the calculation of cpd.

During the first phase of testing with the vertical gratings, M1 detected the 4 cpd grating with 16 out of 20 correct after 31 total trials over 4 days, with only minimal initial confusion with the new visual discrimination task. Subsequently, he passed 6 cpd in only 8 total trials, 8.6 cpd in 20 trials, and 12 cpd in 14 trials. M1 had more difficulty detecting15 cpd, eventually achieving the success criteria after 40 total trials, before failing 20 cpd.

F1 detected the 4 cpd grating with 7 consecutive correct choices after only 12 trials over 2 days, also demonstrating little difficulty learning the new visual discrimination task. Subsequently, she passed 6 cpd in 10 trials, 8.6 cpd in 9 trials, 12 cpd in 15 trials, 15 cpd in 20 trials, and 20 cpd in 14 trials, before finally failing 24 cpd. The 20 cpd and 24 cpd trials involved 2-pixel width gratings for both positive and negative targets, with the only difference being the vertical and horizontal orientation of the grating lines.

During the second phase with the horizontal gratings, M1 detected the 12 cpd grating with 13 out of 16 correct after 20 total trials, then 15 cpd with 11 out of 13 in 14 total trials, before failing 20 cpd again. F1 detected the 15 cpd grating with 13 out of 16 correct after 18 total trials, then 20 cpd with 7 consecutive correct in only 8 trials, before failing 24 cpd again. Both cats achieved an identical maximum cpd for horizontal and vertical targets.

During the final grating confirmation phase, M1 confirmed 15 cpd grating detection acuity (3-pixel horizontal grating versus 2-pixel vertical grating at 992 mm from the choice point) by correctly choosing 25 out of 36 trials (binomial probability = 0.009). F1 confirmed 20 cpd grating orientation discrimination acuity (2-pixel horizontal grating versus 2-pixel vertical grating at 880 mm) by correctly choosing 26 out of 36 trials (binomial probability = 0.004). The results are summarized in Fig. 1.

These results demonstrate that cats are capable of higher grating acuity than previously assumed (Berkley and Watkins, 1973; Blake et al., 1974; Bonds, 1974; Hall and Mitchell, 1991; Harris, 1978; Jacobson et al., 1976; Jarvis and Wathes, 2007; Loop et al., 1981; Pasternak and Merigan, 1981; Pasternak et al., 1983). With optimal focus, high contrast targets, long viewing distances, and adequate lighting, a young cat can discriminate 20 cpd. This grating acuity measurement closely matches the cat's physical limits of optical clarity (Robson and Enroth-Cugell, 1978) and retinal cone density (Blake, 1988; Steinberg et al., 1973), and provides evidence against the contention that upper visual processing or retinal cone pooling into fewer ganglion cells blurs the visual potential of the cat's optical system (Blake, 1988; Hughes, 1975, 1981; Stone, 1965).

These results reinforce the importance of maintaining a physiologic environment to achieving optimal results in behavioral experiments. Unsurprisingly, cats constrained within dark, enclosed

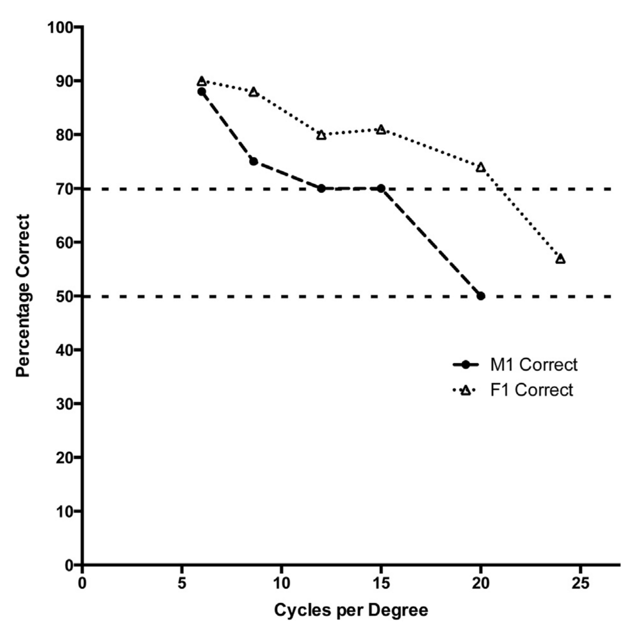

Fig. 1. Percentage of correct responses as a function of spatial frequency. All trials are included – vertical positive gratings, horizontal positive gratings, and the horizontal positive grating confirmation phase at the highest achieved resolution. M1 resolved 15 cycles per degree correctly 70 times over 102 total trials and F1 resolved 20 cycles per degree correctly 52 times over 70 total trials.

testing areas with restricted movement and diet did not perform as well as motivated cats in brightly illuminated, *ad lib* environments. The goal is to allow the experimental subject to perform at peak efficiency, processing all visual information before making a choice.

M1 illustrates the importance of determining the refraction prior to testing visual acuity. Uncorrected refractive error in the cat has been shown to blur the optical system by approximately 25% per 0.50 diopters of defocus (Bonds, 1974). Thus, the two diopters of hyperopia measured in M1 is predicted to create 100% image blur, potentially doubling the size of minimum resolvable details. Accommodation can overcome some of that hyperopia (Bloom and Berkley, 1977), but the diminished accommodative ability of the cat would not be expected to completely overcome hyperopia at the level found in M1. Assuming F1's result represents the highest potential grating acuity in a young cat with near-perfect focus, an increase in the size of discernable details caused by poor focus should easily be sufficient to decrease M1's grating detection from 20 cpd to 15 cpd, his best measured grating acuity.

This study has a few important limitations. Only two subjects took part in the experiment, a small number to base our findings upon but comparable to previous animal behavioral experiments in the literature. In addition, relatively few trials were conducted, giving each trial more weight within the results. Careful planning was required to allow the cats to quickly progress to finer gratings while maintaining their interest in the experiment. The third phase, requiring more successful trials and achieving a high level of statistical certainty, was crucial to validate the results. By the end of the experiment, each cat detected or discriminated its finest grating three different times at a binomial probability less than 0.01, yielding an overall probability of non-random occurrence at less than 10^{-6}.

In conclusion, optimum conditions, including bright lighting, adequate time, and sufficient space, are required to produce accurate results during the physiologic testing of higher cortical functions like grating acuity. Conducting fewer trials per day and allowing more time for completion prevents factors such as intelligence, fatigue, apprehension, and inattentiveness from affecting the results and producing a sub-maximal performance. Uncorrected focusing problems can significantly degrade visual performance, but this study demonstrates that young cats with good focus are capable of discriminating 20 cpd, much higher than previously reported.

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