



Single target acuity is not higher than grating acuity in a bird, the budgerigar

Sandra Chaib^{a,*}, Mikael Ljungholm^a, Olle Lind^b, Almut Kelber^a

^a Department of Biology, Lund University, Sweden

^b Department of Philosophy, Lund University, Sweden



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ABSTRACT

We examined the capacity of budgerigars (*Melopsittacus undulatus*) to visually detect dark single targets against a brighter background and established their spatial resolution limit for such targets. While the sampling density of the retina limits the resolution of gratings, target detection is theoretically limited by contrast sensitivity. This allows many animals to detect single targets smaller than their visual resolution limit, but this is not the case for budgerigars. The budgerigars were able to detect a high contrast circular target with a luminance profile of a single period of a sine wave subtending 0.065 degrees of their visual field, corresponding to a spatial acuity of 7.7 cycles degree⁻¹, a measurement in line with the previously measured grating acuity of budgerigars (7.7 and 10 cycles degree⁻¹). This result is different from findings on the spatial acuity of humans, who can detect single targets much smaller than predicted by their acuity for gratings. The low contrast sensitivity of budgerigar vision might be one of the reasons why the single target acuity is not higher than grating acuity. Adding a bright surround to the target did not influence detection threshold significantly. However, the threshold was slightly higher for a target with a square-wave luminance profile than for a target with a sinusoidal luminance profile.

1. Introduction

Spatial resolution of vision is traditionally measured as the capacity of the eye to resolve a grating of dark and light bars (de Valois & de Valois, 1990). In order to resolve a grating, the images of adjacent dark and light bars must fall on the receptive fields of separate sampling units (photoreceptors or, in many cases, retinal ganglion cells) in the retina (Land & Nilsson, 2012). If the grating is any finer, each unit will sample both light and dark areas, which will reduce the perceived contrast, and ultimately make the image appear uniformly grey. Grating acuity thus is a measure of how fine detail in a visual scene the eye is able to resolve.

It is often assumed that it is possible to deduce, from grating acuity, the size of the smallest single target that an animal can detect. However, different physical mechanisms determine how fine gratings and how small objects an eye can resolve. While the retinal sampling density sets the limit to grating acuity, single target acuity is limited by contrast sensitivity. Thus, a single target smaller than the receptive field of a retinal sampling unit can still be detected if it has high contrast to the background (O'Carroll & Wiederman, 2014).

While gratings have been used extensively when investigating the visual acuity of vertebrates, determining single target acuity has been a

common approach in work with insects (for examples see Giurfa & Vorobyev, 1998, Somanathan, Borges, Warrant, & Kelber, 2017, Spaethe & Chittka, 2003, Vallet & Coles, 1993). Behavioural tests have revealed target detection below the resolution limit for gratings in several insect species. Drone honey bees (*Apis mellifera*) are able to detect a dummy queen bee only subtending an angle of 0.41 degree in their visual field (Vallet & Coles, 1993) and a recent study describes male carpenter bees (*Xylocopa tenuiscapa*) reacting to a flying female covering less than 0.1 degree of their visual field (Somanathan et al., 2017), although the interommatidial angles in both species, 0.5 degree and 0.7 degree respectively, predict much lower grating acuity.

Humans are able to detect a black square against the sky subtending 1/5 of the width of a single line in the finest grating they can resolve, while a black single line is visible even at about 1/100 of the width of a single black stripe in such a grating (Hecht, Ross, & Mueller, 1947). Few such studies have been performed on other vertebrates, but Ehrenhardt (1937) reported that sand lizards (*Lacerta agilis*) were able to detect a single black line against a bright background when it had 1/10 of the width of one stripe in the finest grating that the animals could resolve.

The choice of the most suitable stimulus for investigation of visual acuity thus depends on the question to be asked. Grating acuity is a good measure of how small details in a cluttered environment an

* Corresponding author at: Sölvegatan 35, 223 62 Lund, Sweden.

E-mail address: sandra.chaib@biol.lu.se (S. Chaib).

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animal can detect while target acuity determines in which distance a small single object can be detected on an even background such as the sky (Land, 1997). The visual capabilities of birds have been widely studied but to our knowledge no one has investigated how small single targets or objects they can detect. Budgerigars (*Melopsittacus undulatus*) have been used extensively as model for the avian visual system, and several aspects of their spatial vision have been investigated. The spatial resolution threshold of a budgerigar for a stationary grating is 7.7 to 10 cycles degree⁻¹ (Haller, Lind, Steinlechner, & Kelber, 2014, Lind & Kelber, 2011, Lind, Sunesson, Mitkus, & Kelber, 2012). The maximum contrast sensitivity for stationary achromatic gratings is 10.2 to 14 (corresponding to 9.8–7.1 Michelson contrast, for spatial frequencies around 1–2 cycles degree⁻¹; Haller et al., 2014, Lind & Kelber, 2011, Lind et al., 2012). Budgerigars need a similar achromatic contrast (9 Michelson contrast) to discriminate two spatially separated homogeneous fields (Lind, Karlsson, & Kelber, 2013), while they can detect drifting gratings at only 5.8 Michelson contrast (Haller et al., 2014). Birds in general have low contrast sensitivity, ranging between 7 and 30, compared to humans, which have a contrast sensitivity of about 175 (Lind et al., 2012).

In this study we first determined the detection threshold for dark targets with different achromatic contrasts to the background, in short, the target acuity of budgerigars. To make the results comparable to previous work, we used targets with sinusoidal luminance profiles. Second, we ask whether the luminance profile of the target affects its detectability. Does a target with a square-wave luminance profile have the same detection threshold as the target with sinusoidal luminance profile?

Previous studies on budgerigar grating acuity revealed no difference between visual acuity of sinusoidal patterns and square-wave patterns (Lind & Kelber, 2011, Lind et al., 2012), but in humans a higher detectability for square-wave patterns has been observed (Campbell & Robson, 1968). If the contrast sensitivity was high enough, these two targets could theoretically be detected beneath the resolution limit of the retina. This should not be possible for a target with the same overall luminance as the background. Therefore, we also tested the ability of budgerigars to detect a target with a sinusoidal luminance profile similar to the first stimulus but with a bright surround and thus, the same overall luminance as the background.

2. Methods

2.1. Animals

We used four budgerigars (one female and three males) in our behavioural experiments. The birds were fed a parakeet seed mix as well as fruits and vegetables. One day prior to the weekly training/testing period the seed mix was removed from the cage but the birds always had access to fruits or vegetables. During the training and test sessions, usually on four days/week, the seed mix was used as reward. All experiments were performed following Swedish legislation, under the permit M111-14 from the local authority for animal ethics.

2.2. Experimental apparatus

The experiments took place in a flight cage (length: 1580 mm, width: 860 and height: 670 mm) constructed of metal net except for the floor and one of the short end walls that were made of matte-grey plastic board (Fig. 1). The plastic wall had two circular openings of 90 mm diameter placed 330 mm apart, which allowed the presentation of stimuli on an LCD-screen behind the wall. Beneath each window a feeder with removable lid and a perch was positioned. A vertical grey plastic board divided the cage into two equally sized compartments starting between the stimulus windows and 1160 mm into the cage.

A starting perch was positioned opposite the stimulus windows. Centred on this perch, a bird had a good view of both stimulus

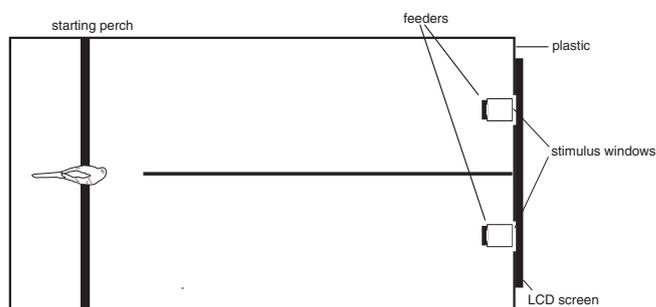


Fig. 1. Sketch of the experimental cage viewed from above with the bird sitting on the starting perch.

windows. The experimenter was always situated behind the grey wall, out of sight for the bird, and monitored the behaviour of the bird on an external screen showing the live feed of a camera attached to the experimental cage.

2.3. Stimuli

Each stimulus pair consisted of one homogeneously grey field (137 candela/m²) and one identical grey field with a circular target in its centre. The stimuli were created in Matlab (v. 8.5.0.197613, The MathWorks Inc.) as PNG-images and presented in Microsoft PowerPoint (v. 14.7.2.170228).

2.3.1. Experiment 1: Sinusoidal targets of different contrasts

In Experiment 1, we determined the detection threshold for a single dark circular target with a gradual transition between the darker centre and the brighter background. The luminance profile of this target resembled a single cycle of a sinusoidal wave, which allowed for direct comparison to previous behavioural tests of grating acuity in the same species (Haller et al., 2014, Lind & Kelber, 2011, Lind et al., 2012). This target was presented with 5 different contrasts to the background (C1, C2, C3, C4, and C5). All stimuli had the same background luminance while the target luminance differed. We give contrast levels as Weber contrast, which is commonly used for contrasts between a single target and its background (O'Carroll & Wiederman, 2014, Rigosi, Wiederman, & O'Carroll, 2017). The equivalent Michelson contrasts are given in Table 1 for easier comparison with previous studies. Target size is given as full width at half amplitude (Fig. 2a), which allows for direct comparison to sine wave gratings.

2.3.2. Experiments 2 and 3: Targets with different luminance profiles

In experiments 2 and 3 we investigated whether the luminance profile of the target affected the detection threshold. The aim of experiment 2 was to compare the detection thresholds for targets with square wave luminance profile to those with a sine wave profile. The stimulus used in experiment 2 had a dark circular target with a sharp edge and a square luminance profile (Fig. 2b). We used the same background luminance as in experiment 1, and the highest contrast (C1) to the background.

A square wave grating and a sine wave grating with the same fundamental frequency and contrast have the same overall luminance.

Table 1

Contrast levels used in the experiments expressed as Weber contrast and Michelson contrast.

	C1	C2	C3	C4	C5
Weber contrast $C_W = \frac{I_0 - I_b}{I_b}$	> 99	89	68	53	41
Michelson contrast $C_M = \frac{I_{\max} - I_{\min}}{I_{\max} + I_{\min}}$	> 99	80	50	35	25

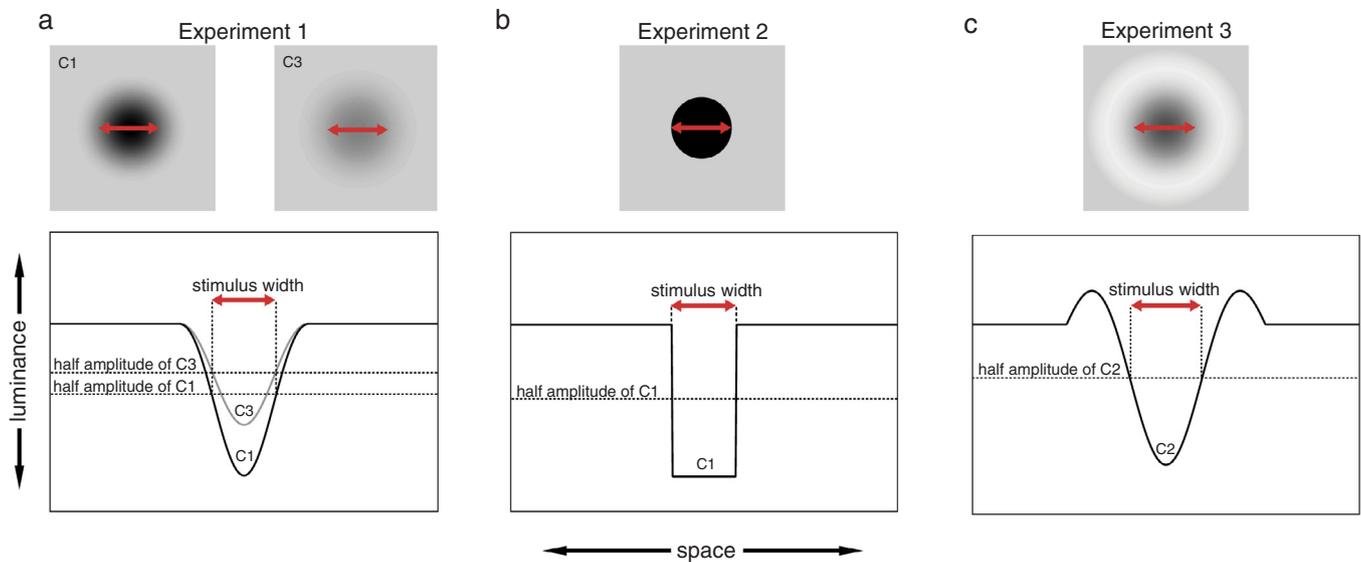


Fig. 2. Luminance profiles of the three types of stimuli. a) The sinusoidal target (Experiment 1), b) the square wave target (Experiment 2) and c) the target with a bright surround (Experiment 3).

However, a circular target with a sine wave luminance profile (the C1 target in experiment 1) decreases the luminance of the stimulus 19% more than a square wave target (the target in experiment 2; see [Supplementary Material A](#) for the calculations).

As we define the size of the sinusoidal target as full width at half maximum, the area of the target with contrast below half amplitude (or 50 Weber contrast to background) will extend outside the defined “target area”. However, budgerigars are able to detect a Michelson contrast of about 10 ([Lind et al., 2013](#), [Lind & Kelber, 2011](#), [Lind et al., 2012](#)). If we measure the size of the targets as the area with at least 10 Michelson contrast to the background, the diameter of the C1 sine wave target will increase with about 59% compared to full width at half maximum, while the diameter of the square wave target will not change.

In experiment 3, we used a target with the same overall luminance as the background. This way, the bird should be unable to discriminate the stimuli with and without targets, if the target was smaller than the acceptance angle of one sampling unit of the eye. This target was similar to the target used in experiment 1, but had a bright surround ([Fig. 2c](#)). The size of the target was measured as the full width at half amplitude between the darkest and brightest part. It was not possible to display this target with the highest contrast (C1) on our monitor without creating sharp transitions between dark and bright areas. In order to avoid such unwanted artefacts we therefore chose to present this target with contrast C2 (89 Weber contrast between target centre and background and 92 Weber contrast between target centre and bright surround)

2.4. Training and testing

We trained each bird individually to associate the stimulus without target, the positive stimulus, with a food reward, and the stimulus with target, the negative stimulus, with absence of a reward. This way, the bird will experience two positive stimuli, if it is unable to resolve the target, and we avoid a scenario in which the bird stops making choices because of the lack of a rewarding stimulus, which would be impossible to separate from the lack of motivation of a different cause.

During the training and test sessions a bird was sitting in the middle of the starting perch facing the two stimulus windows (see [Fig. 1](#)). Each trial started with the screen displaying one stimulus pair – the grey background with the circular dark target as negative stimulus and the background alone as positive stimulus. If the bird flew to the perch in

front of the positive stimulus the feeder was opened and the bird was allowed to eat for around four seconds. If the bird was flying to the negative stimulus, the screen turned black and the feeder remained closed. The bird had unlimited viewing time of the stimuli before making its choice. A new trial began once the bird had returned to and centred on the starting perch. The positive and negative stimuli were presented in the right or left window in a pseudo-random order ([Gellermann, 1933](#)).

In the initial training sessions with a bird, we used a large target (subtending 1 degree of the visual field at the decision point). A bird was considered to have learned to associate the positive stimulus with the food reward when it performed $\geq 80\%$ correct choices in two consecutive training sessions of 20 choices each. Once a bird had fulfilled this criterion we decreased the size of the stimulus stepwise using an adaptive 2-down/1-up staircase procedure ([Levitt, 1971](#)) in each session of 20 trials. This frequently used method implies that, following two correct choices by the subject the experimenter reduces the size of the target presented in the next trial, while after a single incorrect choice stimulus size is increased. Such a process of reversals results in fluctuation around a target size, for which the probability of making two correct choices in a row equals the probability of making one incorrect choice. This corresponds to the point on a psychometric curve, in which the probability of a correct choice is 70.7% ([Levitt, 1971](#), see [Fig. 3](#) for an example). We chose this probability level to allow for easier comparison of our results with previous data sets on spatial resolution and contrast sensitivity of budgerigars, in which stimuli were presented a set number of times in random order. In those experiments, following binomial statistics, a level of 72.5% correct was significantly different from chance ([Lind & Kelber, 2011](#)).

In order to keep the birds motivated, we started each session using a fairly large target and decreased target size in small steps. Over several staircase training sessions, all birds improved in motivation and performance, and we increased the number of trials per session to between 40 and 60. A bird was considered to have reached its detection threshold, when the performance did not improve over three consecutive sessions.

2.5. Analysis

The detection threshold was calculated as the mean stimulus size at the reversals (two correct choices following an incorrect choice or an incorrect choice following two correct choices) during the last 20 trials

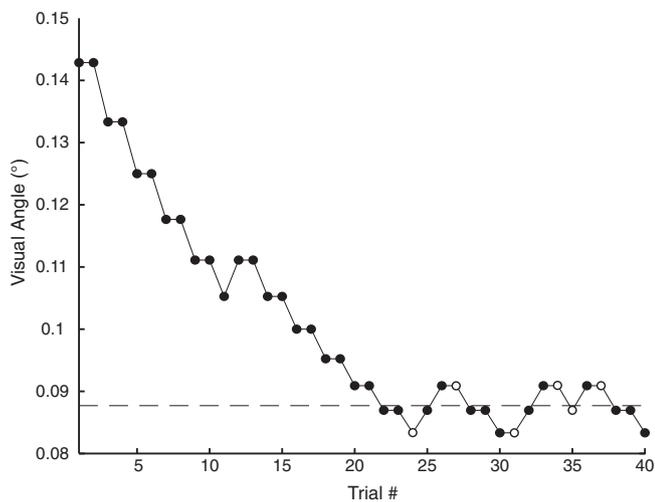


Fig. 3. An example test session with a bird (Pippi) in experiment 1. The detection threshold (indicated by the dashed line) was estimated by calculating the mean of the stimulus sizes in the reversals (indicated by open circles) of the 20 last trials.

in a test session (dashed line in Fig. 3). To avoid estimation bias we used an even number of reversal points per session excluding the first reversal point if needed. The results for each contrast level and experiment include three test sessions per bird.

To examine the effect of contrast level on detection threshold we fitted a linear mixed model (LMM) with random intercepts to our data from experiment 1 using the `{lmerTest}` package (Kuznetsova, Brockhoff, & Christensen, 2017) in RStudio (v. 1.1.463; RStudio Team, 2016). The model had contrast level as fixed effect and bird identity as random effect. This model was compared to a reduced model, excluding the fixed effect of contrast, with a log likelihood ratio test (Quinn & Keough, 2002). We performed a Tukey's HSD test for post-hoc analysis using the `{multcomp}` package (Hothorn, Bretz, & Westfall, 2008) in RStudio.

To test whether detection thresholds differed between targets with different luminance profiles, we compared the results from experiment 2 (targets with C1 contrast and a sharp edge) and the results from experiment 3 (sinusoidal target with contrast C2 and bright surround) to those obtained with the same contrast level in experiment 1. We used the `{lmerTest}` package in R to fit LMMs with random intercepts and luminance profile as fixed effects and bird identity as random effect. These models were analysed by comparing them to reduced models, excluding the fixed effects of luminance profiles, with a log likelihood ratio test.

3. Results

3.1. Experiment 1: Detection threshold for sinusoidal targets

All four birds learned to discriminate the stimulus without the target from the stimulus with the target. Over four to eight staircase training sessions, their performance improved before it reached a constant level (see Supplementary Material Fig. B1). In the test sessions, the birds were able to detect the target with the highest contrast to the background (C1) when it had a diameter of 0.065 ± 0.008 degrees. This corresponds to resolution of a sinusoidal grating with a spatial frequency of $7.7 \text{ cycles degree}^{-1}$ (95% confidence interval: $6.8 - 9.0 \text{ cycles degree}^{-1}$). The smallest target detected by any bird was 0.056 degrees in diameter (Pippi, C1; Fig. 4a). The model including contrast level as fixed effect provided a significantly better fit to the data than a reduced model ($\chi^2 = 110.8$, $df = 4$, $p < 0.001$) and had a lower Akaike Information Criterion (AIC) value (-321.8 versus -219.9),

indicating that detection threshold varied with contrast level. The detection thresholds differed significantly between all contrast levels except between C2 and C3 and between C4 and C5 (for statistics see Supplementary Material Table C1).

3.2. Experiments 2 and 3: Targets with different luminance profiles

In Experiment 2, using a square wave target, the birds reached a detection threshold of 0.098 ± 0.008 degrees (Fig. 5), corresponding to the resolution of a sinusoidal grating of $5.1 \text{ cycles degree}^{-1}$. When the data from Experiment 2 was analysed together with C1 data from Experiment 1, a model including luminance profile as fixed factor had a significantly better fit to our data than a reduced model ($\chi^2 = 37.2$, $df = 1$, $p < 0.001$) and had a lower AIC value (144.8 versus -109.6). This indicates that luminance profile had an effect on the detection thresholds in this experiment.

To test whether this difference resulted from the difference in overall luminance between these two targets, we compared the two targets on a unit-less scale that describes how much each target reduces the overall luminance of the stimulus ("change in luminance"). On this scale, the target in experiment 1 changes the luminance by 19% more than the target in experiment 2, given the same diameter (see Supplementary Material A). Thus, at detection threshold - since the relative change in luminance is a function of the area of the target - the larger square wave target changed overall luminance by almost 90% more than the sinusoidal target. We repeated the statistical analysis using "change in luminance" as the dependent variable and still found the luminance profile to have an effect on detection threshold ($\chi^2 = 24.3$, $df = 1$, $p < 0.001$, AIC: -229.9 versus -207.6).

We also determined which portion of the sinusoidal target had at least 10 Michelson contrast to the background, taking into account that budgerigars are able to detect brightness contrasts of ≈ 10 Michelson contrast (Lind et al., 2013). Measuring the size of the targets in this way, the mean detection threshold for the sine-wave target was 0.094 degrees. We repeated the statistical analysis, and for this comparison, found no significant effect of luminance profile on detection threshold ($\chi^2 = 2.08$, $df = 1$, $p = 0.15$, AIC: -145.2 versus -145.1).

Finally, in experiment 3, we tested the birds using a target with a bright surround. The birds were able to detect a target with a diameter of 0.085 ± 0.008 degrees (Fig. 5). The data from Experiment 3 was analysed together with the C2 data from Experiment 1 and a model including luminance profile as fixed effect did not show a better fit than a reduced model ($\chi^2 = 0.85$, $df = 1$, $p = 0.36$, AIC: -144.1 versus 145.2), indicating no effect of luminance profile on detection threshold in this experiment.

4. Discussion

We tested how small circular targets budgerigars are able to detect, depending on their luminance profiles and contrasts to the background. The targets used in Experiment 1 had a luminance profile similar to one cycle of a sine function allowing us to directly compare the detection thresholds with previously measured spatial resolution and contrast sensitivity of budgerigars for sinusoidal gratings (Haller et al., 2014, Lind & Kelber, 2011). With the highest contrast to the background (C1), the birds could detect a target subtending 0.065 ± 0.008 degrees of the visual field, equivalent to a resolution threshold of $7.7 \text{ cycles degree}^{-1}$. This acuity measurement is similar to the grating acuity obtained by Haller et al. (2014; $7.7 \text{ cycles degree}^{-1}$; Fig. 4b) but the limit obtained by Lind and Kelber (2011) and Lind et al. (2012; $10 \text{ cycles degree}^{-1}$) lies outside the 95% confidence interval of our measurement (see Results). Mitkus, Chaib, Lind, and Kelber (2014) estimated spatial acuity for budgerigars based on maximal ganglion cell density in the retina to be $6.9 \text{ cycles degree}^{-1}$, which is inside the 95% confidence interval of our threshold.

In contrast to humans and other animals, whose detection threshold

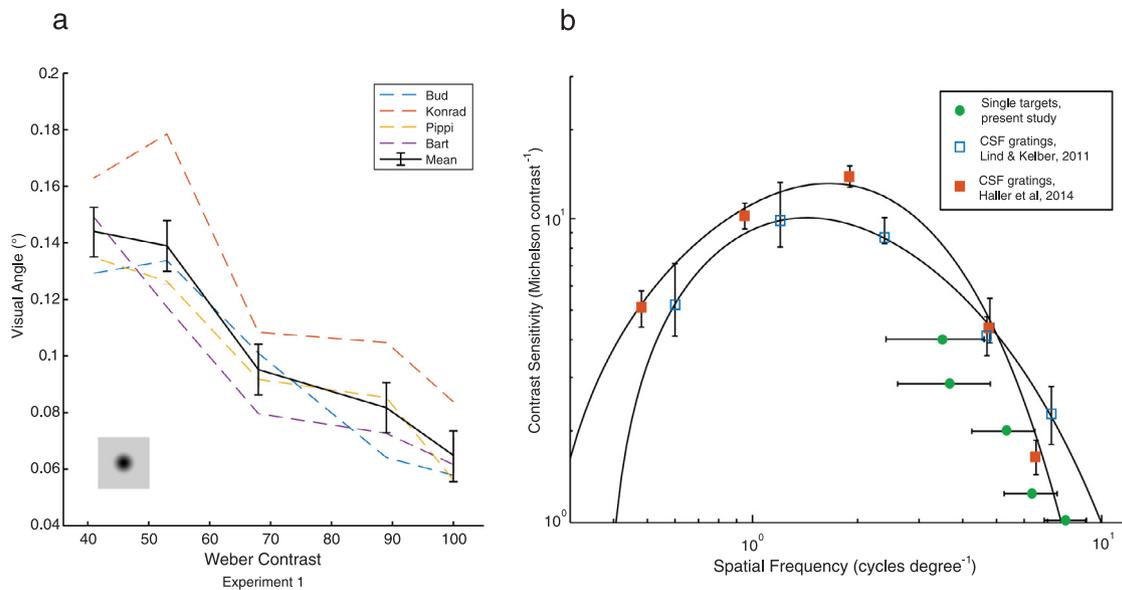


Fig. 4. Detection thresholds of four budgerigars for single targets with different contrasts to the background (Experiment 1). a) Detection thresholds (in degrees) as function of Weber contrast. Solid line: Mean values of all birds (\pm standard errors), dashed lines represent detection thresholds of each bird. b) Comparison between single target and grating acuity and contrast sensitivity (using Michelson contrast). Green circles: detection thresholds from Experiment 1, calculated as cycles degree⁻¹ (\pm 95% confidence interval). Solid lines: Contrast sensitivity functions of budgerigars with achromatic gratings from Lind and Kelber (2011), with open blue squares (\pm 95% confidence interval), and Haller et al. (2014), with filled red squares (\pm standard error).

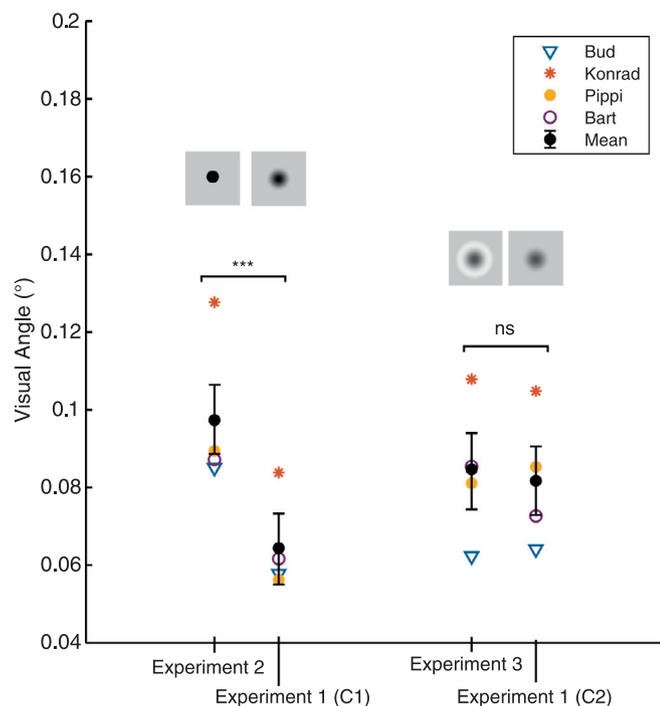


Fig. 5. Detection thresholds of budgerigars for single targets. Left: Targets with square luminance profiles (Experiment 2) compared to targets with sinusoidal luminance profiles (C1 Experiment 1), right: targets with a bright surround (Experiment 3) compared to sinusoidal luminance profiles (C2 Experiment 1). Black filled circles: mean values of all birds. Error bars give standard error. Other symbols: individual birds (see inset).

for single targets has been investigated (Hecht et al., 1947, O’Carroll & Wiederman, 2014), the budgerigars in our study were not better at detecting single targets compared to gratings. A possible reason for this could be their low contrast sensitivity of ≈ 10 , given as inverted Michelson contrast (Lind et al., 2013, Lind & Kelber, 2011). Birds generally have low contrast sensitivity (between 7 and 30; see Lind et al.,

2012, Potier, Mitkus, & Kelber, 2018), compared to humans or cats, which have a contrast sensitivity of 175 and 116, respectively (Lind et al., 2012). Detection of single targets smaller than the resolution threshold is limited by contrast sensitivity since such targets are seen as a small change in luminance in one sampling unit in the retina, and thus appear as having lower contrast to the background (Land & Nilsson, 2012, O’Carroll & Wiederman, 2014). Overall luminance of the stimuli used in Experiment 1 decreases proportionally to the square of target diameter (Eq. (A.3) in supplementary methods), thus the contrast between target and background decreases rapidly with target size.

Fig. 4b shows the detection thresholds for the stimuli in Experiment 1 as function of contrast sensitivity, using the Michelson contrast of the stimuli (see Table 1). Our results are in line with contrast sensitivity functions for budgerigars measured using gratings (Fig. 4b; Haller et al., 2014, Lind & Kelber, 2011, Lind et al., 2012). However, we never tested the budgerigars with low spatial frequencies so we do not know whether the contrast sensitivity function for single targets will have the same band-pass shape as the function for gratings (Lind et al., 2012).

Budgerigars could detect smaller targets with the highest contrast (C1) target in Experiment 1 than in Experiment 2 when we measured the size of the sinusoidal target as full width at half maximum. This difference was even larger when the target was measured as the overall decrease in stimulus luminance, compared to the stimulus without target (see Eq. (A.5) in Supplementary Methods). Interestingly, the contrast sensitivity of humans is $4/\pi$ (1.27) times higher for a square wave grating than for a sinusoidal grating with the same period (Campbell & Robson, 1968). However, this has not been demonstrated in budgerigars (Lind et al., 2012), and it has not been measured for single targets in humans.

For a sinusoidal target diameter adjusted for budgerigar contrast sensitivity (area with contrast ≥ 10 Michelson contrast included), acuity was similar to that of a square-wave target (see Results). This shows that comparisons between single targets require careful considerations of the observer’s visual system.

Humans are better at detecting a single straight line than a single square of the same width (Hecht et al., 1947). A line covers a greater portion of the visual field and the receptive fields of more retinal sampling units than a square. It is thus possible that budgerigars can

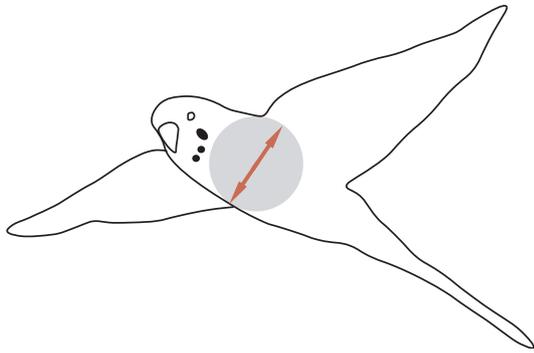


Fig. 6. Illustration of a flying budgerigar. The red arrow marks the core transect diameter.

also detect single lines that are finer than predicted from their target acuity.

The detection threshold for the target with bright surround (Experiment 3) was not different from the detection threshold for the sine-wave target with the same contrast but without surround (Experiment 1, C2; Fig. 5). The luminance profile of the target used in Experiment 3 was designed to have the same overall luminance as the background, which should theoretically make detection impossible when it is smaller than the receptive field of a sampling unit in the retina. Interestingly, “vanishing optotypes” have been used to measure spatial acuity of human subjects using letters. Like single targets or lines, simple black letters can be detected even when they are smaller than the resolution threshold would allow, simply because of the change in luminance. A “vanishing optotype”, with a bright surround similar to the bright surround that we used in Experiment 3, the letter “vanishes” at the level of resolution, as its overall luminance is equal to that of the background (Demirel, Anderson, Dakin, & Thibos, 2012, Howland, Ginsburg, & Campbell, 1978). In a similar way, because the detection limit for the sinusoidal target with and without a bright surround did not differ, we can conclude that the thresholds indeed are limited by the spatial acuity of the birds, and not by contrast sensitivity.

A budgerigar is able to detect a high contrast sharp-edged target subtending ≈ 0.1 degrees of its visual field. If we assume that a flying bird occupies at least an area the size of the core of its body (Fig. 6), we can estimate detection distance. A budgerigar would be able to spot a conspecific against the sky from about 25 m distance and a typical predator on small birds, the Brown falcon (*Falco berigora*), from the safe distance of 85 m.

A bird in flight, however, has a more complex shape than a circle, making this a rather conservative approximation. As a flying bird normally moves across the visual field of the observer (although see Kane & Zamani, 2014) it is possible that image motion also affects its visibility. Budgerigars have higher contrast sensitivity for moving than for stationary gratings (Haller et al., 2014). Therefore, we plan to investigate the influence of motion on the detectability of single targets in our next study.

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Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.visres.2019.04.005>.

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