The Company of Biologists

RESEARCH ARTICLE

More than noise: context-dependent luminance contrast discrimination in a coral reef fish (*Rhinecanthus aculeatus*)

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ABSTRACT

Achromatic (luminance) vision is used by animals to perceive motion, pattern, space and texture. Luminance contrast sensitivity thresholds are often poorly characterised for individual species and are applied across a diverse range of perceptual contexts using over-simplified assumptions of an animal's visual system. Such thresholds are often estimated using the receptor noise limited model (RNL). However, the suitability of the RNL model to describe luminance contrast perception remains poorly tested. Here, we investigated context-dependent luminance discrimination using triggerfish (*Rhinecanthus aculeatus*) presented with large achromatic stimuli (spots) against uniform achromatic backgrounds of varying absolute and relative contrasts. 'Dark' and 'bright' spots were presented against relatively dark and bright backgrounds. We found significant differences in luminance discrimination thresholds across treatments. When measured using Michelson contrast, thresholds for bright spots on a bright background were significantly higher than for other scenarios, and the lowest threshold was found when dark spots were presented on dark backgrounds. Thresholds expressed in Weber contrast revealed lower thresholds for spots darker than their backgrounds, which is consistent with the literature. The RNL model was unable to estimate threshold scaling across scenarios as predicted by the Weber–Fechner law, highlighting limitations in the current use of the RNL model to quantify luminance contrast perception. Our study confirms that luminance contrast discrimination thresholds are context dependent and should therefore be interpreted with caution.

KEY WORDS: Receptor noise limited model, Experimental psychophysics, Perceptual thresholds, Visual ecology, Visual modelling

INTRODUCTION

The perception of chromatic (colour) and achromatic (luminance) information from the surrounding environment enables animals to perform complex behaviours such as navigation, mate choice, territorial defence, foraging and predator avoidance. Chromatic information is largely used to assess the spectral composition and quality of objects or other organisms (Osorio and Vorobyev, 2005), whereas achromatic information is predominantly used for object grouping, pattern and texture detection, figure–ground segregation, and the perception of motion and depth (Anderson, 2011; Brooks, 2014; Elder and Sachs, 2004; Elder and Velisavljevic, 2010; Gilchrist, 2008; Gilchrist and Radonjic, 2009).

Behavioural experiments to examine colour and luminance discrimination thresholds enable inferences on the perception of visual information by non-human observers (for discussion, see Olsson et al., 2018). Thresholds may be influenced by the spatiotemporal and spatiochromatic properties of a visual scene, as the perception of colour, pattern, luminance and motion interact when low-level retinal information is processed along pathways in the visual cortex (Monnier and Shevell, 2003; Shapley and Hawken, 2011; Shevell and Kingdom, 2008), or at even earlier stages (Heath et al., 2020; Zhou et al., 2020 preprint). For example, the perception of luminance contrast in animals is influenced by a range of factors, including perceived illumination and reflectance (which in turn depend on illumination) in addition to various spatial and temporal properties, such as depth perception, adaptation, stimulus geometry and viewer expectation of the position and shape of a stimulus (Corney and Lotto, 2007; Craik, 1938; Gilchrist and Radonjic, 2009; Heinemann and Chase, 1995; Kingdom, 2011; Lind et al., 2012; Pelli and Bex, 2013). The impact of post-photoreceptor and particularly post-retinal neuronal processing on luminance perception is often illustrated by visual displays targeting these effects, such as simultaneous contrast illusions (Fig. 1). To investigate the design, function and evolution of animal visual signals, it is important to define the context sensitivity of visual threshold measurement.

Luminance contrast of objects against their visual background or between objects can be measured in a number of different ways, including Michelson contrast, Weber contrast and root mean square (RMS) (Bex and Makous, 2002; Moulden et al., 1990; Vorobyev and Osorio, 1998). Michelson contrast is commonly used to describe the contrast between two comparably sized objects or sine gratings (Bex and Makous, 2002; Pelli and Bex, 2013). Weber contrast is particularly popular in psychophysics, and is designed to describe the contrast of an object against a dominating background, while accounting for the Weber–Fechner law that states that psychometric thresholds scale with stimulus intensity at a constant ratio: the Weber fraction (Dzhafarov and Colonius, 1999; Norwich, 1987; Treisman, 1964). Luminance discrimination thresholds in animals have been obtained from behavioural experiments and measured in Michelson contrast and most commonly in Weber contrast (e.g. Lind et al., 2013; Scholtyssek et al., 2008). For example, human (Cornsweet and Pinsker, 1965) and seal (Scholtyssek and Dehnhardt, 2013; Scholtyssek et al., 2008) luminance discrimination thresholds are between 0.11 and 0.14 Weber contrast. Other animals have poorer luminance discrimination thresholds, including birds (0.18–0.22 Weber contrast) (Lind et al., 2013), dogs (0.22–0.27 Weber contrast)

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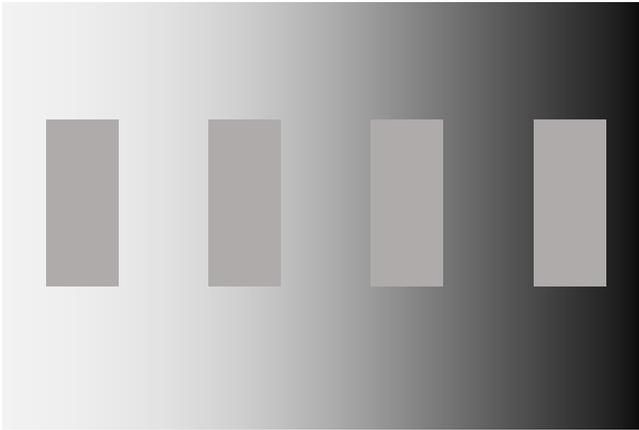
Fig. 1. The simultaneous contrast effect. Despite having identical luminance, the left-most internal square appears darker than the right one as a result of the background contrast against which each square is viewed.

(Pretterer et al., 2004), manatees 0.35 Weber contrast (Griebel and Schmid, 1997) and horses (0.42–0.45 Weber contrast) (Geisbauer et al., 2004).

Behavioural experiments measuring discrimination thresholds are often time consuming and unfeasible, especially when studying non-model organisms. Furthermore, focal species may not be suitable for behavioural testing because of ethical, legal or logistical restrictions. Therefore, in studies on visual ecology, the receptor noise limited (RNL) model (Vorobyev and Osorio, 1998) has been adopted as a means of estimating whether both colour and luminance contrast within and between animal colour patterns, or between animals and their backgrounds, are perceivable to a species. The model was initially designed for colour contrast modelling; however, the achromatic interpretation of the RNL model (Siddiqi et al., 2004) has been used in a large number of studies to quantify the perception of luminance contrast by non-human observers (e.g. Cheney and Marshall, 2009; Marshall et al., 2016; Spottiswoode and Stevens, 2010; Stoddard and Stevens, 2010; Troscianko and Stevens, 2015). In contrast to using Weber contrast or Michelson contrast, the RNL model allows the prediction of contrast discriminability without the need for behavioural experimentation, but instead can even be applied using conservatively chosen estimates of vision parameters (Olsson et al., 2018).

The RNL model assumes that signal discrimination under 'ideal viewing conditions' is limited by noise originating in the receptors and subsequent opponent processing (Vorobyev and Osorio, 1998; Vorobyev et al., 2001). It was designed to estimate when a signal receiver could discriminate between two colours that were spectrally similar, adjacent, and of fixed size and luminance. The point at which the contrast between two stimuli surpasses a behaviourally determined threshold (e.g. 75% correct choices in a pairwise choice paradigm) is then expressed as a 'just noticeable difference' (JND) corresponding to a Euclidean distance (ΔS) in an n-dimensional space, where n is the number of colour or luminance processing channels (Hempel de Ibarra et al., 2001). The model predicts a JND is equal to $1\Delta S$ if all model assumptions (ideal viewing conditions) are met (Vorobyev and Osorio, 1998; Vorobyev et al., 2001).

However, in many animals, the neuronal pathways leading to the perception of luminance contrast vary significantly from those involved in the perception of colour contrast. In humans, for example, the magnocellular and parvocellular pathways segregate colour and luminance tasks (Zeki, 1993), which can interact (to varying degrees) during subsequent neuronal processing (e.g. Bruce et al., 2010;

Gegenfurtner and Kiper, 1992; Shapley and Hawken, 2011; Simmons and Kingdom, 2002; Webster and Wilson, 2000). The pronounced context-dependent sensitivity of luminance contrast perception is partly due to the fact that achromatic vision in vertebrates lacks a process as efficient as colour constancy (Kelber et al., 2003; Land, 1986; Osorio and Vorobyev, 2008; Wallach, 1948), which enables the perceived colour of objects to remain relatively constant under varying illumination conditions (but see Lotto and Purves, 2000; Simpson et al., 2016). However, despite assuming receptor noise levels to be the limiting factor shaping both chromatic and achromatic contrast perception, behavioural validations of perceptual distances calculated using the RNL model are required in various visual contexts (as suggested by Olsson et al., 2018; but see Skorupski and Chittka, 2011; Vasas et al., 2018). Olsson et al. (2018) have further suggested a conservative threshold of up to 1JND=3ΔS for colour discrimination, as both parameter choice and behavioural threshold validation are often difficult. The use of such conservative chromatic discrimination thresholds in perceptually complex contexts has recently been supported by empirical work (Escobar-Camacho et al., 2019; Sibeaux et al., 2019). However, no empirical evidence exists for choosing conservative luminance (achromatic) contrast thresholds using the RNL model.

In this study, we performed behavioural experiments with triggerfish, *Rhinecanthus aculeatus*, to determine luminance discrimination thresholds in a foraging task using large stimuli under well-illuminated (photopic) conditions. This experiment is considered to be a foraging task because the animals needed to locate a visual stimulus to receive a food reward. A non-foraging task would be, for example, a mate choice paradigm without a food reward. We refer to the task of discriminating a stimulus from its background as a detection task, as this reflects a common use of the achromatic RNL model in visual ecology, most prominently when quantifying the efficiency of animal camouflage (e.g. Troscianko et al., 2016). The ability to detect the presence of a potential prey item is the pre-requisite for more complex cognitive processes and decision making by a predator (Endler, 1991) and as such more likely to reflect low-level retinal and post-retinal properties of visual contrast processing, such as the ones the RNL model has been developed to reflect.

Fish were trained to first locate a target spot that was randomly placed on an achromatic background from which the spot differed in terms of luminance, and then peck it to receive a food reward. Luminance discrimination thresholds were measured for both increasing and decreasing luminance, on both a relatively bright and a dark background. We report thresholds in terms of Michelson contrast and Weber contrast. To determine whether the RNL model is capable of predicting achromatic discrimination thresholds across different viewing contexts, we then translated these thresholds into achromatic ΔS using the log-transformed RNL model, as per Siddiqi et al. (2004). To our knowledge, this is the first time that achromatic discrimination thresholds have been quantified in a marine vertebrate, using a 'detection' task (as opposed to a pairwise choice paradigm as in Siebeck et al., 2014), and using animals that have been trained to detect both randomly placed brighter and darker stimuli simultaneously.

MATERIALS AND METHODS
Study species
We used adult triggerfish *Rhinecanthus aculeatus* (Linnaeus 1758) (n=15) of unknown sex, which ranged in size from 6 to 16 cm standard length (SL). This species inhabits shallow tropical reefs and temperate habitats throughout the Indo-Pacific and feeds on algae,

detritus and invertebrates (Randall et al., 1997). They are relatively easy to train for behavioural studies (e.g. Green et al., 2018), and their visual system has been well studied, including their colour vision capabilities (Champ et al., 2016; Cheney et al., 2013; Pignatelli et al., 2010), neuroanatomy (Pignatelli and Marshall, 2010) and spatial vision (Champ et al., 2014). They have trichromatic vision based on a single cone, containing short wavelength-sensitive visual pigment (SW photoreceptor λ_{max}=413 nm), and a double cone, which houses the medium wavelength-sensitive pigment (MW photoreceptor λ_{max}=480 nm) and long wavelength-sensitive pigment (LW photoreceptor λ_{max}=528 nm) (Cheney et al., 2013). The double cone members are used independently in colour vision (Pignatelli et al., 2010), but are also thought to be used in luminance vision (Marshall et al., 2003; Siebeck et al., 2014), as per other animals such as birds and lizards (Lythgoe, 1979). However, it is not clear whether both members of the double cone are used for luminance perception via electrophysiological coupling (Marchiafava, 1985; Siebeck et al., 2014).

We based the current study on the assumption that both members of the double cone contribute to luminance perception, as per previous studies that have modelled luminance perception in *R. aculeatus* (Mitchell et al., 2017; Newport et al., 2017). These studies used the added input of both double cone members (MW+LW), whereas our study uses the averaged output of both members [(MW+LW)/2] as suggested by Pignatelli and Marshall (2010) and Pignatelli et al. (2010). Additionally, Cheney et al. (2013) used the LW receptor response rather than both double cone members for luminance contrast modelling in *R. aculeatus*, based on discussions in Marshall et al. (2003). However, Michelson contrast/Weber contrast/ΔS contrast values are identical for $f_{t/b}$=MW+LW and $f_{t/b}$=(MW+LW)/2 (where $f_{t/b}$ describes the relative luminance contrast between the target and the background; see Eqn 2 below). Using the LW member of the double cone only (as opposed to both members) causes less than 1% difference (well below measurement error) in receptor stimulation because of the lack of chromaticity of the stimuli and the strong overlap of spectral sensitivities of the two double cone members (Cheney et al., 2013). Fish were obtained from an aquarium supplier (Cairns Marine Pty Ltd, Cairns, QLD, Australia), shipped to The University of Queensland, Brisbane, and housed in individual 120 l tanks (40×80×40 cm W×L×H). The fish were kept at 25°C, pH 8.2, at a salinity of 1.025 g cm^{-3} and fed twice daily with a mix of frozen shrimp and squid. Seawater was prepared using aged water mixed with marine salt. Between trials and training, lighting was provided with white fluorescent light on a 12 h (06:00 h–18:00 h) cycle. Fish were acclimatised for at least 1 week before training commenced. Experiments were conducted in September–November 2017. All experimental procedures for this study were approved by the University of Queensland Animal Ethics Committee (SBS/111/14/ARC).

Stimulus creation and calibration
We used a custom program in Matlab (MathWorks, Natick, MA, USA) to create the stimuli (available on GitHub, https://github.com/cedricvandenberg/MakeStimuli). This program allowed us to specify the RGB values of the background and target spot, and randomly allocate the target spot (1.6 cm diameter) to a position on the background. The size of the spot was chosen to be well within the spatial acuity of *R. aculeatus* (Champ et al., 2014) and could be easily resolved by the fish from anywhere in their aquaria. Stimuli, distractors and backgrounds were printed on TrendWhite (Steinbeis Papier GmbH, Steinberg, Germany) ISO 80 A4 recycled paper using a HP Laserjet Pro 400 colour M451dn printer (Hewlett-

Packard, Palo Alto, CA, USA). Stimuli were then laminated using 80 µm matte laminating pouches (GBC, Chicago, IL, USA). Throughout the experiment, any stimuli with detectable scratches or damage were replaced immediately.

To ensure all stimuli were achromatic, reflectance measurements were plotted in colour space as per Champ et al. (2016) and Cheney et al. (2019). Target and background colours were <1ΔS from the achromatic locus in the RNL colour space as per eqns 1–4 in Hempel de Ibarra et al. (2001). Photoreceptor stimulation was calculated using spectral sensitivities of triggerfish from Cheney et al. (2013). Measures of photoreceptor noise are not available in this species; therefore, we assumed a cone ratio of 1:2:2 (SW:MW:LW) with a standard deviation of noise in a single cone of 0.05 as per Champ et al. (2016) and Cheney et al. (2019). The cone abundance was normalised relative to the LW cone, which resulted in channel noise levels (univariant Weber fractions) of 0.07:0.05:0.05 (SW:MW:LW).

We quantified luminance contrast using calibrated digital photography (Stevens et al., 2007) using an Olympus E-PL5 Penlight camera fitted with a 60 mm macro lens (Fig. S1) to take pictures of each stimulus combination outside of the water. Two EcoLight KR96 30 W white LED lights (Eco-lamps Inc., Hong Kong) were used to provide even illumination between 400 and 700 nm wavelength (Fig. S2). Pictures were analysed using the 'Multispectral Image Calibration and Analysis' (MICA) Toolbox (Troscianko and Stevens, 2015) to calculate cone capture quanta of the double cone. The double cone stimulation was calculated as the average stimulation of the medium wavelength (MW) and long wavelength (LW) cone, as per Pignatelli et al. (2010). We used a spatial acuity estimation of 2.75 cycles per degree (Champ et al., 2014) at 15 cm viewing distance using AcuityView (Caves and Johnsen, 2018) implemented in MICA's QCPA package (van den Berg et al., 2020).

Stimulus contrast was measured as Michelson contrast using the MICA-derived cone catch values of the double cones. The stimuli contrasts were evenly spaced around an area of interest in which the threshold was expected to lie, according to pilot trials. Weber contrast of the thresholds was calculated as $\Delta I_t/I_s$, where ΔI_t is the stimulus contrast at threshold and I_s is the intensity of the distractor or background, respectively, as per Lind et al. (2013). Achromatic ΔS values were calculated according to Siddiqi et al. (2004) (Eqn 1):

$$\Delta S = |\Delta f_{dbl}/\omega|, \qquad (1)$$

where Δf_{dbl} describes the contrast in von Kries-corrected double cone stimulation between the stimulus (f_t) and its background (f_b), calculated as per Siddiqi et al. (2004) (Eqn 2) in relation to the Weber fraction (ω) of the double cone channel. When using the natural logarithm of the quantum catches ω=e_i, where e_i is channel-specific noise:

$$\Delta f_{dbl} = \ln(f_t) - \ln(f_b). \qquad (2)$$

A total of 6 stimuli of varying luminance contrast were created for each scenario: detecting a dark spot on a relatively dark background (T_{dd}), detecting a bright spot on a relatively dark background (T_{bd}), detecting a dark spot on a relatively bright background (T_{db}) and detecting a bright spot on a relatively bright background (T_{bb}) (Fig. 2, Table 1). We refer to stimuli with greater luminance than their background as bright or brighter to facilitate reading. However, the perception of luminance is complex, and the term brightness means specifically the perception of surface luminance, which is often used wrongly and/or in confusion with lightness, which refers to the perception of surface reflectance (Kingdom, 2011).
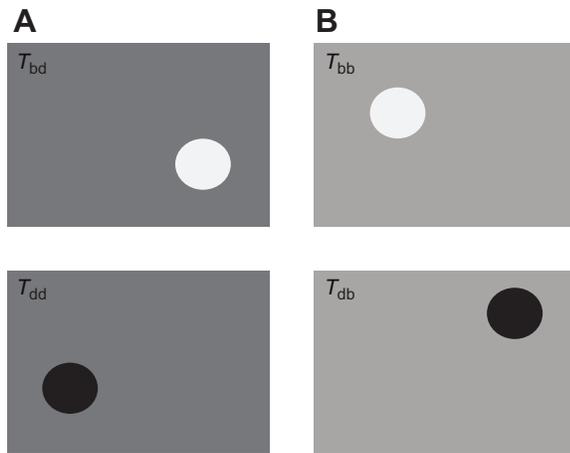
Fig. 2. Schematic representation of detection scenarios. (A) Group 1 (dark background). (B) Group 2 (bright background). Note, figure proportions are not to scale. Stimuli are shown with the maximum contrast used in the experiment. T_{bd}, bright spot on a dark background; T_{dd}, dark spot on a dark background; T_{bb}, bright spot on a bright background; T_{db}, dark spot on a bright background. Backgrounds were A4 size and the spots were 1.6 cm in diameter, randomly placed for each trial.

Experimental setup

Aquaria were divided into two halves by a removable grey, opaque PVC partition. This enabled the fish to be separated from the testing arena while the stimuli were set up. Stimuli were displayed on vertical, grey, PVC boards and placed against one end of the aquaria. Tanks were illuminated using the same white LED lights (EcoLight KR96 30 W) used for stimulus calibration. To ensure equal light levels in all tanks, sidewelling absolute irradiance was measured using a calibrated OceanOptics USB2000 spectrophotometer (Ocean Insight, Orlando, FL, USA), a 180 deg cosine corrector and a 400 nm diameter optic fibre cable fixed horizontally in the tank (Fig. S2).

Animal training

Fish were trained to peck at the target dot using a classic conditioning approach. First, fish were trained to pick a small piece of squid off a black or white (randomly chosen) spot (1.6 cm diameter) on the grey background corresponding to the treatment group ('bright' or 'dark'; Table 1). To reduce possible cues for the fish, the tester was standing behind the fish during a trial so that the fish would move away from the tester when approaching a stimulus. We trained the fish to detect target spots being either brighter or darker than their background to reduce hypersensitivity due to an expected direction of stimulus contrast. This is known as an adaptation of the principle of 'constant stimuli' (Colman, 2008; Laming and Laming, 1992; Pelli and Bex, 2013) aimed at

dissociating perceptual memories associated with a task (e.g. the stimulus being always brighter or darker than its background) and therefore preventing hypersensitivity. Training fish to react to stimuli being either brighter or darker was intended to produce thresholds more closely related to a natural context, as prey items in the natural environments can be both brighter and darker than their natural background. Second, once fish consistently removed the food reward from the black and white target spots, a second food reward was presented from above using forceps. Once fish were confident with this, the final stage of training was a food reward given from above once they had tapped at the target stimulus (without food). Training consisted of up to two sessions per day, with 6–10 trials per session. Fish moved to the testing phase when successful in performing the task in >80% trials over at least 6 consecutive sessions. A trial was considered unsuccessful if the fish took longer than 90 s to make a choice or if it pecked at the background more than twice. This criterion was chosen as the fish are sometimes distracted by small particles or reflections, which they often peck at. A fish doing this twice was a more reliable indicator of the inability to find the stimulus while being motivated enough to guess. Testing was suspended for the day if the fish showed multiple timeouts for obviously easy contrasts, with the assumption that the fish was not motivated to perform the task. However, this occurred rarely (<1% of trials), with smaller fish being more susceptible to having been fed enough to lose appetite.

Animal testing

We randomly allocated fish into two groups: group 1 (n=7) had to find and peck at target spots that were brighter (T_{bd}) or darker (T_{dd}) than a relatively dark background; group 2 (n=8) had to find and peck target spots that were brighter (T_{bb}) or darker (T_{db}) than a relatively bright background (Fig. 2, Table 1). As with the training of the animals, the target spots were presented in a random position against an A4-sized achromatic background in two sessions per day consisting of 6–10 trials per session depending on the appetite of the fish. The trials for each session were chosen pseudo-randomly from all possible contrasts (shuffling the stack of all printed stimuli and choosing a random set of stimuli); thus, fish were presented with both darker and brighter spots compared with their background in each session. Each stimulus was presented a minimum of 6 times (Table 1). We ensured that both easier and harder contrast stimuli were presented in each session to maintain fish motivation; thus, if a chosen series consisted of only hardly detectable stimuli, we would manually add one or two easy ones and vice versa. While stimulus placement on the background using the Matlab script was truly random, we only ever had two or three different versions of each stimulus printed, which, because of the random selection of stimulus sequence as well as the random rotation of the printed stimuli and

Table 1. Summary of all stimulus contrasts across both groups in ΔS and Michelson contrast

Group 1 (dark background, n=7)		Group 2 (bright background, n=8)	
Bright spot (T_{bd})	Dark spot (T_{dd})	Bright spot (T_{bb})	Dark spot (T_{db})
15.34/0.37* (6.0±0.5)	9.26/0.23* (7.0±1.1)	17.87/0.42* (8.5±1.5)	15.51/0.37* (9.0±1.8)
5.98/0.15 (8.0±1.3)	6.55/0.16 (6.0±0.4)	8.84/0.22 (8.5±1.8)	7.99/0.20 (8.0±1.3)
4.82/0.12 (6.0±0.5)	5.04/0.13 (8.0±1.7)	5.19/0.13 (7.5±0.9)	5.92/0.15 (8.5±1.5)
3.94/0.10 (8.0±1.5)	3.03/0.08 (9.0±1.5)	3.98/0.10 (9.0±1.7)	4.65/0.12 (8.5±1.3)
2.34/0.06 (8.0±1.2)	1.24/0.03 (9.0±1.6)	1.82/0.05 (8.0±1.3)	2.46/0.06 (6.0±1.6)
0.58/0.01 (7.0±1.1)	0.89/0.02 (9.0±1.6)	0.84/0.02 (6.5±1.0)	1.58/0.04 (7.0±1.4)

Data are ΔS/Michelson contrast (where ΔS is Euclidean distance), with the median number of trials per fish (±s.d.) indicated in parentheses beside each stimulus contrast. Each scenario consisted of 6 stimuli ranging from low to high luminance contrast. The number of animals tested (n) for each treatment group is noted in the column heading. Asterisks indicate stimuli used for training.

re-printing of damaged stimuli (placed in new random positions by the Matlab script), would result in a non-predictable, pseudo-random placement of stimuli. Motivation was considered to be low when the animal did not engage in the trial immediately, and if this occurred, trials were ceased for that fish until the next session. However, this rarely occurred and was further minimised by carefully avoiding overfeeding the animals. A trial was considered unsuccessful if the fish took longer than 90 s to make a choice or if it pecked at the background more than twice. Incorrect pecks were recorded, and time to detection was defined from when the fish swam past the divider to when they successfully pecked at the target spot.

Statistical analysis

Psychometric curves were fitted to the pooled data of each scenario with percentage correct detection per stimulus as the response variable and stimulus contrast measured in Michelson contrast as the independent variable, using the R package *quickpsy* (Linares and Lopez-Moliner, 2015; http://www.R-project.org/). The best model fit (cumulative normal or logistic) was determined using the lowest AIC as per Yssaad-Fesselier and Knoblauch (2006) and Linares and Lopez-Moliner (2015) and is expressed both individually for each scenario and as the sum across all scenarios. Prior to pooling individuals for each scenario, we conducted a median absolute distance (MAD) test for outliers (Leys et al., 2013) with adjusted, moderately conservative criteria based on a Shapiro–Wilk test of normality (Royston, 1982). We interpolated the 50% correct detection thresholds with a 95% confidence interval (CI) from these curves. Thresholds between the fitted curves for each pooled scenario were compared as per Jörges et al. (2018) using the Bootstrap (Boos, 2003) implemented in *quickpsy* (100

permutations). The Bonferroni method (Bland and Altman, 1995) was used to adjust the significance level of the confidence intervals to $1-0.05/n$, with n corresponding to the number of comparisons.

RESULTS

A total of 1365 trials were conducted across all animals and treatments (Table 1). The total success rate was 68.5% across all 24 stimuli with a median (±s.d.) time to detection of 3.1±12.6 s, with the fastest success at 0.3 s and the slowest at 89.9 s. The median (±s.d.) time for successful detection was uniform across all scenarios: T_{dd} 2.9±12.9 s, T_{bd} 2.8±10.8 s, T_{db} 3.1±13.5 s and T_{bb} 3.22±12.58 s.

Detection thresholds (50% correct detection) using pooled data across all individuals for a given scenario are presented in Fig. 3 and Table 2; individual detection thresholds are shown in Fig. 4 (see also Figs S3 and S4). No outliers were detected prior to pooling the data. The sum of AIC across all four detection scenarios (fit=cumulative normal) was 162.4 (T_{dd} 24.2, T_{bd} 50.8, T_{bb} 50.1, T_{db} 37.3). In group 1 (dark background), the detection thresholds for the bright and dark spot were not significantly different from each other, with the threshold for detecting a spot brighter than a dark background being slightly higher than a spot darker than a dark background ($T_{bd}-T_{dd}$: 0.007 Michelson contrast, CI_{diff} [0.002/0.017]; Fig. 3A). However, the detection thresholds in group 2 (bright background) were significantly different from each other, with the threshold for detecting a dark spot against a bright background being significantly lower than the threshold for detecting a bright spot against a bright background ($T_{db}-T_{bb}$: −0.028 Michelson contrast, CI_{diff} [0.014/0.041]; Fig. 3B).
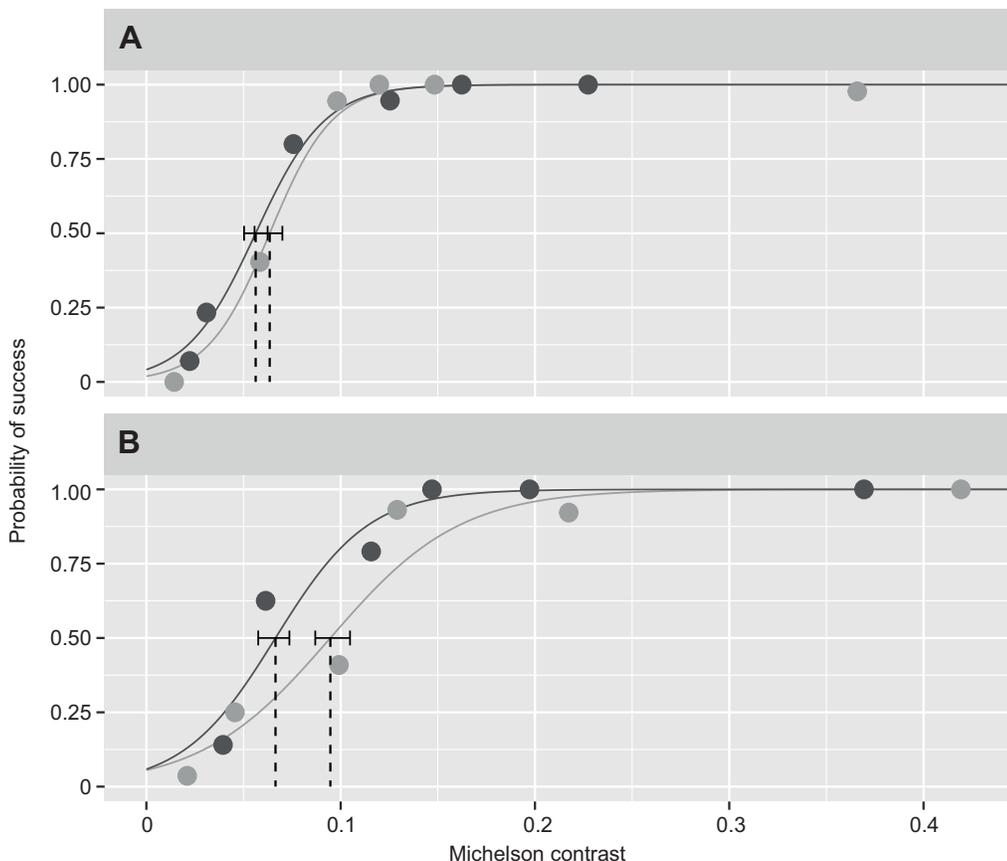

Fig. 3. Cumulative normal curves fitted to the pooled detection success of each scenario. (A) Group 1 (dark background). (B) Group 2 (bright background). Dashed lines indicate thresholds for each scenario in Michelson contrast; error bars represent the 95% confidence interval at the 50% correct detection threshold. Black dots indicate the 'dark spot' scenario and grey spots indicate the 'bright spot' scenario for each group.

Table 2. Summary of results for the 50% correct detection threshold contrasts

	Scenario significance (MC/ΔS)	Michelson contrast	Weber contrast	ΔS
Group 1				
T_{bd}	(abd/a)	0.063 (0.057–0.071)	0.313 (0.282–0.349)	2.543 (2.286–2.831)
T_{dd}	(b/a)	0.056 (0.051–0.063)	0.278 (0.241–0.309)	2.252 (1.955–2.510)
Group 2				
T_{bb}	(c/b)	0.095 (0.086–0.104)	0.322 (0.287–0.354)	3.799 (3.379–4.118)
T_{db}	(d/a)	0.066 (0.060–0.073)	0.226 (0.197–0.253)	2.662 (2.317–2.979)

Treatment groups and scenario abbreviations are indicated on the far left. Letters in parentheses above scenario drawings indicate significant differences in Michelson contrast (MC) thresholds as per bootstrap sampling or a 1ΔS receptor noise limited (RNL) contrast. For example, in terms of MC, scenario T_{bb} is significantly different from all other scenarios, whereas T_{bd} does not differ from T_{dd} or T_{db}. Michelson contrast, Weber contrast and ΔS values are shown with 95% confidence intervals in parentheses.

While the threshold for detecting a bright spot against a dark background was not different from that for detecting a dark spot against a bright background (its 'inverse' scenario) ($T_{bd}-T_{db}$: −0.003 Michelson contrast, CI_{diff} [−0.013/−0.016]), all other detection thresholds varied significantly from each other when compared across groups 1 and 2 (Figs 3 and 4, Table 2).

DISCUSSION

Our study demonstrates that for triggerfish, *Rhinecanthus aculeatus*, the ability to discriminate a large, well-illuminated achromatic stimulus against a uniform achromatic background depends on both the relative luminance contrast between target and background (f_t versus f_b) and the absolute luminance level (f_t+f_b) at which the
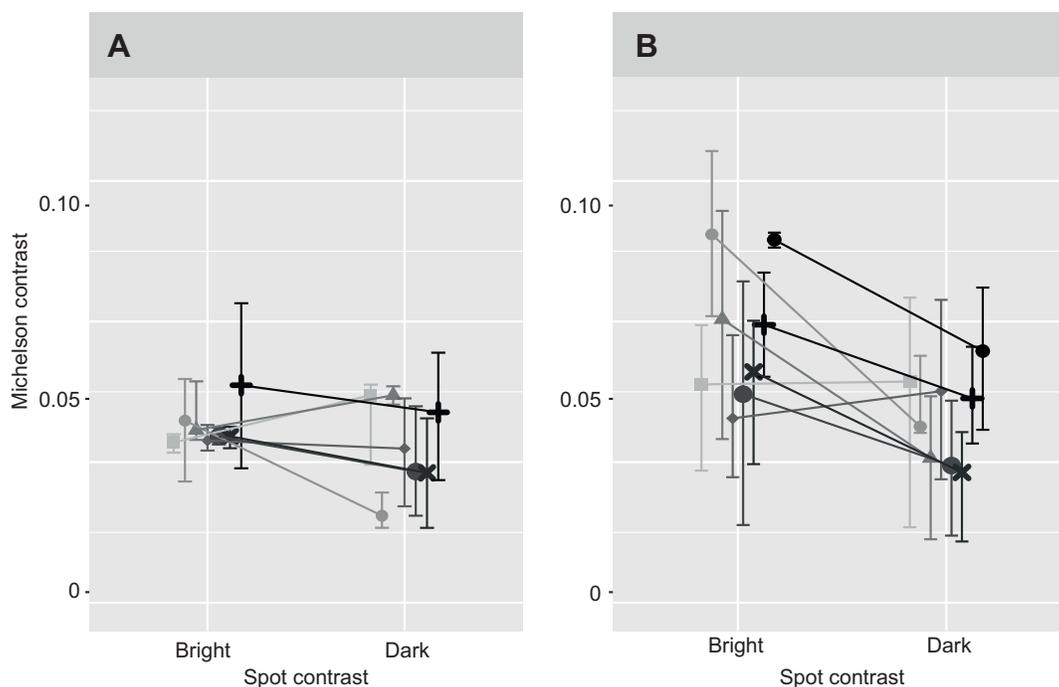

Fig. 4. Detection thresholds for individual fish. Individually estimated discrimination thresholds in Michelson contrast for each scenario. (A) Group 1 (dark background). (B) Group 2 (bright background). Error bars represent the 95% confidence intervals.

contrast is perceived (Eqn 2). For example, discrimination thresholds, measured as Michelson contrast, were significantly lower when fish were presented with a bright spot against a dark background, as opposed to a bright spot against a bright background (Table 2). However, when expressed in terms of Weber contrast (i.e. scaling the contrast with the luminance level at which the luminance contrast is perceived), these two thresholds were almost identical (Table 2). This finding supports the Weber–Fechner law that states the ability to discriminate a target stimulus against its background scales with the intensity at which the discrimination is made. The same holds true for the discrimination thresholds of a dark spot against a dark background (T_{dd}) as opposed to a bright background (T_{db}), which have an almost identical Weber contrast (Table 2). Furthermore, the contrast sensitivity depends on the direction of the contrast ($f_t > f_b \neq f_t < f_b$); that is, the Weber contrast for detecting stimuli darker than their respective backgrounds is lower (i.e. more sensitive) than that for stimuli which are brighter than their backgrounds (0.23–0.28 Weber contrast for dark spots and 0.31–0.32 Weber contrast for bright ones) (Table 2).

Our results agree with previous findings that human (e.g. Bowen et al., 1989; Emran et al., 2007; Lu and Sperling, 2012), non-human vertebrate (e.g. Baylor et al., 1974) and invertebrate visual systems (e.g. Smithers et al., 2019) are consistently better at detecting stimuli darker than their visual background. Increasing and decreasing luminance changes are thought to be processed differently: darker stimuli are detected by off-centre ganglion cells, while lighter ones are detected by on-centre ganglion cells (Schiller et al., 1986). Dark stimuli cause depolarization of photoreceptors, whereas light ones are detected as hyperpolarization (Baylor et al., 1974). For example, investigation of turtle photoreceptors has shown that dark stimuli result in much greater depolarization of photoreceptors than the magnitude of hyperpolarization resulting from light ones (Baylor et al., 1974). This asymmetry is thought to be a crucial contributor to object and motion detection in post-retinal processing (e.g. Oluk et al., 2016; Vidyasagar and Eysel, 2015).

Behavioural calibration of the RNL

The relationship of absolute (background+stimulus) and relative luminance (background versus stimulus) contrast does not hold when expressing thresholds as achromatic ΔS (Table 2). The exclusion of signal intensity is a fundamental assumption when calculating chromatic contrasts using the RNL model (Vorobyev and Osorio, 1998), which was designed to quantify contrast perception between two closely opposed chromatic stimuli viewed against an achromatic background. As a result, the RNL equations used by Siddiqi et al. (2004) calculate a relative comparison of two background-adapted receptor responses without scaling the difference in photoreceptor stimulation between stimulus and background in relation to the overall brightness of a scene. Thus, the commonly used RNL equations in Siddiqi et al. (2004) fail to reflect the Weber–Fechner law for the discrimination of a stimulus from its background. Olsson et al. (2018) proposed the use of an adaptation where the Weber contrast at the behaviourally determined discrimination threshold (WC$_t$) should be used in place of the receptor noise:

$$\Delta S = |\Delta f_{dbl}/WC_t|. \quad (3)$$

This renders the following ΔS values at threshold: $T_{dd}=T_{bd}$ 0.41ΔS ±0.0001 and $T_{bb}=T_{db}$ 0.59ΔS±0.001, using the Weber contrast determined in this experiment. This makes the RNL model, as modified by Olsson et al. (2018), conform with the Weber–Fechner law while preserving the difference in contrast sensitivity regarding

increments and decrements. Furthermore, the thresholds are well below 1ΔS, making the assumption of a JND corresponding to a threshold of 1ΔS a comfortably conservative (but not extreme) threshold. It should be noted that the general conclusion of Siddiqi et al. (2004) that poison dart frogs display powerful visual signals, which can be used for detection by predators and conspecifics, remains probably correct, especially as the authors discuss their thresholds in the context of a conservative threshold (0–3ΔS are considered poorly discriminable).

Olsson et al. (2018) propose the use of Michelson contrast in place of receptor noise in order to estimate the channel-specific noise (e_i). First, the contrast sensitivity (CS) is calculated as the inverse of the behaviourally determined Michelson contrast (C_t):

$$CS = \frac{1}{C_t}. \quad (4)$$

Next, this CS (which is sensitive to the absolute level of luminance as our results confirm) can be used to calculate the relative quantum catch of stimulus 2 (q_{stim2}):

$$q_{stim2} = \frac{1 - C_t}{1 + C_t}. \quad (5)$$

We can then use q_{stim2} as f_t and our originally measured f_b in Eqn 2 to derive the channel noise (e_i) (see Olsson et al., 2018, for further details). With the assumption of $\Delta S=1$ at threshold, this produces:

$$e_i = \ln \frac{\Delta S}{q_{stim2}}. \quad (6)$$

Thus, we obtain the following channel noise estimates (e_i with 95% CI): $e_{Tdd}=0.113$ (0.098–0.125) and $e_{Tbd}=0.127$ (0.114–0.142) for group 1 (dark background) and $e_{Tdb}=0.133$ (0.116–0.149) and $e_{Tbb}=0.190$ (0.169–0.209) for group 2 (bright background). This is the same as setting ω (which is equal to e_i) in Eqn 1 so that the observed ΔS in our experiments (Table 2) would be equal to 1 (as we determined f_t at threshold by fitting a model to the observed Michelson contrast). This is interesting, as these noise values are up to almost 4 times as high as the 'conservative' (!) standard deviation of noise (in a single photoreceptor) estimate of 0.05, currently used for modelling vertebrate vision across the field of visual ecology.

Given that Weber contrast is meant to be used for comparably small stimuli against large backgrounds and Michelson contrast is meant to be used for contrasts between stimuli of comparable size, we recommend a differentiated use of either Eqn 3 or Eqns 4–6 depending on the visual context in which a discrimination threshold is used. For example, as the scenario in this study involved the discrimination of a single spot against a much larger background, we would assume Eqn 3 to be more relevant than Eqns 4–6 [e.g. Eqns 4–6 still produce a higher noise ratio for group 2 (bright background), especially T_{bb}]. Thus, Eqns 4–6 would probably be more relevant when discriminating between two objects of equal size. This further implies that one could plot the discrimination curves as a function of Weber contrast rather than Michelson contrast to obtain the discrimination threshold. The thresholds would then only be distinguishable based on the relative direction of the contrast (bright spot or dark spot) and not the background intensity (Table 2). It also implies that thresholds obtained from experiments using a discrimination scenario more fitting to Eqns 4–6 (e.g. Lind et al., 2013) should not be used to infer the detectability of most likely relatively small prey items against their most likely large visual backgrounds.

Conclusions, future directions and recommendations

Our findings provide insight into the processing of achromatic information as well as the use of the RNL model to quantify achromatic discrimination by non-human observers. We show that the current use of the RNL model for the quantification of luminance contrast sensitivity thresholds warrants caution. More specifically, our study suggests the lack of adequate scaling of thresholds by the RNL model to the average luminance of a scene and the need for context-specific behavioural experimentation whenever possible.

Our results warrant caution in the use of uniform contrast sensitivity thresholds (be it achromatic or chromatic) across widely diverse perceptual contexts, independently of which models are used to describe them. Luminance discrimination, as expected, is not just limited by photoreceptor noise and therefore cannot be adequately represented by the use of a singular detection or discrimination threshold determined using the equations in Siddiqi et al. (2004) as currently common in behavioural ecology studies. This realisation shares many parallels with ongoing discussions regarding the use of the RNL model outside of model assumptions (Marshall, 2018; Olsson et al., 2018; Osorio and Vorobyev, 2018; Sibeaux et al., 2019; Stuart-Fox, 2018; Vasas et al., 2018). Our results suggest that the use of a conservative achromatic RNL threshold assumption of $3\Delta S$ (e.g. Spottiswoode and Stevens, 2010) without adaptations such as those proposed by Olsson et al. (2018) might warrant caution.

We show that the noise in the achromatic channel of *R. aculeatus* can be substantially higher than anticipated in previous studies modelling its luminance contrast sensitivity using 'conservative' receptor noise estimates. However, this increase in channel noise (e_i) could originate from many potential sources, including electrophysiological coupling of receptors in the double cone of *R. aculeatus* (but also a generally higher noise level in receptors responsible for luminance contrast detection) or downstream (post-receptor) processing of visual information. As such it is wrong to conclude receptor noise from such behavioural calibration (Vasas et al., 2018) and it would be more appropriate to refer to the noise of the entire pathway involved in the performance of a task based on the animal's ability to perceive luminance contrast in a specific visual context.

The specific mechanisms causing the observed difference in Weber contrast between the detection of a dark spot and a bright spot (or mathematical approximations thereof), or an explanation as to why $e_{\mathrm{achromatic}}$ is much higher than the conservatively chosen receptor noise of 0.05, remain speculative. Further investigations might seek advances in the understanding of neurophysiological mechanisms underlying luminance contrast perception in *R. aculeatus*. These include knowledge of the detailed anatomy and receptor noise of double cone photoreceptors, the relative contribution of each double cone member to luminance contrast sensitivity (Siebeck et al., 2014) as well as the precise mechanism by which photoreceptor stimulation is integrated in post-receptor structures such as edge-detecting receptive fields (e.g. Szatko et al., 2020). Behavioural experiments with closely related species with different retinal morphologies would be of interest to further investigate, for example, the role of retinal neuroanatomy on luminance contrast perception.

The adaptations to the RNL model in Olsson et al. (2018), while apparently effective, do not account for the effects of spatial frequency on luminance contrast sensitivity when discriminating objects against visual backgrounds. This is probably the most notable confounding effect on low-level processing of luminance contrast as a result of post-receptor lateral inhibition (Veale et al., 2017). One possible approach would be the use of contrast sensitivity functions to scale Weber fractions as a function of spatial frequency in a visual scene. However, given that these are determined using a perceptually different experimental setup (da Silva Souza et al., 2011), this should be investigated using context-specific behavioural experimentation.

Despite having investigated luminance contrast sensitivity using two different levels of background luminance, our study only considered discrimination of large, uniform and achromatic circular target stimuli against a uniform grey background. In future studies, more realistic backgrounds and illumination should be taken into account (e.g. Matchette et al., 2020), as a variety of factors can fundamentally influence luminance contrast perception in most circumstances (Gilchrist, 2014; Gilchrist and Radonjic, 2009; Gilchrist et al., 1999; Kingdom, 2011; Maniatis, 2014). Unsurprisingly then, there is evidence that luminance contrast modulates the salience of objects at stages well beyond the retina (Einhäuser and König, 2003).

One of the main reasons why researchers use the RNL model is that, presumably, the discriminability of visual contrasts can be reliably predicted by using a set of conservatively estimated physiological parameters such as photoreceptor noise, abundance and spectral sensitivity. While this seems to work satisfyingly well for colour contrast perception across a range of animals and viewing contexts, our study suggests quite the opposite to be the case for achromatic contrast. Despite the possibility of calibrating the RNL (determination of a relevant ΔS contrast) using contextualised behavioural experiments (as suggested by Olsson et al., 2018), the result of doing so in an achromatic context remains difficult because of the context sensitivity of luminance contrast perception. However, given the lack of general applicability of the RNL model in an achromatic context, we recommend the use of behaviourally determined discrimination thresholds suitable to the given visual context in which they are to be applied (and the mathematical consequences thereof, as discussed above) as well as generous caution when predicting the discriminability of luminance contrast. Recent advances in methodology used to determine such thresholds (Cheney et al., 2019) can be used to drastically reduce the amount of time needed to obtain relevant threshold estimates.

The need for behaviourally validated and contextualised threshold estimates has direct implications for the design of behavioural experiments where validated discrimination thresholds are unavailable. For example, given the difficulty of predicting luminance discriminability, luminance contrast should be thoroughly randomised (as opposed to attempting iso-luminance between stimuli) in any behavioural experiment than can potentially be influenced by luminance contrast perception.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: C.P.v.d.B.; Methodology: C.P.v.d.B.; Software: C.P.v.d.B.; Validation: C.P.v.d.B.; Formal analysis: C.P.v.d.B.; Investigation: C.P.v.d.B., M.H., L.J.M., E.J.W.; Resources: L.J.M., K.L.C.; Data curation: C.P.v.d.B., M.H., E.J.W.; Writing - original draft: C.P.v.d.B.; Writing - review & editing: C.P.v.d.B., L.J.M., N.F.G., K.L.C.; Visualization: C.P.v.d.B.; Supervision: N.J.M., K.L.C.; Project administration: K.L.C.; Funding acquisition: N.J.M., K.L.C.

Data availability
Data are available from the UQ eSpace digital repository: https://doi.org/10.14264/uql.2020.993

Supplementary information
Supplementary information available online at
https://jeb.biologists.org/lookup/doi/10.1242/jeb.232090.supplemental

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