

## Research



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## Evolutionary biology

## Colour and luminance contrasts predict the human detection of natural stimuli in complex visual environments

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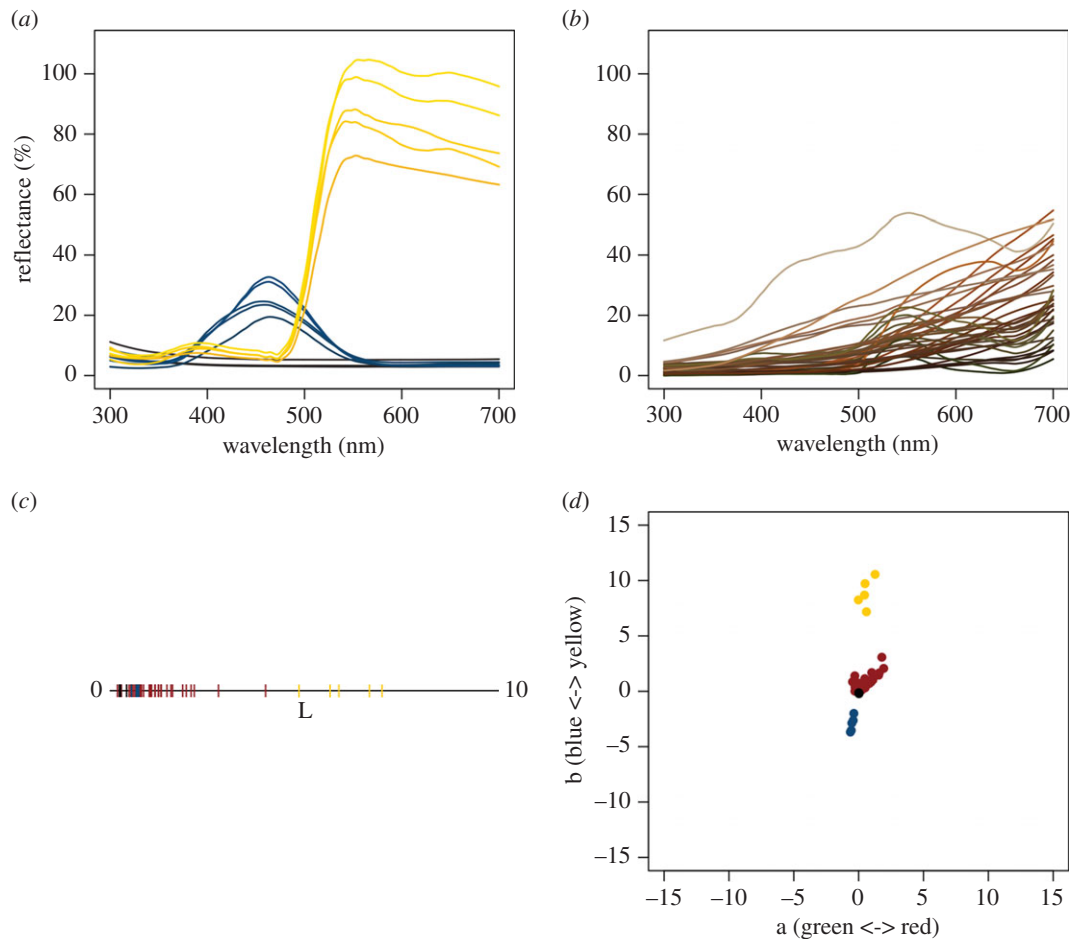
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Much of what we know about human colour perception has come from psychophysical studies conducted in tightly-controlled laboratory settings. An enduring challenge, however, lies in extrapolating this knowledge to the noisy conditions that characterize our actual visual experience. Here we combine statistical models of visual perception with empirical data to explore how chromatic (hue/saturation) and achromatic (luminance) information underpins the detection and classification of stimuli in a complex forest environment. The data best support a simple linear model of stimulus detection as an additive function of both luminance and saturation contrast. The strength of each predictor is modest yet consistent across gross variation in viewing conditions, which accords with expectation based upon general primate psychophysics. Our findings implicate simple visual cues in the guidance of perception amidst natural noise, and highlight the potential for informing human vision via a fusion between psychophysical modelling and real-world behaviour.

## 1. Introduction

The interactions of light and matter offer a rich source of information about the world, and vision often dominates the sensory ecology of animals. Regardless of ocular structure, visual processing begins with the absorption of photons by one or more receptors sensitive to a limited range of wavelengths [1,2]. In humans, the perception of luminance is mediated by the pooled stimulation of mid- and long-wavelength cones, which is broadly used to judge form, motion and texture [3]. This enables rapid characterization of entire panoramas because the greatest spectral power—hence ‘information’—generally exists in the achromatic channel [2,4]. Unlike achromatic cues, however, the chromatic features of stimuli (i.e. hue and saturation) are relatively invariant, and so tend to be used for higher tasks such as object recognition, categorization and memory [3,5]. Humans, as old world primates, possess a trichromatic visual system that enables colour perception via two independent ‘opponency’ channels [6]. One channel arises via comparison of relative stimulation among mid-versus-long-wave sensitive cones, and the second arises through comparing the stimulation of mid- and long-wave receptors with that of short-wave receptors [7].

This initial extraction of colour and luminance information is critical for higher-level cognitive functions and ultimately defines our ability to judge spatial perspective, detect movement, classify scenes, and locate objects within them. Present knowledge of how such information is weighted among these tasks stems from exacting laboratory-based psychophysical study



**Figure 1.** The spectral reflectance ( $n = 5$  samples) of (a) model stimuli components and (b) background material, along with their position in the (c) luminance and (d) colour-opponent dimensions of the CIELAB model of human colour sensation. The colours of each point/line (yellow, blue, black and brown) approximate the colour of the elements comprising each model 'morph' as seen by a human observer. (Online version in colour.)

[3,6,7], which has generated precise models of colour perception [8]. The world at large, however, is visually dynamic. Information must be continuously integrated, and the most salient cues may shift with the broader viewing context [9,10]. An outstanding challenge therefore lies in extrapolating laboratory-gained knowledge to colour sensation under the noisy environments that characterize our historical (evolutionary) and contemporary visual experience. Integrative, 'top-down' approaches that combine physiological knowledge with natural-behavioural data hold particular promise [11], though remain largely untested in the context of human visual ecology.

In this study we used empirical data of human performance in an object detection task to explore which spectral cues best guide detection and classification amidst gross visual noise. We used an information-theoretic approach to define the linear combination of parameters that (additively and/or interactively) best explained subject performance in a forest environment under varied visual conditions. In doing so, we explicitly tested the prediction derived from primate psychophysics that detection should rely upon both luminance and chromatic contrasts [3,6,7].

## 2. Methods

### (a) Data provenance

We used data from an experiment in which human viewers were tasked with finding objects under two forest-light environments

[12]. The focal stimuli consisted of paraffin wax models of four different morphs of the dyeing poison frog *Dendrobates tinctorius* (fig. 1e–h in [12]), whose patterns differed in the arrangement and constitution of 'yellow', 'blue' and 'black' patches (see [12] for model-construction details). Reflectance spectra (figure 1a) were captured from representative patches using an OceanOptics USB4000-FL spectrometer and a PX-2 pulsed xenon light source, calibrated against a Spectralon (Labsphere, Congleton, UK) white standard. Measurements of a haphazard sample of leaf-litter background material—upon which models were presented—were collected at the same locality.

During the human-detection assay, 20 model stimuli (five of each morph) were placed randomly in two  $6 \times 6$  m quadrats that differed in their light environment; one was located under a large canopy gap, and the other under a wholly closed-canopy. All trials were conducted on a single overcast day between 07.00 and 11.00, in an effort to minimize within-treatment environmental variation between trials. Twenty-five volunteers (12 women, 13 men) were asked to find as many models as possible in each quadrat within 30 s. Twelve of the participants started in the canopy gap environment, while the other 13 started in the closed forest environment. Upon completing their search in the first environment, each participant repeated the task in the second environment. Participants had no experience with the focal stimuli prior to their first trial, and individual trials were independent from one another.

### (b) Visual modelling

We used the CIELAB model of human perception to estimate the subjective chromatic and achromatic visual information

**Table 1.** Full model-selection table, detailing the relative strength of candidate models for the relationship between target detection and one or more linear combinations of: luminance contrast ( $\Delta L$ ), saturation contrast ( $\Delta S$ ), hue contrast ( $\Delta h$ ), maximum colour difference ( $\Delta C$  max.), integrated colour difference ( $\Delta C$  int.), and the gross between-environment deviation for each (dev.). Estimates of the log-likelihood (LL), adjusted Akaike's information criterion (AICc), change in AICc relative to the leading model ( $\Delta AICc$ ), and relative weights ( $w$ ) are provided for each model. Bolded estimates denote the most informative models, as broadly indicated by a relative increase in AICc of less than 2.

model	d.f.	LL	AICc	$\Delta AICc$	$w$
$\Delta L + \Delta S$	5	<b>-264.18</b>	<b>538.70</b>	<b>0.00</b>	<b>0.505</b>
$\Delta L$	4	<b>-265.91</b>	<b>540.10</b>	<b>1.35</b>	<b>0.258</b>
$\Delta L * \Delta S$	6	-264.32	541.10	2.43	0.150
$\Delta S$	4	-267.95	544.10	5.43	0.033
$\Delta S + S$ dev.	5	-267.40	545.10	6.44	0.020
$\Delta L + \Delta S + L$ dev. + $S$ dev.	7	-265.46	545.60	6.87	0.016
$\Delta L + L$ dev.	5	-268.46	547.30	8.57	0.007
$\Delta C$ int.	4	-270.23	548.70	9.99	0.003
$\Delta L + \Delta h$	5	-269.26	548.90	10.17	0.003
null (intercept only)	3	-271.62	549.40	10.67	0.002
$\Delta h$	4	-271.88	552.00	13.29	0.001
$\Delta S + \Delta h$	5	-271.02	552.40	13.69	0.001
$\Delta C$ max.	4	-273.74	555.70	17.01	0.000
$\Delta C$ int. + $C$ dev.	5	-273.43	557.20	18.51	0.000
$\Delta L * \Delta h$	6	-272.54	557.60	18.88	0.000
$\Delta h + h$ dev.	5	-275.82	562.00	23.28	0.000
$\Delta S + \Delta h + S$ dev. + $h$ dev.	7	-273.74	562.10	23.44	0.000
$\Delta C$ max. + $C$ dev.	5	-276.94	564.20	25.54	0.000
$\Delta L + \Delta h + L$ dev. + $h$ dev.	7	-275.29	565.20	26.54	0.000

presented by each stimulus. We used the 10-degree standard observer colour-matching functions, and modelled all stimuli under two illumination conditions ('forest shade' for full canopy cover, and 'blue sky' to simulate large canopy gaps; [13]) to capture the environmental treatment effects from the original study. We otherwise followed standard calculations for the CIELAB model and its CIELCh cylindrical transformation [14]. All visual modelling was run using 'pavo' for R [15].

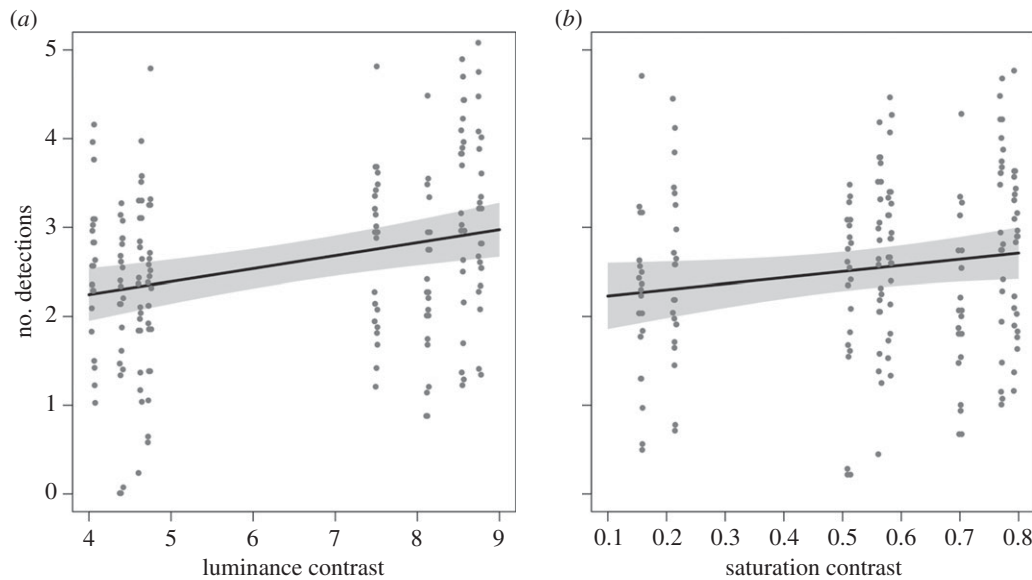
As noted above, each stimulus comprised four distinct coloured elements that varied in their relative proportions; the yellow, blue, and black paints of the models themselves, and the brown leaf-litter of the presentation background (figure 1*a,b*). We therefore estimated between-element hue, saturation, and luminance contrasts as the mean of the pairwise differences in each. We also estimated the pairwise 'colour difference' between each patch—which broadly captures the combined contributions of hue, saturation and luminance contrasts—as the distance between the centroids of each group in CIELAB/LCh space calculated using the CIEDE2000 colour-difference formula (a Euclidean distance adjusted for perceptual non-uniformity). We then estimated the information offered by each of the four focal stimuli by combining these values in a way that accounted for the difference in their relative contribution to the overall pattern. To estimate the hue, saturation and luminance contrast generated by stimuli, we simply took the maximum of any between-patch comparison in each variable, weighted by their combined relative area.

We estimated the overall colour contrast of stimuli in two ways, representing subtly different mechanisms by which this information may be perceived by a human viewer [3]. We estimated the maximum colour difference as above, by taking the maximum colour difference of any pairwise comparison

weighted by the combined relative area of both elements. We also estimated the integrated, or average, colour difference by combining all pairwise colour-difference estimates, and weighting each by its relative area.

### (c) Statistical modelling

We used a restricted maximum likelihood (REML) based information-theoretic approach ([16]; and electronic supplementary material, methods) to rank a set of generalized linear mixed-effect models (table 1) that represent alternate hypotheses for the way in which subjective visual cues guide object-detection in noisy environments, as informed by knowledge of primate psychophysics [3,6,7]. In all cases we modelled the number of stimuli detected as a Gaussian response (as supported by normally distributed data and residuals), and included participant ID as a random covariate. Six models were constructed of all individual and two-way linear combinations of luminance, hue, and saturation contrasts. A further six models were built using the same combinations, with the addition of the between-environment deviation for each factor. That is, the absolute difference in the mean value of each factor (hue, saturation and/or luminance contrast) between participants' starting and finishing environments, thereby estimating any effects of the order in which environmental treatments were completed. We included two models comprised of the main effects and two-way interaction of luminance and either hue or saturation, which represents a differential, shifting reliance on chromatic and achromatic cues across the two viewing environments. We built a further four models of overall 'colour-difference' using estimates of maximum and integrated colour difference individually, as well as each with their associated between-environment



**Figure 2.** Conditional plots of predictors from the most parsimonious model of stimulus detection (table 1), comprised of (a) luminance contrast and (b) saturation contrast. Points denote partial residuals, black lines are the restricted maximum-likelihood fits of a given predictor with the other held at its median value, and shaded areas demarcate 95% confidence bands.

deviation. Finally, we included an intercept-only model as our null, which represented stimulus detections as a random process. We used the R package nlme to build GLMEs, and MuMIn for information-theoretic model selection [17].

### 3. Results

The most parsimonious model of stimulus detection indicated a positive contribution of both luminance and saturation contrast (tables 1 and 2). Of all models tested, it was approximately twice as informative as the second-best model (in terms of minimizing the estimated relative Kullback–Leibler distance; [16]), which included a positive contribution of luminance contrast alone ( $\Delta\text{AICc} = 1.35$ ,  $w_1/w_2 = 1.96$ ). Both models clearly outperformed the null ( $(w_1 + w_2)/w_{\text{null}} = 299$ ). The strength of the individual effects of luminance and saturation contrast were modest (figure 2). However, the presence of luminance contrast in both leading models, and the minimal change in log-likelihood between them despite the extra parameter (table 1, bold), imply a more fundamental role in stimulus detection. Hue contrast was uninformative, with all models containing it performing no better than the null (table 1).

### 4. Discussion

Extensive laboratory-based work continues to develop our understanding of the physiology and psychology of human colour sensation [3,7]. Here we built upon recent empirical data [12], in an effort to identify the basis of stimulus detection/classification across complex, natural visual environments. The most parsimonious models indicated a simple additive contribution of both luminance and saturation contrast; brighter and more ‘chromatic’ stimuli were more likely to be found by human viewers across environments (table 1; figure 2).

The primacy of luminance contrast as a predictor of detections is consistent with our knowledge of primate visual

**Table 2.** Parameter estimates and standard errors from the most parsimonious GLME models of stimulus detections (table 1, bold), along with their overall fit.

model	parameter	est.	s.e.	cond. $R^2$
$\Delta L + \Delta S$	intercept	1.27	0.30	0.20
	$\Delta L$	0.15	0.04	
	$\Delta S$	0.69	0.36	
$\Delta L$	intercept	1.52	0.28	0.19
	$\Delta L$	0.16	0.04	

ecology, and likely represents a number of concurrent processes. For example, reflexive attentional shifts triggered by the appearance of objects in the visual periphery are mediated by achromatic, rather than chromatic, cues [18]. Luminance contrast also guides the rapid characterization of panoramic scenes, and affords the location and fixation of target objects [4,7]. This is exemplified by recent work on new world monkeys, in which achromatic contrast alone predicted individual success in short-range fruit foraging [19]. Finally, this channel mediates the perception of edges and shapes that underlie finer-scale object recognition; a specialization echoed in the distribution of receptors across the human retina [7].

Under variable illumination, chromatic cues provide the most reliable information about the material properties of objects (a truth partly credited for the evolution of colour vision itself; [6,20]). Given that our experimental data were drawn from a task that demanded both the detection and categorization of objects amidst noise [12], we would expect a role for chromatic contrast in leading models (table 1). As with luminance, the predictive strength of this parameter (figure 2b) is likely to reflect several visual processes. These include object detection, segregation and discrimination under trying conditions (as noted above), along with higher-level processes involving memory and spatial recall [3]. However, given that hue is typically a more reliable cue

than saturation—which is also susceptible to shifts in illumination—its lack of influence here is of interest. In the current context, this is likely a consequence of humans' ability to alternate the use of chromatic cues depending on whether they are diagnostic features of the target [20]. This is further supported by extensive psychological work demonstrating that viewers' selective attention may be captured by locally salient features of stimuli, such as discrepancies in hue, saturation and/or motion [18,21,22]. The inclusion of saturation over hue contrast in our most parsimonious models, then, may simply be a function of the greater range of between-stimulus variation in that feature (i.e. its particular salience as a visual cue, or 'singleton' [22]). This is of course a general limitation of our experimental data in that the focal targets imitate a limited range of natural pattern variation, rather than the spread of colour and luminance contrasts required for more general inference.

Accessing the perceptual world of animals remains a fundamental challenge, and progress will stem from a diversity of approaches. Given the ultimate importance of behaviour in questions of sensory ecology and evolution, underexplored potential lies in drawing on traditional psychophysical

knowledge to inform manipulative, natural-behavioural experiments. Our results support the promise of this approach, and implicate relatively simple cues in guiding human visual behaviour under naturally dynamic conditions.

**Ethics.** All experimental data were drawn from a previously published study [12] for which research permits were obtained from CNRS-Guyane, and all participants gave written consent for the use of anonymised data in a scientific publication.

**Data accessibility.** All raw data are available via Figshare [23].

**Authors' contributions.** B.R., J.M., D.J.K. and T.E.W. conceived the present study, B.R. and P.R. collected the data, T.E.W. analysed the data, T.E.W. and B.R. wrote the manuscript, and all authors critically revised the manuscript. All authors approved the final version, and agree to be held accountable for all aspects of the work.

**Competing interests.** The authors have no competing interests to declare.

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## References

- Kelber A, Vorobyev M, Osorio D. 2003 Animal colour vision—behavioural tests and physiological concepts. *Biol. Rev. Camb. Philos. Soc.* **78**, 81–118. (doi:10.1017/S1464793102005985)
- Osorio D, Vorobyev M. 2005 Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc. R. Soc. B* **272**, 1745–1752. (doi:10.1098/rspb.2005.3156)
- Gegenfurtner KR, Kiper DC. 2003 Color vision. *Annu. Rev. Neurosci.* **26**, 181–206. (doi:10.1146/annurev.neuro.26.041002.131116)
- Delorme A, Richard G, Fabre-Thorpe M. 2000 Ultra-rapid categorisation of natural scenes does not rely on colour cues: a study in monkeys and humans. *Vision Res.* **40**, 2187–2200. (doi:10.1016/S0042-6989(00)00083-3)
- Wichmann FA, Sharpe LT, Gegenfurtner KR. 2002 The contributions of color to recognition memory for natural scenes. *J. Exp. Psychol. Learn. Mem. Cogn.* **28**, 509–520. (doi:10.1037/0278-7393.28.3.509)
- Vorobyev M. 2004 Ecology and evolution of primate colour vision. *Clin. Exp. Optom.* **87**, 230–238. (doi:10.1111/j.1444-0938.2004.tb05053.x)
- Nathans J. 1999 The evolution and physiology of human color vision: insights from molecular genetic studies of visual pigments. *Neuron* **24**, 299–312. (doi:10.1016/S0896-6273(00)80845-4)
- Renoult JP, Kelber A, Schaefer HM. 2015 Colour spaces in ecology and evolutionary biology. *Biol. Rev.* **92**, 292–315. (doi:10.1111/brv.12230)
- Blake R, Lee SH. 2005 The role of temporal structure in human vision. *Behav. Cogn. Neurosci. Rev.* **4**, 21–42. (doi:10.1177/1534582305276839)
- Schaefer HM, Levey DJ, Schaefer V, Avery ML. 2006 The role of chromatic and achromatic signals for fruit detection by birds. *Behav. Ecol.* **17**, 784–789. (doi:10.1093/beheco/arl011)
- Kemp, DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett AT, Dyer AG, Hart NS, Marshall J, Whiting MJ. 2015 An integrative framework for the appraisal of coloration in nature. *Am. Nat.* **185**, 705–724. (doi:10.1086/681021)
- Rojas B, Rautiala P, Mappes J. 2014 Differential detectability of polymorphic warning signals under varying light environments. *Behav. Processes* **109**, 164–172. (doi:10.1016/j.beproc.2014.08.014)
- Endler JA. 1993 The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27. (doi:10.2307/2937121)
- Westland S, Ripamonti C, Cheung V. 2012 *Computational colour science using MATLAB*. New York, NY: John Wiley & Sons.
- Maia R, Eliason CM, Bitton PP, Doucet SM, Shawkey MD. 2013 Pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* **4**, 906–913. (doi:10.1111/2041-210X.12069)
- Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
- Bartoń K. 2013 MuMIn: multi-model inference. R package version, 1(5).
- Theeuwes J. 1995 Abrupt luminance change pops out; abrupt color change does not. *Percept. Psychophys.* **57**, 637–644. (doi:10.3758/BF03213269)
- Hiramatsu C, Melin AD, Aureli F, Schaffner CM, Vorobyev M, Matsumoto Y, Kawamura S. 2008 Importance of achromatic contrast in short-range fruit foraging of primates. *PLoS ONE* **3**, e3356. (doi:10.1371/journal.pone.0003356)
- Oliva A, Schyns PG. 2000 Diagnostic colors mediate scene recognition. *Cogn. Psychol.* **41**, 176–210. (doi:10.1006/cogp.1999.0728)
- Parkhurst D, Law K, Niebur E. 2002 Modeling the role of salience in the allocation of overt visual attention. *Vision Res.* **42**, 107–123. (doi:10.1016/S0042-6989(01)00250-4)
- Theeuwes J. 1992 Perceptual selectivity for color and form. *Percept. Psychophys.* **51**, 599–606. (doi:10.3758/BF03211656)
- White TE, Rojas B, Mappes J, Rautiala P, Kemp DJ. 2017 Data from: Simple visual cues predict the human detection of stimuli amidst natural noise. Figshare (doi:10.6084/m9.figshare.5235079)