

**Title:** Spatial structure, phase, and the contrast of natural images

**Author names and affiliations:**

Reuben Rideaux <sup>1,\*</sup>

Rebecca K. West <sup>2,\*</sup>

Thomas S. A. Wallis <sup>3</sup>

Peter J. Bex <sup>4</sup>

Jason B. Mattingley <sup>1,2</sup>

William J. Harrison <sup>1,2</sup>

<sup>1</sup> Queensland Brain Institute, The University of Queensland, St Lucia 4072, Australia

<sup>2</sup> School of Psychology, The University of Queensland, St Lucia 4072, Australia

<sup>3</sup> Institut für Psychologie & Centre for Cognitive Science, Technische Universität Darmstadt, Darmstadt 64283, Germany

<sup>4</sup> Department of Psychology, Northeastern University, Boston 02115, USA

\* Contributed equally

**Corresponding author and email:** William J Harrison ([willjharri@gmail.com](mailto:willjharri@gmail.com))

**Key words:** contrast sensitivity, visual search, image statistics, natural images

## 1 Abstract

2 The sensitivity of the human visual system is thought to be shaped by environmental  
3 statistics. A major endeavour in vision science, therefore, is to uncover the image statistics  
4 that predict perceptual and cognitive function. When searching for targets in natural images,  
5 for example, it has recently been proposed that target detection is inversely related to the  
6 spatial similarity of the target to its local background. We tested this hypothesis by  
7 measuring observers' sensitivity to targets that were blended with natural image  
8 backgrounds. Targets were designed to have a spatial structure that was either similar or  
9 dissimilar to the background. Contrary to masking from similarity, we found that observers  
10 were most sensitive to targets that were most similar to their backgrounds. We hypothesised  
11 that a coincidence of phase-alignment between target and background results in a local  
12 contrast signal that facilitates detection when target-background similarity is high. We  
13 confirmed this prediction in a second experiment. Indeed, we show that, by solely  
14 manipulating the phase of a target relative to its background, the target can be rendered  
15 easily visible or undetectable. Our study thus reveals that, in addition to its structural  
16 similarity, the phase of the target relative to the background must be considered when  
17 predicting detection sensitivity in natural images.

## 18 Introduction

19 The human visual system is tasked with parsing the complexity of natural environments  
20 into a coherent representation of behaviourally relevant information. These operations have  
21 been shaped by various selective pressures over evolutionary and developmental  
22 timescales. Therefore, the perceptual computations that guide cognition and behaviour  
23 ultimately serve to extract functional information from rich and complex naturalistic  
24 environments (Carandini et al., 2005; Field, 1987; Olshausen & Field, 2005; Parraga et al.,  
25 2000; Simoncelli & Olshausen, 2001). For example, a common task is to find a pre-defined  
26 target object in a complex or cluttered visual environment. The vast majority of our  
27 knowledge of the visual system, however, has been derived from experiments using  
28 relatively sparse stimulus displays that are not representative of our typical visual diets. The  
29 aim of the present study was to investigate how natural image structure influences target  
30 detection. We tested how detection is influenced by the spatial structure, phase, and  
31 contrast of natural image backgrounds to determine the features that best predict detection  
32 sensitivity.

33 Luminance contrast plays a critical role in most visual tasks. The human visual system  
34 is tuned to detect contrast across a range of spatial and temporal frequencies. Neurons in  
35 primary visual cortex (V1) are classically understood as processing local regions of oriented  
36 contrast that can define the borders of objects (Hubel & Wiesel, 1959). Such properties of  
37 individual neurons govern phenomenal perception and are thought to be shaped by the  
38 statistics of natural environments (Barlow, 1961, 1972). The encoding of contrast within the  
39 visual system is most commonly studied with oriented grating stimuli, such as Gabor  
40 wavelets. Grating stimuli are conveniently characterised by a simple set of parameters:  
41 orientation, contrast, position, and spatial frequency. From a computational perspective,  
42 "Gabor wavelet analyses" allow the decomposition of any image into mathematically  
43 tractable component features. Such analyses are relatively simple and are common in many  
44 computer vision applications. Early theory suggested that analogous decomposition  
45 processes occur in the visual system (Campbell & Robson, 1968). However, more recent  
46 studies suggest that individual visual neurons encode complex higher-order statistical  
47 information that is not necessarily predicted by Gabor parameters (e.g. Cadena et al., 2019).

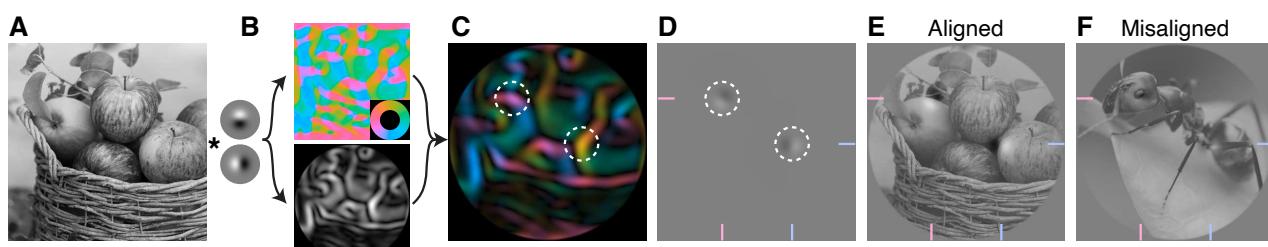
48 One common approach to investigate contrast sensitivity in natural conditions is to  
49 have observers detect contrast-defined targets embedded in digital photographs or movies.  
50 Relative to sensitivity as typically quantified with a uniform background, spatio-temporal  
51 contrast sensitivity is diminished when viewing dynamic movies, particularly for lower  
52 frequencies (Bex et al., 2009). Furthermore, during free viewing of natural movies, the large-  
53 scale retinal changes caused by saccadic eye movements also diminish sensitivity likely  
54 due to forward and backward masking (Dorr & Bex, 2013; Wallis et al., 2015). In general,  
55 such studies have revealed that the sensitivity of the visual system does indeed depend on  
56 naturalistic context (Bex & Makous, 2002; Geisler, 2008).

57 Researchers have further sought to understand the statistical regularities of natural  
58 scenes that impact the detectability of targets. For example, various image structures, such  
59 as the density of edges within close proximity to the target, negatively impact detection  
60 sensitivity (Bex et al., 2009; see also Wallis et al., 2015). Indeed, the discriminability of visual  
61 objects can be predicted from the spatial proximity of surrounding visual clutter (Balas et al.,  
62 2009; Greenwood et al., 2010, 2012; Harrison & Bex, 2014, 2015, 2017; Rosenholtz et al.,  
63 2012; Wallis et al., 2019). More recently, it has been found that sensitivity scales inversely  
64 with the *structural similarity* between target and background (Sebastian et al., 2017, 2020).  
65 Structural similarity describes how similar two stimuli are in terms of the spatial distribution  
66 of phase-invariant contrast. Sebastian et al found that observers' detection sensitivity  
67 decreases with increasing similarity. These studies thus predict that targets are most difficult  
68 to detect when they are similar to their backgrounds (Sebastian et al., 2017), particularly  
69 when those backgrounds are dense with edges (Bex et al., 2009). Other studies that have  
70 attempted to quantify the relationship between image statistics and sensitivity use post-hoc  
71 computational means to estimate the influence of natural image structure on target detection  
72 or apparent contrast (e.g. Haun & Peli, 2013; Wallis et al., 2015; Wallis & Bex, 2012). Very  
73 few studies, to the best of our knowledge, explicitly manipulated the consistency of a target's  
74 appearance with the appearance of a natural image background in an experimental design  
75 (e.g. Neri, 2014, 2017; Teufel et al., 2018).

## 76 The present study

77 The aim of the present study was to test observers' sensitivity to targets presented on  
78 natural image backgrounds. Importantly, we designed the test stimuli a priori such that  
79 targets approximated the appearance of, and were aligned with, the local structure of a  
80 natural image background, or differed from the local structure. We therefore distinguish  
81 target-background *alignment* from target-background *similarity* in terms of the stimulus  
82 generation procedure (alignment) versus an image statistic (similarity). As shown in Figure  
83 1, we automated the placement of targets within natural backgrounds according to oriented  
84 contrast energy at different image regions. We created two conditions, one in which targets  
85 were aligned with their backgrounds and one in which targets were misaligned with their  
86 backgrounds. In contrast to this stimulus generation procedure, target-background similarity  
87 is a measure of the correlation between a target and a background without a target. While  
88 target-background similarity ranges from 0 – 1 for all stimuli, our stimulus generation method  
89 results in higher similarity scores for aligned targets than misaligned targets (on average).  
90 Based on previous studies showing a negative impact of increasing target-background  
91 similarity on detection (Bex et al., 2009; Sebastian et al., 2017), we expected to find worse  
92 detection sensitivity when targets were aligned with the background – and were therefore  
93 highly similar – than when they were misaligned relative to the background – and were  
94 therefore relatively dissimilar. To anticipate our results, however, we found the opposite,  
95 instead revealing that the influence of target-background similarity on detection sensitivity  
96 depended almost entirely on the relative phase of the target.

97



98  
99  
100  
101  
102  
103  
104  
105  
106  
107  
108  
109  
110  
111  
112  
113

**Figure 1. Stimulus generation method for testing sensitivity to contrast in natural images.** A) An example source image taken from a collection of over 26,000 labelled images in the THINGS database (Hebart et al., 2019). B) We used a complement of derivative of Gaussian wavelets to filter each source image and compute the dominant orientation (top panel) and contrast energy (bottom panel) at each pixel location. Orientation is indicated by the inset colour wheel, which spans the full range (0 – 2pi) to indicate the preservation of the phase of the dominant filter. C) As shown by the white dashed circles, we selected target image regions according to the peaks of the oriented contrast maps. The number of targets varied from trial to trial from 1 to 16 in equally spaced log steps. D) Targets were oriented filters generated from the oriented contrast maps. These target features are thus aligned to the natural structure within the source image. Targets were then added to a natural image background, and observers were required to detect in which of two images the targets had been added. E and F) Targets were either aligned (E) or misaligned (F) with the background structure. Note that the same targets have been added to both examples but are more apparent in the aligned condition than the misaligned condition. As a guide, target filters are located at the intersection of pink and blue lines at the edges of panels D – F.

114

## Methods

115  
116  
117  
118  
119  
120  
121

**Participants.** We used a single-subjects design in which we measured observers' perceptual performance with high precision and treat each observer as a replication (Smith & Little, 2018). All observers were authors of the paper and had normal vision (RR, RW & WH). RW and RR were naïve to the specific experimental manipulations at the time of testing. The experiment was designed and carried out during a COVID-19 lockdown in Brisbane, Australia, in March 2021. Testing occurred, therefore, in each observer's private residence.

122  
123  
124  
125

**Design.** We measured observers' sensitivity to contrast changes in natural images in a 2 (target-background alignment: aligned or misaligned) x 5 (number of targets: 1, 2, 4, 8, or 16) x 5 (target amplitude: 0, 0.05, 0.1, 0.2, or 0.4 of maximum) design. Each observer completed 40 trials per condition for a total of 2000 trials in a fully within-participants design.

126  
127  
128  
129  
130  
131  
132

**Stimuli.** Stimuli were programmed with the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) in MATLAB (v2018b, Mathworks) and were displayed either on a 15" MacBook Pro Retina or a 16" MacBook Pro Retina. Natural images of objects were taken from the THINGS database (Hebart et al., 2019), available via the Open Science Framework (<https://osf.io/jum2f/>). Images were converted to greyscale using the `rgb2grey()` function in MATLAB, and we assumed digital photos were encoded with a gamma of 2, and displays had a decoding gamma of 2.

133  
134  
135  
136  
137  
138  
139  
140

We describe the stimulus generation process in detail below, but provide a brief overview here. On each trial, two different natural images were displayed, both of which were normalised in their contrast. Images had a diameter of 2° and were presented to the left and right of a red fixation spot. We chose this relatively small stimulus size for two reasons. First, we wanted to display images side by side, but close enough to central vision so as to mitigate effects of e.g. crowding. Second, because we were not able to monitor observers' fixation compliance, the smaller stimulus size reduced the tendency for observers to make reflexive eye movements to high contrast image regions in their periphery. The

141 target stimulus was the one in which wavelet filters had been blended with the natural image;  
142 the distractor was a natural image with no target filters. The filters were designed to be  
143 similar or dissimilar from the underlying natural image structure. We generated target stimuli  
144 by blending a source image of a natural object with derivative of Gaussian wavelets  
145 (henceforth: *filters*). The blending process followed four steps: 1) find the dominant  
146 orientation of each pixel in a source image, 2) find the relative contrast of each pixel in the  
147 image, 3) draw some number of filters at the highest contrast image regions, and 4) combine  
148 the filters with a source image. We expand on these steps below.

149 First, we used a steerable filter approach to determine the dominant orientation at  
150 every pixel in a given source image (Freeman & Adelson, 1991). Filters were directional first  
151 derivative of Gaussians oriented at 0° and 90°:

152 *Equation 1* 
$$G^{0^\circ} = -2 \frac{x}{\sigma} e^{-\frac{x^2+y^2}{\sigma^2}}$$

153 *Equation 2* 
$$G^{90^\circ} = -2 \frac{y}{\sigma} e^{-\frac{x^2+y^2}{\sigma^2}}$$

154 Where  $\sigma$  is the standard deviation of the Gaussian,  $x$  and  $y$  are the coordinates of each  
155 image pixel with point (0,0) at the centre, and  $G^\theta$  is the resulting filter. The Gaussian standard  
156 deviation was 0.08°. Within a trial, each filter was convolved with a source image:

157 *Equation 3* 
$$R^{0^\circ} = G^{0^\circ} * I$$

158 *Equation 4* 
$$R^{90^\circ} = G^{90^\circ} * I$$

159 Where  $I$  is the source image with a mean of 0 and in the range [-1 1] and  $R$  is a filter  
160 response at each pixel location. We combined the filter responses to find the dominant  
161 orientation,  $\hat{\theta}$ , at each location:

162 *Equation 5* 
$$\hat{\theta} = \text{atan2}(\sum_{\theta=0^\circ}^{90^\circ} R^\theta \sin(\theta), \sum_{\theta=0^\circ}^{90^\circ} R^\theta \cos(\theta))$$

163 Second, we created a contrast map,  $C$ , of the filtered image by combining the filter  
164 outputs as follows:

165 *Equation 6* 
$$C = \sqrt{\sum_{\theta=0^\circ}^{90^\circ} R_\theta^2}$$

166 Third, we found the dominant orientation at the location of the contrast maxima:

167 *Equation 7* 
$$C_0 = \text{argmax } C$$

168 *Equation 8* 
$$\hat{\theta}_{cmax} = \hat{\theta}_{C_0}$$

169  $C_0$  indexes the x-y coordinates of the contrast maxima, and  $\hat{\theta}_{cmax}$  is the orientation at  
170 this location. We then steered a filter at this location as follows:

171 *Equation 9* 
$$S = \cos(\hat{\theta}_{cmax}) G_{C_0}^{0^\circ} + \sin(\hat{\theta}_{cmax}) G_{C_0}^{90^\circ}$$

172 Here,  $S$  is the resulting filter stimulus in the range -1 to 1. Note the additional subscript  
173 of the filters that indicates that the filters were centred on the location of the contrast maxima,  
174  $C_0$ . This is trivially achieved by centring the x-y coordinates in Equations 1 and 2 on the  
175 coordinates of  $C_0$ .

176 Finally, we created the target stimulus,  $\tau$ , by combining the filter stimulus,  $S$ , with a  
177 normalised source image:

178 *Equation 10* 
$$\tau = 0.5 + \frac{2\alpha S + I_{norm}}{2}$$

179 Where  $\alpha$  is the filter amplitude expressed as a proportion of maximum possible  
180 contrast, and

181 *Equation 11* 
$$I_{norm} = 2\rho \frac{I}{sd(I)}$$

182 Here,  $\rho$  is the image root mean square (RMS) contrast, and  $sd(I)$  is the standard  
183 deviation of the source image. RMS contrast was set to 0.2 based on the findings of  
184 Sebastian et al (2017). The addition of 0.5 and denominator in Equation 10 normalises the  
185 range of the source image to [0 1] for display. Prior to this step, the target image was  
186 windowed in a circular aperture with a diameter matching the width of the source image (i.e.  
187 2°) and a raised cosine edge, transitioning to zero contrast in 6 pixels. To constrain the filters  
188 generated by Equation 9 to appear within the windowed portion of the stimulus, the same  
189 aperture was applied to the contrast map,  $C$ , prior to generating the stimulus. Any values  
190 lower or higher than 0 or 1, respectively, in  $I_{norm}$  were clipped.

191 For trials in which multiple filters were combined with a source image, we used an  
192 iterative procedure to draw  $n$  local maxima from the contrast image. Following the argmax  
193 operation in Equation 7, we updated the contrast map to minimise the contrast at the  
194 maxima:

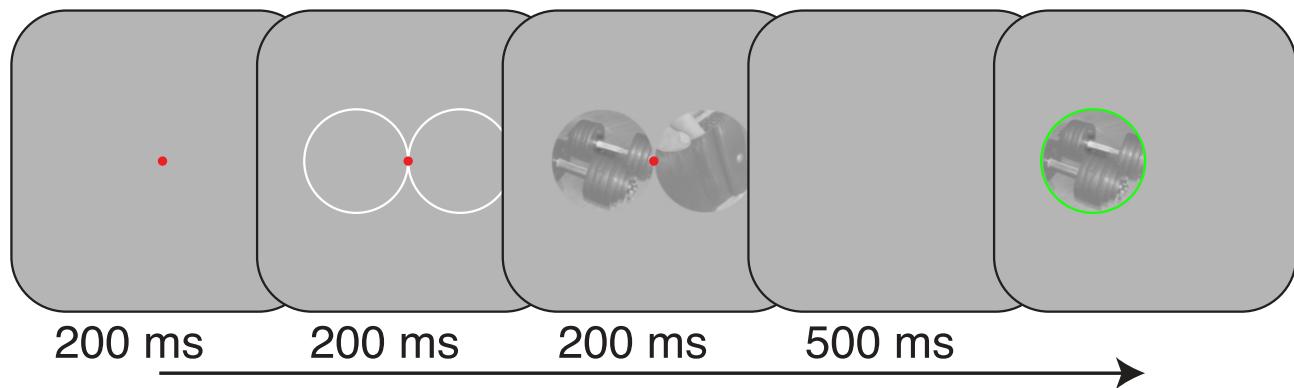
195 *Equation 12* 
$$C_n = \begin{cases} C_{n-1}[1 - f(C_0, \Delta\sigma)] & n > 1 \\ C & n = 1 \end{cases}$$

196 Where  $C_n$  is the contrast map for the  $n$ -th filter, and  $f(C_0, \Delta\sigma)$  is a two-dimensional  
197 Gaussian with a peak of 1 centred on the location of the maxima  $C_0$ , and a standard deviation  
198 of  $\Delta\sigma$ .  $\sigma$  is the standard deviation of the basis filters, while  $\Delta$  is a scaling factor that  
199 determines the spatial extent of change in the contrast map. The effect of this adjustment is  
200 the creation of a new local maxima at a different location than in the previous iteration. The  
201 greater the value of  $\Delta$ , the greater the spatial spread of filters. The first filter location is always  
202 the image region with highest contrast. After accounting for the effect of  $\Delta$ , subsequent filters  
203 are placed in regions of diminishing contrast. In trials in which multiple filters were present,  
204 backgrounds were randomly selected as described above.

205 **Image selection.** The 26,107 images in the THINGS database are grouped into 1,854  
206 concepts (e.g. “dog”, “cup”, “brush” etc), such that there are at least 12 unique, high quality  
207 images for each concept (Hebart et al., 2019). In each testing session (500 trials), we  
208 selected 1000 source images from unique concepts such that no two images were drawn  
209 from the same concept. The target background was thus always drawn from a different  
210 concept than the distractor image. However, it was necessary that some concepts were  
211 repeated across testing sessions, and it was also possible that some individual images were  
212 also repeated across sessions (but never within sessions).

213 On each trial, we selected two images from the set of 500: one image for the target  
214 background, and a second image was the distractor. On half the trials, the target filters were  
215 generated from the target background and were therefore aligned with the background,  
216 while on the other half of trials they were generated from the distractor image – but blended  
217 with the target background – and were therefore misaligned relative to the target  
218 background. Target filters were generated from the distractor background on misaligned  
219 trials, as opposed to an unused image, so that the filters and their source image were  
220 presented on every trial, but we doubt this decision was important to our results. We chose  
221 to present two different background images on each trial, rather than, for example,  
222 presenting two of the same background images, because we did not want observers to  
223 attempt to simply spot the difference between two similar images. Instead, observers had to  
224 perform a more natural task of searching unfamiliar and unique backgrounds for targets.

225 **Procedure.** A typical trial sequence is shown in Figure 2. Each trial began with a small  
226 red fixation spot in the centre of the display, followed by outlines of the upcoming stimulus  
227 locations. Natural image backgrounds were followed by a blank of 500ms, after which time  
228 the observer reported which of the two patches contained the target filter(s) using the  
229 keyboard. Following the observer's response, the image patch with target filters was re-  
230 displayed for an additional 500ms, outlined in green or red depending on whether the  
231 observer's response was correct or incorrect, respectively. Feedback was provided to  
232 facilitate observers reaching a stable level of performance. No breaks were programmed  
233 but could be taken by withholding a response. Each session included ten repeats of each  
234 trial type, all presented in random order, giving 500 trials per session and taking  
235 approximately 15 minutes when no breaks were taken.



236  
237 **Figure 2. Schematic of typical trial sequence. The target and background could appear on the left or**  
238 **right of the screen with equal probability. Following an observer's response, the background**  
239 **containing the target filters was framed by a green or red circle depending on whether the response**  
240 **was correct or incorrect, respectively.**

241 **Sensitivity analyses.** We quantified observers' sensitivity to the target filters in natural  
242 images in a generalised linear model (GLM) framework. We describe the most pertinent  
243 aspects of the framework below, but, for the impatient reader, we note that these equations  
244 accumulate to the `fitglme()` function in MATLAB, or, equivalently, the `lmer()` function in R  
245 with the `lme4` package (Bates et al., 2015).

246 In a standard single-interval detection paradigm in which a target is either present or  
247 absent, sensitivity,  $d'$ , is calculated as:

$$248 \quad \text{Equation 13} \quad d' = \phi H - \phi F$$

249 Where  $\phi$  is the normal integral function,  $H$  is the proportion of hits, and  $F$  is the  
 250 proportion of false alarms, under the assumption of equal variance. An observer's criterion,  
 251  $c$ , is calculated as:

$$252 \quad \text{Equation 14} \quad c = \frac{1}{2}(\phi H + \phi F)$$

253 In a GLM,  $d'$  and  $c$  (bias) are computed as predictor weights  $\beta_1$  and  $\beta_0$ , respectively,  
 254 that are passed through a probit link function, which is the normal integral function:

$$255 \quad \text{Equation 15} \quad \eta_{[i]} = \beta_0 + \beta_1 S_{01[i]}$$

$$256 \quad \text{Equation 16} \quad p(\text{present}_i) = \phi \eta_i$$

257 Where  $\eta$  is the sum of weighted linear predictors and  $S_{01}$  is the absence or presence  
 258 of the signal (i.e. 0 or 1, respectively) on the  $i$ -th trial. By fitting such a probit model, estimates  
 259 of the predictor weights  $\beta_1$  and  $\beta_0$  are identical to  $d'$  and  $c$ , respectively, as calculated in  
 260 Equation 13 and Equation 14. Whereas these equations fully specify sensitivity and bias in  
 261 a single interval present/absent judgement task, some small modifications are needed to

262 quantify sensitivity in a two-alternative forced choice task (2AFC) as in our experiment. First,  
263  $S_{01}$  denotes whether the target filter(s) appeared in the left or right spatial interval, defined  
264 as -.5 or .5, respectively. Similarly, observers' reports (i.e. "target appeared in the left or right  
265 interval"), were defined as -1 and 1, respectively. Finally, in a 2AFC, observers have two  
266 opportunities to detect the target – once per spatial interval – and so raw  $d'$  will be greater  
267 than in a single-interval detection design. Therefore, sensitivity (but not bias) must be scaled  
268 by  $\frac{1}{\sqrt{2}}$  (Macmillan & Creelman, 2004):

269 *Equation 17* 
$$d'_{2AFC} = \frac{1}{\sqrt{2}}\beta_1 = \frac{1}{\sqrt{2}}(\phi H - \phi F)$$

270 Importantly, we can extend Equation 15 to quantify sensitivity to any number of other  
271 predictors,  $x_\omega$ :

272 *Equation 18* 
$$\eta_{[i]} = \beta_0 + \beta_1 S_{01[i]} + \dots + \beta_\omega x_{\omega[i]}$$

273 Consider, for example, the influence of filter amplitude ( $\alpha$ ) on an observer's sensitivity:

274 *Equation 19* 
$$\eta_{[i]} = \beta_0 + \beta_1 \alpha_{[i]} S_{01[i]}$$

275 Note that filter amplitude is entered into the model as an interaction with target location  
276 because the model's predicted outcome is a spatial report; target amplitude alone can only  
277 predict a change in bias. In preliminary model fits, we found that such bias was not  
278 significantly different from zero, and thus included only interactive terms to facilitate  
279 interpretability of the standard bias term,  $\beta_0$ . We selected other model predictors according  
280 to the model that produced the lowest Akaike information criterion (AIC; see below).

281 Finally, we implemented this model as a multilevel GLM (GLMM) to partially pool  
282 coefficient estimates across observers (Gelman & Hill, 2007). By using a GLMM, we model  
283 each observer's predictor weights as having come from a population distribution with mean  
284  $\mu$  and variance  $\sigma^2$ :

285 *Equation 20* 
$$\eta_{[i]} = \beta_{0,j} + \beta_{1,j} \alpha_{j[i]} S_{01,j[i]} + \dots$$

286 Where

287 *Equation 21* 
$$\beta_{\omega,j} = \mu_\omega + \epsilon_{\omega,j} \mid \sigma_\omega^2$$

288 Here,  $\epsilon_{\omega,j}$  is the offset for each predictor  $\omega$  and observer  $j$ , relative to the parameter's  
289 mean  $\mu$ , contingent on the parameters' estimated population variance  $\sigma^2$ . The partial pooling  
290 of observers' data in a GLMM results in more extreme values being pulled toward the  
291 population mean estimate. Note that in our experiment, however, such pooling is relatively  
292 minor due to the large number of trials, and therefore high precision, of each observer's  
293 estimated performance, as well as the relatively small number of observers. Because  
294 images were drawn randomly from trial to trial from a pool of tens of thousands of images,  
295 we did not expect many, if any, repeats of each image. We therefore did not model the  
296 background images as a random effect, but we note that such a design could be chosen in  
297 future to estimate the variance associated with each tested background.

298 We entered into the model the factors target amplitude, number of filters, and target-  
299 background alignment, which, as noted above, were each entered as an interaction with the  
300 spatial interval of the target. In hindsight, our inclusion of the condition in which target  
301 amplitude was 0 was unnecessary. For all such trials, therefore, we set all predictors to have  
302 a value of 0 so they were omitted from model calculations. The model fit was improved by  
303 including nonlinear terms by raising amplitude and number of Gabors to the exponents 0.5  
304 and 2, respectively. We further tested all combinations of interactions, but none improved  
305 the model fit as assessed by the Akaike information criterion.

306 **Post-hoc analysis of interaction between the number of filters and filter**  
307 **amplitude.** We modelled the joint influence of number of filters and filter amplitude on  
308 proportion correct as a two-dimensional surface (see Figure 5B). The surface is defined as:

309 *Equation 22* 
$$z = 0.5 + \frac{1}{2}(f(\alpha_\mu, \alpha_\sigma) \odot f(n_\mu, n_\sigma))$$

310 Where  $z$  is the surface of estimated proportion correct,  $f(\alpha_\mu, \alpha_\sigma)$  is a cumulative  
311 probability function relating target amplitude to accuracy according to a threshold and  
312 variance,  $\alpha_\mu$  and  $\alpha_\sigma$ , respectively, and  $f(n_\mu, n_\sigma)$  is a cumulative probability function relating  
313 the number of filters to accuracy according to a threshold and variance,  $n_\mu$  and  $n_\sigma$ ,  
314 respectively. Here,  $\odot$  refers to the element wise product of cumulative distributions. This  
315 function can be thought of as a two-dimensional psychometric function, with separable  
316 means and standard deviations. The input parameters into the cumulative functions were  
317 free parameters, fit by minimising the summed squared error between the average  
318 proportion correct and  $z$  using Matlab's fminsearch(). While there are no doubt other ways  
319 of quantifying the interaction between filter amplitude, number of filters, and proportion  
320 correct, this model suffices for our purposes.

321 **Structural similarity.** We quantified the similarity between targets and their  
322 backgrounds using the same approach as Sebastian et al (2017 see their equation S9):

323 *Equation 23* 
$$r_{[i]} = \frac{A_{S[i]} \cdot A_{I[i]}}{\|A_{S[i]}\| \|A_{I[i]}\|}$$

324 Where  $r_{[i]}$  is the similarity between the steered filter targets (i.e.  $S$  in Equation 9) and  
325 the background image  $I$  on trial  $i$ .  $A_{S[i]}$  is the Fourier amplitude spectrum of the filters, and  
326  $A_{I[i]}$  is the Fourier amplitude of the natural image background, both of which are vectors and  
327 were computed by taking the absolute of the complex values of the Fourier transforms.  $r_{[i]}$   
328 is thus a phase-invariant metric. Prior to computing  $A_{I[i]}$ , we windowed the natural image  
329 background to include only the same regions as the locations of target filters. This was  
330 achieved by first computing a contrast map in which two-dimensional Gaussians were  
331 positioned at each target location. Gaussians had the same standard deviation as the target  
332 filters and had their peaks normalised to one. We then computed the elementwise product  
333 of the source image and this contrast map, which produced the background image entered  
334 into Equation 23. Note that our method to generate stimuli and target-background similarity  
335 both depend on oriented contrast within the frequency band of the target. Variations in  
336 structural similarity for the aligned and misaligned targets are shown in Figure 6.

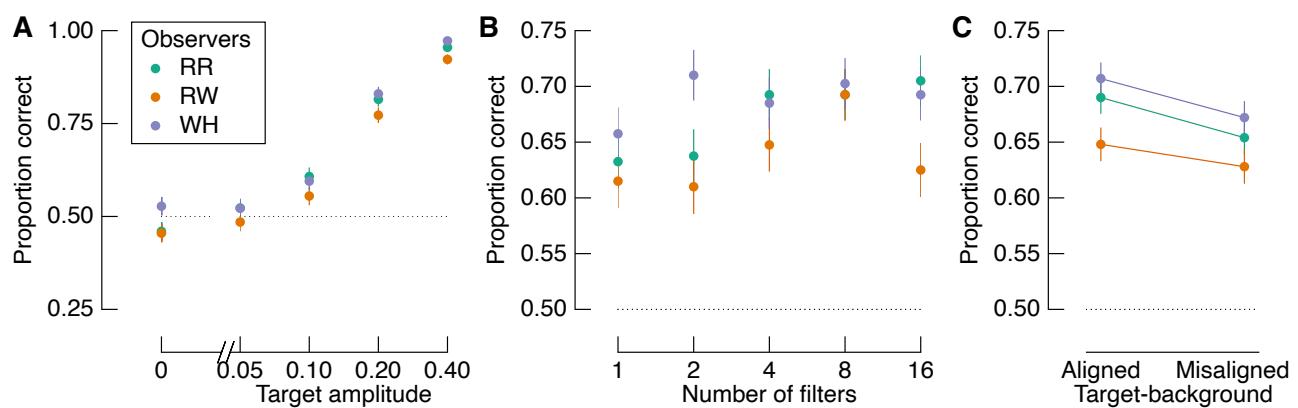
## 337 Results

338 We tested observers' ability to detect target filters that were blended with natural image  
339 backgrounds. Targets were designed such that they were either aligned or misaligned with  
340 the structure of the background. We tested detection of 1, 2, 4, 8 and 16 target filters and  
341 across a range of target amplitudes. We first describe our results in terms of raw accuracy,  
342 and then report the results of our modelling analysis in which we quantified observers'  
343 sensitivity in terms of  $d'$ .

## 344 The influence of target amplitude, number of filters, and target-background alignment

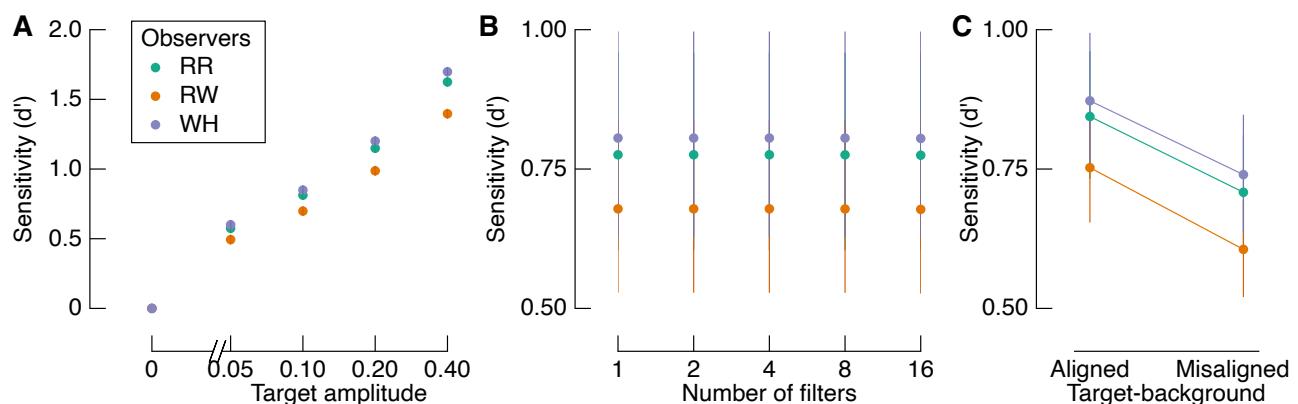
345 The proportion of correct responses as a function of each factor is shown in Figure 3.  
346 The amplitude of the target most clearly impacts accuracy, such that accuracy increases  
347 approximately linearly with (log) target amplitude (Figure 3A). Although the relationship  
348 between proportion correct and the number of filters is less consistent (Figure 3B), there is  
349 a general increase in accuracy with increasing number of target filters. As described below,

350 however, the relationship between number of filters and sensitivity was not significant. We  
 351 also found a highly consistent effect of target-background alignment across observers  
 352 (Figure 3C). Contrary to our expectations based on recent reports of similarity masking  
 353 (Sebastian et al., 2017), however, we found better performance when target filters were  
 354 aligned with their backgrounds than when they were misaligned with their backgrounds. This  
 355 difference in performance is significant at the group level ( $t(2) = 5.862, p = 0.028, d = 3.38$ ),  
 356 but we more formally quantify the relationship between these factors in a GLMM below.  
 357 Importantly, given the high measurement precision of these data (1000 observations per  
 358 data point shown in Figure 3C), we can treat each observer as an independent replication  
 359 of the effect, regardless of any specific inferential statistic (Smith & Little, 2018).



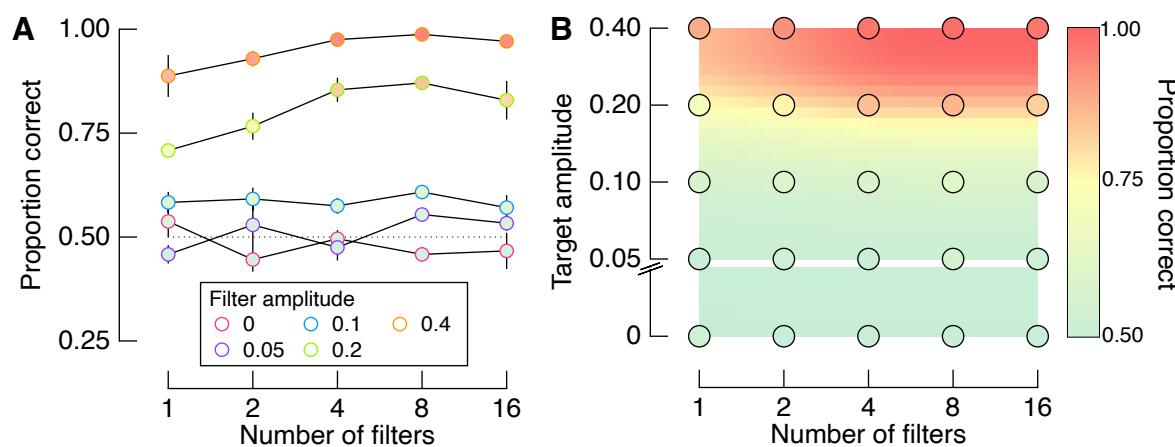
360  
 361 **Figure 3. Proportion correct target identifications based on the three experimental factors: A) Target**  
 362 **amplitude, B) Number of filters, and C) Target-background alignment. Colours represent different**  
 363 **observers, as indicated by the legend in panel (A). The dotted line in each panel shows chance**  
 364 **performance. There were 400 trials per data point in panels (A) and (B), and 1000 trials per data point**  
 365 **in panel (C). Error bars show one binomial standard deviation.**

366 We estimated detection sensitivity as a function of the experimental factors with a  
 367 GLMM. Modelled sensitivity is shown in Figure 4 in the same format as Figure 3. Target  
 368 amplitude and target-background alignment were both significant contributors to the model.  
 369 Importantly, as shown in Figure 4C, sensitivity was greater when target filters were aligned  
 370 with the background than when they were misaligned. The number of filters did not predict  
 371 sensitivity, which is consistent with the relatively noisy relationship between accuracy and  
 372 the number of filters as shown in Figure 3B.



373  
 374 **Figure 4. Modelled target detection sensitivity. A) Sensitivity varies systematically with target**  
 375 **amplitude, but not the number of filters (B). C) Sensitivity depends on the target-background**  
 376 **alignment, such that it is greater when filters are aligned with the background than when they are**  
 377 **misaligned. Error bars in all panels show one standard error across marginalised conditions, but are**  
 378 **smaller than the point size in (A).**

379 We manipulated the number of filters because we expected to find an improvement in  
380 performance with increasing filter number. The lack of a main effect of filter number in the  
381 results above, therefore, was unexpected. Although not critical to our primary interest in the  
382 influence of target-background alignment, we tested whether the number of filters interacted  
383 with target amplitude using a more direct test than the full GLMM above. Data points in  
384 Figure 5A show mean proportion correct responses, marginalised to show the influence of  
385 the number of filters for each target amplitude. At the two highest target amplitudes tested  
386 (top two lines), there is indeed an effect of the number of filters: as the number of filters  
387 increases, so too does observers' accuracy. The same data points are shown in Figure 5B  
388 arranged as a surface that maps proportion correct as conditional on the combination of  
389 conditions. We interpolated these points as a two-dimensional surface function that  
390 quantifies the interaction between number of filters and amplitude (see Methods). The warm  
391 colours clustering in the top right corner reveal that increasing the number of filters in the  
392 targets has the strongest effect at higher target amplitudes.



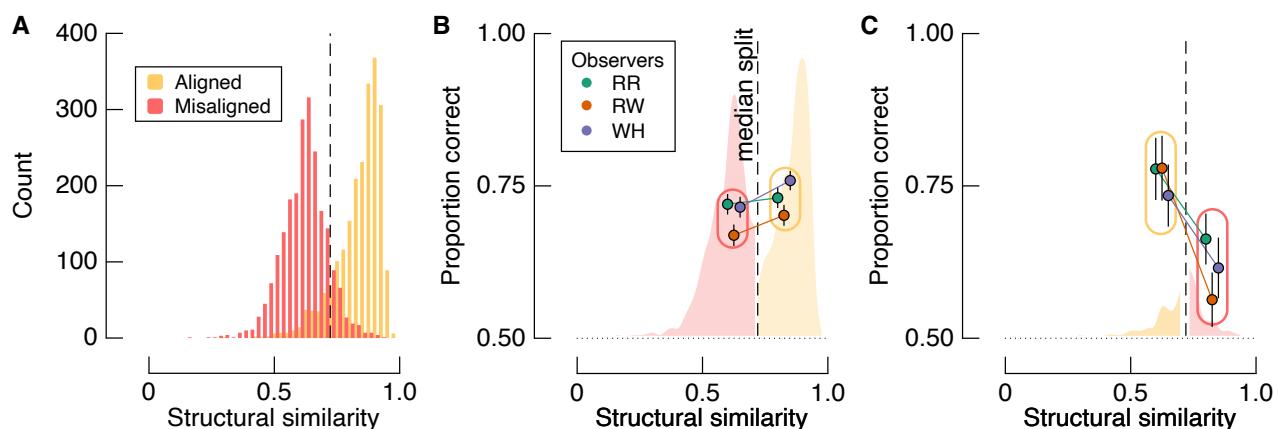
393  
394 **Figure 5. Interaction between the number of filters and filter amplitude.** A) Proportion correct for each  
395 number of filters at each amplitude level, averaged across the three observers. B) Points show the  
396 same data as in (A), but arranged as a surface, while the background is interpolated from these points.  
397 Error bars in (A) show one standard error across observers, which is smaller than the point size in  
398 many cases.

### 399 The influence of target-background similarity

400 The perceptual performance described above reveals that observers were better able  
401 to detect targets on natural image backgrounds when the targets were aligned with the  
402 underlying spatial structure of the background than when the targets were misaligned with  
403 the background. These results are contrary to our expectations based on the data of  
404 Sebastian et al (2017) who found that sensitivity is negatively correlated with the *structural*  
405 *similarity* between target and background, a metric that scales from zero (no similarity) to  
406 one (perfect similarity). We therefore next tested whether observers' performance was  
407 instead *positively* correlated with target-background similarity using the same analysis of  
408 similarity as in this previous study (Equation 23).

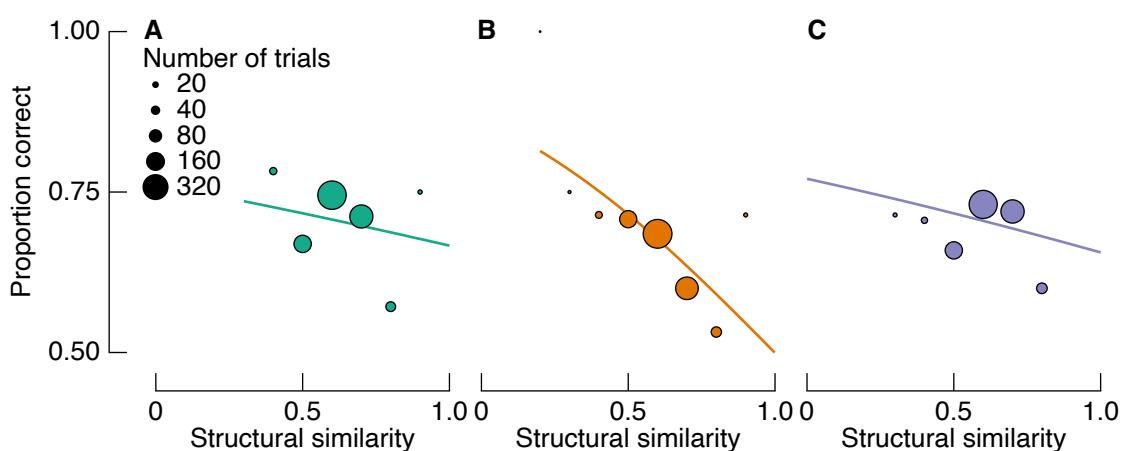
409 Shown in Figure 6A are the histograms of similarity for all trials across observers,  
410 which, by design, can be separated according to the filter alignment relative to the  
411 background. The dashed vertical line shows the median similarity of all trials, regardless of  
412 target-background alignment. By isolating trials from each condition according to whether  
413 they fall above or below this arbitrary cut-off, we can test whether accuracy depends more  
414 on similarity or target-background alignment. Figure 6B shows the proportion of correct  
415 target detections for aligned and misaligned targets that were most and least similar to the  
416 background, respectively. As per the main analyses above, accuracy was greater for aligned

417 than misaligned trials. The more diagnostic analysis is shown in Figure 6C, in which the  
418 proportion of correct target detections are shown for aligned trials that were *less* similar than  
419 the included misaligned trials (i.e. we limit the analyses to the tails of the similarity  
420 distributions). We again find that accuracy was higher for the aligned condition than the  
421 misaligned condition, despite the aligned targets having lower similarity with the background  
422 than the misaligned trials. Therefore, target-background alignment predicts performance  
423 much more strongly than target-background similarity.



424  
425 **Figure 6. Analysis of the influence of target-background similarity on perceptual performance.** A)  
426 Histograms show structural similarity between targets and background separately for the aligned and  
427 misaligned conditions. The vertical dashed line is the median similarity of all trials. B) Proportion  
428 correct for misaligned trials that were lower in similarity than aligned trials, and vice versa, as  
429 determined by median split. Accuracy for the misaligned trials is shown to the left of the median, and  
430 accuracy for the aligned trials is shown to the right of the median. C) Proportion correct for aligned  
431 trials that were lower in similarity than misaligned trials, and vice versa, as determined by median split.  
432 Accuracy for the aligned trials is shown to the left of the median, and accuracy for the misaligned trials  
433 is shown to the right of the median. Note that proportion correct is higher in the aligned condition  
434 regardless of similarity. Error bars in (B) and (C) show one binomial standard deviation.

435 In a final analysis of perceptual performance, we attempted to replicate the findings of  
436 Sebastian et al (2017) using the condition in our experiment that is most analogous to the  
437 one in theirs, namely, the misaligned condition. In both this previous study and the  
438 misaligned condition of the present study, the blending of target filters and their backgrounds  
439 did not depend on any structural alignment. Instead, any incidental alignment can be  
440 quantified in terms of structural similarity. We therefore tested whether we found an inverse  
441 relationship between target-background similarity and detection accuracy for the misaligned  
442 condition. Figure 7 shows proportion correct for trials in similarity bins (bin width = 0.1) for  
443 each observer. We modelled these data with logistic regression, with random intercept and  
444 slopes grouped by observer (i.e. a logistic GLMM). Fits are shown as solid lines in Figure 7.  
445 There is a clear negative relationship between structural similarity and accuracy, with a  
446 mean slope of -0.96 (population standard deviation = 0.75). Similarity was not a significant  
447 predictor in the model ( $p=0.13$ ), but the trends are nonetheless consistent across observers  
448 and also with the data of Sebastian et al.



449  
450  
451  
452  
453

Figure 7. Proportion correct as a function of target-background similarity for misaligned trials only. A-C show data for each observer, colour coded as in Figure 3. Solid lines are fits from a logistic GLMM, showing a negative relationship between similarity and detection accuracy, as reported by Sebastian et al (2017).

454

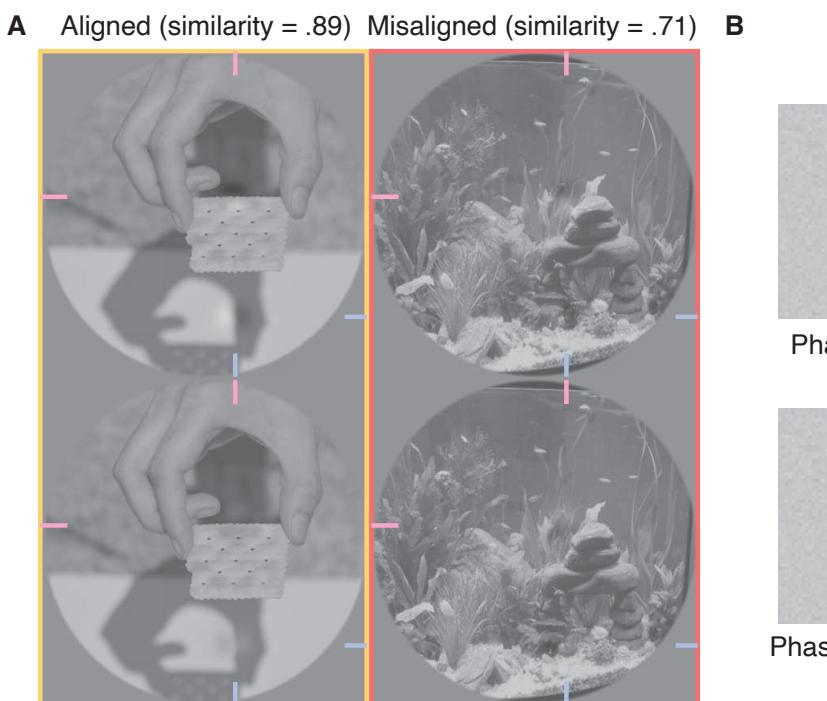
## Discussion

455  
456  
457  
458  
459  
460  
461  
462  
463  
464

We found that observers are better at detecting contrast-defined targets when they are aligned with a natural image background compared with when they are misaligned with the natural image background. The superior performance on aligned than misaligned trials did not depend on the structural similarity of targets relative to backgrounds, in contrast to the results of Sebastian et al (2017). Because the target filters tended to be aligned with object edges (i.e. the points of highest contrast in natural images; see Figure 1 and Methods), these data also appear to contradict the findings of Bex et al (2009; see also Wallis & Bex, 2012). Bex et al found that sensitivity was lower in image regions of relatively high edge density, whereas we found higher sensitivity when targets were aligned with edges than when they are randomly positioned.

465  
466  
467  
468  
469  
470  
471  
472  
473  
474  
475  
476  
477  
478  
479  
480  
481

A potentially simple explanation for the discrepancy between our data and earlier work concerns the phase alignment of target filters and backgrounds: the *phase* of a target filter relative to the phase of the local natural image background determines local contrast. This fact is demonstrated in Figure 8A. When target filters are designed to be aligned with their background structure (left panels), local contrast depends strongly on phase. When the targets and background are phase-matched, target-background amplitude is additive, resulting in greater local contrast (top left panel). By inverting the phase of those same filters, target-background amplitude is subtractive, reducing local contrast (bottom left panel). Indeed, Bex and Makous (2002) speculated that this dependence of local contrast on phase alignment explains a loss of sensitivity to phase-scrambled natural images. We tested this hypothesis directly in Experiment 2. Note, however, that, while phase-mismatched target filters reduce local contrast, they may not be less visible. See, for example, the demonstrations in Figure 8B. While the phase-mismatched filter has a lower local contrast than the phase-matched filter, the phase-mismatched filter is conspicuous. Indeed, within each half of these images, the absolute change of luminance is the same, regardless of filter phase. It therefore remains an open question as to how this manipulation will affect observers' sensitivity.



482  
483  
484  
485  
486  
487  
488  
489  
490  
491  
492  
493  
494

**Figure 8. A demonstration of the influence of filter phase on local contrast, and examples of conditions tested in Experiment 2.** A) Added to all panels are the same two target filters that were designed to be phase-matched with the local spatial structure in the top left panel. Filters in the bottom row have an inverse phase, and are therefore mismatched relative to the source image. Filters are most apparent in the top left panel: one filter is aligned with the top horizontal edge of the cracker, and the other is aligned to the left side of the vertical shadow of the thumb. Note that the structural similarity metric is phase invariant, and therefore the filters have the same similarity score within each column. Target filters are located at the intersection of pink and blue lines at the edges of each panel. In Experiment 2, we averaged observers' performance over the misaligned conditions (right column), because phase alignment is relative only to the source image. B) Simplified demonstrations of phase-matched and phase-mismatched filters aligned to an edge. Note that, while the phase-mismatched filter reduces contrast, it appears similarly visible to the phase-matched edge.

495

## Experiment 2

496  
497  
498  
499  
500  
501  
502

The results presented above reveal that the alignment of target filters with the spatial structure of the background determines detection sensitivity at least somewhat independently of target-background similarity. In Experiment 2 we tested our hypothesis that aligned targets are easier to detect because their amplitude is additive with the background amplitude, increasing local contrast. We therefore compared detection sensitivity to target filters that were either aligned or misaligned, and were either phase-matched or phase-mismatched with the original source image.

503

## Methods

504  
505  
506  
507  
508  
509  
510  
511  
512  
513  
514

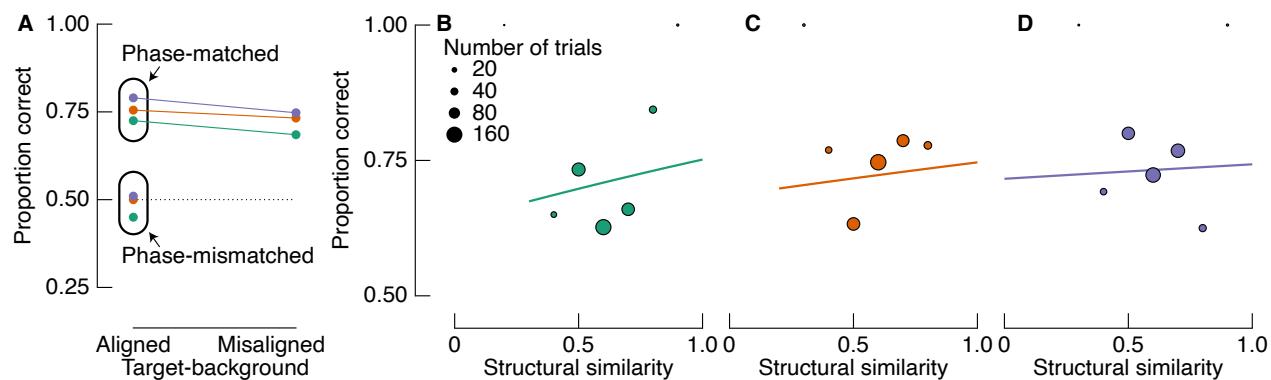
All methods were identical to those of the preceding experiment, with the following changes. This experiment was carried out in our testing lab on a Display++ monitor (Cambridge Research Systems) with 14bit luminance precision (i.e. our local lockdown had lifted). The experimental design was a 2 (alignment: aligned versus misaligned) x 2 (phase: phase-matched versus phase-mismatched) factorial design (see Figure 8 for example stimuli). All target filters had an amplitude of 0.15, which, based on the data shown in Figure 4, we expected to yield a mean  $d'$  of approximately 1. In all trials, there were four filters. Importantly, on half the trials, target filters were blended with the background as per Experiment 1, whereas in the other half of the trials the phase of the filters were reversed before blending. Note that, in the misaligned condition, the phase of the filters relative to the background is somewhat arbitrary, so in the analysis we average across these trials. Each

515 observer completed a total of 800 trials, giving 200 trials per unique condition demonstrated  
516 in Figure 8. Testing took approximately 30 minutes per observer.

517

## Results

518 In Experiment 2, we included conditions that provided an opportunity to replicate our  
519 findings from Experiment 1. As demonstrated in the top left panel of Figure 8, we included  
520 a condition in which target filters were both aligned and phase-matched to the natural  
521 background structure, as per the aligned condition of Experiment 1. We first compare  
522 observers' accuracy in this condition with the accuracy in the misaligned condition. The  
523 results are shown as connected points in Figure 9A, and reveal better performance in the  
524 (phase-matched) aligned condition than the misaligned condition for all observers. We  
525 therefore replicate the results from Experiment 1 under strict laboratory conditions. Also  
526 shown in Figure 9A are the results from the phase-mismatched condition, in which target  
527 filters were aligned with their backgrounds, but had their phase inverted. Importantly, phase-  
528 matched and phase-mismatched targets were well equated on similarity (phase-matched  
529 and phase-mismatched average similarities were .7 and 0.71, respectively). In the phase-  
530 mismatched condition, however, all observers were close to chance level, revealing they  
531 were unable to detect these targets (mean accuracy = 49%; RR = 45%, RW = 50%, WH =  
532 51%).



533

534 **Figure 9. Proportion of correct target detections in Experiment 2.** A) Results are shown according to  
535 the two main experimental factors: target-background alignment (x-axis) and target-background phase  
536 alignment (grouped data points). Note that target-background similarity is matched across aligned  
537 conditions (see left column of Figure 8). Colours indicate different observers as per Figure 3. B-D)  
538 Proportion correct as a function of target-background similarity for misaligned trials only. Solid lines  
539 are fits from a logistic GLMM, showing a positive relationship between similarity and detection  
540 accuracy, in contrast to the fits of Experiment 1 data and results reported by Sebastian et al (2017).

541

542 We again tested whether there was an inverse relationship between accuracy and  
543 similarity in the condition most closely matching the condition tested by Sebastian et al  
544 (2017), i.e. the misaligned condition (see Figure 7). We again used a logistic GLMM, and  
545 similarity was binned in 0.1 steps. In contrast to the fitted model in Experiment 1, however,  
546 we found a non-significant positive relationship between similarity and proportion correct  
547 (slope = 0.33, population standard deviation = 0.28,  $p = 0.596$ ). Fits to observers' data are  
548 shown in Figure 9B-D.

549

## Discussion

550

551 The aim of Experiment 2 was to test the prediction that targets aligned with their natural  
552 image backgrounds are easier to identify than targets that are misaligned with their  
553 backgrounds (i.e. the results of Experiment 1) due to a difference in local contrast. The  
554 differences in local contrast across these conditions results from contrast additivity in the  
555 aligned condition when filters are phase-matched with their background. We tested this

554 prediction in Experiment 2 by inverting the phase of target filters on half of the trials in which  
555 the filters were aligned with the background structure. Inverting the phase of target filters  
556 aligned with their background has a subtractive effect on local contrast, and, as we  
557 expected, rendered observers incapable of detecting the targets (Figure 9). The results of  
558 Experiment 2 thus support the notion that target-background similarity is not a useful metric  
559 of the detectability of targets per se, whereas the interaction between relative phase and  
560 structural alignment is critical.

### 561 Generative model of task performance

562 We next aimed to develop a model that captures the key results reported for  
563 Experiment 1 and Experiment 2. We hoped to account for the finding that aligned targets  
564 are more accurately detected than misaligned targets, and that this effect of alignment  
565 depends on the relative phase of target and background. These effects suggest that  
566 observers are tuning to local changes in the images caused by the additivity of filter and  
567 background luminance. The model is therefore based on simple luminance and contrast  
568 detection mechanisms like those involved in the generation of our stimuli (Figure 1). On  
569 each trial, the model detects difference in various image statistics across the target and  
570 distractor images, and then generates a response based on these differences. Simulated  
571 responses were determined by fitting the model output to observers' responses in  
572 Experiment 1. We then tested whether the fitted model reproduced the key Experiment 2  
573 results.

574 On each trial, the model was given the target image and the distractor image. The  
575 maximum contrast of each image was found by taking the maximum value of contrast maps  
576 as computed in Equations 1 – 6. The maximum luminance extreme of each image was the  
577 maximum absolute deviation of each image from mid-grey, capturing both local minima and  
578 maxima in images across trials. For each trial and each metric, we computed a ratio between  
579 left and right images:

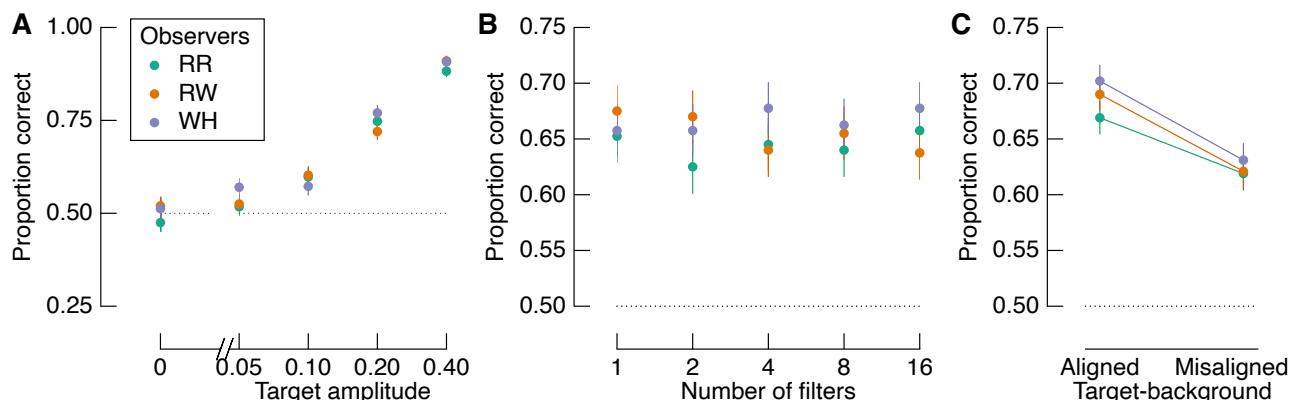
580 *Equation 24* 
$$LR_{[i]} = \ln\left(\frac{L_{max,right}}{L_{max,left}}\right)$$

581 *Equation 25* 
$$CR_{[i]} = \ln\left(\frac{C_{max,right}}{C_{max,left}}\right).$$

582 LR and CR refer to ratios of the most extreme luminance and contrast values,  
583 respectively, where negative values indicate greater extremes in the left image, and positive  
584 values indicate greater extremes in the right image. We weighted these metrics by fitting  
585 them to observers' responses (i.e. left or right spatial interval) using logistic regression. We  
586 then analysed the model predictions as per the behavioural analyses. We built different  
587 models that included 1) just the absolute luminance peak of stimuli, 2) just the contrast  
588 energy maxima of stimuli, or 3) both.

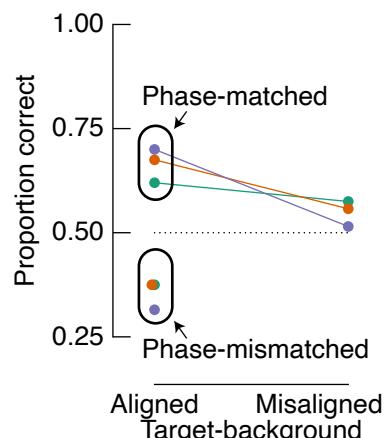
589 The best model was one that detects the absolute luminance peak and the maximum  
590 contrast energy within the target and distractor images. As shown in Figure 10, this model  
591 reproduces the qualitative patterns of performance observed in Experiment 1 (compare the  
592 model data in Figure 10 with the empirical data in Figure 3). Importantly, each image statistic  
593 significantly contributes to the model ( $p$ 's  $< 0.001$ ), and including both parameters provided  
594 a better fit than including either parameter alone based on formal model comparison (chi-  
595 square test compared with the next best model:  $\chi^2(\Delta df = 4) = 114.3, p < 0.001$ ). Note that  
596 the generative model responses are fit to the observer data based solely on the image-  
597 computable features, not on the labels of the experimental conditions (e.g. the data are not  
598 fit to aligned vs misaligned conditions) – yet the model reproduces the same patterns of data  
599 across conditions as observers. Adding the model's predicted response to the signal

600 detection model also improved estimates of observers'  $d'$  ( $\chi^2(\Delta df = 6) = 163.1, p < 0.001$ ).  
 601 These model results are consistent with the notion that adding filters to the image causes  
 602 local peaks in absolute luminance and contrast that can differentiate the target image from  
 603 the distractor image (Bex & Makous, 2002). As described next, however, this model cannot  
 604 account for the findings in Experiment 2.



605  
 606 **Figure 10. Model performance for Experiment 1. Compare with Figure 3. The model captures the key**  
 607 **results from Experiment 1. Error bars show one binomial standard deviation.**

608 We fit the model to observers' responses from Experiment 1, as shown above, and  
 609 tested whether the fitted model could predict observers' responses to Experiment 2. The  
 610 critical test is whether the model falls to chance when filters were spatially aligned but phase-  
 611 inverted relative to their backgrounds (i.e. the phase-mismatched condition). As shown in  
 612 Figure 11, however, model performance was well *below* chance in this condition. This below-  
 613 chance performance occurs because phase-inversion reduces the luminance and contrast  
 614 peaks of the target image to below those of the distractor image, resulting in the model  
 615 reporting the distractor as the target more often than not. The model again reproduces the  
 616 effect of alignment, but overestimates the size of the effect. The overestimation may have  
 617 resulted from the changes we made between experiments, including using different displays  
 618 and filter amplitudes. These differences are less relevant than the model's gross  
 619 misestimation of the phase-mismatched condition as described below.



620  
 621 **Figure 11. Model performance for Experiment 2. Compare with Figure 9A. The model performs below**  
 622 **chance in the phase mismatched condition, whereas observers were at chance (Figure 9A).**

623 The relatively poor fit to the phase-mismatched condition of Experiment 2 is  
 624 informative. Observers' data cannot be explained fully by assuming that they adopted a  
 625 simple rule in which they detected luminance and contrast peaks. For phase-matched trials,  
 626 therefore, the superior sensitivity to aligned filters over misaligned filters cannot be solely  
 627 accounted for by tuning to local peaks. We attempted to improve the fit using other image

628 metrics, such as contrast energy combined across spatial scales and the energy of a “back  
629 pocket” filter-rectify-filter model (Harrison & Bex, 2016; Landy, 2013), but none improved the  
630 fits of the model. Rather than taking the maximum contrast or luminance extreme, we also  
631 tried using k-maxima (up to  $k = 1000$ ), which also did not improve the fits. Observers’  
632 performance, therefore, escapes a relatively straightforward low-level explanation.

### 633 General Discussion

634 The aim of the present study was to test observers’ ability to detect contrast-defined  
635 targets that have been blended with natural image backgrounds. We designed the target  
636 filters so that their orientations were either aligned or misaligned with the local background  
637 structure. Based on the recent report that detection sensitivity is inversely related to target-  
638 background similarity (Sebastian et al., 2017), we expected to find worse performance in  
639 the aligned condition relative to the misaligned condition based on the notion that aligned  
640 targets would have higher target-background similarity than misaligned targets. Across two  
641 experiments, however, we found superior detection of targets that were designed to be  
642 aligned and phased-matched to the structure of the background compared with targets that  
643 were designed to be misaligned with their backgrounds and were thus lower in similarity. As  
644 noted below, our goal was not to replicate the study by Sebastian et al, but instead to test  
645 the role of target-background similarity in target detection using a novel approach.

646 Our experiments show that observers’ sensitivity does not linearly scale with similarity  
647 in all cases. In Experiment 1 we found a positive relationship between similarity and  
648 sensitivity: observers were most sensitive to targets in which target filters were aligned with,  
649 and most similar to, background structure (Figure 3C and Figure 4C). We replicated this  
650 finding in Experiment 2 (Figure 9A). When we limited our analyses to only trials in which  
651 target filters were misaligned with the background structure, we found mixed results across  
652 the two experiments: a negative relationship between detection accuracy and target-  
653 background similarity in Experiment 1 (Figure 7), but a positive relationship in Experiment 2  
654 (Figure 9C-D). The cause of this difference in results across experiments is not clear, but  
655 we note that we did not design either experiment to specifically measure the relationship  
656 between similarity and sensitivity in this way, and neither model was significant. Regardless,  
657 there was no clear evidence of an inverse relationship as we expected.

658 The limitation of a specific structural similarity metric as a predictor of sensitivity in our  
659 study is most apparent in our Experiment 2 results. By matching or inverting the phase of  
660 filters aligned with the background structure, we produced target-background images that  
661 were equivalent in similarity but were different in their detectability (Figure 8 and Figure 9A).  
662 When phase was inverted relative to the background, observers’ performance was at  
663 chance level. The phase-mismatched condition therefore removed the information  
664 observers depended on to perform the task (i.e. contrast). A variant of the metric of similarity  
665 used here and by Sebastian et al (2017) may better predict sensitivity if it encodes phase  
666 information. Computationally, similarity is analogous to a normalised correlation coefficient;  
667 retaining phase would yield similarity scores ranging from -1 (perfectly matched counter-  
668 phase) and 1 (perfectly matched in-phase). However, Sebastian et al. used targets and a  
669 template-matching ideal observer model that had a fixed phase, in which case sensitivity  
670 may indeed scale inversely with phase-invariant similarity. We also note that the similarity  
671 between target filters and backgrounds in our study was approximately double those  
672 reported by Sebastian et al, and so it is possible that a linear inverse influence of similarity  
673 on sensitivity holds for relatively low levels of similarity.

674 In Experiment 1, there was no clear relationship between the number of filters added  
675 to the target image and observers’ performance (Figure 3B and Figure 4B). We expected to

676 find such a relationship based on the simple principle that there is an additional opportunity  
677 to detect a target for each filter added (Macmillan & Creelman, 2004). On closer inspection  
678 of the proportion correct data presented in Figure 3B, only a single data point in each of RW  
679 and WH's data are inconsistent with the expected trend for all observers. The lack of a  
680 statistically robust finding, therefore, may be due to our limited number of observers. A clear  
681 main effect of the number of filters was possibly also obscured by an interaction with target  
682 amplitude as shown in Figure 5. It is interesting that our generative model also produced a  
683 somewhat noisy relationship between accuracy and the number of filters. It is possible that  
684 observers outperformed our model in the phase-mismatched condition of Experiment 2  
685 because they integrated information over multiple locations rather than using the maximum  
686 in each image. However, even when our model had access to the top 1000 maxima in the  
687 images, it still performed below chance.

688 Detection thresholds in our experiments are approximately an order of magnitude  
689 greater than those reported by Sebastian et al. This is not particularly surprising given that  
690 we did not attempt to replicate their design, and instead used stimuli and methods that  
691 differed from theirs. One aspect of our experiments that would have likely decreased  
692 sensitivity was the lack of spatial certainty in the position of targets. Target filters could  
693 appear anywhere within the natural image background, maximising spatial uncertainty. The  
694 ability to identify targets depends on spatial (un)certainty, particularly in peripheral vision  
695 (Bennett & Banks, 1991; Harrison & Bex, 2015, 2017; Levi et al., 1987). Sebastian et al  
696 reduced spatial uncertainty by presenting targets at the same location on each target-  
697 present trial. Lower thresholds should be expected with such reduced uncertainty relative to  
698 our experiment in which observers had to search the entire background region. When  
699 observers are required to search for a potential target in a new background, false alarms  
700 can occur anywhere in the image. Computationally, such search can be performed using  
701 the same basic processes as involved in detection of a target at a cued location. In addition  
702 to determining whether a filter response is greater than a threshold (e.g. Sebastian et al.,  
703 2017), however, search involves determining which of several locations is most likely a  
704 target. We modelled this by taking the spatial interval with maximum luminance and contrast  
705 energy.

706 Despite the differences between our study and previous studies, we can confidently  
707 conclude that phase plays an important role in target detection for at least the sorts of targets  
708 used in our study (i.e. directional first-derivative of Gaussians). This result was  
709 foreshadowed by Bex and Makous (2002), who suggested detection thresholds for natural  
710 images depend on local phase-alignment within or across frequency bands. Our modelling  
711 suggests that observers detected the target interval by using local luminance extremes and  
712 contrast maxima. These local visual cues were most apparent in conditions in which the  
713 target phase was additive with the background. Phase, therefore, played an important role  
714 in our experiments. However, the failure of this model to capture observers' accuracy in the  
715 phase-mismatched condition of Experiment 2 reveals that a rule using local extremes is  
716 overly simple. We do not think it is likely that observers were switching strategies across  
717 conditions, because observers could not have known on a given trial which condition was  
718 displayed. In phase-mismatched trials in which the extremes of the target image were  
719 reduced to below the level of the extremes of the distractor image, observers must have  
720 been using other image cues that have escaped our description. Anecdotally, all observers,  
721 who are experienced psychophysical observers, reported using a template-matching  
722 strategy. This insight is obviously limited in its usefulness, because a template-matching  
723 strategy is equivalent to the computations performed in our model.

724 Our results are consistent with those of Neri (2011), who investigated the influence of  
725 target phase relative to the structure of a natural image background and how these effects  
726 differ when the stimulus is inverted. Neri found that, when the background is upright,  
727 observers tune to feature detectors that are in-phase with a natural edge. When the  
728 background is inverted, observers' tuning is less phase-aligned with the natural edge. These  
729 results suggest that upright scenes produce a bias in visual processing that steers  
730 observers' filtering toward the local phase of natural structures. These results are consistent  
731 with our own finding that observers are most sensitive to filters that are spatially aligned,  
732 and in-phase, with the background.

733 The extent to which the design of visual targets determines detectability in natural  
734 backgrounds is thus clearly an important consideration. As shown in a demonstration by  
735 Sebastian et al., it is incontrovertible that there are some targets for which phase is  
736 unimportant for visibility. We reproduce such a demonstration in the top row of Figure 12.  
737 We question, however, the relevance of a similarity metric in explaining the visibility of the  
738 target in this demonstration, considering that similar demonstrations can be produced in  
739 which target-background similarity is greater, and yet the target is easily visible (bottom row,  
740 Figure 12). The importance of target-background phase (in)variance likely depends on  
741 multiple factors, such as target design, as well as differences in the background in the region  
742 of the target (i.e. 'partial masking', see Sebastian et al., 2020). In addition to testing target  
743 visibility in different backgrounds based on contrast, luminance, and similarity (Sebastian et  
744 al., 2017, 2020), binning backgrounds according to their phase-similarity with targets may  
745 clarify these interactions in future experiments.

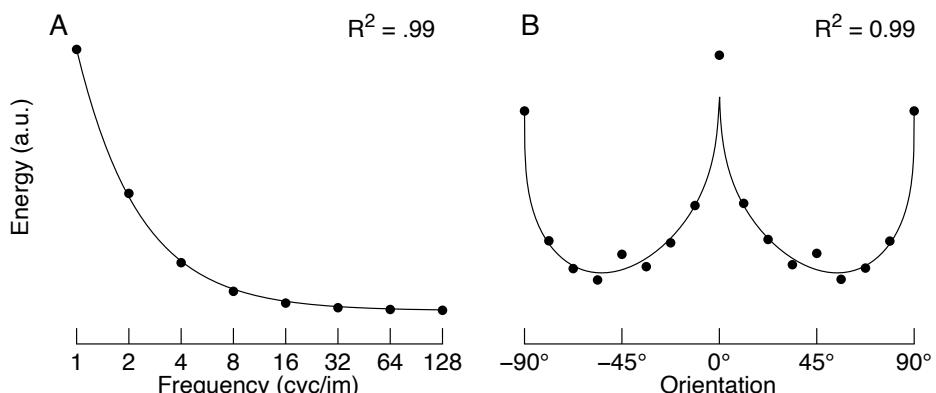


746  
747 **Figure 12. Similarity alone is a poor predictor of visibility.** Top and bottom panels show a 16 cyc/image  
748 target and Gaussian-derivative target, respectively, in each of three backgrounds (left to right): zero  
749 noise, vertical noise, and horizontal noise. Noise is 1D Gaussian (standard deviation = 0.15), and  
750 targets have the same amplitude in all panels (0.1). Similarity masking is demonstrated in the top right  
751 panel, in which the high-frequency target is rendered invisible. Such a masking effect is phase-  
752 invariant. As shown in the bottom right panel, however, a broader-band target with the same amplitude  
753 remains unmasked by the same noise. Importantly, the structural similarity between the target and  
754 background is greatest in the bottom right panel (0.15 bottom vs 0.12 in the top right).

755 We used images from the THINGS database as naturalistic backgrounds. The  
756 THINGS database is a recently released database with over 26,000 images from 1854  
757 categories (Hebart et al., 2019). Relatively little has been reported about the basic statistical  
758 properties of the images in this database, and so it is possible that they may deviate from  
759 what one may expect from typical natural images<sup>1</sup>. In Figure 13 we show the mean image  
760 spectra as a function of spatial frequency and orientation. This analysis shows that THINGS  
761 images have, on average, the same basic image spectra as typically found in natural  
762 images: contrast energy decreases with increasing spatial frequency (Figure 13A), and  
763 there is an over representation of cardinal orientations (Figure 13B). It is therefore unlikely

<sup>1</sup> Since originally submitting this manuscript, a more thorough description of the luminance and luminance contrast properties of THINGS images was presented by Harrison (2021).

764 that something in particular about the distribution of contrast energy in the THINGS images  
765 played a key role in our results. However, it is likely that the visual system performs different  
766 operations when processing visual objects like those in the THINGS images compared with  
767 visual textures (Wallis et al., 2019). Sebastian et al (2017) used images of scenes that had  
768 no particular focus on objects per se. To the best of our knowledge, no study has  
769 systematically investigated whether target detection differs on backgrounds of things versus  
770 backgrounds of stuff.



771  
772 **Figure 13. Mean spectra of all images in the THINGS database. A) Mean contrast energy as a function**  
773 **of spatial frequency. The solid line is the fit of the function  $1/f^a$ , which explains 99% of the variance.**  
774 **The free parameter,  $a$ , was 1.2. B) Mean contrast energy as a function of orientation. We computed**  
775 **contrast energy in the frequency domain using a series of raised cosine filters centred on a given**  
776 **orientation and spanning all spatial frequencies ("bow-tie filters"; full width half height = 12.5°). These**  
777 **data were then fit with a function that captures the over-representation of cardinals, as well as the**  
778 **greater contrast energy for horizontal contrast compared with vertical contrast <sup>2</sup>. This function**  
779 **explains 99% of the variance.**

780 Several studies suggest that there are high-level influences over the tuning of low-level  
781 feature detectors like those used to detect targets in the present study. For example, Teufel  
782 et al (2018) found that prior knowledge about image content influences the detectability of  
783 oriented targets aligned to locally occluded edges. Neri (2017) similarly found that sensitivity  
784 is greatest on edges implied by image content, regardless of whether local contrast  
785 detectors would respond at the region of the target. Harrison & Rideaux (2019) further  
786 showed that edge detection in visual noise can be greatly influenced by the allocation of  
787 visual attention. Taken together, these findings suggest that the detectability of targets in  
788 the present study may have depended on the specific objects in background images, and  
789 how combinations of low-level and high-level factors guided observers' visual attention.  
790 However, we did not design our experiments to examine such possible differences across  
791 object images. The availability of repositories such as the THINGS database makes such  
792 questions possible to address in future studies.

793 In summary, we tested observers' ability to detect targets in natural image  
794 backgrounds. Observers were most sensitive to targets when they were aligned and phase-  
795 matched with their backgrounds. Inverting the phase of aligned targets reduced observers'  
796 detection performance to chance. To best model the image factors that predict human  
797 sensitivity to contrast defined targets in natural backgrounds, therefore, the phase of the  
798 target relative to the background must be considered.

<sup>2</sup> This function has the form:  $E = (a - mag * |\sin(2\theta)|^b) * (p * (\cos(2\theta)) + p + 1)$ , where  $E$  is contrast energy,  $\theta$  is orientation in radians, and  $a$ ,  $mag$ ,  $b$ , and  $p$  are free parameters. See Harrison (2021) for a more detailed analysis of the THINGS images.

799

800

### Author contributions

801 WJH and PJB designed the stimulus generation method and conceived the general  
802 idea. WJH designed Experiment 1. WJH, RR, and JBM designed Experiment 2. WJH, RR,  
803 and RKW conducted the experiments. WJH conducted all analyses and generated all  
804 figures. TSAW advised on the multilevel modelling and was involved in many discussions  
805 leading to the conception of the study. RR, RKW and WJH wrote the first draft of the  
806 manuscript. All authors reviewed and edited the manuscript.

807

### Acknowledgements

808 This research was supported by an Australian Research Council Discovery Early  
809 Career Award to WJH (DE190100136) and RR (DE210100790). JBM was supported by  
810 the Australian Research Council (ARC) Centre of Excellence for Integrative Brain Function  
811 (ARC Centre Grant CE140100007). PJB was supported by a National Institute of Health  
812 R01 (EY029713).

813

814

815

## References

- 816 Balas, B., Nakano, L., & Rosenholtz, R. (2009). A summary-statistic representation in  
817 peripheral vision explains visual crowding. *Journal of Vision*, 9(12), 1–18.  
818 <https://doi.org/10.1167/9.12.13>
- 819 Barlow, H. B. (1961). Possible Principles Underlying the Transformations of Sensory  
820 Messages. In W. A. Rosenblith (Ed.), *Sensory Communication* (Vol. 1, pp. 216–234).  
821 The MIT Press. <https://doi.org/10.7551/mitpress/9780262518420.003.0013>
- 822 Barlow, H. B. (1972). Single Units and Sensation: A Neuron Doctrine for Perceptual  
823 Psychology? *Perception*, 1(4), 371–394. <https://doi.org/10.1068/p010371>
- 824 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models  
825 Using lme4. *Journal of Statistical Software*, 67(1), 1–48.  
826 <https://doi.org/10.18637/jss.v067.i01>
- 827 Bennett, P. J., & Banks, M. S. (1991). The effects of contrast, spatial scale, and orientation  
828 on foveal and peripheral phase discrimination. *Vision Research*, 31(10), 1759–1786.
- 829 Bex, P. J., & Makous, W. (2002). Spatial frequency, phase, and the contrast of natural  
830 images. *Journal of the Optical Society of America A*, 19(6), 1096–1106.  
831 <https://doi.org/10.1364/JOSAA.19.001096>
- 832 Bex, P. J., Solomon, S. G., & Dakin, S. C. (2009). Contrast sensitivity in natural scenes  
833 depends on edge as well as spatial frequency structure. *Journal of Vision*, 9(10), 1–  
834 19. <https://doi.org/10.1167/9.10.1>
- 835 Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436.
- 836 Cadena, S. A., Denfield, G. H., Walker, E. Y., Gatys, L. A., Tolias, A. S., Bethge, M., & Ecker,  
837 A. S. (2019). Deep convolutional models improve predictions of macaque V1  
838 responses to natural images. *PLOS Computational Biology*, 15(4), e1006897.  
839 <https://doi.org/10.1371/journal.pcbi.1006897>
- 840 Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of  
841 gratings. *The Journal of Physiology*, 197(3), 551–566.
- 842 Carandini, M., Demb, J. B., Mante, V., Tolhurst, D. J., Dan, Y., Olshausen, B. A., Gallant, J.  
843 L., & Rust, N. C. (2005). Do we know what the early visual system does? *Journal of  
844 Neuroscience*, 25(46), 10577–10597. <https://doi.org/10.1523/JNEUROSCI.3726-05.2005>
- 846 Dorr, M., & Bex, P. J. (2013). Peri-Saccadic Natural Vision. *Journal of Neuroscience*, 33(3),  
847 1211–1217. <https://doi.org/10.1523/JNEUROSCI.4344-12.2013>
- 848 Field, D. J. (1987). Relations between the statistics of natural images and the response  
849 properties of cortical cells. *JOSA A*, 4(12), 2379–2394.  
850 <https://doi.org/10.1364/JOSAA.4.002379>
- 851 Freeman, W. T., & Adelson, E. H. (1991). The design and use of steerable filters. *IEEE  
852 Transactions on Pattern Analysis & Machine  
853 Intelligence*, 13(9), 851–857. <http://www.computer.org/csdl/trans/tp/1991/09/i0891.pdf>
- 854 Geisler, W. S. (2008). Visual Perception and the Statistical Properties of Natural Scenes.  
855 *Annual Review of Psychology*, 59(1), 167–192.  
856 <https://doi.org/10.1146/annurev.psych.58.110405.085632>

- 857 Gelman, A., & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical*  
858 *Models*. Cambridge University Press.
- 859 Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2010). Crowding changes appearance. *Current*  
860 *Biology*, 20(6), 496–501. <https://doi.org/10.1016/j.cub.2010.01.023>
- 861 Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2012). Crowding follows the binding of relative  
862 position and orientation. *Journal of Vision*, 12(3). <https://doi.org/10.1167/12.3.18>
- 863 Harrison, W. J. (2021). Luminance and contrast of images in the THINGS database. *BioRxiv*,  
864 2021.07.08.451706. <https://doi.org/10.1101/2021.07.08.451706>
- 865 Harrison, W. J., & Bex, P. J. (2014). Integrating retinotopic features in spatiotopic  
866 coordinates. *Journal of Neuroscience*, 34(21), 7351–7360.  
867 <https://doi.org/10.1523/JNEUROSCI.5252-13.2014>
- 868 Harrison, W. J., & Bex, P. J. (2015). A unifying model of orientation crowding in peripheral  
869 vision. *Current Biology*, 25(24), 3213–3219.  
870 <https://doi.org/10.1016/j.cub.2015.10.052>
- 871 Harrison, W. J., & Bex, P. J. (2016). Reply to Pachai et al. *Current Biology*, 26(9), R353–  
872 R354. <https://doi.org/10.1016/j.cub.2016.03.024>
- 873 Harrison, W. J., & Bex, P. J. (2017). Visual crowding is a combination of an increase of  
874 positional uncertainty, source confusion, and featural averaging. *Scientific Reports*,  
875 7, 45551. <https://doi.org/10.1038/srep45551>
- 876 Harrison, W. J., & Rideaux, R. (2019). Voluntary control of illusory contour formation.  
877 *Attention, Perception, and Psychophysics*, 81(5), 1522–1531.  
878 <https://doi.org/10.3758/s13414-019-01678-8>
- 879 Haun, A. M., & Peli, E. (2013). Perceived contrast in complex images. *Journal of Vision*,  
880 13(13), 3. <https://doi.org/10.1167/13.13.3>
- 881 Hebart, M. N., Dickter, A. H., Kidder, A., Kwok, W. Y., Corriveau, A., Wicklin, C. V., & Baker,  
882 C. I. (2019). THINGS: A database of 1,854 object concepts and more than 26,000  
883 naturalistic object images. *PLOS ONE*, 14(10), e0223792.  
884 <https://doi.org/10.1371/journal.pone.0223792>
- 885 Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate  
886 cortex. *The Journal of Physiology*, 148, 574–591.
- 887 Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's  
888 new in psychtoolbox-3. *Perception*, 36(14), 1–16.
- 889 Landy, M. S. (2013). Texture analysis and perception. In *The New Visual Neurosciences*  
890 (pp. 639–652). MIT Press.
- 891 Levi, D. M., Klein, S. A., & Yap, Y. L. (1987). Positional uncertainty in peripheral and  
892 amblyopic vision. *Vision Research*, 27(4), 581–597.
- 893 Macmillan, N. A., & Creelman, C. D. (2004). *Detection theory: A user's guide*.  
894 [https://doi.org/10.1016/0376-6357\(93\)90083-4](https://doi.org/10.1016/0376-6357(93)90083-4)
- 895 Neri, P. (2011). Global Properties of Natural Scenes Shape Local Properties of Human Edge  
896 Detectors. *Frontiers in Psychology*, 2. <https://doi.org/10.3389/fpsyg.2011.00172>
- 897 Neri, P. (2014). Dynamic engagement of human motion detectors across space-time  
898 coordinates. *Journal of Neuroscience*, 34(25), 8449–8461.  
899 <https://doi.org/10.1523/JNEUROSCI.5434-13.2014>

- 900 Neri, P. (2017). Object segmentation controls image reconstruction from natural scenes.  
901 *Plos Biology*, 15(8), e1002611. <https://doi.org/10.1371/journal.pbio.1002611>
- 902 Olshausen, B. A., & Field, D. J. (2005). How close are we to understanding v1? *Neural*  
903 *Computation*, 17(8), 1665–1699. <https://doi.org/10.1162/0899766054026639>
- 904 Parraga, C. A., Troscianko, T., & Tolhurst, D. J. (2000). The human visual system is  
905 optimised for processing the spatial information in natural visual images. *Current*  
906 *Biology*. <http://www.sciencedirect.com/science/article/pii/S0960982299002626>
- 907 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming  
908 numbers into movies. *Spatial Vision*, 10(4), 437–442.
- 909 Rosenholtz, R., Huang, J., & Ehinger, K. A. (2012). Rethinking the role of top-down attention  
910 in vision: Effects attributable to a lossy representation in peripheral vision. *Frontiers*  
911 *in Psychology*, 3, 13. <https://doi.org/10.3389/fpsyg.2012.00013>
- 912 Sebastian, S., Abrams, J., & Geisler, W. S. (2017). Constrained sampling experiments  
913 reveal principles of detection in natural scenes. *Proceedings of the National Academy*  
914 *of Sciences of the United States of America*, 114(28), E5731–E5740.  
915 <https://doi.org/10.1073/pnas.1619487114>
- 916 Sebastian, S., Seemiller, E. S., & Geisler, W. S. (2020). Local reliability weighting explains  
917 identification of partially masked objects in natural images. *Proceedings of the*  
918 *National Academy of Sciences*, 117(47), 29363–29370.  
919 <https://doi.org/10.1073/pnas.1912331117>
- 920 Simoncelli, E. P., & Olshausen, B. A. (2001). Natural image statistics and neural  
921 representation. *Annual Review of Neuroscience*, 24, 1193–1216.  
922 <https://doi.org/10.1146/annurev.neuro.24.1.1193>
- 923 Smith, P. L., & Little, D. R. (2018). Small is beautiful: In defense of the small-N design.  
924 *Psychonomic Bulletin & Review*, 1–19. <https://doi.org/10.3758/s13423-018-1451-8>
- 925 Teufel, C., Dakin, S. C., & Fletcher, P. C. (2018). Prior object-knowledge sharpens  
926 properties of early visual feature-detectors. *Scientific Reports*, 8(1), 10853.  
927 <https://doi.org/10.1038/s41598-018-28845-5>
- 928 Wallis, T. S. A., & Bex, P. J. (2012). Image correlates of crowding in natural scenes. *Journal*  
929 *of Vision*, 12(7), 1–19. <https://doi.org/10.1167/12.7.6>
- 930 Wallis, T. S. A., Dorr, M., & Bex, P. J. (2015). Sensitivity to gaze-contingent contrast  
931 increments in naturalistic movies: An exploratory report and model comparison.  
932 *Journal of Vision*, 15(8), 3. <https://doi.org/10.1167/15.8.3>
- 933 Wallis, T. S. A., Funke, C. M., Ecker, A. S., Gatys, L. A., Wichmann, F. A., & Bethge, M.  
934 (2019). Image content is more important than Bouma's Law for scene metamers.  
935 *ELife*, 8, e42512. <https://doi.org/10.7554/eLife.42512>
- 936