

1 **Contextual influences of visual perceptual inferences**

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6

Abstract

7 Humans have well-documented priors for many features present in nature that
8 guide visual perception. Despite being putatively grounded in the statistical
9 regularities of the environment, scene priors are frequently violated due to the inherent
10 variability of visual features from one scene to the next. However, these repeated
11 violations do not appreciably challenge visuo-cognitive function, necessitating the
12 broad use of priors in conjunction with context-specific information. We investigated
13 the trade-off between participants' internal expectations formed from both longer-term
14 priors and those formed from immediate contextual information using a perceptual
15 inference task and naturalistic stimuli. Notably, our task required participants to make
16 perceptual inferences about naturalistic images using their own internal criteria, rather
17 than making comparative judgements. Nonetheless, we show that observers' performance
18 is well approximated by a model that makes inferences using a prior for low-level image statistics, aggregated over many images. We further show that the
19 dependence on this prior is rapidly re-weighted against contextual information,
20 whether relevant or irrelevant. Our results therefore provide insight into how apparent
21 high-level interpretations of scene appearances follow from the most basic of
22 perceptual processes, which are grounded in the statistics of natural images.

24

25

Introduction

26 We move through different environments many times each day. Each
27 environment exposes our visual system to a unique combination of features that guide
28 cognition and behaviour (Frazor & Geisler, 2006; Torralba & Oliva, 2003). When
29 entering a new environment, we can readily categorise and identify how its features
30 relate to our current goals (Greene & Oliva, 2009; Walther et al., 2009). Our ability to
31 make such flexible assessments suggests that visual cognition leverages internally
32 stored sets of rules that help to make sense of new sensory information.

33

The sets of rules that guide visual cognition can be considered as expectations,
34 or priors, for visual features that are common across environments. Priors putatively
35 represent the average of features on any number of dimensions (Series & Seitz, 2013;
36 Summerfield & Egner, 2009). When incoming sensory information deviates from a set
37 of priors, our expectations are violated. However, the inherent variability in image
38 features across environments (Hansen et al., 2003, 2008) does not appreciably
39 challenge our visual or cognitive capacities. While priors may be a useful guiding tool

40 when interpreting our environment, therefore, they must be flexible, allowing
41 functional interpretation of a vast array of possible visual scenes. Indeed, expectations
42 shift depending on context-specific information (Brockmole & Le-Hoa Vo, 2010; Wolfe
43 et al., 2011), suggesting a trade-off between priors that generally apply in the longer
44 term versus those that depend on a specific context.

45 Visual information can be quantified at any arbitrary level, but in the present
46 study we broadly categorise features as being either low- or high-level. By low-level
47 information, we refer to basic visual features, such as orientation, contrast, or hue.
48 Under the same framework as Neri (2014), we consider high-level information to
49 include features which convey meaningful information (e.g., the arrangements of
50 chairs and a table that imply a dining room setting as opposed to an office).
51 Importantly, two images can be matched on a subset of low-level features, but have
52 these features arranged such that only one conveys meaning (Neri, 2014). Low-level
53 features, such as contrast energy across spatial frequency bands, are relatively stable
54 across contexts, whereas many attributes of high-level features are scene-specific
55 (Harrison, 2022; Torralba & Oliva, 2003), and their respective statistical regularities
56 across scenes influence decision making. For example, cardinally oriented features
57 are overrepresented in natural images (Coppola et al., 1998; Essock et al., 2003;
58 Girshick et al., 2011; Hansen et al., 2003; Hansen & Essock, 2004; Keil & Cristóbal,
59 2000), leading to well-known biases in perceptual judgments of orientation (Appelle,
60 1972; Berkley et al., 1975; Campbell et al., 1966; Dakin, 2001; Dakin et al., 2009;
61 Dakin & Watt, 1997; de Gardelle et al., 2010; Emsley, 1925; Girshick et al., 2011;
62 Pratte et al., 2016; Westheimer & Beard, 1998). Similarly, relationships between high-
63 level visual objects can be predicted from scene context, leading to errors in object
64 detection and recognition when objects are positioned at uncommon locations (Bar,
65 2004; Bar & Ullman, 1993; Biederman et al., 1982). Despite their differences in
66 content and contextual stability, we combine low- and high-level features with great
67 ease to allow a seamless percept of our environment. However, the relative
68 contribution of low- and high-level information to our interpretations of a scene remain
69 largely unknown.

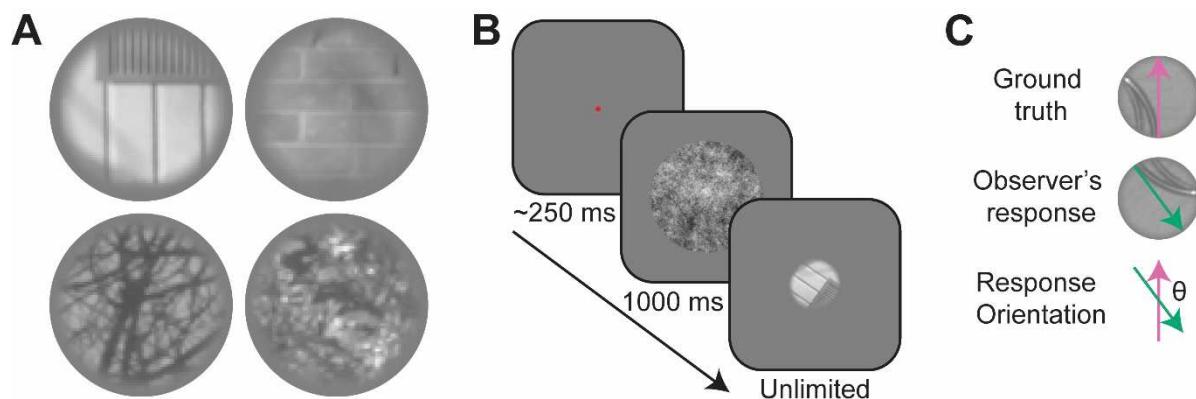
70 In the present study, we investigated the interplay between relatively long-term
71 priors and context-dependent information in forming visual expectations. To force
72 observers to use and combine previous experience with changing high-level
73 contextual information, we took advantage of the statistical distributions of features

74 present in naturalistic stimuli (David et al., 2004; Harrison, 2022; Olshausen & Field,
75 1996; Simoncelli & Olshausen, 2001). Targets were randomly oriented natural image
76 patches that participants rotated to appear subjectively “upright” based on their own
77 internal criteria (see Methods for specific task design information). By windowing the
78 targets within a small aperture, we removed large-scale contextual information. In the
79 absence of such high-level information, we anticipated that observers would base their
80 responses on how closely target features match their internal priors for low-level image
81 features alone. In some conditions, the surrounding region of the target was presented
82 briefly prior to target presentation, allowing observers to incorporate contextual
83 information to inform their judgments. Our task, therefore, required participants to align
84 targets with their internal expectations formed from both longer-term priors as well as
85 immediate contextual information, thereby enabling us to disentangle the relative
86 contribution of each.

87 **Results**

88 **Natural image statistics predict perceptual inferences in the absence of context**

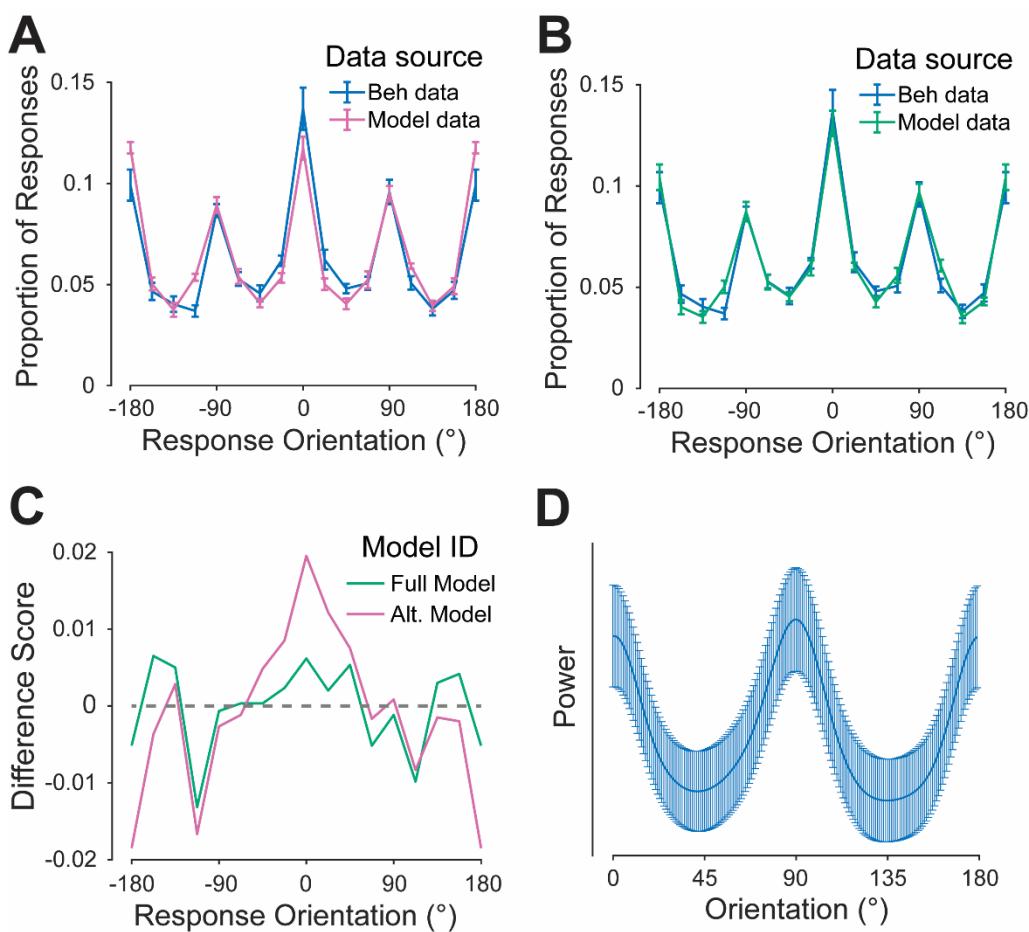
89 Participants rotated natural image target patches to make the targets appear
90 upright (see Fig. 1A-B). Targets contained very little high-level structure that could
91 unambiguously inform responses, as we confirmed in control experiments (described
92 below and in Supplemental Materials). By having participants rotate the targets, they
93 were able to control various low-level image features, such as the relative frequency
94 of orientations present. In Experiment 1, targets were presented without context. If
95 participants responded randomly, their responses would be uniformly distributed. If
96 instead participants used any sort of strategy that depended on the target image
97 features, their responses would be systematically biased by their strategy. For
98 example, if participants were biased by orientation information present in the targets,
99 then we might observe response orientations biased towards particular orientations,
100 such as cardinals.



101

102 Figure 1. Overview of paradigm. **A)** Example windowed image patches used as targets, shown to
103 participants at random orientations from trial to trial. **B)** Example schematic for a trial in Study 1 (stimuli
104 are not to scale). Participants saw a fixation point, followed by a brief pink noise patch. Subsequently,
105 the target was presented at a random orientation. Participants used the mouse to rotate the target to
106 appear upright and clicked to input their response. **C)** Observers' judgments were circularly distributed
107 deviations from the known objective vertical axis of the target. Note that the top left target patch in (A)
108 is rotated 90° from upright, demonstrating the inherent ambiguity in the stimuli.

109 The blue curve in Figure 2A shows the frequency distribution of participants'
110 responses relative to the objective upright orientation of each target. Participants'
111 responses have a clear cardinal bias: the most frequent response orientation is
112 centred on 0°, demonstrating participants' modal response was highly accurate, with
113 smaller peaks at the other cardinal orientations ($\pm 90^\circ$ and $\pm 180^\circ$). The multimodal
114 distribution of responses reveals that participants were not simply guessing. Instead,
115 observers must have combined target information with some internal representation
116 of the most appropriate orientation given the features in the image.



117

118 Figure 2. Perceptual inferences are predicted by natural image statistics. **A)** Proportion of response
 119 orientations (bin size = 22.5°) as measured from model and human observers in Experiment 1. The
 120 model judged the same targets as participants using an orientation heuristic. The model judged the
 121 same targets as participants using an orientation heuristic. **B)** The same behavioural data from Panel
 122 A, however model data in Panel B represent proportions of reported orientations yielded from a model
 123 that judged the same targets as participants using an orientation *and* lighting heuristic. **C)** Difference
 124 scores between model predictions and participant data, comparing the full model incorporating lighting
 125 and orientation heuristics (green) and the alternative model using an orientation heuristic only (pink). A
 126 difference score of 0 indicates the model predicted the same frequency of responses that participants
 127 displayed, positive values indicate the model predicted less responses than participants displayed, and
 128 negative values indicate the model predicted more responses than participants displayed. **D)** The mean
 129 distribution of contrast energy for each target when rotated to the orientation reported by the observer.
 130 Note this includes only the trials where participants responded with a $\geq 90^\circ$ response orientation. N =
 131 10; error bars = ± 1 SEM.

132 To understand how observers made their judgments in the absence of
 133 meaningful contextual information, we built a model observer that rotates each target
 134 so that the distribution of low-level features approximates the average distribution
 135 across many thousands of natural images. For each target we computed contrast

136 energy across orientations, and calculated the circular shift required to minimise the
137 difference between this distribution and the distribution of oriented contrast typically
138 found in natural images, as reported previously (e.g., Hansen et al., 2003; Hansen &
139 Essock, 2004; Harrison, 2022; see Methods). Note that this model is equivalent to
140 asking what pattern of data would result from solely matching low-level target features
141 to a prior acquired from averaging image statistics across many different scenes.

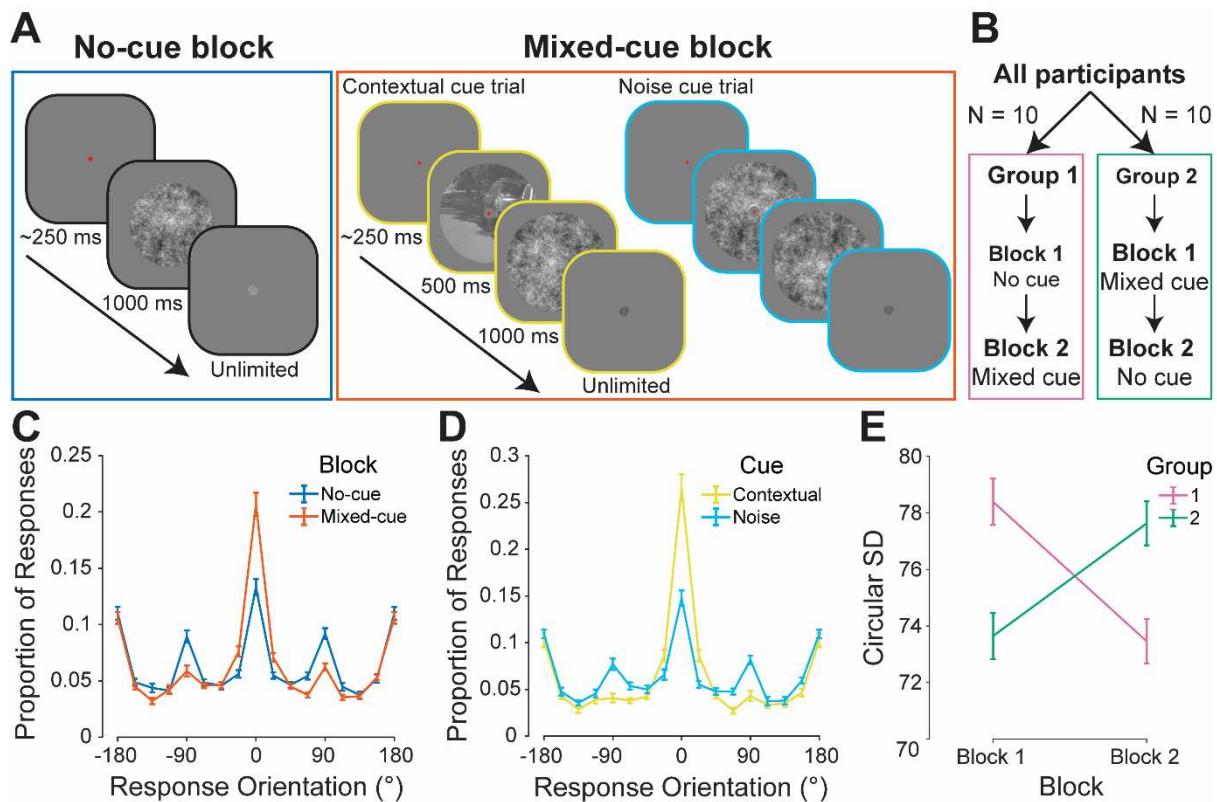
142 The output of this model is shown as the pink function in Figure 2A. Importantly,
143 we did not fit the model to the observers' data. Nonetheless, the model provides a very
144 good approximation of their responses, with clear cardinal biases. However, the model
145 underrepresents the frequency of responses around 0°, and overrepresents the
146 frequency of responses around ±180°. This model error arises because oriented
147 contrast energy is phase invariant, and so the orientation distribution is very similar for
148 an upright or inverted image. We therefore added a second stage of the model that,
149 after rotating the image to align its oriented contrast distribution to the prior, determines
150 whether the target needs to be rotated a further 180°. This stage involved using a
151 broadscale filter to estimate the lighting direction, which we fit to observers' data with
152 a single free parameter. The output of this full model is shown in Figure 2B, and now
153 correctly estimates the frequency of responses for all orientations. Indeed, the two-
154 stage model minimises the error in the overall model fit (Fig. 2C).

155 The results for Experiment 1 suggest that observers judge the appropriate
156 appearance of an image patch by matching a relatively simple set of low-level image
157 statistics to an average of these statistics over many images. If this is the case,
158 observers' responses should reflect the statistics of natural images even when their
159 responses are highly inaccurate. We tested this prediction using reverse correlation to
160 analyse the distribution of oriented structure for trials in which observers' absolute
161 response orientation was at least 90° from the ground truth orientation. For such trials,
162 we computed oriented contrast energy for each target after rotating the target to the
163 orientation reported by the observer. The mean distribution of contrast energy is
164 shown in Figure 2D. There are clear peaks and troughs at cardinal and oblique
165 orientations, respectively, aligning closely with contrast energy distributions in nature.
166 Taken together, our model and reverse correlation analyses suggest that observers'
167 perceptual inferences depend on their prior expectations for the statistics of natural
168 images.

169 **Contextual information enhances perceptual inferences**

170 In Experiment 2, we next investigated the extent to which participants integrate
171 context-specific information when inferring the upright orientation of novel target
172 patches. Participants completed two blocks of trials in which we manipulated
173 contextual information. In the “no-cue” block, the trial design was identical to that used
174 in Experiment 1 above. In the “mixed-cue” block, participants performed the same
175 task, but the target was preceded by either a contextual cue or a pink noise cue (see
176 Fig. 3A). Contextual cues were the surrounding image from which a given target was
177 drawn, with the target cropped out. By providing target-relevant contextual
178 information, we directly investigated how observers weigh immediate contextual
179 information relative to their longer-term priors. Furthermore, the use of a blocking
180 design (Fig. 3B) allowed investigation into the temporal nature of contextual impacts
181 on perceptual decisions. By interleaving contextual cues with noise cues in the mixed-
182 cue block, we could further assess the degree to which contextual information carries-
183 over from one trial to the next.

184 The distributions of response orientations for the no-cue and mixed-cue
185 conditions are shown in Figure 3C. The proportion of responses close to the objective
186 upright (i.e., 0°) is almost two-fold greater in the mixed-cue condition than the no-cue
187 condition, showing a clear facilitation of judgments when targets were preceded by a
188 cue. Indeed, observers’ circular standard deviation was significantly lower in the
189 mixed-cue condition ($M = 73.55$, $SD = 3.52$) than the no-cue condition ($M = 78.01$, SD
190 = 1.58; $BF_{10} = 42244.747$; see Fig. 3C). By including contextual cues and noise cues
191 in the mixed-cue condition, we further found that the changes in performance in the
192 mixed-cue condition were driven by judgements only when contextual information was
193 provided (Fig. 3D). These contextual effects cannot be accounted for by simple
194 practice effects because there was no effect of block order on task performance (BF_{10}
195 = 0.366; see Fig. 3B/E). Instead, the findings suggest participants’ judgements are
196 influenced by transient contextual information, enhancing such judgements above the
197 use of long-term priors alone. However, when contextual information is removed,
198 observers again rely on priors to make their judgments about novel stimuli.



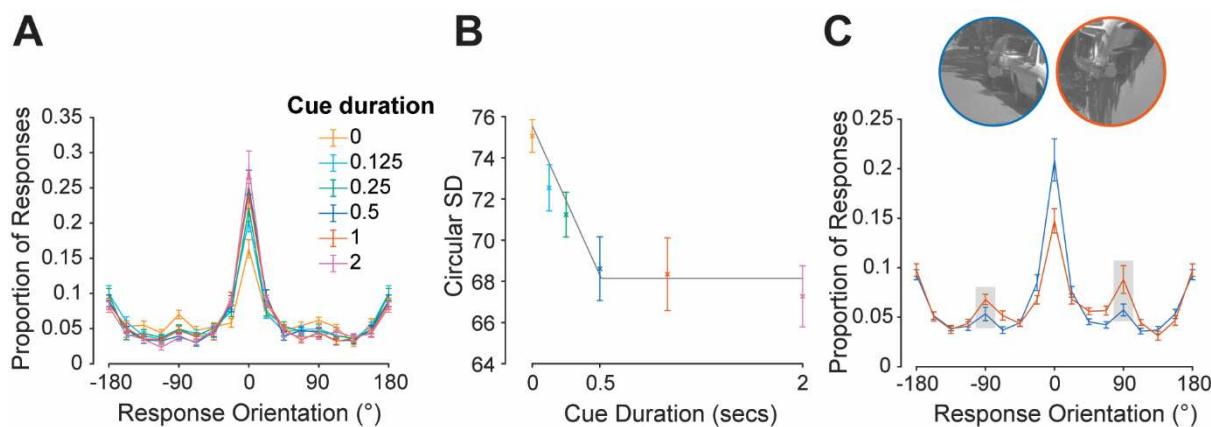
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200 Figure 3. Contextual information enhances perceptual inferences above long-term priors. **A**) Example
 201 trial schematics for both tasks (no-cue and mixed-cue) in Experiment 2. **B**) Depiction of the mixed
 202 design of Experiment 2. Participants were split into two groups of 10. Each group did both tasks, but in
 203 different orders to eliminate the impact of potential practice effects on result interpretations. **C**)
 204 Comparison of mean responses for the no-cue (blue) and mixed-cue (orange) conditions. **D**)
 205 Comparison of performance for the two cue types *within* the mixed-cue condition: contextual cues
 206 (yellow) and pink noise cues (blue). **E**) Comparison of response variability for the two groups depicted
 207 in panel B: Group 1 (no-cue condition first; pink) and Group 2 (mixed-cue condition first; green). The x-
 208 axis indicates the block (a temporal category, indicating the order in which the two conditions were
 209 undertaken). The y-axis indicates the circular standard deviation of response orientations. N = 20; error
 210 bars: ± 1 SEM.

211 **Contextual benefits arise rapidly, but are image-specific**

212 The results of Experiment 2 revealed that observers' perceptual inferences
 213 involve a trade-off between their prior expectations and transient contextual
 214 information. Recent evidence suggests that contextual information is incorporated
 215 rapidly in the initial feedforward processing of an image (Neri, 2017). To determine
 216 when contextual effects emerge in our paradigm, we conducted Experiment 3 in which
 217 the duration of the contextual cue was manipulated: cues were presented for either
 218 0.125, 0.25, 0.5, 1.0, 2.0 seconds, or not at all. This allowed us to investigate the time
 219 course over which contextual information is integrated.

220 The distributions of response orientations as a function of cue duration are
221 shown in Figure 4A. The proportion of inverted responses is similar across cue
222 durations, most likely because some targets are approximately symmetric across the
223 horizontal axis (e.g., the bricks in Figure 1A). Nonetheless, the positive relationship
224 between cue duration and proportion of responses centred on 0° demonstrates the
225 increasing influence context-specific evidence with exposure. We summarise the data
226 from each condition using circular standard deviation in Figure 4B, which shows an
227 inverse relationship between response variability and cue duration, and reveals that
228 contextual influences emerge rapidly, consistent with previous findings (Neri, 2017).
229 We fit a hinged line to these data, which further reveals that contextual benefits accrue
230 with increasing presentation times but then plateau after approximately 0.5 seconds,
231 suggesting a maximal benefit of contextual exposure (Fig. 4B, hinged line). Hence,
232 while contextual benefits appear to arise rapidly, their influences strengthen only up to
233 a particular exposure time, after which additional benefits become negligible.



234 Figure 4. The timing and orientation of the cues influence contextual benefits. **A)** Results of Experiment
235 3, comparing mean response proportions for the six cue presentation time conditions (different
236 conditions depicted by different colours). **B)** Comparison of response variability for the six cue durations
237 (x-axis) as measured by circular standard deviation. A hinged line has been fit to the data to illustrate
238 the point of maximal contextual benefit (grey). **C)** Results of Experiment 4, comparing performance in
239 the upright-cue condition (blue) and rotated-cue (orange) condition, specifically for trials where
240 contextual cues were given. Given that rotated cues were presented at +90° and -90°, responses for -
241 90° trials have been reverse-coded such that any expected biases away from a 0° response orientation
242 due to rotated cues can be expected in the same direction (i.e., towards 90°). For ease of interpretation,
243 data points of interest have been highlighted by grey boxes. We see a biasing of responses towards
244 the presented cue orientation, with a greater proportion of 90° response orientations in the rotated cue
245 condition compared to the upright cue condition, revealing a biasing effect of the cues' low-level
246 features. N = 20 per experiment; error bars: ± 1 SEM.

248 **Contextual benefits arise regardless of relevance**

249 Experiments 2 and 3 elucidated a strong influence of relevant contextual
250 information on participants' responses. However, it remains unclear whether
251 participants utilise and become biased by contextual information because it is directly
252 relevant to the task, or simply because observers automatically use any information
253 regardless of its relevance. We investigated this in Experiment 4, presenting
254 participants with upright contextual cues as well as cues rotated by $\pm 90^\circ$. Importantly,
255 participants were explicitly told whether cues were going to be upright or rotated in
256 separate blocks and were instructed to rotate the target to be upright (i.e., not
257 necessarily aligned with the contextual cue). In doing so, participants were actively
258 discouraged from using rotated cues, allowing us to investigate whether participants
259 still become biased by these less relevant cues.

260 We first standardised responses in the $\pm 90^\circ$ rotated-cue conditions by reverse-
261 coding responses for trials where cues were rotated by -90° . As shown by the
262 highlighted regions of the distributions in Figure 4C, responses were biased toward
263 90° in the rotated-cue condition compared to in the upright cue condition. We also
264 observed an increase in responses in the opposite direction, i.e., toward -90° . This is
265 consistent with participants being influenced by the rotated cue and inverting their
266 response on a subset of trials. The presence of such biasing by unhelpful rotated cues
267 suggests perceptual inferences cannot be made entirely independently of contextual
268 information, even if that information is explicitly known to be irrelevant.

269 **Discussion**

270 We investigated the contributions of long-term priors and immediate contextual
271 information to perceptual inferences. Observers performed a task in which they rotated
272 a target stimulus to its upright orientation, which required them to match the image
273 features to some internal representation. Across four main experiments, we found that
274 such perceptual inferences follow from priors for natural image statistics, and that the
275 availability of transient contextual information enhances such inferences above the
276 use of long-term priors alone.

277 **Perceptual inferences from natural image statistics**

278 We found converging evidence that participants use priors for low-level image
279 structure when interpreting isolated naturalistic image regions. In Experiment 1,
280 participants' inferences were explained by a model that matches targets to the
281 distribution of orientation contrast seen in the natural world on average. Our reverse

282 correlation analyses revealed that even large errors were aligned with the statistics of
283 natural images on average (Fig. 2D). Therefore, our results demonstrate that
284 judgments about the appearance of naturalistic images depend on priors accumulated
285 over many scenes over a relatively long period of time.

286 While the tendency for observers' responses to be biased toward cardinal
287 orientations is similar to the oblique effect (Appelle, 1972; Berkley et al., 1975;
288 Campbell et al., 1966; Dakin, 2001; Dakin et al., 2009; Dakin & Watt, 1997; de Gardelle
289 et al., 2010; Emsley, 1925; Girshick et al., 2011; Pratte et al., 2016; Westheimer &
290 Beard, 1998), our results cannot be explained by an oblique effect alone. Oriented
291 contrast energy can only elucidate the horizontal and vertical axes of an image, not
292 which half of the image should be at the top. Our full model therefore included a free
293 parameter that estimated observers' preferred lighting direction, analogous to the well-
294 known light-from-above prior (Brewster, 1826; Metzger, 1936; Murray, 2013;
295 Ramachandran, 1988), and aligned with behavioural responses. Hence, our results
296 show that a relatively simple set of priors derived from natural image statistics is
297 sufficient to drive heterogeneous patterns of perceptual inferences.

298 Despite the abstract appearance of many targets, observers' modal response
299 was accurate in all experiments. We designed targets so that there was no information
300 that could unambiguously inform participants' responses. We nonetheless ruled out
301 any meaningful contribution of high-level structure in two control experiments: these
302 experiments showed that the targets' size and image content precluded observers'
303 use of high-level or semantic image content to inform their judgments (see
304 Supplemental Materials). That observers' modal response was accurate therefore
305 reveals that low-level features provide sufficient information to interpret complex
306 stimuli, such as natural image regions.

307 **Contextual information is assimilated rapidly**

308 Our study demonstrates that perceptual inferences are guided by contextual
309 information on the sorts of timescales that are behaviourally relevant. Such shifts in
310 biases of perceptual judgements have been demonstrated for low-level features such
311 as orientation (Lorenc et al., 2018; Rademaker et al., 2015; Taylor & Bays, 2018) and
312 lighting (Adams et al., 2004; Morgenstern et al., 2011; Series & Seitz, 2013).
313 Contextual influences have also been observed with high-level structures, with
314 superior object detection and recognition when objects are embedded within
315 contextually relevant scenes relative to contextually incongruent scenes or in isolation

316 (Bar, 2004; Bar & Ullman, 1993; Biederman et al., 1982; Oliva & Torralba, 2007;
317 Palmer, 1975). Importantly, we observe response bias shifts in response to contextual
318 cues displayed for short durations. Such a time course is consistent with studies
319 demonstrating our ability to rapidly process high-level information (e.g., scene
320 categorisations and descriptions; Fei-Fei et al., 2007; VanRullen & Thorpe, 2001;
321 Walther et al., 2009) and low-level information (e.g., feature averaging; Chong &
322 Treisman, 2003; Parkes et al., 2001; Wolfe et al., 2011). Beyond supporting previous
323 findings, our results suggest that the brain not only prioritises the rapid encoding and
324 interpretation of complex stimuli, but that it is also able to utilise this information
325 extremely effectively to inform judgements about subsequent stimuli.

326 **Contextual information is assimilated even when task-irrelevant**

327 In Experiment 4, we found evidence suggesting that contextual information had
328 an effect on perceptual inferences, even when participants were aware it was task-
329 irrelevant. Previous literature has demonstrated detrimental impacts of incongruent
330 context on visual detection/recognition tasks (Bar, 2004; Bar & Ullman, 1993;
331 Biederman et al., 1982; Oliva & Torralba, 2007; Palmer, 1975). Such visual search
332 tasks typically investigate the impact of irrelevant contextual information on an
333 embedded target that cannot be separated from its contextual surroundings. Our
334 study, however, allows us to investigate contextual influences under circumstances
335 where participants are both aware of the unhelpfulness of the contextual information,
336 and do not need to use it or explicitly engage with it to complete the task. The fact
337 that we observe biasing towards irrelevant contextual information suggests that we
338 interpret and incorporate contextual information regardless of relevance. Such a
339 strategy should be beneficial under most circumstances, reflecting our experience in
340 the real world where information is most commonly observed within its relevant
341 context.

342 **Low-level image statistics and cognitive judgments**

343 In the context of visual perception research, there has been substantial debate
344 around the interactions between perceptual/bottom-up and cognitive/top-down
345 processing (Firestone & Scholl, 2016; Pylyshyn, 1999). Relatively little is known about
346 how such processes interact with one another in the context of interpreting natural
347 scenes, with many investigations focusing on the contribution of high-level structures
348 alone, and very few assessing the contributions of low-level perceptual processing.
349 Such a focus on the contributions of high-level structure to cognitive tasks risks

350 underestimating the potential contribution of low-level structure. Indeed, there is a
351 precedent for such a notion, with evidence to suggest that systematic biases in visual
352 working memory for simple stimuli can be accounted for by changes in basic image
353 statistics (Taylor & Bays, 2018). Our results are in line with this finding: although our
354 novel task involved what may be considered a relatively high-level task – to orient a
355 random natural image patch to the subjective upright – observers' performance can
356 be captured by basic low-level image properties. Further, we have found clear
357 contextual influences on such processes, with participants rapidly becoming biased by
358 such information (whether relevant or irrelevant). Our results therefore provide insight
359 into how interpretations of scene appearances follow from the most basic perceptual
360 processes, which effectively assess a scene based on existing priors for such low-
361 level information in tandem with available contextual information.

362

363

Methods

364 General task design

365 On each trial, participants were presented with one target patch, which was
366 randomly oriented in the centre of the display (see Fig. 1A-B). Participants' task was
367 to infer the "upright" orientation of the target by rotating it using a mouse. Specifically,
368 participants were instructed that they would see a series of "targets", each cut out from
369 a larger image, the "source image", and presented at a random orientation.
370 Participants were instructed to rotate these targets to their upright orientation.
371 Performance was measured using the orientations reported by the participant for each
372 trial relative to the objective upright orientation of the patch (see Fig. 1C).

373 Participants

374 Numbers of participants differed across experiments, ranging from N=10-20.
375 Participants had varying degrees of experience participating in psychophysical
376 experiments, but all participants were naïve to the purpose of the experiments except
377 for one participant in Experiment 1 (an author). Ethics approval was granted by the
378 University of Queensland Medicine, Low & Negligible Risk Ethics Sub-Committee.

379 Stimuli

380 Targets and contextual cues were generated in the same manner across all
381 experiments unless otherwise specified. Digital natural images were taken from a
382 database of high-resolution colour photos, cropped to 1080x1080 pixel regions (Burge
383 & Geisler, 2011). For Experiments 1-4, target patches were circular patches cropped
384 from the centre of the 1080x1080 images, subtending 2° of visual angle in diameter.
385 In experiments where contextual cues were given, the 1080x1080 images that the
386 target patches were cropped from were used. These were cropped to an annulus with
387 a 27° outer diameter and a 2° inner diameter (i.e., cropping out the target patch). All
388 stimuli were converted to greyscale using Matlab's `rgb2gray()` function.

389 Apparatus

390 Stimuli were displayed on a Dell Precision T1700 computer (running Windows
391 7 Enterprise) with the Psychophysics Toolbox (3.0.12; Brainard, 1997; Pelli, 1997) for
392 MATLAB (R2015a). Stimuli were presented on a 24-inch Asus VG428QR 3D monitor
393 with 1920 x 1080-pixel resolution and a refresh rate of 100 Hz. A gamma correction
394 was applied to the display, assuming that gamma was 2.

395 **Experiment 1 Design**

396 Participants (N=10; no exclusions) completed 600 trials. For each participant,
397 150 unique target patches were pseudorandomly selected from a bank of 9,361
398 potential targets. Participants performed the task of re-orienting a randomly oriented
399 target patch to be “upright” on each trial with no additional contextual information given
400 about the patches (see Fig. 1A-B). Prior to completing the experiment, participants
401 did 20 practice trials. Trial order was randomised and sessions were split into six
402 blocks of 100 trials with self-timed breaks in between.

403 In Experiment 1, four copies of each target patch were made, with each copy
404 having a different level of white noise (0%, 2.5%, 5%, and 10%) applied through
405 manipulating the RMS contrast of the image. This was an initial line of interest in the
406 current study, however there was no significant effect of target noise on participants’
407 performance as measured by circular standard deviation ($BF_{10} = 0.933$). We therefore
408 combined these conditions in the data shown in Figure 2 and the manipulation was
409 not explored in further experiments.

410 **Experiment 2 design**

411 Twenty-one participants completed 600 trials split into two blocks (see Fig. 3A).
412 One dataset was not analysed because the participant did not finish the experiment.
413 In one block, each participant performed the basic task of re-orienting 300 target
414 patches to be “upright” (the “no-cue” block). In the other block, participants completed
415 the same task, but a contextual cue (i.e., the surrounding source image the target was
416 drawn from with the target cropped out) or a random pink noise patch was displayed
417 for a duration of 500 ms prior to the target (the “mixed-cue” block). For the mixed-cue
418 block, 150 target patches were pseudorandomly selected for each participant: each
419 unique target patch was presented twice – once preceded by a pink noise patch (noise
420 cue) and once preceded by the surrounding image from which the target was drawn
421 (contextual cue). Participants completed 20 practice trials prior to completing each
422 block, with practice trials implementing the same cue types as the blocks. Block order
423 was counterbalanced across participants (see Fig. 3B). Trial order for each block was
424 randomised and each block was split into three sets of 100 trials with self-timed breaks
425 in between. On average, participants took 29 minutes to complete each block
426 (excluding three participants, due to a duration recording error).

427 **Experiment 3 design**

428 Participants (N=21; one excluded due to not finishing the experiment)
429 completed 450 trials. For each participant, 75 unique target patches were
430 pseudorandomly selected. Unique target patches were presented six times, preceded
431 by the surrounding image from which the target was drawn – once for each
432 presentation length: 0, 0.125, 0.25, 0.5, 1.0, and 2.0 seconds. Prior to completing the
433 experiment, participants did 20 practice trials. Trial order was randomised and
434 sessions were split into six blocks of 75 trials with self-timed breaks in between. On
435 average, participants took 48 minutes to complete the task.

436 **Experiment 4 design**

437 Participants (N=20; no exclusions) completed 600 trials split into two blocks. In
438 one block, participants completed the base task, however before seeing the target
439 patch participants were either shown a typical contextual cue or a random pink noise
440 patch, with 150 pseudorandomly selected target patches for each participant (the
441 “upright-cue” block; see Fig. 4C). The other block had an identical design, however
442 contextual cues (when presented) were rotated by $\pm 90^\circ$ (the “rotated-cue” block; see
443 Fig. 4C). Block order was counterbalanced across participants. Participants
444 completed 20 practice trials prior to completing each block, with practice trials
445 implementing the same cue types as the blocks. Each block was split into three sets
446 of 100 trials with self-timed breaks in between. On average, participants took 31
447 minutes to complete each block.

448 **Control experiments**

449 Targets were generated in a uniform manner across images in our database
450 and were not screened for their content before being shown to participants. Therefore,
451 in cases where participants were not given contextual information, the possibility
452 remained that the targets themselves included sufficient high-level structure to
453 unambiguously cue their objective upright orientation. The presence of such high-level
454 information could potentially explain participants’ performance. For example, if
455 participants happened to be shown a picture of a car, they would be expected to know
456 from their semantic knowledge which way is upright. As such, two control experiments
457 were conducted to investigate the potential contribution of high-level structure in the
458 isolated target patches to participants’ performance. These experiments are
459 summarised below and described in detail in the Supplemental Materials.

460 The first control experiment had participants categorise individual patches
461 according to whether there was sufficient high-level information present to
462 unambiguously indicate the “correct” upright orientation of the image (informative) or
463 not (uninformative). This experiment found there was neither sufficient numbers of
464 informative images shown to participants, nor consistently accurate responses made
465 in response to informative images to account for levels of performance observed.
466 Thus, informative image regions are unable to account for participants’ inference
467 judgements of the upright appearance of naturalistic images.

468 The second control experiment involved the same trial structure and task as
469 Experiment 1, but the size of the target patch was manipulated to include varying
470 amounts of the source image. We found that as target size increased (and therefore
471 the amount of high-level structure), so did performance. This pattern suggests that
472 the decision to limit the target size was effective in eliciting task difficulty by limiting the
473 amount of high-level information present. Together, our two control experiments
474 revealed relevant high-level information content that disambiguated the perceptual
475 task was almost entirely absent for our target stimuli and therefore cannot account for
476 participants’ performance.

477 **Analyses**

478 Where inferential statistics were performed, Bayesian analyses were
479 implemented in JASP, using circular standard deviation (i.e., response orientation
480 variance, where greater variance indicates poorer performance) as the dependent
481 variable. For Experiment 3 response variability data (Fig. 4B), we fit a hinged line by
482 finding the parameters that minimised the square error between each participant’s
483 data and the model using MATLAB’s fminsearch() function.

484 **A “pretty good observer” model of upright inferences**

485 We developed an observer model that estimates the upright orientation of a
486 target patch by matching the target’s statistics with the anisotropic distribution of
487 orientation energy found in nature (e.g., Hansen et al., 2003; Hansen & Essock, 2004;
488 Harrison, 2022). We refer to this model here as a *pretty good* observer model, rather
489 than an *ideal* observer model, because we only exploit orientation energy and ignore
490 other statistical features that could further improve performance (e.g., conditional
491 orientation statistics; Geisler et al., 2001). For a given target patch, we computed
492 orientation energy in 180 equally spaced orientation bands, each of which covered all
493 spatial frequencies. These operations were performed in the frequency domain;

494 energy was the absolute of the Fourier-transformed target values. Oriented filters were
495 also constructed in the frequency domain: filters were raised cosines with a bandwidth
496 of 45°. Energy was summed within each orientation band, giving a distribution of
497 energy across orientations. We then compared the target's energy distribution to a
498 prior derived from studies of natural images (e.g., Wei & Stocker, 2015):

499 $p(\theta) \propto 2 - |\sin\theta|$ Equation 1

500 Where $p(\theta)$ is the probability of observing contrast energy with an orientation
501 of θ , in radians. Whereas Equation 1 assumes equal prevalence of horizontal and
502 vertical orientations, Hansen and colleagues noted there tends to be a horizontal bias
503 (see also Harrison, 2022). We therefore modified Equation 1 by increasing the
504 proportion of horizontal energy according to a von Mises function:

505 $p(\theta) \propto 2 - |\sin\theta| + C \exp(\kappa(\cos(\theta) - 1))$ Equation 2

506 Where C is the strength of the horizontal bias, and κ is the width of the von
507 Mises function, which we set to 2.5. Small changes in κ did not change the results.
508 Before summing the distributions, we first normalised the von Mises function to have
509 a peak of one.

510 The model selects the upright orientation of a target by computing the rotational
511 offset that minimises the sum of the squared difference between the target patch's
512 energy and $p(\theta)$, performed using MATLAB's `fminsearch()` function. Prior to this step,
513 we further normalised the target's energy distribution and $p(\theta)$ to both fall within the
514 range 0 – 1. To avoid local minima, we fit the model with varying starting parameters
515 and took the rotational offset at the global minimum from all fits. Note that this fitting is
516 entirely independent of an observer's response – we fit the target's image statistics to
517 the prior, but nonetheless approximate observers' responses very closely (Figure 1A).
518 However, as described in the Results, this model produces an equal proportion of 0°
519 and ±180° responses, which is different than observers' reports. We therefore added
520 a second stage of the model that, after finding the best rotational offset, estimates
521 lighting direction from a broadscale filter positioned at the centre of the target. The
522 orientation of this filter matched the fitted offset. Crudely, this filter can be considered
523 an estimate of the relative phase of a horizon running through the middle of the target.
524 Depending on the polarity of the filter's response, the image was either rotated a
525 further 180°, or left as is. This step considerably improved the match between the
526 model responses and observers' data, as shown in Figures 1A - 1C.

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530 **Competing interests**

531 The authors have no conflicts of interest to declare.

532

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701 Contextual influences of visual perceptual inferences

Supplemental Materials

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Control Experiments

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Targets were generated in a uniform manner across images in our database and were not screened for their content before being shown to participants. Therefore, in cases where participants were not given contextual information, the possibility remained that the targets themselves included sufficient high-level structure to unambiguously cue their objective upright orientation. The presence of such high-level information could potentially explain participants' performance. For example, if participants happened to be shown a picture of a car, they would be expected to know from their semantic knowledge which way is upright. As such, two control experiments were conducted to investigate the potential contribution of high-level structure in the isolated target patches to participants' performance.

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Participants

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Numbers of participants differed across experiments, ranging from $N=2-3$. Participants had varying degrees of experience participating in psychophysical experiments, and all participants were naïve to the purpose of the experiments except for one participant in both experiments (an author). Ethics approval was granted by the University of Queensland Medicine, Low & Negligible Risk Ethics Sub-Committee.

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Apparatus

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Stimuli were generated on a Dell Precision T1700 computer (running Windows 7 Enterprise) with the Psychophysics Toolbox (3.0.12; Brainard, 1997; Pelli, 1997) for MATLAB (R2015a). Stimuli were presented on a 24-inch Asus VG428QR 3D monitor with 1920 x 1080-pixel resolution and a refresh rate of 100 Hz. A gamma correction was applied to the display, assuming that gamma was 2.

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Control Experiment 1

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Stimuli. Stimuli were made up of targets used in Experiment 1 and 2, as well as an additional unreported experiment that implemented the same design as Experiment 2 but did not involve a no-cue block. In total, there were 7176 unique targets shown to participants across these three experiments. Briefly, these targets were digital natural images taken from a database of high-resolution photos (Burge & Geisler, 2011) cropped to subtend 2° of visual angle in diameter and converted to greyscale (see Methods for more detail).

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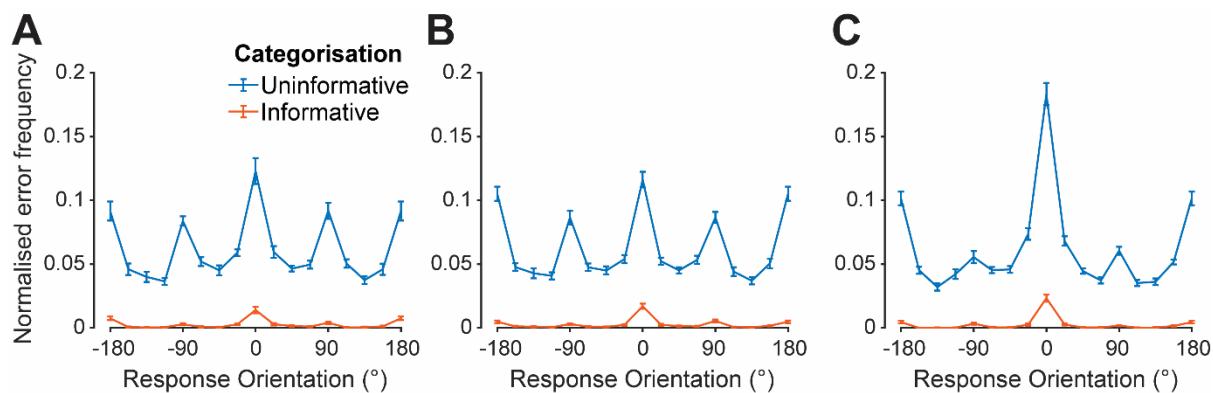
Design. Participants ($N = 2$; one author) completed 7176 trials. On each trial, participants were shown a target in its upright position. For each target, participants judged whether there was sufficient high-level information present to unambiguously

742 indicate the “correct” upright orientation of the image (“informative”) or not
743 (“uninformative). For example, patches that contained identifiable objects such as
744 cars or signs were classified as informative. Categorisations were made using the 0
745 (uninformative) and 1 (informative) keys on a keyboard. Targets were presented until
746 a response was made, and participants had the ability to backtrack using the
747 ‘Backspace’ key. Participants completed the experiment across self-selected block
748 lengths.

749 **Analyses.** Results presented here are based on Rater 2’s (non-author) data,
750 who categorised more images as “informative” (295 of 7176) than Rater 1 (66 of 7176;
751 an author). Results are based on Rater 2 as we want to be conservative in attributing
752 effects to low-level features relative to high-level features in our targets. Hence, by
753 basing analyses on Rater 2’s more liberal informative categorisations, we give
754 informative images the greatest chance of explaining the observed patterns of data
755 across experiments.

756 **Results.** In Experiment 1, there was a sub-sample of image patches
757 categorised as informative (58 of 1400 unique targets across 10 participants; 4%). On
758 average, 6.20 ($SEM = 0.63$) unique informative images were shown to each
759 participant, accounting to 4% of the total number of unique targets seen. Across
760 participants, we see a range of response orientations when informative images are
761 shown (Fig. S1A), with informative images responded to accurately on 29% of trials
762 when they are shown. Hence, even when presented with informative image regions,
763 participants do not necessarily perform optimally, diminishing the explanatory power
764 of informative images accounting for accurate responses. Indeed, on average,
765 accurate responses attributed to informative images account for just 1% of
766 participants’ responses (Fig. S1A).

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Figure S1. The contribution of informative images to participants' responses. **A**) Proportion of responses made in Experiment 1, split by responses made to targets categorised as informative (orange) and uninformative (blue). **B**) Proportion of responses made in the no-cue block of Experiment 2, split by responses made to targets categorised as informative (orange) and uninformative (blue). **C**) Proportion of responses made in the mixed-cue block of Experiment 2, split by responses made to targets categorised as informative (orange) and uninformative (blue). N = 10 (A) & 20 (B/C); error bars: ± 1 SEM.

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This was reflected in Experiment 2 stimuli. In the no-cue block, 190 (4%) of the 4510 unique targets used were rated as informative. On average, 13.5 ($SEM = 0.92$) unique informative images were shown to each participant, accounting for 5% of the total number of unique targets seen. Again, a range of response orientations for informative images was observed (Fig. S1B), with informative images responded to accurately on 34% of trials when they are shown. Similarly, on average, accurate responses attributed to informative images account for just 1% of participants' responses (Fig. S1B).

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Similarly, in the mixed-cue block, 107 (4%) of the 2609 unique targets were rated as informative. On average, 6.3 ($SEM = 0.54$) unique informative images were shown to each participant, accounting for 4% of the total number of unique targets seen. Again, a range of response orientations for informative images was observed (Fig. S1C), with informative images responded to accurately on 50% of trials when they are shown. On average, accurate responses attributed to informative images account for just 2% of participants' responses (Fig. S1C).

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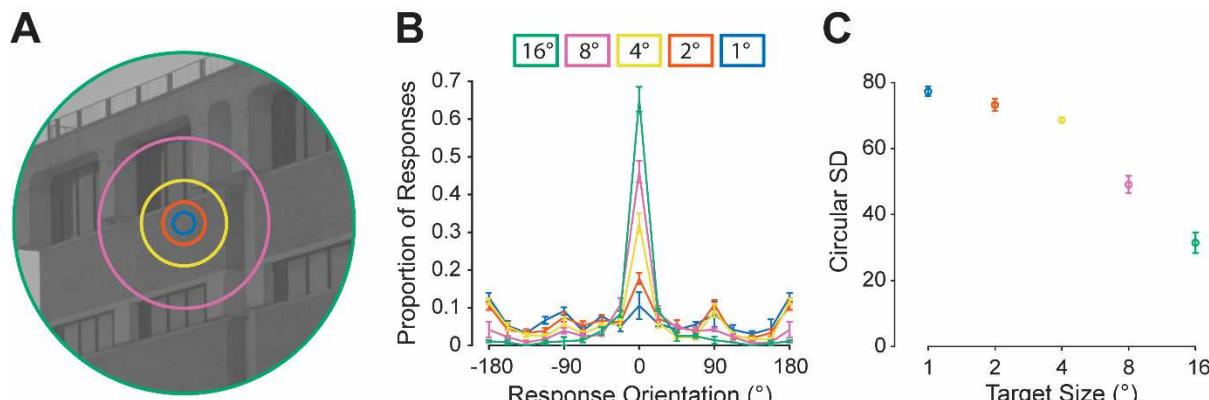
Taken together, these results demonstrate there was neither sufficient numbers of informative images shown to participants, nor consistently accurate responses made in response to informative images to account for levels of performance observed. Thus, informative image regions are unable to account for participants' inference judgements of the upright appearance of naturalistic images.

797 **Control Experiment 2**

798 **Stimuli.** Targets were digital natural images were taken from a database of
799 high-resolution photos (Burge & Geisler, 2011). For each participant, 120 unique
800 images were selected from the database. Each unique image had five copies
801 generated, each cropped to circular patches of different sizes (1, 2, 4, 8, and 16°),
802 such that different target sizes included varying amounts of the source image (Fig.
803 S2A). All stimuli were converted to greyscale.

804 **Design.** Participants ($N = 3$; one author) completed five blocks of 120 trials,
805 where each block corresponded to one target size (i.e., 1, 2, 4, 8, or 16°). Block order
806 was randomised for each participant. The task was identical to Experiment 1, requiring
807 participants to rotate a randomly oriented target patch to be perceptually upright.

808 **Results.** As anticipated, when the area of the original image presented
809 increased beyond that used in Experiments 1-4 (2° of visual angle), performance
810 steadily increased, supported by large increases in the number of responses centred
811 on a response orientation of 0° (Fig. S2B) and large decreases in response variability
812 as measured by circular standard deviation (Fig. S2C). Improved performance with
813 larger patch sizes suggests that providing larger patches, and therefore more high-
814 level structure, makes the patches more informative and decreases the difficulty of the
815 task.



816
817 Figure S2. The impact of image size on perceptual inferences for naturalistic images. **A)** Depiction of
818 target sizes used (1, 2, 4, 8, and 16°; smaller than actual size, but to scale relative to one another). **B)**
819 Comparison of mean response proportions for the five target size conditions (different conditions
820 depicted by different colours). **C)** Comparison of response variability for the five target sizes (x-axis) as
821 measured by circular standard deviation. $N = 3$; error bars: ± 1 SEM.

822 **Overview**

823 Overall, results from our informativeness and patch size control experiments
824 suggest that limiting the targets to a windowed patch, particularly at our chosen patch
825 size, was effective at removing much of the high-level structure present. Taken
826 together with the four main experiments, the results presented suggest that priors for
827 statistical regularities of low-level features in nature are sufficient to make informed
828 interpretations of isolated naturalistic stimuli.