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Article

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Fearful Faces Have a Sensory Advantage in the Competition for Awareness

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Abstract

Only a subset of visual signals give rise to a conscious percept. Threat signals, such as fearful faces, are particularly salient to human vision. Research suggests that fearful faces are evaluated **without awareness** and preferentially promoted to conscious perception. This agrees with evolutionary theories that posit a dedicated pathway specialised in processing threat-relevant signals. We propose an alternative explanation for this “fear advantage”. Using psychophysical data from continuous flash suppression (CFS) and masking experiments, we demonstrate that awareness of facial expressions is predicted by effective contrast: the relationship between their Fourier spectrum and the contrast sensitivity function. Fearful faces have higher effective contrast than neutral expressions and this, not threat content, predicts their enhanced access to awareness. Importantly, our findings do not support the existence of a specialised mechanism that promotes threatening stimuli to awareness. Rather, our data suggest that evolutionary or learned adaptations have moulded the fearful expression to exploit our general-purpose sensory mechanisms.

Keywords: threat; awareness; vision; contrast

50 An important predictor of survival is the ability to detect threat. However, given the
51 capacity limits of our sensory systems, not all visual inputs give rise to a conscious percept -
52 many stimuli within our field of view go undetected in the competition for neural resources
53 (Dehaene & Changeux, 2011). How does a limited-capacity system selectively process those
54 inputs of most significance for survival? A widely held view is that humans have a
55 specialised, subcortical visual pathway that expedites the processing of threatening stimuli
56 (Ohman, 2005). An important component of this proposal is that this pathway is thought to
57 operate independently of conscious awareness (Tamietto & de Gelder, 2010). In the context
58 of survival, it would be advantageous if threats in the environment could influence behaviour
59 before, or without, an observer's awareness of them.

60 Evidence that threat can be processed **preconsciously, or without awareness**, comes
61 from paradigms in which visual input is dissociated from awareness (Kim & Blake, 2005). In
62 backward masking, **awareness of a briefly presented image is restricted** by the subsequent
63 presentation of a co-located mask. Neuroimaging evidence indicates that masked fearful
64 faces can increase amygdala activity, which is indicative of emotional arousal (Whalen et al.,
65 1998; Whalen et al., 2004). Behaviourally, an observer's response to a peripheral "probe"
66 stimulus is faster when preceded by a masked fearful face than a masked neutral face
67 (**Carlson & Reinke, 2008**; Fox, 2002). Continuous flash suppression (CFS) is a technique in
68 which a stable image shown to one eye is suppressed from perception by a dynamic stream of
69 images presented to the other (Tsuchiya & Koch, 2005). Fearful faces break into awareness
70 from CFS more quickly than neutral faces (Sylvester, Brennan, & Lilienfeld, 2011; Yang, Zald,
71 & Blake, 2007). Together, these findings suggest that fear faces are evaluated without
72 awareness and gain prioritised access to conscious vision. **Interestingly, our own meta-**
73 **analyses show that fearful faces are the only threat stimuli to be reliably prioritised over**
74 **neutral stimuli across the masked visual probe, binocular rivalry and continuous flash**

75 suppression paradigms (Hedger, Adams, & Garner, 2014). Thus, subliminally presented
76 fearful expressions do appear to elicit prioritised processing, relative to other threat stimuli,
77 and this effect warrants careful investigation.

78 Ecological models distinguish between two components of visual signals: content and
79 efficacy (Guilford & Dawkins, 1991). The former relates to the “message” of the signal,
80 whereas the latter relates to the efficient transmission of the signal in relation to the sensory
81 biases of an observer. It is often assumed that fearful faces are prioritised in the competition
82 for awareness due to their *content*, since they signal important information about potential
83 threats (Sylvers et al., 2011; Yang et al., 2007). However, fearful faces may also be
84 prioritised due to their *efficacy*; fast detection could be mediated by purely low-level factors,
85 such as the high contrast physical signal emanating from the eye region – i.e. the increased
86 exposure of the iris and scleral field (Lee, Susskind, & Anderson, 2013). This latter position
87 is in-line with the ‘sensory bias hypothesis’ (Horstmann & Ansorge, 2009; Horstmann &
88 Bauland, 2006), which states that facial expression signals are salient to sensory biases of
89 human observers. Thus, without characterising the sensory properties of facial signals, we
90 risk attributing prioritised detection to threat-sensitive processes, when it may be better
91 explained by the low-level physical salience of the expression.

92 Here, we consider this dilemma. There are two possible mechanisms via which fear
93 faces, or other threat-relevant stimuli might gain prioritised access to conscious vision. First,
94 humans might have evolved specialised mechanisms that evaluate the threat content of visual
95 signals prior to their conscious registration. Second, the physical expression of fear might
96 exploit the sensory tuning of early, general-purpose visual processing. In this latter case, the
97 apparent “threat advantage” could be parsimoniously explained by sensory efficacy, without
98 the involvement of pre-conscious mechanisms sensitive to threat.

99 Typically, these two accounts are conflated, since the low-level characteristics of
100 facial expressions define the content of the communicated emotion (e.g. wide eyes signal
101 fear). To resolve this issue, therefore, one must experimentally dissociate a stimulus' sensory
102 and affective properties. In the present study, we addressed this issue with a combination of
103 image analyses and behavioural data. First, we use known properties of early visual processes
104 to estimate the efficacy with which emotional expressions are received by human observers.
105 Second, we use stimulus manipulations that modulate the threat content of our images,
106 without affecting sensory efficacy. Third, we present behavioural data from CFS and
107 masking paradigms that quantify the extent to which emotional expressions gain access to
108 awareness. Lastly, we determine whether this is **better** predicted by (i) the images' low-level,
109 effective contrast (a quantity indifferent to threat), or (ii) their threat-content.

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Image Analyses

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Stimulus detection is influenced by low-level properties such as luminance and contrast. Moreover, humans are more sensitive to contrast at certain spatial frequencies, as defined by their contrast sensitivity function (De Valois & De Valois, 1990). Thus, differences in detection between stimuli (e.g. fearful vs. neutral faces) that differ in these low-level properties cannot be considered a valid measure of threat-related processing. The contrast sensitivity function can be conceptualised as a modulation transfer function for spatial contrast energy at early visual stages. Measuring the extent to which stimuli exploit this sensitivity thus provides an estimate of their sensory efficacy. We asked whether fearful and neutral expressions differ in the extent to which they exploit the contrast sensitivity function (i.e. do they differ in “*effective contrast*”?).

Effective Contrast

123 We analysed the NimStim face set, a collection of face stimuli that is widely used in
124 studies of emotion recognition and is subsequently employed in our behavioural experiments.
125 The set includes 24 male and 19 female models from multiple ethnicities (Tottenham et al.,
126 2009). First, we applied an opaque elliptical mask to eliminate external features before
127 equating mean luminance and root mean squared contrast (RMS) of the images (following
128 standard practice in psychophysical experiments). For our initial analyses, we mirrored the
129 average size (13.5 cm bizygomatic diameter, see Katsikitis, 2003) and a typical distance
130 (220cm) of a human face during social interactions.

131 To calculate effective contrast we followed the procedure of Baker and Graf (2009),
132 implemented in MATLAB (Mathworks). This measure of effective contrast has previously
133 been found to be a good predictor of stimulus salience in binocular rivalry competition
134 (Baker & Graf, 2009). We obtained the amplitude spectrum (contrast energy as a function of
135 spatial frequency) of each face image (figure 1a, left panel). We then fitted a second order
136 polynomial to the contrast sensitivity data set “ModelFest” (Watson & Amuhada, 2005) to
137 obtain a continuous contrast sensitivity distribution (figure 1a, middle panel, normalised to
138 the 0-1 range). By multiplying this distribution by the amplitude spectrum, we obtained
139 effective contrast as a function of spatial frequency, for each stimulus (figure 1a, right panel).

140 Summing this contrast across spatial frequency produces an overall estimate of
141 contrast energy after attenuation by the contrast sensitivity function, i.e. the image’s effective
142 contrast. Fear faces had higher effective contrast than neutral faces for 41 of the 43 models,
143 and this difference was large in magnitude ($d = 0.76$, 95% CI [0.31 1.21], $p < .001$).

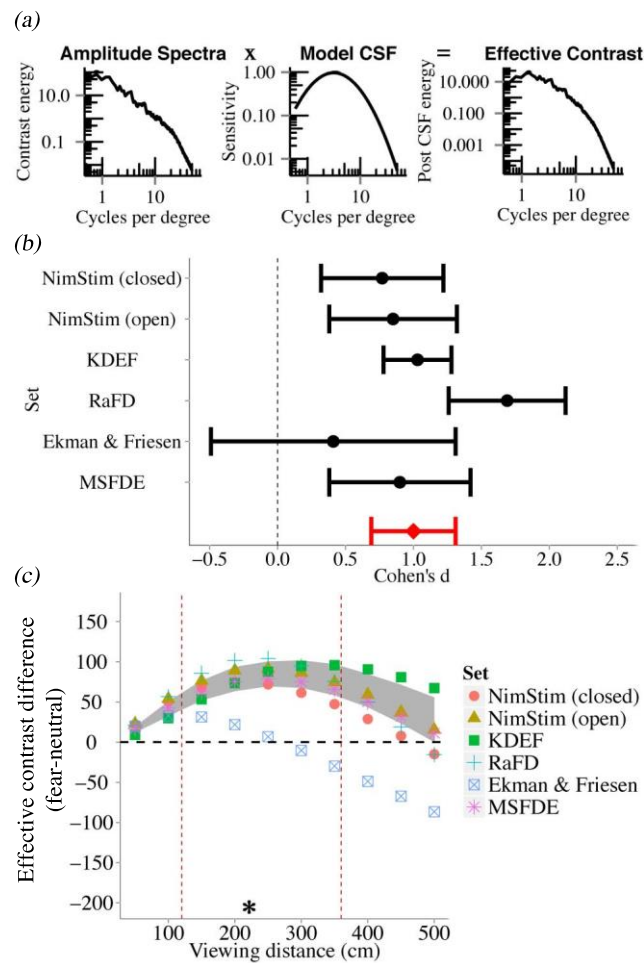
144 To confirm that this finding generalised beyond this particular image set, we
145 extended our analysis to 641 images by including 4 other widely used face sets (fronto-
146 parallel faces only): the Karolinska Directed Emotional Faces (KDEF: Lundqvist, Flykt, &
147 Ohman, 1998), The Radboud Faces Database (RaFD: Langer et al., 2010), The Pictures of

148 Facial Affect Dataset (Ekman & Friesen, 1976), The Montreal Set of Facial Displays of
149 Emotion (MSFDE: Beaupre & Hess, 2005). The sensory advantage of fear was large and
150 significant in all but the Ekman & Friesen set¹ (figure 1b). The pooled effect size across face
151 sets, calculated via a random effects model, was large and significant ($k=6$, $N= 641$, $d= 1.00$,
152 95% CI [0.69 1.31], $p < .001$). Based on this pooled estimate, the “probability of superiority”
153 (Grissom & Kim, 2005), i.e. the likelihood that a randomly sampled fearful face will have a
154 sensory advantage over a randomly sampled neutral face, is 84% (95% CI [75% 90%]).

155 **Stability Across Viewing Distances**

156 The effective contrast differences described above are not scale-invariant; they
157 depend on the particular retinal size of the images. If our physical expression of fear is
158 optimised to be salient in everyday social contexts (Gray, Adams, Hedger, Newton, &
159 Garner, 2013) then this sensory advantage of fear should be robust over distances at which
160 humans typically socialise and communicate. To test this possibility, we extended our
161 analyses to simulated viewing distances of 50 - 500 cm. As shown in figure 1c, the sensory
162 benefit of fear is largest within interpersonal proximities that characterise human social
163 interactions (120 to 360 cm, region within dotted lines, see Argyle, 2013).

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165

166 *Figure 1.* (a) Image analysis for one example fearful face. (CSF = contrast sensitivity
 167 function). (b) Forest plot depicting the effect sizes for effective contrast differences between
 168 fearful and neutral faces (open = open mouthed, closed = closed mouthed). Error bars are
 169 95% confidence intervals. The diamond depicts the pooled effect size. (c) The difference in
 170 effective contrast (arbitrary units) between fearful and neutral models as a function of
 171 viewing distance. Coloured symbols indicate the mean within each face set, shaded grey
 172 region is the bootstrapped 95% confidence interval. The asterisk indicates the viewing
 173 distance used for the initial analyses. Dashed vertical lines span the distances that
 174 characterise typical human social interactions.

175

176 Importantly, our measure of effective contrast is derived from “classic” contrast
 177 sensitivity data (i.e. from challenging threshold conditions). It could be argued, therefore, that

178 most normal (non CFS or unmasked) viewing conditions are *suprathreshold*, to which the
179 shape of this *threshold* contrast sensitivity function may not apply. Indeed, contrast matching
180 experiments have found that perceived suprathreshold contrast is largely invariant with
181 spatial frequency (Georgeson & Sullivan, 1975). However, as De Valois and De Valois
182 (1990) note, contrast matching is not a direct sensitivity measurement and as such, one
183 cannot conclude what the suprathreshold contrast response function is for different spatial
184 frequencies. In fact, other measures, such as magnitude estimation, show that the high and
185 low frequency attenuation of the contrast sensitivity function is maintained at suprathreshold
186 levels (Cannon, 1979). It is therefore inappropriate to conceptualise the contrast sensitivity
187 function as an epiphenomenon restricted to threshold conditions. By extension, the detection
188 of stimuli in natural viewing conditions can be understood, at least to a first approximation, in
189 terms of the properties of the contrast sensitivity function.

190 Our analyses suggest that fearful expressions are optimised to excite the early visual
191 processes of proximal observers: fear faces contain greater contrast energy at the spatial
192 frequencies that humans are sensitive to, relative to neutral faces. This advantage is purely
193 sensory, and generalises across gender and race. This sensory advantage could be either an
194 evolutionary or learned adaptation.

195 The case for an unconscious processing advantage for threatening stimuli is most
196 often evidenced by the prioritisation of fearful over neutral expressions. However, angry
197 faces, although also signalling threat, have typically yielded smaller effects (Hedger, Adams,
198 & Garner, 2014) and in some cases a *disadvantage* has been found for angry faces, relative to
199 neutral faces in CFS paradigms (Gray, et al., 2013). Moreover, happy faces, although not
200 signalling threat, have also been found to be prioritised over neutral stimuli in detection
201 paradigms (Becker, Anderson, Mortensen, Neufeld & Neel, 2011) and there is some evidence
202 that they are processed subliminally (Dimberg, Thunberg, & Elmehed, 2000; Schupp et al.,

203 2004). Given the inconsistent nature of these findings, it is important to understand whether
204 processing differences between these expressions are better explained by their sensory or
205 affective characteristics. To this end, we used CFS (Experiment 1) and masking paradigms
206 (Experiment 2) to investigate whether effective contrast can predict conscious perception of
207 fearful, angry, happy and neutral faces.

208

209 **Behavioural Experiment: Access to Awareness from CFS**

210 Under most viewing conditions, our two eyes receive slightly different views of the
211 world and we perceive a single “fused” percept (Howard & Rogers, 1995). However, when
212 dissimilar images are presented to our two eyes at corresponding retinal locations, conscious
213 perception alternates between the two images as their neural representations compete for
214 awareness (Blake & Logothetis, 2002)- a phenomenon termed binocular rivalry. In some
215 respects, this is a controlled phenomenon that can be used to mimic aspects of natural vision,
216 which involves selection amongst multiple sensory inputs, which are assigned to or omitted
217 from conscious perception. In CFS, a dynamic masking pattern is presented to one eye,
218 which can render a stimulus presented to the other eye invisible for seconds before it breaks
219 suppression and enters conscious awareness (Tsuchiya & Koch, 2005). The length of this
220 initial suppression has been used as an index of the unconscious salience of the suppressed
221 image (the bCFS paradigm, Stein & Sterzer, 2014). Here, we use this bCFS paradigm to
222 measure the extent to which stimuli gain access to conscious perception.

223 **Methods**

224 We selected 4 NimStim models, on the basis of their high emotional validity (mean
225 expression recognition accuracy was 87% - see Tottenham et al., 2009), portraying fearful,
226 happy, angry and neutral expressions. Stimuli subtended 6.2 x 4.1 degrees of visual angle
227 (DVA) at the viewing distance of 60 cm on a 1280 x 1024 pixel resolution, gamma corrected

228 monitor. In order to decouple our images' low-level, effective contrast from their affective
229 properties, we presented the face stimuli in two different conditions (figure 2a). *Normal* faces
230 were presented upright with veridical contrast polarity. *Control* faces were rotated 180
231 degrees with reversed contrast polarity, producing an image similar to a photographic
232 negative. Together, these manipulations severely disrupt the recognition and affective
233 evaluation of facial expressions (Gray et al., 2013). Critically, however, they do not alter
234 effective contrast². Thus, if the threat or valence of face images is the critical factor in
235 driving access to awareness, we would expect any threat advantage to be reduced or
236 eliminated for the control images. Conversely, if effective contrast is the key predictor for a
237 'threat advantage', then a similar advantage for the fear expression should be observed within
238 normal and control stimuli.

239 The trial sequence is shown in figure 2b. A central fixation cross was presented to
240 each eye via a mirror stereoscope for 1 second. Subsequently, observers viewed a CFS
241 display for 800 milliseconds, during which one eye viewed a pair of dynamic masking
242 patterns and the other viewed a face stimulus at 1.4 DVA to the left or right of fixation. **The**
243 **masking patterns were randomly generated ellipses. This ensured that suppression was not**
244 **biased towards any particular orientation or spatial frequency.** Face stimuli were introduced
245 gradually by linearly increasing RMS contrast from 0-100% over the 800 millisecond period.
246 Each eye's display was framed by a random dot surround (9.5 x 11.4 DVA) to assist
247 binocular alignment. Temporal frequency influences the strength of CFS suppression, with
248 mask frequencies above 10Hz exerting weaker suppression than those below (Yang & Blake,
249 2012). We therefore used a 20Hz mask to ensure that faces broke suppression on a substantial
250 proportion of trials. After the CFS presentation, observers were required to make a forced
251 choice decision as to whether "anything other than the mask" was visible during the trial.

252 This unspeeded measure does not measure response times, or recognition of the target
253 stimulus, which are susceptible to criterion effects (Stein & Sterzer, 2014)

254 Twenty-two undergraduate students completed 256 experimental trials (4 expressions
255 (anger, happy, fear, neutral) x 2 stimulus manipulations (normal, control) x 32 repetitions),
256 balanced across face location (left or right of fixation). Our sample size provides in excess of
257 95% power to detect a large effect size (Cohen's $d = 1.15$, the magnitude of difference in
258 detection between fearful vs. neutral faces from a similar CFS paradigm- Yang et al., 2007).

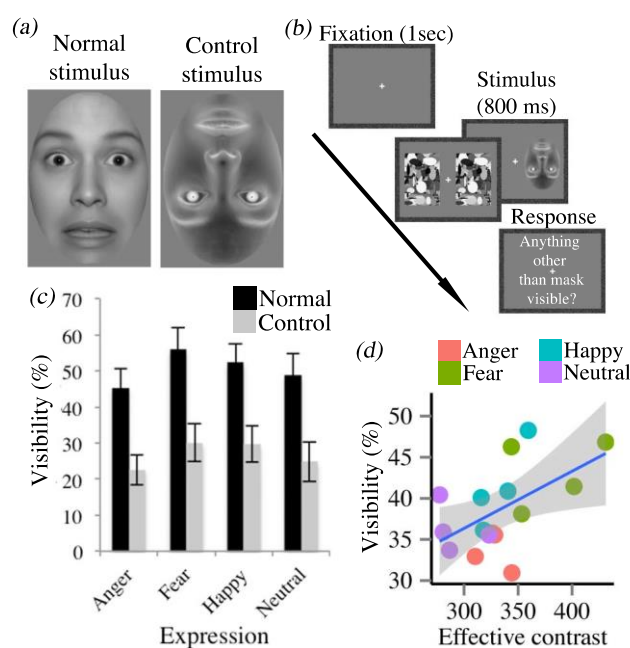
259 **Results**

260 The percentage of CFS trials in which face stimuli became visible is shown in figure
261 2c. Visibility was modulated by expression ($F(3, 63) = 5.33, p = .002$) with fear faces visible
262 most often, followed by happy, neutral, then angry faces. It is notable that angry faces were
263 detected least often, as this conflicts with the notion that threat is selectively prioritised.
264 Pair-wise comparisons revealed fear and happy faces were both detected more frequently
265 than angry faces ($ps < .05$). In addition, stimulus manipulation strongly modulated visibility
266 ($F(1, 21) = 33.31, p < .001, d = 1.06, 95\% CI [0.57 1.54]$): normal faces ($M = 50.56, SE =$
267 5.11) were detected more frequently than control faces ($M = 26.85, SE = 4.34$). Critically,
268 expression and manipulation did not interact in their effects on visibility ($F(3, 63) = 0.18, p =$
269 $.905$): the main effect of expression was similar for both the normal ($F(3, 63) = 3.14, p =$
270 $.031$) and control ($F(3, 63) = 3.00, p = .028$) stimuli, with fear detected most often, followed
271 by happy, neutral and anger in both cases. Importantly, this means that the same modulation
272 of visibility by expression and the same “fear advantage” was observed with control stimuli,
273 whose emotional content *severely disrupted*. Thus, some physical property, that is unaffected
274 by the stimulus manipulations, must be driving the effect of expression.

275 Does effective contrast predict visibility? Visibility was closely related to effective
 276 contrast (figure 2d) and a linear regression across the 16 facial models revealed that this was
 277 significant, $R^2 = .301$, $p = .026$.

278 Importantly, however, the main effect of stimulus manipulation (normal vs. control)
 279 cannot be explained by low-level properties, as the two stimulus categories have equivalent
 280 effective contrast. **The mechanisms that govern visual awareness may therefore** discriminate
 281 faces from non-faces (Stein, Sterzer, & Peelen, 2012), but we found no evidence that emotion
 282 or threat had an effect on detection beyond that explained by basic low-level variability
 283 between expressions.

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286

287 *Figure 2.* Experiment 1. (a) Examples of normal and control stimuli. (b) Schematic of CFS

288 trial sequence. (c) Stimulus visibility in the CFS task, as a function of expression and

289 stimulus manipulation. Error bars are ± 1 SEM. (d) Stimulus visibility as a function of

290 effective contrast, collapsed across manipulation, shaded region is ± 1 SEM.

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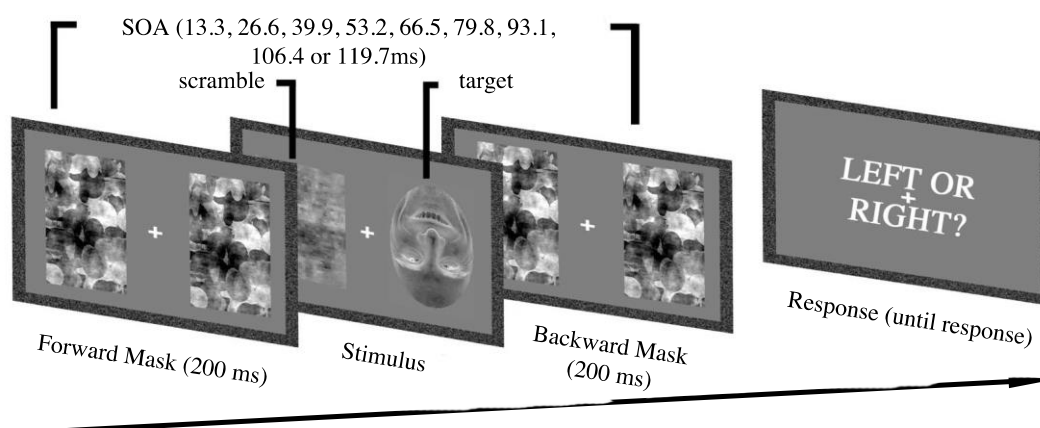
292 **Behavioural Experiment 2: Access to Awareness from Visual Masking**

293 The bCFS paradigm has been widely used to investigate the competition for visual
 294 awareness. However, we might question whether this represents a naturalistic example of
 295 how stimuli compete for awareness; binocular rivalry is infrequently encountered in daily life
 296 (Arnold, 2011). In contrast, backward masking involves conditions more typical of everyday
 297 vision; observers frequently encounter brief glimpses of stimuli when sampling dynamic
 298 scenes via saccades and fixations. In our second experiment, therefore, we investigated
 299 whether effective contrast can predict the detection of briefly presented, masked facial
 300 expressions. In addition, we asked observers to provide affective ratings of the face stimuli,
 301 allowing us to assess the contributions of (i) low-level contrast and (ii) affective factors in
 302 stimulus detection.

303 **Method**

304 Figure 3 shows the masking paradigm. At the beginning of each trial, observers
 305 viewed the fixation cross for one second. Next, two masks were presented either side of
 306 fixation for 200 ms, followed by a target (intact) and non-target (block-scrambled) face for a
 307 variable duration (13.3, 26.6, 40, 53.3, 66.7, 80, 93.3, 106.7 or 120ms). Subsequently, two
 308 new mask stimuli were presented for 200ms, immediately following the face presentation.
 309 Participants were asked to indicate, as accurately as possible, whether the intact face had
 310 appeared to the left or right of fixation.

311



312

313 *Figure 3.* Schematic of trial sequence in the masking task.

314

315 All stimulus dimensions matched those in Experiment 1. The scrambled face matched
316 the amplitude spectrum averaged across all target face stimuli, ensuring the target could not
317 be localised via non-specific differences in luminance or contrast between the two sides of
318 the display. Mask stimuli also matched the averaged spectral slope of all face stimuli. This
319 prevented interactions between the spatial frequency profile of the target and mask from
320 influencing detection.

321 An independent sample of 11 participants completed 1152 randomly ordered trials (4
322 expressions (anger, fear, happy, neutral) x 2 stimulus manipulations (normal, control) x 9
323 stimulus onset asynchronies (SOAs: 13.3, 26.6, 40, 53.3, 66.7, 80, 93.3, 106.7 or 120ms) x 16
324 repetitions), balanced across the location of the face stimulus (left, right). Our sample size
325 provided in excess of 95% power to detect the same target effect size as defined for
326 experiment 1.

327 Observers also completed a Self-Assessment Manikin (SAM) to evaluate face stimuli
328 on the three dimensions of emotional assessment: valence, arousal and dominance (see
329 Bradley & Lang, 1994). On each trial, observers initiated face presentation, which was
330 displayed (unmasked) for 120ms (maximum SOA in the masking task). Valence, arousal and
331 dominance ratings (1-9 scale) were made in separate blocks, consisting of 32 randomly
332 ordered trials.

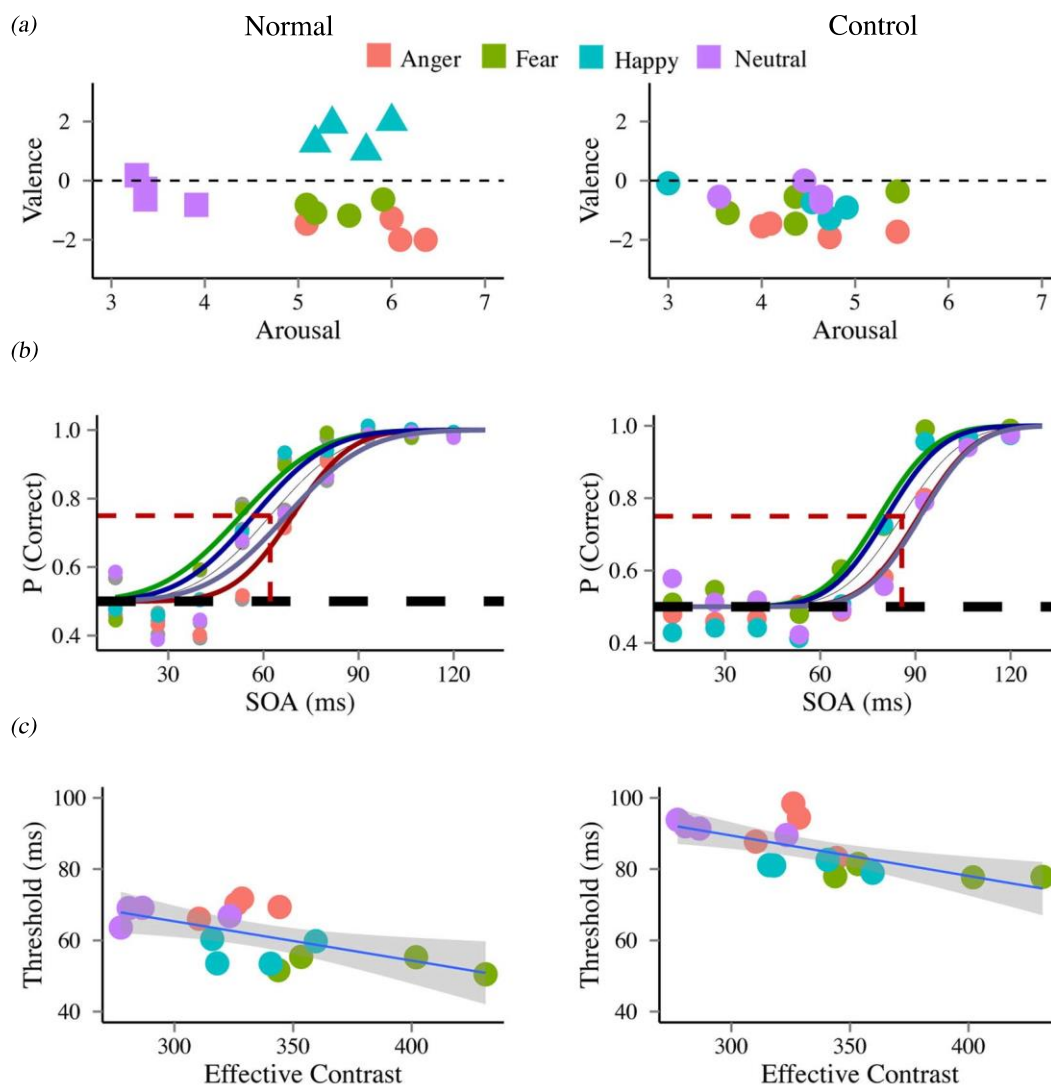
333 **Results**

334 Following standard practice, valence and arousal ratings are summarised in “affective
335 space” (figure 4a). For normal faces, the distribution of stimuli follows the expected
336 “boomerang” shape (Bradley, Codispoti, Cuthbert, & Lang, 2001) with higher arousal levels
337 reported for stimuli with large positive or negative valence. However, no such pattern is

338 visible for the control stimuli. A cluster analyses confirms this – the distribution of normal
339 stimuli is optimally explained (as determined by Bayesian Information Criterion) by a 3
340 cluster model that clearly differentiates between the positive (happy) negative (fear, anger)
341 and neutral (neutral) expressions. In contrast, the distribution of control stimuli is optimally
342 explained by a one-cluster model; expressions are not differentiated in affective space. This,
343 consistent with previous work (Gray et al., 2013) confirms that our stimulus manipulations of
344 spatial and contrast inversion severely alter the emotional evaluation of facial expressions. **It**
345 **is possible that increased statistical power may have detected residual discrimination**
346 **(Reingold & Merikle, 1988). Nonetheless, it is clear from figure 4a that control stimuli elicit**
347 **a qualitatively different pattern of affective evaluations. Thus, if affective dimensions are**
348 **important in prioritising emotional stimuli, this difference should be reflected in a different**
349 **pattern of detection across expression for control stimuli vs. normal stimuli.**

350 Figure 4b displays the 2AFC performance accuracy from the masking task. Data were
351 fitted with cumulative normal distributions free to vary in position and slope. Detection
352 thresholds were estimated from these fits for 75% correct performance (upper binomial
353 limit). Thresholds were significantly and substantially modulated by stimulus manipulation,
354 with observers requiring longer SOAs to detect control faces than normal faces (normal: $M =$
355 60.6 ms, control: $M = 84.6$ ms, $t(10) = 10.7$, $p < .001$, $d = 2.54$, 95% CI [1.38 3.69]). **Notably,**
356 **these detection thresholds correspond to much briefer stimulus exposures (72 ms on average)**
357 **than those at which observers made affective judgements in the SAM task (120 ms). Thus,**
358 **we expect that discrimination of expressions would have been *even worse* under conditions**
359 **that are sufficient for any fear advantage.** Similarly to Experiment 1 there was a main effect
360 of expression on detection in both the normal ($F(3, 30) = 9.95$, $p < .001$) and control
361 conditions ($F(3, 30) = 9.22$, $p < .001$). This effect was again similar in the two conditions,
362 with no interaction between expression and stimulus manipulation ($F(3, 30) = 1.15$, $p =$

363 .345). In other words, although spatial and contrast inversion inhibited emotional recognition
 364 of the control stimuli, this did not affect the ‘fear advantage’ for detection. Normal and
 365 control fearful faces were detected at shorter SOAs than both neutral and angry faces (p s <
 366 .05, pairwise comparisons). Figure 4c illustrates the relationship between effective contrast
 367 and detection threshold, for all stimuli. Effective contrast was a similarly good predictor of
 368 detection thresholds in both the normal ($R^2 = 0.36, p = .014$) and control ($R^2 = 0.41, p = .004$)
 369 configurations.
 370



371
 372 *Figure 4.* (a) Distribution of stimuli in affective space, according to valence and arousal
 373 ratings. Valence is normalised to a -4 to +4 range such that 0 indicates neutral. Symbol colour

374 represents facial expression, symbol shape represents clusters obtained via Bayes criteria (i.e.
375 normal = 3 clusters, control = 1 cluster). (b) The proportion of correct face localisation
376 responses is plotted as a function of SOA and expression, with cumulative normal fits. The
377 dashed red lines indicate the mean thresholds for normal and control stimuli (c) Detection
378 threshold as a function of effective contrast. Shaded region indicates ± 1 SEM.

379

380 Interestingly, adding expression as a predictor significantly increased the variance
381 explained by effective contrast alone (normal: $F(3,11) = 15.96, p < .001$, control: $F(3,11) =$
382 $5.60, p = .014$). However, as we have discussed, it is important not to conflate ‘expression’
383 (the physical signal) with ‘emotion’ (i.e. a semantic or affective evaluation of the signal).
384 Thus, the fact that expression improves the model fit simply means that effective contrast
385 cannot *entirely* account for the effect of expression. Other, unspecified stimulus attributes
386 may also play a role; it does not, in itself, imply an influence of emotion sensitive processes
387 on detection. To strengthen this conviction, we performed regression analyses with valence,
388 arousal and dominance as predictors of thresholds. For both the normal and control
389 configurations, none of these variables significantly predicted detection thresholds (all ps
390 $> .05$). Notably, the same was true when these affective ratings were used as predictors of the
391 bCFS visibility data from Experiment 1. Moreover, tests for zero partial association revealed
392 that the relationship between effective contrast and detection thresholds remained significant
393 after controlling for the influence of all these variables (normal: $t(11) = -2.57, p = .026$,
394 control: $t(11) = -3.47, p = .005$). In summary, we found that low-level effective contrast
395 predicts stimulus visibility, but found no effect of emotion sensitive processes on detection.

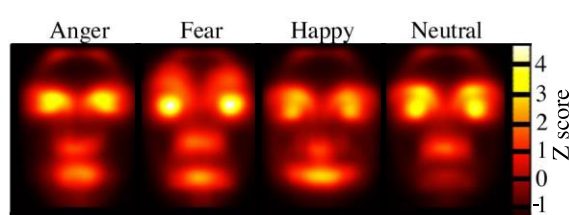
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Local Image Analyses

398 Our data establish that global differences in effective contrast can predict the
399 prioritisation of faces in the competition for awareness. However, we can refine our analyses
400 further to ask whether this is driven by particular image regions. These regions were defined
401 by symmetric Gaussian windows whose size and standard deviation (2 DVA, 0.5 DVA
402 respectively) matched the stimuli used to derive the Modelfest data (Watson & Amuhada,
403 2005). These windows were applied to 130 uniformly distributed, overlapping locations
404 within each image and effective contrast was calculated for each region. The relative (z
405 scored) effective contrast, averaged across the models used in our experiments is shown in
406 figure 5. Consistent with previous suggestions (Gray et al., 2013; Lee et al., 2013) it is clear
407 that the eye region is highly salient within all expressions, but particularly so for fear faces.
408 This can be attributed to the increased exposure of the white scleral field and dark iris. These
409 features are unique amongst primates and probably co-evolved with human social
410 communication to enhance detectability of gaze (Kobayashi & Kohshima, 1997). Expressing
411 fear amplifies this sensory benefit by increasing the vertical dimension of the scleral field
412 (see Hedger, 2014 for a demonstration).

413



414

415 *Figure 5.* Local variations in effective contrast. Image colour/luminance represents the Z-
416 scored effective contrast.

417

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Discussion

419

420 Shaped by sociobiological pressures, human signals are designed to reliably convey
information to observers. In the context of threat, a sender may express fear to warn others of

421 danger, or to signal appeasement. However, before a signal can be acted upon, it must be
422 detected. Theories of enhanced signal function by design (Dukas, 1998) thus predict that the
423 facial expression of fear would converge on a form that exploits the sensory processes of a
424 proximal observer. By analysing the Fourier content of faces in the context of human
425 interactions, we found that facial expressions differ in the extent to which they stimulate low-
426 level visual processes. This mechanism, effective contrast, provides a parsimonious
427 explanation for the prioritisation of fearful faces in the competition for awareness, across
428 rather different paradigms: CFS and masking. Critically, this ‘threat advantage’ was **poorly**
429 **explained** by perceived emotion; it was unchanged for stimuli with the same effective
430 contrast, **but altered emotional content**. Moreover, face detection was not predicted by
431 observers’ affective ratings. Our data are inconsistent with the notion that the threat value of
432 fear faces is evaluated outside of awareness and determines access to conscious vision.
433 Instead, our data suggest that access is **best explained** by the tuning of very early visual
434 processes, i.e. the contrast sensitivity function.

435 Previous work has speculated that the prioritised detection of threat relevant stimuli
436 (including fearful faces) may be linked to simple, low-level stimulus properties (Bar, & Neta,
437 2006; Coelho, Cloete, & Wallis, 2010; Gray et al., 2013; Stein & Sterzer, 2012; Lee et al.,
438 2013; Yang et al., 2007). However, these studies have not quantified these properties with
439 respect to underlying human sensory processes. Moreover, to our knowledge, our study is the
440 first to explicitly quantify both sensory (effective contrast) and affective properties (SAM) of
441 facial expressions as predictors in a detection paradigm. We found that low-level sensory
442 properties were by far the best predictor of stimulus detection and found no evidence that
443 detection was modulated by threat-sensitive processes. The data thus suggest that the fear
444 advantage is most parsimoniously explained by low-level properties of the fear expression,
445 negating the need to invoke the role of threat, or emotion sensitive processes.

446 Detectability is unlikely to be the only factor that has shaped the fear expression.
447 Expressing fear enhances the expresser's field of view, eye movement velocity and nasal
448 airflow- linking it to functional advantages in the context of threat (Susskind et al., 2008).
449 Fear may also enhance the expresser's stimulus detection by shaping how light is cast onto
450 their retina (Lee, Mirza, Flanagan, & Anderson, 2014). In other words, the expression of fear
451 appears to be adaptive for both senders and receivers, in terms of efficient transmission and
452 reception of visual information.

453 We observed a robust "face advantage" in both experiments. Normal faces were better
454 detected than control faces, despite being equivalent in effective contrast. This suggests that
455 the visual system is sensitive to stimuli that are specifically face-like, and this sensitivity is
456 not yoked to awareness of the stimuli. It has been found in bCFS studies that stimulus
457 inversion has a detrimental effect on the detection of human faces but no effect on detection
458 of chimpanzee faces (Stein, et al., 2012). This suggests that pre-conscious visual processes
459 selectively promote stimuli that resemble conspecific faces to conscious perception,
460 presumably because of their social relevance. However, our data suggest that this sensitivity
461 does not extend to **the evaluation of facial emotion; emotional evaluations** had no effect on
462 stimulus detection beyond that explained by low-level image properties.

463 How can we reconcile a robust face advantage with the absence of emotion-sensitive
464 processes? Determining whether a stimulus is a face represents a coarser-level judgement
465 than identifying its emotional expression. Visual masking studies have shown that identifying
466 a specific object requires substantially more processing time than identifying its general
467 category, whilst determining an object's category co-occurs with its detection (Grill-Spector
468 & Kanwisher, 2005). The present data are thus consistent with a framework in which the
469 detection and categorisation of faces (i.e. face vs. non face), but not the evaluation of facial
470 expression, is performed at an early processing stage by the same perceptual mechanisms. In

471 contrast, the data are poorly explained by models suggesting that emotional evaluation
472 precedes and drives face detection (Palermo & Rhodes, 2007).

473 It is important to consider well-documented phenomena that appear to conflict with
474 our “low-level” account of the fear advantage. One relevant example is that anxious
475 populations exhibit enhanced processing of fear faces, which is commonly attributed to
476 dysfunction in threat-sensitive mechanisms that operate without awareness (Bar Haim, Lamy,
477 Pergamin, Bakermans-Kranenberg, & van IJzendoorn, 2007). However, differences in
478 perceptual selection observed in anxious populations are not limited to threat relevant
479 contexts. For instance, anxiety is associated with enhanced attentional capture by
480 perceptually salient neutral stimuli (Moser, Becker, & Moran, 2012, Moran & Moser, 2014).
481 Correspondingly, enhanced biases for fear faces in anxious populations could be a function of
482 either the perceptual or emotional properties of the stimuli. Thus, processing differences
483 displayed by anxious populations may not be inconsistent with our account.

484 Another interesting phenomenon is that eye gaze direction can modulate detection of
485 fearful faces, such that averted fearful gazes are prioritised over directed fearful gazes
486 (Milders, Hietan, Leppanen, & Braun, 2011). This makes good ecological sense in terms of
487 perceived threat, since the presence of an unknown threat in the environment (averted gaze)
488 may be more dangerous than a threat directly from the target (directed gaze). Importantly,
489 however, Chen and Yeh (2012) found directly contradictory results using schematic faces, in
490 which low-level variability is reduced. In a bCFS paradigm, Chen and Yeh found that
491 schematic fearful faces with directed gaze were detected faster than those with averted gaze.
492 Notably, the removal of the salient eye white in schematic stimuli also resulted in a lack of an
493 overall “fear advantage” for detection. These opposing findings, likely due to simple physical
494 variations between the particular stimulus sets employed, pose problems for accounts that

495 posit specialised threat detection mechanisms as the cause of processing biases (see Becker,
496 et al., 2011 for a related discussion).

497 Several studies have observed differential amygdala responses to fearful and neutral
498 faces rendered invisible by masking and CFS (Jiang & He, 2006; Whalen et al., 2004), which
499 has been interpreted as evidence that fearful faces are evaluated without awareness via a
500 pathway involving the amygdala. However, whether this neural activity is linked to adaptive
501 changes in perception is hard to determine without convergent behavioural measures.
502 Importantly, patients with amygdala lesions nonetheless show prioritised detection of fear in
503 bCFS and visual search tasks (Piech et al., 2010; Tsuchiya, Moradi, Felsen, Yamakazi, &
504 Adolphs, 2009). Moreover, recent work using a CFS paradigm suggests that attentional
505 orienting to threat stimuli may be dependent on their conscious detection (Hedger, Adams, &
506 Garner, in press). Whether amygdala activity to unconsciously presented threat stimuli (in
507 response to either low-level or affective properties) has a functional role in promoting their
508 detection, therefore, remains an interesting question.

509 How do our data fit with suggestions that processing of threatening stimuli is driven
510 by evaluation of content in the low spatial frequencies? (Mermillod, Droit-Volet, Devaux,
511 Schaefer, & Vermeulen, 2010; Willenbockel, Leopre, Nguyen, Bouthillier, & Gosselin,
512 2012). Such observations are thought to support the notion that coarse, rapid, magnocellular
513 input to the amygdala is sufficient for the evaluation and subsequent detection of threat
514 stimuli (Tamietto & de Gelder, 2010; Vuileumier, Armony, Driver, & Dolan, 2003).
515 Importantly, human contrast sensitivity is greater for low spatial frequencies, i.e. they have
516 more influence on our measure of effective contrast. Thus, our data also suggest that low
517 spatial frequencies are important, but that this relates to the distribution of contrast at these
518 spatial scales, not the semantic content that is available, or evaluated at these scales.

519 In summary, our data suggest that, through evolutionary or learned adaptations,
520 fearful faces are optimised to stimulate human sensory biases. This mechanism may provide
521 a parsimonious explanation of the “fear advantage” in the competition for awareness that
522 negates the need to invoke preconscious processes sensitive to threat.

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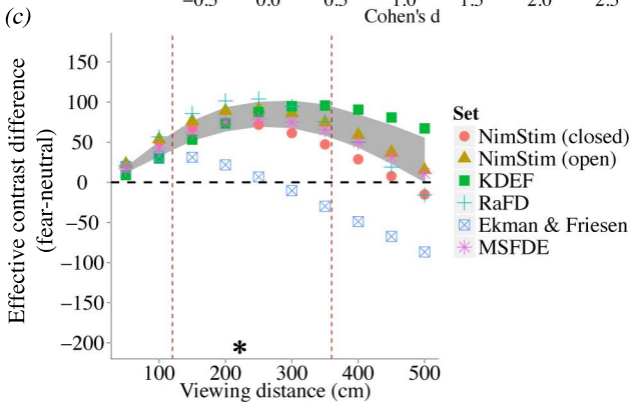
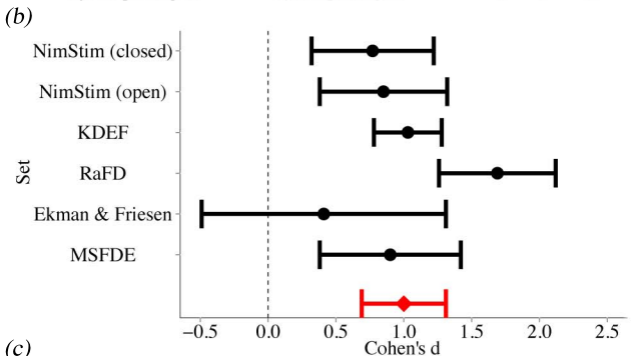
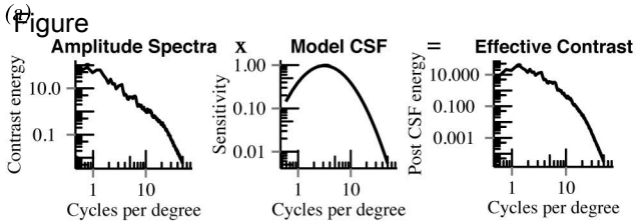
Footnotes

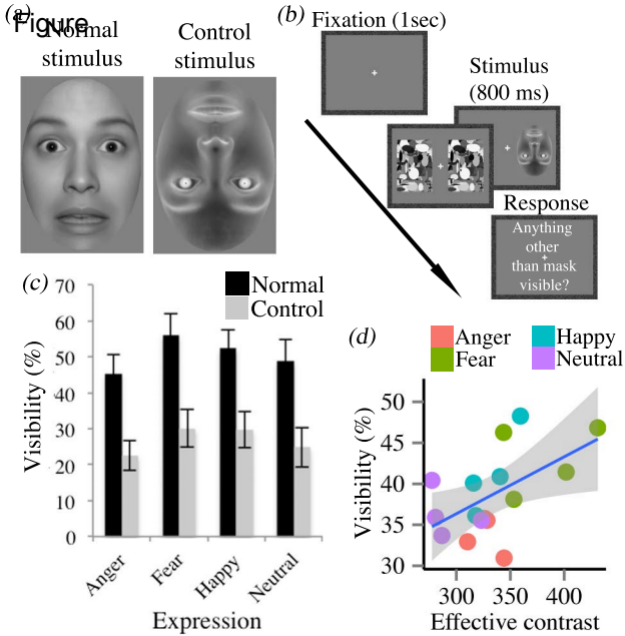
¹This outlying result may be attributed to the low control of head orientation, lighting and lower image resolution compared to other, more recent sets. Moreover i) the effect is directionally consistent and ii) statistical power is lower, given the significantly smaller number of images in the Ekman set. Thus, this discrepancy should not greatly impact on the interpretation of our main findings.

² *Perceived* contrast is affected more by low than high luminances (Haun & Peli, 2013). All normal faces had luminance histograms that were negatively skewed (third moment: $M=-0.10$, $SD=0.21$). Thus, luminance profile reversal may have marginally *increased* the perceived contrast of control faces, relative to normal faces (which is in contrast to their *decreased* detection). Therefore, the effect of stimulus type (normal v control detection) cannot be explained by changes in the skew/ luminance histogram. Importantly, all relationships between effective contrast and detection remained significant after controlling for skew.

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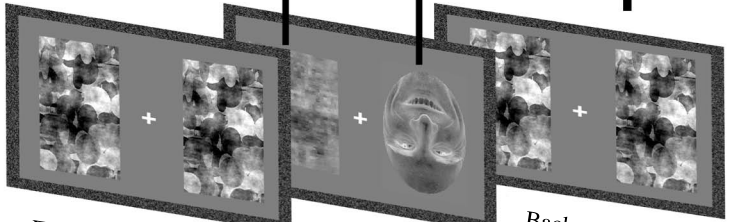


Figure

SOA (13.3, 26.6, 39.9, 53.2, 66.5, 79.8, 93.1,
106.4 or 119.7ms)

scramble

target



Forward Mask (200 ms)

Stimulus

Backward Mask
(200 ms)

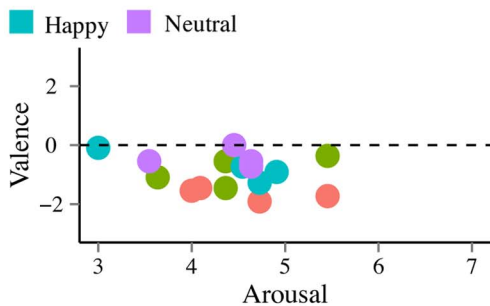
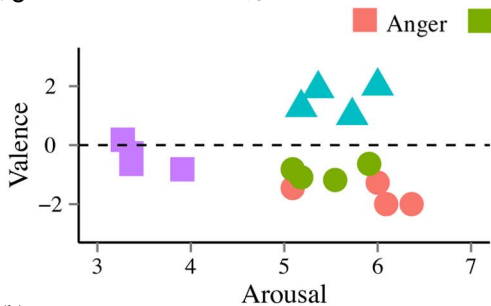


Response (until response)

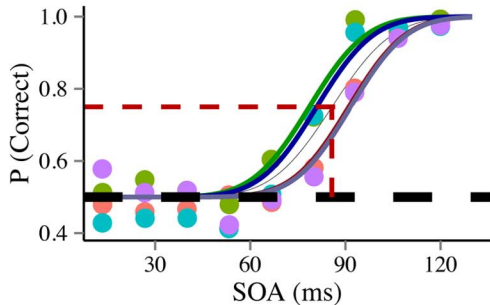
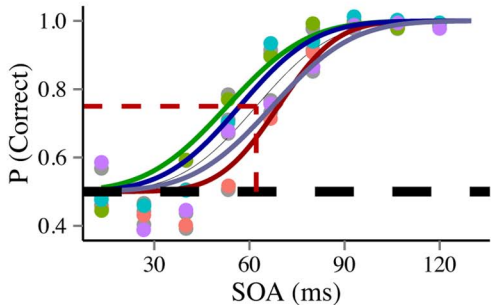
Figure

Normal

Control



(b)



(c)

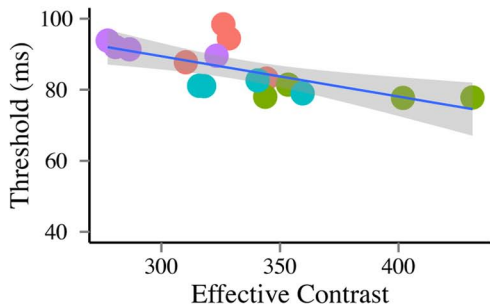
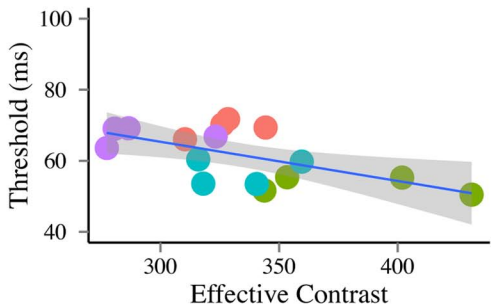


Figure 1
Anger

Fear

Happy

Neutral

