

1 **Visual contrast and color in rapid learning of novel patterns by chicks**

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12

13 **ABSTRACT**

14 Biological communication signals often combine bright and dark colors, such as
15 yellow and black, but it is unclear why such patterns are effective. The literature on
16 aposematism suggests that high contrast patterns may be easily learnt or innately
17 avoided, whereas studies of sexual signaling refer to their attractiveness or to their
18 cost. Here in experiments with poultry chicks trained to find food in patterned
19 containers, we confirm that elevated contrast dramatically increases the rate of initial
20 attack on novel stimuli, but this response is labile. The chicks peck once at a novel
21 unrewarded stimulus and then ignore it for at least 24 hours. Such single trial learning
22 has not previously been reported for birds without a positively aversive unconditioned
23 stimulus such as quinine. We then test and reject two hypotheses about the function of
24 high contrast patterns: first that the preferential responses are due to novelty, and
25 second that elevated contrast enhances learning about a novel color. More generally,
26 the observations are consistent with the idea that elevated contrast attracts attention,
27 thereby enhancing both initial responses - whether positive or negative - and the rate
28 of learning.

29

30 **INTRODUCTION**

31

32 The beautiful and conspicuous patterns of animals and plants pose fundamental
33 questions about the function of biological communication signals. Darwin (1871)
34 argued that these displays are attractive to potential mates, whereas Müller's (1879)
35 work on butterfly mimicry suggests that colorful aposematic signals facilitate learning
36 by predators (Halpin et al., 2008; Riipi et al., 2001; Roper and Redston, 1987; Stevens
37 and Ruxton, 2012). High contrast patterns also promote unlearned wariness – or
38 neophobia (Lindstrom et al., 2001; Marples and Kelly, 1999; Rowe and Guilford,
39 1999). Thus high contrast patterns and bright colors are important in both positive and
40 negative innate responses and in learning.

41

42 Broadly speaking there are three main theories about the evolution of colorful signals
43 (which may not be mutually exclusive). Firstly, they convey specific information
44 about the signaler, for example they may be costly; secondly, they evolve to be
45 different from the background or competitors' signals; and thirdly that they simply
46 attract attention. This study tests how contrast in a simple pattern affects foraging
47 poultry chicks' responses to novel patterns and colors, and what they learn on their
48 first and subsequent encounters. The strength of the effects and the speed of learning
49 imply that pattern contrast is crucial for controlling birds' responses to visual signals.

50

51 In classical models of animal learning (Pearce, 1997; Pearce and Bouton, 2001) the
52 rate of associative learning depends only on stimuli being discriminable from one
53 another. However, Pearce and Hall (Pearce and Hall, 1980) introduced a factor,
54 termed 'associability', to model the rate of reinforcement learning. Associability can
55 be equated to the attention given to the conditioned stimulus (Dayan et al., 2000;
56 Pearce and Hall, 1980). Bayesian models of learning relate associability (and
57 attention) to the level of confidence in the predictive value of a signal: poorly known
58 stimuli should receive more attention and have higher associability than familiar
59 stimuli (Courville et al., 2006; Dayan et al., 2000). This idea accords with the
60 intuition that new evidence is most significant when one initially knows little about
61 what to expect. Poultry chicks do indeed learn about novel colors more quickly than
62 familiar colors (Baddeley et al., 2007; Osorio et al., 2009).

63

64 Does novelty alone account for the attention given to a stimulus (Itti and Baldi,
65 2009)? A simple prediction is that for an (otherwise naïve) animal familiar with
66 stimulus *A*, the novelty of stimulus *B* would be equal to that for *A* following
67 experience with *B*. If the rate of learning is dependent on the magnitude of the
68 difference between familiar and novel stimuli, but not the polarity of this difference,
69 then one can expect signals that need to be learnt, such as warning colors, to evolve to
70 be detectable, but there need not be in any particular polarity to this difference - say to
71 high rather than low contrasts. Conversely, if associability depends on factors other
72 than difference, such as the contrast in a pattern or the saturation of a color, then one
73 might expect signals that need to be learnt to evolve accordingly.

74

75 Previous work showed that when week-old poultry chicks are trained appetitively to
76 patterned food containers and then encounter a pattern bearing either a novel color or
77 novel achromatic contrast they have a strong fidelity to the familiar color (or, more
78 accurately, chromaticity) but prefer elevated contrast (Osorio et al., 1999b). This
79 observation conflicts with the finding that chicks avoid unfamiliar high contrast
80 patterns (Roper and Cook, 1989), but is perhaps simply indicative of context
81 dependence for such effects.

82

83 We know also that when chicks are trained to two colors, such as red and yellow, they
84 initially prefer novel intermediate colors, in this case orange (Jones et al., 2001), but
85 this preference is labile; if the chicks are tested in extinction (i.e. without reward) the
86 rate of response to the novel color declines faster than to the familiar rewarded colors
87 (Osorio et al., 2009). The rapid learning about novel stimuli demonstrates that the
88 chicks classify the novel color separately from the known colors (contrary to simple
89 models of sensory generalization (Osorio et al., 2009; Osorio et al., 1999b), and is
90 consistent with the novel stimulus having high associability, owing to a low
91 confidence in the predicted relationship between the color and the food reward.

92

93 These observations lead to questions about how signal design affects an animal's
94 initial response and its subsequent learning. Does contrast in visual patterns affect
95 unlearned responses or learning, and are any effects due to contrast being conspicuous,
96 unusual, or simply inherently more effective? Here we test how changes in contrast

97 affect poultry chicks' initial responses and subsequent learning about novel patterns.
98 We then study the interactions between color and contrast. There are two questions:
99 first, are the strength of the initial response and the subsequent rate of learning linked,
100 and second, does elevated contrast affect responses independently of novelty?

101 **MATERIALS AND METHODS**

102 Male poultry chicks (*Gallus gallus*; Bovans Goldline) from a commercial hatchery
103 lived communally from hatching to a week of age. The room temperature was 21°C
104 with additional warmth from an infra-red lamp under a 12:12 L:D lighting regime.
105 Walls of the communal enclosure were grey, the substrate was sawdust, and chicks
106 had free access to food crumbs and water. At one week the chicks were rehoused as
107 pairs in 24 x 27 cm cages. The birds had free access to standard food and water,
108 except for 2 hours before training or testing when food was removed. In experiments
109 the chicks were trained and tested in pairs in a 40 x 30 cm arena, the floors and walls
110 of which were painted grey, lit by an overhead 250W tungsten-halogen light (color
111 temperature c. 3.4K). All experimental work was carried out under Home Office
112 licence.

113

114 *Stimuli*

115 Stimuli for training and testing were conical paper food containers of 25mm length
116 and 7mm base diameter printed (Canon Pro9000 printer) with a stimulus pattern of
117 2mm x 6mm rectangular tiles. The tilings (created using purpose-written code in
118 MATLAB) were either all grey (achromatic), or tiles selected at random were colored
119 red, orange or yellow with a probability of 0.3. The achromatic tiles were designed at
120 two contrast levels: 1) *Low Contrast*, with a random pattern of two tiles of the same
121 average luminance and a Michelson contrast ($I_{max}-I_{min}/I_{max}+I_{min}$) of 0.3, and 2)
122 *High Contrast* with black and white background tiles with nominal Michelson
123 contrast of 1.0 (the actual contrast is close to 0.85). The mean intensity of the black
124 and white tiles was slightly lower than for the lower contrast backgrounds, but this is
125 very unlikely to have had any effect in this study as the chicks do not easily learn
126 average luminance. For the *Low Contrast* condition the mean grey-level of the
127 achromatic tiles matched the intensity of the colored tiles for the chicks' double cones
128 (Jones and Osorio, 2004; Osorio et al., 1999c). The colored tiles had fixed
129 chromaticities (i.e. hue and saturation), but the brightness varied randomly with a

130 contrast range of 0.3 (Osorio et al., 1999c). Different sets of stimuli were used for
131 training and testing and all the stimuli had different (random) patterns, so that the
132 patterns were uninformative. These tiled patterns allow the chicks to learn colour
133 accurately and quickly against an achromatic background. The presence of luminance
134 noise reduces the chance that the birds will learn the brightness rather than the
135 chromaticity (i.e. hue and saturation of the colour). Full details and rationale for the
136 design of stimuli can be found in Osorio et al. (1999c).

137

138 *General training procedure*

139 The experiments used up to 36 pairs of naïve chicks, with a new group of chicks used
140 in each experiment. Chicks were housed, trained and tested in pairs because they
141 become stressed in isolation. Members of each pair were distinguishable by marking
142 one bird with a spot on the top of the head using a permanent marker pen. Training
143 started on day 7 after hatching. Pairs of chicks were placed in the arena with eight of
144 the conical food-containers. Four colored rewarded cones (S^+), contained standard
145 crumbs, which the chicks could extract by pecking. The other four cones (S^-), which
146 were entirely achromatic but otherwise similar to the rewarded stimuli, were empty.
147 Chicks were trained to two S^+ colors that could be easily discriminated (S^{+1} and S^{+2}),
148 which were red and yellow to the human eye. Each color was equally rewarded (see
149 below for details of individual experiments). Training sessions lasted six minutes with
150 rewarded stimuli refilled with food at one-minute intervals. All chicks had two
151 training sessions a day, separated by a two-hour interval, for three days.

152

153 *General test procedure*

154 Tests were carried out in extinction (i.e. without reward) on the fourth day after
155 training started (i.e. ten days after hatching). For Experiments 1-3 the arena contained
156 nine clean printed cones: three of S^{+1} or S^{+2} (as learnt during training but without
157 food), three of S^- , and three of the novel test stimulus S' . For Experiment 4 there were
158 eight cones: two S^+ , two S^- , two high contrast S' , and two low contrast S' .

159

160 We recorded the sequence of the first ten selections made by one chick of the pair
161 after entering in the test arena. The same chick was scored in each test, and its
162 companion was ignored. Rapid repeated pecks at a single cone were discounted as
163 they represented a continued attempt to retrieve food from that cone rather than a

164 further choice. Obvious incidences of mimicking the second bird's actions, where the
165 bird being scored would see the other peck at a cone and run over to peck at the same
166 stimulus, were also discounted. Chicks were tested on three occasions for each
167 experiment to assess initial responses and subsequent learning about the novel
168 stimulus (Osorio et al., 2009): T1 at 24 hours after the final training session, T2 at 4
169 hours after the first test, and T3 at 24 hours after the first test. Food was provided
170 between T2 and T3 tests and removed 2 hours before.

171

172 As the chicks first encountered the novel stimulus in the initial test, and all tests were
173 in extinction, the initial response reveals preferences established during training,
174 while the subsequent responses were influenced by learning about the novel stimulus.
175 Details of the experimental stimuli and numbers of individuals tested are given in the
176 Results section.

177

178 Statistical analyses were carried out in MATLAB R2012b (MathWorks) and R
179 v2.14.0 using the lme4 package (R, 2008). Mean responses over 10 stimulus
180 selections were compared using Wilcoxon matched-pairs signed-rank tests (two-
181 tailed). Within-trial S' preferences were tested using generalized linear mixed models
182 (GLMMs), with color, condition, and peck (at ten levels) as fixed factors and
183 individual chick as a random factor, and a binomial error term. Models were then
184 tested using analysis of deviance. Correlation between choice and peck order were
185 tested with Spearman's rank correlation in SPSS (SPSS Inc., Chicago, IL. USA).

186 **RESULTS**

187 *Experiment 1: responses to novel high-contrast patterns.*

188 This experiment examined how elevated contrast affects the initial responses to and
189 learning about novel stimuli. We trained 36 pairs of chicks to both red (S⁺¹) and
190 yellow (S⁺²) patterns with low-contrast (range 0.3) grey backgrounds. The
191 unrewarded training stimuli (S⁻) were similar to the S⁺, but all grey. The tests
192 compared chicks' responses to the S⁻ and S⁺ training stimuli to responses to novel (S')
193 stimuli with the familiar training colors, but having the low contrast grey tiles
194 replaced with black and white tiles (i.e. high contrast: S'¹ (red) and S'² (yellow)
195 respectively). There were two test conditions: *Condition 1* (n=18) where the S⁺ and S'

196 stimuli had the same color (i.e. both either red or yellow: S^{+1} with S'^1 or S^{+2} with S'^2 ;
197 Figure 1A), and *Condition 2* (n=18) where the S^+ and S' colors were different (i.e.
198 one red and the other yellow: S^{+1} with S'^2 or S^{+2} with S'^1 ; Figure 1A). In the first test
199 (T1) *Condition* proved to have a highly significant effect on the preference for S' over
200 the first 10 selections (GLMM analysis of deviance; $X^2(3) = 19.39$; $p = 0.0002$), hence
201 we analysed them separately. However, S^+ color *per se* proved to have no effect on
202 stimulus preference (GLMM analysis of deviance; $X^2(4) = 0.04$; $p = 0.99$). We
203 therefore pooled the red and yellow responses for each condition to improve the
204 power of our subsequent tests.

205
206 In the initial extinction tests (T1), the novel stimuli S' with elevated background
207 contrast were initially greatly preferred to S^+ (Figure 1B; (Osorio et al., 1999a)).
208 Overall, 32 of 36 (89%) first pecks were directed at the novel stimuli (Figure 1B).
209 This preference for S' then rapidly declined over the subsequent nine selections
210 (Spearman's rank correlation; $r_s = -0.914$, $p < 0.0001$). When S^+ and S' colors were
211 different in the test (*Condition 2*), fewer than half of the second choices were for the
212 S' high-contrast pattern, which was thereafter (selections 3-10) no more attractive
213 than S^+ . The rate of decline was slower in *Condition 1* where S^+ and S' colors were
214 alike in the test (Figure 1B).

215
216 Mean stimulus choice across 10 selections at T1 for *Condition 1* shows no significant
217 preference for S^+ over S' (Wilcoxon matched-pairs signed-ranks; $z = 32$, $p > 1$). For
218 *Condition 2* there appeared to be a strong preference for S^+ over S' (Wilcoxon
219 matched-pairs signed-ranks; $z = -3.64$, $p = 0.0003$), which can be explained by the very
220 rapid extinction of and subsequent low preference for initial preference for S' (see
221 above and figure 1B). A simple explanation for the difference between *Condition 1*
222 and *Condition 2* is that chicks were more readily able to distinguish the novel from
223 the previously reinforced stimuli by color.

224
225 The chicks' preferences were retested 4-hours (T2) and 24-hours (T3) after the first
226 test. The choice for the novel patterns with elevated contrast (S') remained uniformly
227 low in both conditions, and did not differ significantly from that to S^+ , with the
228 exception of *Condition 1* where at 24 hours the preference for S^+ was significantly
229 greater than for S' (Wilcoxon matched-pairs signed-ranks comparing mean selection

230 for S' and S⁻; *Condition 1*: T2 $z = -0.96$, $p = 0.339$, $p = 0.558$; T3 $z = -2.67$, $p = 0.0075$.
231 *Condition 2*: T2 $z = -1.98$, $p = 0.052$; T3 $p = 0.783$; Figure 1B).

232

233 *Experiment 2: Responses to novel low-contrast patterns.*

234 Experiment 1 showed that chicks respond strongly to novel stimuli bearing a high-
235 contrast pattern, but quickly learn to reject the stimuli, and continue to ignore them
236 for 24 hours. Experiment 2 examined the effect of reduced contrast on responses to
237 novel stimuli, and hence distinguishes between the effects of novelty and elevated
238 contrast in Experiment 1. Here, twenty pairs of chicks were trained to red or yellow
239 tiles mixed with black and white (i.e. the high contrast S' stimulus from Experiment
240 1), and then tested with low contrast stimuli (i.e. the low contrast training stimulus S⁺
241 used in Experiment 1; Figure 1A). Analysis of deviance of the GLMMs showed that
242 neither the training color nor differences between test and training colors (i.e.
243 *Conditions 1* and *2* in Experiment 1) had an effect on novel stimulus choice at T1
244 (Color: $X^2(4) = 0.878$, $p = 0.928$; Condition: $X^2(3) = 3.162$, $p = 0.367$), and so data were
245 pooled to improve the power of subsequent tests.

246 Reduction in background contrast abolished the initial attractiveness for the novel
247 stimuli seen in Experiment 1, with S⁺ receiving around 80% of all selections at T1.
248 Peck number had no effect on choice for S' in the GLMMs ($X^2(3) = 5.745$, $p = 0.123$).
249 Mean preference for S⁺ was significantly greater than for S' at T1, T2 and T3
250 (Wilcoxon matched-pairs signed-ranks; T1: $z = 3.945$, $p = 0.00008$; T2: $z = -3.929$, $p =$
251 0.00007 ; T3: $z = -3.916$, $p = 0.00008$; Figure 1C). There was a preference for S' over
252 S⁻ at T1 (Wilcoxon matched-pairs signed-ranks; $z = 3.796$, $p = 0.0014$; Figure 1C), but
253 no preference for S' over S⁻ at T2 or T3 (T2: $p = 0.274$; T3: $z = 0.907$, $p = 0.365$; Figure
254 1C).

255

256 *Experiment 3: Effect of elevated achromatic contrast on responses to a novel color*

257 Chicks trained to two colors, such as red and yellow, generalise to intermediate
258 colors, such as orange (Jones et al., 2001; Osorio et al., 1999a). Without reward the
259 initial preference for the novel color relative to the familiar training (S⁺) stimulus is
260 sustained though the initial test (i.e. T1) but then drops (Osorio et al., 2009).

261 Experiments 3 and 4 examine the interaction between novel color and achromatic
262 contrast on the chicks' responses.

263

264 For Experiment 3, 36 pairs of chicks were trained as in Experiment 1. They were then
265 tested with orange, either in high or in low contrast conditions (i.e. as with experiment
266 1 and 2 respectively, but orange replacing red or yellow color panels for S'; Figure
267 2A). Eighteen pairs were then tested with orange mixed with same grey levels as
268 training stimuli (*Condition 1*, low contrast, S'^{lc}; Figure 2A), and 18 pairs were tested
269 with orange mixed with high contrast black and white tiles as described for S' in
270 Experiment 1 (*Condition 2*, high contrast, S'^{hc}; Figure 2A). Chicks were tested in the
271 presence of either the red or yellow training stimulus with nine pairs tested with each
272 color, and these data were pooled as analysis of deviance of GLMMs showed that
273 color had no effect on novel stimulus choice at T1 ($X^2(4) = 0.012, p = <1$).

274

275 When the novel orange color was presented with a low-contrast background
276 resembling that used for the training stimuli (*Condition 1*, S'^{lc}), the results were much
277 like those in previous studies of color generalization (Jones et al., 2001; Osorio et al.,
278 2009). In the first test (T1) the chicks showed a preference for S'^{lc} over S⁺ and S⁻
279 (Wilcoxon matched-pairs signed-ranks; $z = -3.223, p = 0.0013$; $z = 2.589, p = 0.0097$
280 respectively). However, in contrast to the rapid learning seen to elevated contrast with
281 a novel color (Experiment 1), preference for S'^{lc} was random over the 10 selections
282 and not correlated with selection number (Spearman's rank correlation; $r_s = -0.110, p =$
283 0.762). At T2 chicks showed no preference for S'^{lc} over S⁺ (Wilcoxon matched-pairs
284 signed-ranks; $z = 0.259, p = 0.795$). After 24 hours (T3) preference for S'^{lc} fell further,
285 with S⁺ significantly preferred over S'^{lc} and S⁻ (Wilcoxon matched-pairs signed-ranks;
286 $z = -2.6128, p = 0.009$ and $z = -3.6326, p = 0.003$ respectively). Thus, at least in our
287 experimental conditions, learning about color is slower than learning about elevated
288 contrast.

289

290 Presenting the novel color with high contrast components (*Condition 2*, S'^{hc})
291 markedly affected the initial choice and rate of learning; the chicks' preference for
292 S'^{hc} resembled that for a familiar color on a high-contrast background, as in
293 Experiment 1. Preference for S'^{hc} was highly correlated with selection number over
294 10 selections (Spearman's rank correlation; $r_s = -0.841, p = 0.002$; Figure 2B); in the

295 first test about 90% of initial pecks are directed at S^{hc} , but this preference dropped
296 over subsequent choices. As with Experiment 1, mean preference for S^{hc} at T1 was
297 not significantly different from S^+ because of the rapid loss of preference within the
298 trail (Wilcoxon matched-pairs signed-ranks; $z = 1$, $p = 0.379$; Figure 2B), with S^+ and
299 S^{hc} both preferred to S^- (Wilcoxon matched-pairs signed-ranks; $z = 3.614$, $p = 0.0003$
300 and $z = 3.2829$, $p = 0.001$ respectively). Choice for S^{hc} remained low at T2 and T3,
301 with S^+ greatly preferred to S^{hc} (Wilcoxon matched-pairs signed-ranks; T2: $z = -$
302 3.7364 , $p = 0.0002$; T3: $z = -3.7422$, $p = 0.0001$; Figure 2B), and no preference for S^{hc}
303 over S^- (Wilcoxon matched-pairs signed-ranks; T2: $p = 0.8633$; T3: $p = 0.1083$; Figure
304 2B). Thus the high contrast pattern enhances the rate of learning about a novel
305 stimulus, regardless of whether the color is familiar or novel.

306

307 *Experiment 4: simultaneous presentation of low and high contrast with novel color*

308 This experiment tests the effect of achromatic contrast on learning about a novel
309 color. Ten pairs of chicks were trained to red and yellow on a low contrast
310 background as in Experiments 1 and 3, and then tested with a novel orange on both
311 low (S^{lc}) and high (S^{hc}) contrast backgrounds simultaneously, along with one of the
312 two S^+ stimuli, and S^- (Figure 2A).

313

314 As expected from the results of Experiment 2, the chicks showed a strong initial
315 preference for the novel color/ high contrast stimulus at T1, with S^{hc} being chosen for
316 all first pecks. As in Experiments 1 and 3, this preference dropped sharply after the
317 first peck (significant negative correlation between preference and selection number;
318 Spearman's rank correlation; $r_s = -0.852$, $p = 0.002$), while the preference for the novel
319 color/ low contrast stimulus S^{lc} increased throughout the trial. At T1 S^{hc} was
320 preferred over S^+ and S^{lc} when considered as a mean over the 10 recorded selections
321 (Wilcoxon matched-pairs signed-ranks; $p = 0.002$ and $p = 0.002$ respectively; Figure
322 2C), but was subsequently strongly avoided over the next 24 hours (no significant
323 preference for S^{hc} over S^- at T2 or T3; Wilcoxon matched-pairs signed-ranks; $p =$
324 0.5313 and $p = 0.3125$ respectively). Preference for the novel color with a low
325 achromatic contrast declined more slowly: S^{lc} was significantly preferred to S^- at T2
326 (Wilcoxon matched-pairs signed-ranks; $p = 0.0039$) but not at T3 ($p = 0.1758$; Figure
327 2C).

328

329 **DISCUSSION**

330 When week-old chicks are trained to a single colored pattern their initial preference in
331 test is not for the training color but for elevated achromatic contrast (Osorio et al.,
332 1999a). This suggests that chicks learn color accurately, but have an unlearned
333 preference for high contrast patterns. We have found also that male chicks (though of
334 a different strain) tested under the same conditions as these experiments learn to avoid
335 a novel color after a small number of selections, but with a delay of about an hour
336 between the initial encounter and the change in preference (Osorio et al., 2009).

337

338 Here, within our experimental conditions, Experiment 1 shows that elevated
339 background contrast is not only attractive, but also greatly increases the rate of
340 learning. Experiment 2 suggests that rapid learning about elevated contrast is not an
341 effect of novelty, because it does not apply when the novel pattern is of lower contrast
342 than the training stimuli. Experiment 3 shows that rapid learning about the elevated
343 contrast occurs in the presence of a novel color. Experiment 4 indicates that the
344 effects of color and contrast are independent, because chicks that learn (in one peck)
345 to avoid a pattern including a novel color and elevated contrast then transfer their
346 attention to the novel color in a background of familiar contrast. The high contrast
347 pattern does not appear to enhance learning about the color, and may even distract
348 from it.

349

350 The procedure used in these experiments resembles natural foraging. During training
351 chicks are free to move about the test arena and to peck any of the paper cones, which
352 are arbitrarily spread across the floor (and often moved by the chicks). There is no
353 penalty for selecting an empty container, other than lost time. Previous
354 demonstrations of one-trial learning by chicks have used aversive conditioning,
355 normally a bitter taste (Roper and Cook, 1989). Here the training procedure, with
356 chicks foraging freely amongst small food containers, means that they are used to not
357 getting food each time they peck at the S^+ patterns. Thus the rapid extinction of the
358 responses to novel unrewarded stimuli can be compared to the well-known
359 observation that such intermittent reinforcement slows the rate of extinction (Hull,
360 1943), as seen here in the sustained preference for S^+ over S^- .

361

362 The findings emphasize the separate roles of color and achromatic contrast in
363 controlling how chicks respond to and learn about visual signals. Firstly, contrast is
364 not learnt accurately (without differential training), but elevated contrast strongly
365 enhances the rate of learning. Secondly, the rapid learning about high-contrast
366 patterns (Figure 1B) contrasts with the delayed effects of learning about color where
367 the elevated preference for the novel color persists for about an hour after the initial
368 extinction trial (Experiment 3; Osorio et al., 2009 (2009)). Thirdly, color is learnt
369 separately from contrast. There is no evidence here for color and contrast acting
370 synergistically to potentiate learning, as with multimodal stimuli, especially color and
371 odor (Rowe and Guilford, 1999).

372

373 A review of research into aposematic coloration (Ruxton et al., 2004) concluded that
374 little known about recognition of warning coloration patterns by predators, and that
375 virtually nothing is known about the memorability of such signals. There has been no
376 definitive demonstration that visual contrast alone accelerates simple avoidance
377 learning, irrespective of the rate at which prey are attacked. For example recent
378 studies on the role of pattern and color in appetitive learning by poultry chicks
379 (Aronsson and Gamberale-Stille, 2008; Aronsson and Gamberale-Stille, 2012) find
380 that pattern is less well learnt than color, and there is little if any potentiation of
381 avoidance learning by adding a high contrast feature to a color pattern. Previous tests
382 of single trial learning have involved a strong aversive (bitter tasting) stimulus, such
383 as methyl anthranilate or quinine. Chicks learn in a single trial to reject colored beads
384 coated with bitter tasting methyl anthranilate (Roper and Cook, 1989), but Ruxton and
385 co-authors (Ruxton et al., 2004) argue that the odor of the methyl anthranilate means
386 such a signal could be multimodal. The single learning about the simple absence of
387 food here is especially striking because the chicks are not invariably rewarded for
388 selecting stimuli in training, as the containers are often empty.

389

390 *Achromatic contrast in visual displays*

391 High contrast patterns are common in many biological communication signals but the
392 significance of achromatic contrast remains elusive. The strong effects of contrast on
393 both unlearned responses and the rate of learning suggest that they would be significant
394 in natural conditions, and could influence the evolution of achromatic contrast in
395 signals directed at birds. Related studies with poultry chicks find the opposite effect;

396 that raised contrast increases unlearned avoidance of novel patterns, i.e. the chicks
397 demonstrate neophobia (Lindstrom et al., 2001; Roper and Cook, 1989) (but see
398 Aronsson and Gamberale-Stille (2008)). As the stimuli in each case are generally
399 roughly comparable in their size and appearance it seems that this difference between
400 avoidance and attraction depends upon the context. The finding is not wholly
401 consistent with dietary conservatism being an overriding factor (Marples and Mappes,
402 2011; Marples and Kelly, 1999), as this would always predict avoidance of novelty.

403

404 Under our experimental conditions high contrast patterns appear to promote rapid
405 learning by attracting attention. Thus their unrewarded state might be more quickly
406 established due to a greater initial interaction compared to the previously rewarded
407 stimulus; the effect on the rate of learning would in this case be an encounter
408 frequency effect. Innate bias or an “enhanced novelty” effect due prior experience
409 being limited to low contrast objects could account for the initial attraction to the high
410 contrast stimulus. Therefore, while it is tempting to suggest that high contrast patterns
411 attract attention, and hence increase the general affective strength of any signal
412 including its associability (c.f. Pearce and Hall, 1980), this concept should be treated
413 with the caution in the absence of a separate measure of attention for birds.

414

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420

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- 491
- 492

493 **FIGURE CAPTIONS**

494

495 **Figure 1**

496 **A)** S^+ and S' stimuli used in Experiments 1 and 2. Experiment 1 had two test
497 conditions: *Condition 1* where the training color and the novel stimulus in the test
498 were the same, and *Condition 2* where the training color and the novel stimulus were
499 different (chicks were equally familiar with red and yellow training colors as both
500 were used in all training). Experiment 2 acted as a control for Experiment 1, testing
501 the effect of novelty on the preferences, with chicks trained to high contrast stimuli
502 and tested on low contrast. **B)** Left: Results from Experiment 1, show the relative
503 preference (proportion of selections by 36 chicks) for S' over the 10 recorded
504 selections. At T1 the chicks directed most first pecks to the novel stimulus, but that
505 this preference rapidly declined over the subsequent 9 selections. This was
506 particularly true in *Condition 2*, where the color of S^+ and S' were different. Right:
507 Mean preferences over 10 selections for S' , S^+ and S^- at T1, T2 and T3 for Condition
508 1 (upper) and Condition 2 (lower). After the initial choice for S' is lost preference for
509 this novel stimulus remains low throughout these tests (right). **C)** Results from
510 Experiment 2, showing (left) that there was no in-trial change in preference for S' at
511 T1, which remained low over the 10-peck trial, and over T2 and T3 subsequently
512 (right).

513

514 **Figure 2**

515 **A.** S^+ and S' stimuli used in Experiments 3 and 4, where an intermediate novel color
516 was introduced in either low contrast (*Condition 1*) or high contrast (*Condition 2*)
517 form during tests. In Experiment 3 these were tested separately on different pairs of
518 chicks. In Experiment 4 they were experienced simultaneously. **B.** Results for
519 Experiment 3, showing that for *Condition 1* (S'^{lc}) chicks showed a consistent elevated
520 preference for the intermediate color at T1 (left), which became slowly reduced over
521 subsequent trials (right). Chicks tested under *Condition 2* showed a great preference
522 for S'^{hc} on initial contact at T1 (left), but this preference fell rapidly within this first
523 trial, and was not recovered in subsequent trials (right). **C.** When chicks first
524 encountered the novel intermediate color in both high and low conditions
525 simultaneously, they directed all pecks at the high contrast stimulus (left). Over the 10
526 recorded selections of T1 this preference had altered, with S'^{hc} and S'^{lc} afforded equal

527 attention. Over subsequent trials (right), preference for S^{hc} did not recover, while S^{lc}
528 fell slowly.

FIGURE 1

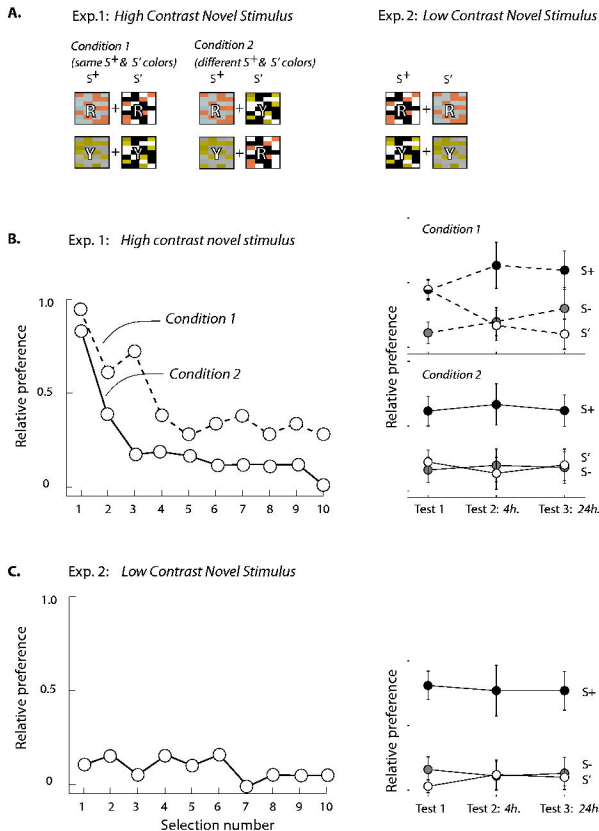
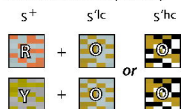
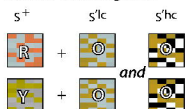


FIGURE 2

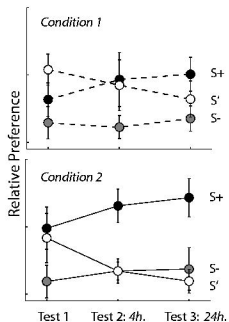
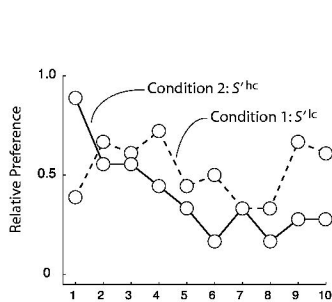
A. Exp. 3: *Novel orange low and high contrast tested seperately*



Exp. 4: *Novel orange low and high contrast tested together*



B. Exp. 3: *Novel orange low and high contrast tested seperately*



C. Exp. 4: *Novel orange low and high contrast tested together*

