RESEARCH ARTICLE

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

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SUMMARY

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

INTRODUCTION

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

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

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

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

Previous work showed that when 1 week old poultry chicks are trained appetitively to patterned food containers and then encounter a pattern bearing either a novel color or a novel achromatic contrast they have a strong fidelity to the familiar color (or, more accurately, chromaticity) but prefer elevated contrast (Osorio et al., 1999b). This observation conflicts with the finding that chicks avoid unfamiliar high contrast patterns (Roper and Cook, 1989), but is perhaps simply indicative of context dependence for such effects.

We know also that when chicks are trained to two colors, such as red and yellow, they initially prefer novel intermediate colors, in this case orange (Jones et al., 2001), but this preference is labile; if the chicks are tested in extinction (i.e. without reward), the rate

of response to the novel color declines faster than to the familiar rewarded colors (Osorio et al., 2009). The rapid learning about novel stimuli demonstrates that the chicks classify the novel color separately from the known colors (contrary to simple models of sensory generalization) (Osorio et al., 2009; Osorio et al., 1999b), and is consistent with the novel stimulus having high associability, owing to a low confidence in the predicted relationship between the color and the food reward.

These observations lead to questions about how signal design affects an animal's initial response and its subsequent learning. Does contrast in visual patterns affect unlearnt responses or learning, and are any effects due to contrast being conspicuous, unusual or simply inherently more effective? Here, we tested how changes in contrast affect poultry chicks' initial responses and subsequent learning about novel patterns. We then studied the interactions between color and contrast. We addressed two questions: first, are the strength of the initial response and the subsequent rate of learning linked, and second, does elevated contrast affect responses independently of novelty?

MATERIALS AND METHODS

Male poultry chicks, *Gallus gallus* (Linnaeus 1758) (Bovans Goldline), from a commercial hatchery lived communally from hatching to 1 week of age. The room temperature was 21°C with additional warmth from an infrared lamp under a 12 h:12 h light:dark regime. The walls of the communal enclosure were gray, the substrate was sawdust, and chicks had free access to food crumbs and water. At 1 week the chicks were rehoused as pairs in 24×27 cm cages. The birds had free access to standard food and water, except for 2 h before training or testing when food was removed. In experiments the chicks were trained and tested in pairs in a 40×30 cm arena, the floors and walls of which were painted gray, lit by an overhead 250 W tungsten–halogen light (color temperature *ca*. 3.4 K). All experimental work was carried out under UK Home Office licence.

Stimuli

Stimuli for training and testing were conical paper food containers (25 mm length, 7 mm base diameter) printed (Canon Pro9000 printer) with a stimulus pattern of 2×6 mm rectangular tiles. The tiling (created using purpose-written code in MATLAB) was either all gray (achromatic), or included tiles selected at random that were colored red, orange or yellow with a probability of 0.3. The achromatic tiles were designed at two contrast levels: (1) low contrast, with a random pattern of two tiles of the same average luminance and a Michelson contrast ($I_{max}-I_{min}/I_{max}+I_{min}$) of 0.3, and (2) high contrast, with black and white background tiles with a nominal Michelson contrast of 1.0 (the actual contrast is close to 0.85). The mean intensity of the black and white tiles was slightly lower than that for the lower contrast backgrounds, but this is very unlikely to have had any effect in this study as the chicks do not easily learn average luminance. For the low contrast condition, the mean gray-level of the achromatic tiles matched the intensity of the colored tiles for the chicks' double cones (Jones and Osorio, 2004; Osorio et al., 1999c). The colored tiles had fixed chromaticities (i.e. hue and saturation), but the brightness varied randomly with a contrast range of 0.3 (Osorio et al., 1999c). Different sets of stimuli were used for training and testing, and all the stimuli had different (random) patterns, so that the patterns were uninformative. These tiled patterns allow the chicks to learn color accurately and quickly against an achromatic background. The presence of luminance noise reduces the chance that the birds will learn the brightness rather than the chromaticity (i.e. hue and saturation of the color). Full details and rationale for the design of stimuli can be found elsewhere (Osorio et al., 1999c).

General training procedure

The experiments used up to 36 pairs of naive chicks, with a new group of chicks used in each experiment. Chicks were housed, trained and tested in pairs because they become stressed in isolation. Members of each pair were distinguishable by marking one bird with a spot on the top of the head using a permanent marker pen. Training started on day 7 after hatching. Pairs of chicks were placed in the arena with eight of the conical food containers. Four colored rewarded cones (S^+) contained standard crumbs, which the chicks could extract by pecking. The other four cones (S^-), which were entirely achromatic but otherwise similar to the rewarded stimuli, were empty. Chicks were trained to two S^+ colors that could be easily discriminated (S^{+1} and S^{+2}), which were red and yellow to the human eye. Each color was equally rewarded (see below for details of individual experiments). Training sessions lasted 6 min with rewarded stimuli refilled with food at 1 min intervals. All chicks had two training sessions a day, separated by a 2 h interval, for 3 days.

General test procedure

Tests were carried out in extinction (i.e. without reward) on the fourth day after training started (i.e. 10 days after hatching). For experiments 1–3, the arena contained nine clean printed cones: three of S^{+1} or S^{+2} (as learnt during training but without food), three of S^- and three of the novel test stimulus S′. For experiment 4 there were eight cones: two S^+, two S^-, two high contrast S′ and two low contrast S′.

We recorded the sequence of the first 10 selections made by one chick of the pair after entering the test arena. The same chick was scored in each test, and its companion was ignored. Rapid repeated pecks at a single cone were discounted as they represented a continued attempt to retrieve food from that cone rather than a further choice. Obvious incidences of mimicking the second bird's actions, where the bird being scored would see the other peck at a cone and run over to peck at the same stimulus, were also discounted. Chicks were tested on three occasions (T1–3) for each experiment to assess initial responses and subsequent learning about the novel stimulus (Osorio et al., 2009): T1 at 24 h after the final training session, T2 at 4 h after T1, and T3 at 24 h after T1. Food was provided between T2 and T3 and removed 2 h before testing.

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

Statistical analyses were carried out in MATLAB R2012b (MathWorks, 2012) and R v2.14.0 using the lme4 package (R Development Core Team, 2008). Mean responses over 10 stimulus selections were compared using Wilcoxon matched-pairs signed-rank tests (two-tailed). Within-trial S′ preferences were tested using generalized linear mixed models (GLMMs), with color, condition and peck (at 10 levels) as fixed factors and individual chick as a random factor, and a binomial error term. Models were then tested using analysis of deviance. Correlation between choice and peck order was tested with Spearman's rank correlation in SPSS (SPSS Inc., Chicago, IL, USA).

RESULTS
Experiment 1: responses to novel high contrast patterns

This experiment examined how elevated contrast affects the initial responses to and learning about novel stimuli. We trained 36 pairs of chicks to both red (S^{+1}) and yellow (S^{+2}) patterns with low contrast (range 0.3) gray backgrounds. The unrewarded training stimuli (S^-) were similar to the S^+, but all gray. The tests compared chicks' responses to the S^- and S^+ training stimuli with their responses to novel (S') stimuli with the familiar training colors, but having the low contrast gray tiles replaced with black and white tiles [i.e. high contrast: S'^1 (red) and S'^2 (yellow), respectively]. There were two test conditions: condition 1 (N=18) where the S^+ and S' stimuli had the same color (i.e. both either red or yellow: S^{+1} with S'^1 or S^{+2} with S'^2; Fig. 1A), and condition 2 (N=18) where the S^+ and S' colors were different (i.e. one red and the other yellow: S^{+1} with S'^2 or S^{+2} with S'^1; Fig. 1A). In the first test (T1), condition proved to have a highly significant effect on the preference for S' over the first 10 selections (GLMM analysis of deviance; χ^2_3=19.39; P=0.0002), hence we analysed them separately. However, S^+ color *per se* proved to have no effect on stimulus preference (GLMM analysis of deviance; χ^2_4=0.04; P=0.99). We therefore pooled the red and yellow responses for each condition to improve the power of our subsequent tests.

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

Mean stimulus choice across 10 selections at T1 for condition 1 showed no significant preference for S^+ over S' (Wilcoxon matched-pairs signed-ranks; z=32, P>1). For condition 2 there appeared to be a strong preference for S^+ over S' (Wilcoxon matched-pairs signed-ranks; z=–3.64, P=0.0003), which can be explained by the very rapid extinction of and subsequent low preference following initial preference for S' (see above and Fig. 1B). A simple explanation for the difference between condition 1 and condition 2 is that chicks were more readily able to distinguish the novel from the previously reinforced stimuli by color.

The chicks preferences were retested 4 h (T2) and 24 h (T3) after the first test. The choice for the novel patterns with elevated contrast
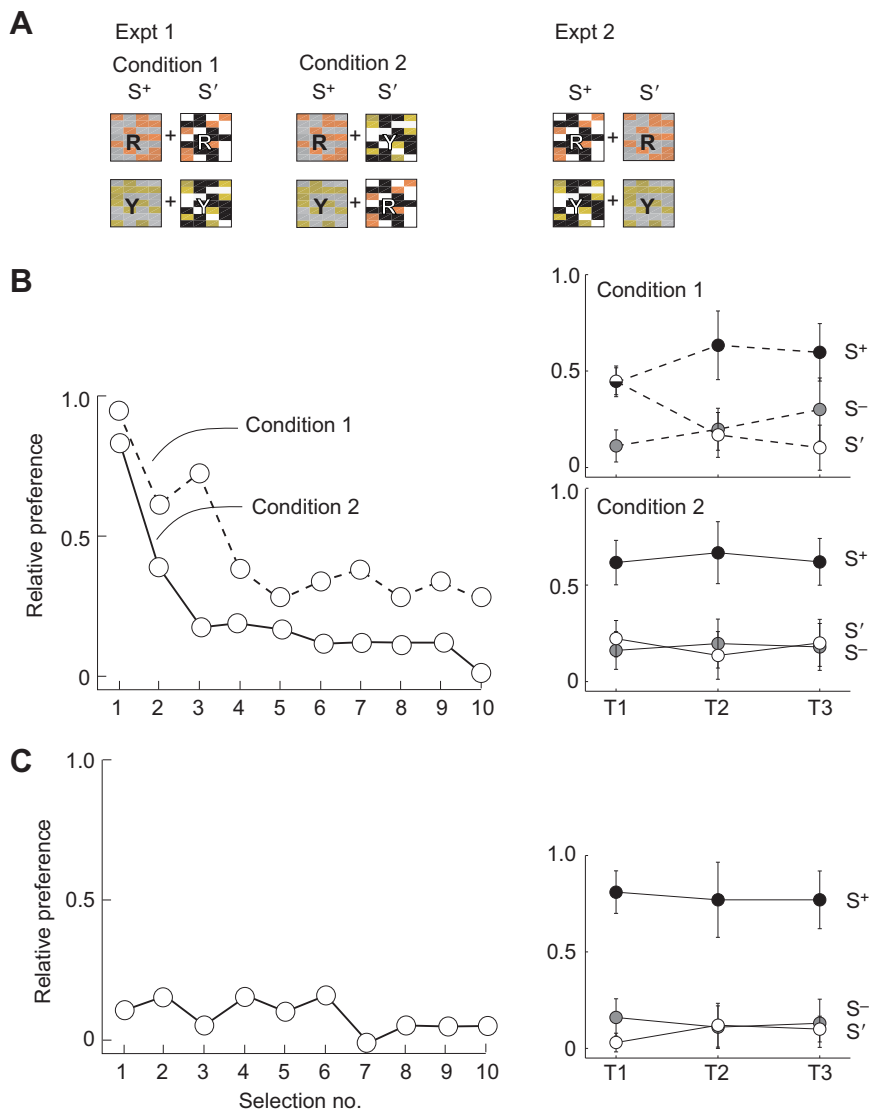

Fig. 1. (A) S^+ and S' stimuli used in experiment 1 (high contrast novel stimulus) and experiment 2 (low contrast novel stimulus). Experiment 1 had two test conditions: condition 1 where the training color (S^+) and the novel stimulus (S') in the test were the same, and condition 2 where the training color and the novel stimulus were different (chicks were equally familiar with red and yellow training colors as both were used in all training). Experiment 2 acted as a control for experiment 1, testing the effect of novelty on the preferences, with chicks trained to high contrast stimuli and tested on low contrast stimuli. R, red; Y, yellow. (B) Left: results from experiment 1, showing the relative preference (proportion of selections by 36 chicks) for S' over the 10 recorded selections. At test 1 (T1) the chicks directed most first pecks to the novel stimulus, but this preference rapidly declined over the subsequent nine selections. This was particularly true in condition 2, where the colors of S^+ and S' were different. Right: relative preference over 10 selections for S', S^+ and S^- at T1, T2 (4 h after T1) and T3 (24 h after T1) for condition 1 (upper) and condition 2 (lower). After the initial choice for S' is lost, preference for this novel stimulus remains low throughout these tests. (C) Results from experiment 2, showing (left) that there was no in-trial change in preference for S' at T1, which remained low over the 10 peck trial, and over T2 and T3 subsequently (right).

(S′) remained uniformly low in both conditions, and did not differ significantly from that for S$^-$, with the exception of condition 1 where at 24 h the preference for S$^-$ was significantly greater than that for S′ (Wilcoxon matched-pairs signed-ranks comparing mean selection for S′ and S$^-$; condition 1: T2 $z=-0.96$, $P=0.339$; T3 $z=-2.67$, $P=0.0075$; condition 2: T2 $z=-1.98$, $P=0.052$; T3 $P=0.783$; Fig. 1B).

Experiment 2: responses to novel low contrast patterns

Experiment 1 showed that chicks respond strongly to novel stimuli bearing a high contrast pattern, but quickly learn to reject the stimuli, and continue to ignore them for 24 h. Experiment 2 examined the effect of reduced contrast on responses to novel stimuli, and hence distinguishes between the effects of novelty and elevated contrast in experiment 1. Here, 20 pairs of chicks were trained to red or yellow tiles mixed with black and white (i.e. the high contrast S′ stimulus from experiment 1), and then tested with low contrast stimuli (i.e. the low contrast training stimulus S$^+$ used in experiment 1; Fig. 1A). Analysis of deviance of the GLMMs showed that neither the training color nor differences between test and training colors (i.e. conditions 1 and 2 in experiment 1) had an effect on novel stimulus choice at T1 (color: $\chi^2_4=0.878$, $P=0.928$; condition: $\chi^2_3=3.162$, $P=0.367$), and so data were pooled to improve the power of subsequent tests.

Reduction in background contrast abolished the initial attractiveness for the novel stimuli seen in experiment 1, with S$^+$ receiving around 80% of all selections at T1. Peck number had no effect on choice for S′ in the GLMMs ($\chi^2_3=5.745$, $P=0.123$). Mean preference for S$^+$ was significantly greater than for S′ at T1, T2 and T3 (Wilcoxon matched-pairs signed-ranks; T1: $z=3.945$, $P=0.00008$; T2: $z=-3.929$, $P=0.00007$; T3: $z=-3.916$, $P=0.00008$; Fig. 1C). There was a preference for S$^-$ over S′ at T1 (Wilcoxon matched-pairs signed-ranks; $z=3.796$, $P=0.0014$; Fig. 1C), but no preference for S$^-$ over S′ at T2 or T3 (T2: $P=0.274$; T3: $z=0.907$, $P=0.365$; Fig. 1C).

Experiment 3: effect of elevated achromatic contrast on responses to a novel color

Chicks trained to two colors, such as red and yellow, generalize to intermediate colors, such as orange (Jones et al., 2001; Osorio et al., 1999a). Without reward, the initial preference for the novel color relative to the familiar training (S$^+$) stimulus is sustained through the initial test (i.e. T1) but then drops (Osorio et al., 2009). Experiments 3 and 4 examined the interaction between novel color and achromatic contrast on the chicks' responses.

For experiment 3, 36 pairs of chicks were trained as in experiment 1. They were then tested with orange, either in high or in low contrast conditions (i.e. as with experiment 1 and 2, respectively, but with orange replacing red or yellow color panels for S′; Fig. 2A). Eighteen pairs were then tested with orange mixed with the same grey levels as the training stimuli (condition 1, low contrast, S′^{lc}; Fig. 2A), and 18 pairs were tested with orange mixed with high contrast black and white tiles as described for S′ in experiment 1 (condition 2, high contrast, S′^{hc}; Fig. 2A). Chicks were tested in the presence of either the red or yellow training stimulus with nine pairs tested with each color, and these data were pooled as analysis of deviance of GLMMs showed that color had no effect on novel stimulus choice at T1 ($\chi^2_4=0.012$, $P\leq1$).

When the novel orange color was presented with a low contrast background resembling that used for the training stimuli (condition 1, S′^{lc}), the results were much like those in previous studies of color generalization (Jones et al., 2001; Osorio et al., 2009). In the first test (T1) the chicks showed a preference for S′^{lc} over S$^+$ and S$^-$ (Wilcoxon matched-pairs signed-ranks; $z=-3.223$, $P=0.0013$;

$z=2.589$, $P=0.0097$, respectively; Fig. 2B). However, in contrast to the rapid learning seen with elevated contrast with a novel color (experiment 1), preference for S′^{lc} was random over the 10 selections and not correlated with selection number (Spearman's rank correlation; $r_s=-0.110$, $P=0.762$). At T2, chicks showed no preference for S′^{lc} over S$^+$ (Wilcoxon matched-pairs signed-ranks; $z=0.259$, $P=0.795$; Fig. 2B). After 24 h (T3), preference for S′^{lc} fell further, with S$^+$ significantly preferred over S′^{lc} and S$^-$ (Wilcoxon matched-pairs signed-ranks; $z=-2.6128$, $P=0.009$; $z=-3.6326$, $P=0.003$, respectively; Fig. 2B). Thus, at least in our experimental conditions, learning about color is slower than learning about elevated contrast.

Presenting the novel color with high contrast components (condition 2, S′^{hc}) markedly affected the initial choice and rate of learning; the chick S′ preference for S′^{hc} resembled that for a familiar color on a high contrast background, as in experiment 1. Preference for S′^{hc} was highly correlated with selection number over 10 selections (Spearman's rank correlation; $r_s=-0.841$, $P=0.002$; Fig. 2B); in the first test about 90% of initial pecks are directed at S′^{hc}, but this preference dropped over subsequent choices. As with experiment 1, mean preference for S′^{hc} at T1 was not significantly different from that for S$^+$ because of the rapid loss of preference within the trial (Wilcoxon matched-pairs signed-ranks; $z=1$, $P=0.379$; Fig. 2B), with S$^+$ and S′^{hc} both preferred over S$^-$ (Wilcoxon matched-pairs signed-ranks; $z=3.614$, $P=0.0003$; $z=3.2829$, $P=0.001$, respectively). Choice for S′^{hc} remained low at T2 and T3, with S$^+$ greatly preferred to S′^{hc} (Wilcoxon matched-pairs signed-ranks; T2: $z=-3.7364$, $P=0.0002$; T3: $z=-3.7422$, $P=0.0001$; Fig. 2B), and no preference for S′^{hc} over S$^-$ (Wilcoxon matched-pairs signed-ranks; T2: $P=0.8633$; T3: $P=0.1083$; Fig. 2B). Thus, the high contrast pattern enhances the rate of learning about a novel stimulus, regardless of whether the color is familiar or novel.

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

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

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

DISCUSSION

When 1 week old chicks are trained to a single colored pattern, their initial preference in a test is not for the training color but for elevated
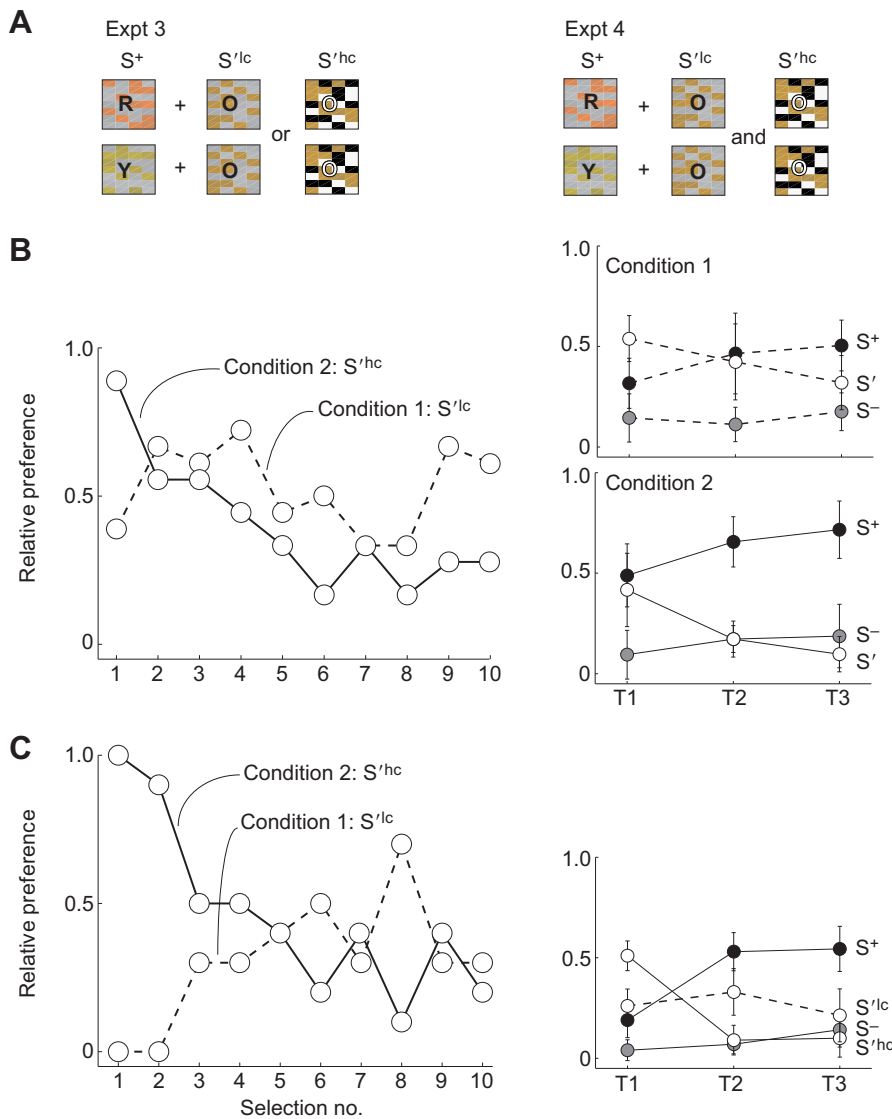
A

Expt 3

Expt 4

B

Fig. 2. (A) S$^+$ and S′ stimuli used in experiments 3 and 4, where an intermediate novel color (orange) was introduced in either low contrast (lc, condition 1) or high contrast (hc, condition 2) form during tests. In experiment 3 these were tested separately on different pairs of chicks. In experiment 4 they were experienced simultaneously. R, red; Y, yellow; O, orange. (B) Results for experiment 3, showing that for condition 1 (S′^{lc}) chicks had a consistent elevated preference for the intermediate color at T1 (left), which became slowly reduced over subsequent trials (right). Chicks tested under condition 2 showed a great preference for S′^{hc} on initial contact at T1 (left), but this preference fell rapidly within this first trial, and was not recovered in subsequent trials (right). (C) When chicks first encountered the novel intermediate color in both high and low conditions simultaneously, they directed all pecks at the high contrast stimulus (left). Over the 10 recorded selections of T1 this preference had altered, such that S′^{hc} and S′^{lc} afforded equal attention. Over subsequent trials (right), preference for S′^{hc} did not recover, while S′^{lc} preference fell slowly.

C

achromatic contrast (Osorio et al., 1999a). This suggests that chicks learn color accurately, but have an unlearnt preference for high contrast patterns. We have found also that male chicks (though of a different strain) tested under the same conditions as in these experiments learn to avoid a novel color after a small number of selections, but with a delay of about an hour between the initial encounter and the change in preference (Osorio et al., 2009).

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

The procedure used in these experiments resembles natural foraging. During training, chicks are free to move about the test

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

The findings emphasize the separate roles of color and achromatic contrast in controlling how chicks respond to and learn about visual signals. Firstly, contrast is not learnt accurately (without differential training), but elevated contrast strongly enhances the rate of learning. Secondly, the rapid learning about high contrast patterns (Fig. 1B) contrasts with the delayed effects of learning about color, where the elevated preference for the novel color persists for about an hour after the initial extinction trial (experiment 3) (Osorio et al., 2009). Thirdly, color is learnt separately from contrast. There is no evidence here for color and

contrast acting synergistically to potentiate learning, as with multimodal stimuli, especially color and odor (Rowe and Guilford, 1999).

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

Achromatic contrast in visual displays

High contrast patterns are common in many biological communication signals but the significance of achromatic contrast remains elusive. The strong effects of contrast on both unlearnt responses and the rate of learning suggest that they would be significant in natural conditions, and could influence the evolution of achromatic contrast in signals directed at birds. Related studies with poultry chicks find the opposite effect; that raised contrast increases unlearnt avoidance of novel patterns, i.e. the chicks demonstrate neophobia (Lindström et al., 2001; Roper and Cook, 1989) (but see Aronsson and Gamberale-Stille, 2008). As the stimuli in each case are generally roughly comparable in their size and appearance, it seems that this difference between avoidance and attraction depends upon the context. The finding is not wholly consistent with dietary conservatism being an overriding factor (Marples and Mappes, 2011; Marples and Kelly, 1999), as this would always predict avoidance of novelty.

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

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