



Receiver bias for colourful signals

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Animals tend to respond more strongly to signals that are more colourful and such signals are also common in nature. This is the first study to explore experimentally the possibility that response biases arising in an animal's recognition mechanisms can explain these findings. We trained domestic fowls, *Gallus gallus domesticus*, to respond by pecking or not pecking to different colours displayed on a touch-sensitive computer screen. The colours changed in response to the birds' choices, which mimicked a simple evolutionary process. Discrimination training generated response biases for the colours more distinct from the nonrewarding colour. As a result the signals evolved towards distinct coloration. The biases developed in directions towards more intense and towards less intense colour, depending on the colour of the nonrewarding stimulus. The result may be applicable to all sorts of visual signals encountered during the same kind of experiences, that is, when one signal should be avoided and another should be approached.

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The inclination of animals to react more strongly to more bright or colourful (high saturation or chroma) stimuli has been demonstrated in species of various taxa, especially in experiments concerning mate choice (Ryan & Keddy-Hector 1992), but also in the avoidance of aposematic prey by predators (Gamberale & Tullberg 1996, 1999) or egg retrieving by birds (Baerends & Drent 1982). Such responding is a plausible evolutionary cause of the widespread occurrence of colourful signals. The intriguing question, however, is why animals have this inclination. The receiver bias hypothesis offers an explanation that is applicable to all contexts in which visual displays occur (reviewed by Endler & Basolo 1998; Enquist & Arak 1998; Ryan 1998). According to this hypothesis, a bias inherent in the animals' recognition mechanisms is a sufficient explanation for the evolution of exaggerated signals such as bright or saturated coloration (Ryan et al. 1990; Enquist & Arak 1998). Empirical data unambiguously show that animals will respond more strongly to certain novel variants of stimuli (Purtle 1973; Mackintosh 1974; Ghirlanda & Enquist 2003). This biased responding has been referred to as supernormal stimuli in ethology (Tinbergen 1948) and as peak shifts in psychology (Hanson 1959; Mackintosh 1974). Despite different terminology, both concepts seem to refer to the same phenomenon and appear both when responding is learned and when it is genetically

determined (Hogan et al. 1975; Ghirlanda & Enquist 2003). Data show that the direction and magnitude of such receiver bias can be predicted from knowledge about the individual's or the species' experiences of similar stimuli (Spence 1937; Mackintosh 1974). For instance, an animal trained to peck a slightly red key but not a grey one will respond more strongly to a more saturated red. Theoretical work suggests that such bias can explain both the initial evolution and the maintenance of visual signals that are both colourful and distinct from other stimuli (Leimar et al. 1986; Weary et al. 1992; Enquist & Arak 1994, 1998). The present study is an attempt to evaluate this hypothesis empirically.

Our study was inspired by computer simulation of colour evolution in arms races between signals and receivers. Enquist & Arak (1998) showed that receiver biases could drive evolution towards distinct coloration. Their simulations were conducted with simplified models of receiver mechanisms: feed-forward artificial neural networks. We repeated some of these simulations using real animals as receivers while keeping the signal electronic. Generally, there is a lack of empirical studies of the receiver bias hypothesis compared with other theories of signal evolution. Existing empirical studies of receiver bias have used comparative methods to identify biases that have emerged prior to the signal (Basolo 1990; Ryan et al. 1990). However, no one has yet tried to study the actual process by investigating the effect of peak shift on the evolution of colours when driven by live animals.

Colours that humans perceive as colourful are generated by light spectra that strongly stimulate one or

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two of our three light receptors (red, green and blue) while not stimulating the remaining ones. Such colours are often referred to as saturated or chromatic (Coren et al. 1999). Colour vision in other animals does not exactly correspond to that of humans but is still based on a limited number of receptors distributed over a range of light frequencies (see Varela et al. 1993 regarding colour vision in birds). Two colours that stimulate different light receptors in humans will also mainly stimulate different receptors in a bird such as the domestic fowl, *Gallus gallus domesticus*. We trained domestic fowls to discriminate between rewarding and nonrewarding colour signals that were displayed on a peck-sensitive computer screen. The colours varied along the green-cyan dimension and were created by mixing intense green with varying amounts of blue. Discrimination that occurs along such an intensity dimension (amount of blue) is likely to generate a strong response bias (Mackintosh 1974). With two complementary experiments we assessed the potential role of the fowl's receiver bias on signal evolution by letting its choices of signal drive the succeeding evolution of the colour. Stimuli eliciting more pecks continued to be displayed, while the others stopped being displayed, a method developed by Forkman & Enquist (2000).

GENERAL METHODS

Subjects and Housing

Twelve chickens (one male and 11 females) were brought to the laboratory as newly hatched and started in the experiment at 4–6 months. Each cage (1 × 1 × 1 m) was equipped with sawdust bedding, a perch and a water bowl, and housed one to three birds. All cages were placed in a laboratory room, at 20°C, with windows providing daylight (the study was conducted in January) in addition to a 12:12 h light:dark artificial light cycle. The birds were given free access to water, except during the experimental sessions, and free access to food (commercial chicken pellets) after their daily session for the rest of the day. Food access was completely free during the session-free weekends. This is a very low restriction schedule, compared to those normally used in operant conditioning experiments, which typically involves keeping the animals at 80–90% of their ad libitum body weight. The use of the current schedule ensured that the birds remained at their ad libitum body weight and were still motivated to work for food (B. Forkman, unpublished data). The study was approved by 'Stockholms norra försöksdjursetiska nämnd' Dnr: N148/98 (the relevant Swedish authority).

Test Equipment

The birds were tested in an operant chamber placed in front of a touch-sensitive PC-computer screen (Philips 15 inches, Digital Autoscan Colour Monitor, 105S). The computer registered all pecks made on the screen. The chamber (40 × 50 cm and 44 cm high), was made of a wooden frame coated with chicken wire. A feeder

delivered food rewards in a feeding tray (12 × 3 cm) fixed in the lower right corner of the computer screen. The displayed stimuli, or the background colour of the computer screen, served as the only light sources in the experimental room. Before the experiment, we measured the reflectance spectra of the colours included in the experiment, with a S1000-2LOS25U spectrometer (Ocean Optics, Dunedin, FL, U.S.A.). The green screen colour had one distinct intensity peak at 520 nm. Cyan, which is generated by combining green and blue, had two peaks, one corresponding to green and one equally distinct at 444 nm, corresponding to blue. (We use the words green and cyan because it is convenient, and we do not imply that the chickens had such experiences.) The matter of interest is the relative change in stimulation of the different receptors of the birds' eyes caused by the change in colour, and the two wavelengths used (444 and 520 nm) clearly stimulate different light receptors in the domestic fowl (Zeigler & Bischof 1993).

Shaping Procedure

Before the experiment, the birds were trained to peck on the computer screen by differential reinforcement for about 5–10 min per day. This means that they were initially rewarded with mealworms for all attempts to approach the screen. They were then rewarded with commercial pellets for attempts to peck on the screen. Finally, they were rewarded only for pecks within an area of 20 mm of a grey spot (7 mm in diameter) displayed on different locations on the screen. When a bird had met the criterion of pecking 70% of all pecks within the allowed area in three consecutive sessions we considered it to be ready for the experiment.

Experimental Stimuli

The stimuli consisted of round coloured spots, 7 mm in diameter, which we displayed six at a time in six fixed evenly dispersed locations on the computer screen, 5 and 10 cm from the top of the screen. At each new trial, each stimulus was randomly assigned for any of the locations. However, to prevent place preferences, the location of the previously pecked rewarding stimulus became unavailable for any rewarding stimuli in the successive trial. The stimuli could take any of 11 hues, which we produced by using the Red, Green and Blue (RGB) colour model. All hues were along the colour dimension between green and cyan. Thus, the red colour was never used. The RGB model is implemented on computers where each of the three colours is assigned a numerical value between 0 and 255, higher values corresponding to greater colour intensity. Using this model, we produced the cyan colour by combining the maximum amount of blue (B=255) with the maximum amount of green (G=255). To produce the other 10 colours, we kept green at maximum (G=255) while varying the amount of blue, creating a series of colours that ranged from cyan to green. The amount of blue was changed in steps of 25 units. Thus, we varied only the amount of blue. We conducted two

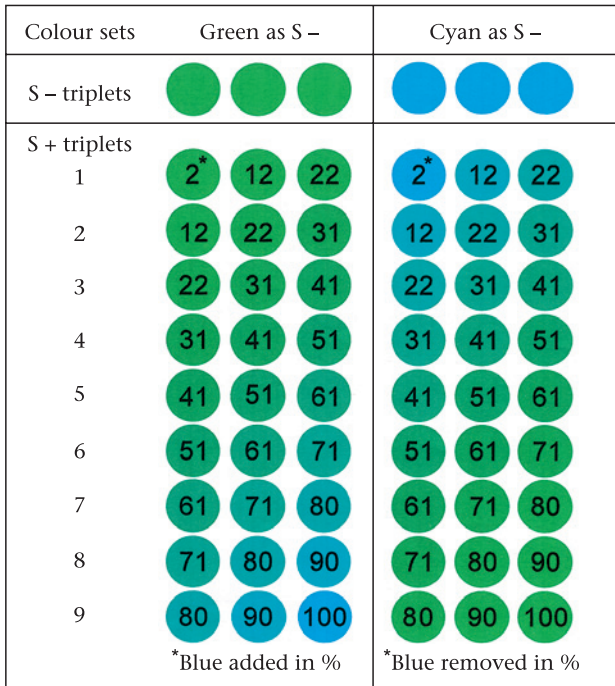


Figure 1. The two sets of rewarding (S₊) and nonrewarding (S₋) stimulus triplets used.

experiments; the few methodological differences are described in connection with the particular experiment.

The six simultaneously displayed stimuli consisted of one triplet with rewarding stimuli (S₁₊, S₂₊, S₃₊) and one triplet with nonrewarding stimuli (S₁₋, S₂₋, S₃₋). All stimuli of a nonrewarding triplet were identically coloured and never changed. In contrast, all stimuli of a rewarding triplet varied slightly in colour. Between S₁₊ and S₂₊ the difference was 25 units of blue and between S₁₊ and S₃₊ 50 units. In addition, the total amount of blue within the rewarding triplet could change during the experiment. We used two different colour sets for different groups of birds. In set 1, green was the colour of the nonrewarding triplet and blue was added to the stimuli in the rewarding triplet when the stimuli evolved. In set 2, cyan was the colour of the nonrewarding triplet and blue was removed from the rewarded stimuli. This means that each group of birds worked with nine differently coloured rewarding stimulus triplets combined with one nonrewarding triplet. **Figure 1** shows the different hues and amount of blue within the triplets.

Recording of Pecks and Colour Evolution

The birds were tested once a day except at weekends. Sessions lasted for about 20 min. The first session, of both experiments, started with the nonrewarding stimulus triplet displayed together with the rewarding stimulus triplet number 1, that is, the triplet containing colours most similar to the nonrewarding triplet (**Fig. 1**). During a trial, all stimuli were shown for 10 s or until the bird pecked on any stimulus. If the bird did not peck at all, the stimuli disappeared and were repeated after 2 s. Only

Table 1. Algorithm for updating the rewarding stimulus triplet

Current triplet (T ₀)	Number of pecks on	New triplet (T)
1	(S ₁₊) ≥ (S ₃₊) (S ₁₊) < (S ₃₊)	1 2
2–8	(S ₁₊) > (S ₃₊) (S ₁₊) = (S ₃₊) (S ₁₊) < (S ₃₊)	T ₀ - 1 T ₀ T ₀ + 1
9	(S ₁₊) > (S ₃₊) (S ₁₊) ≤ (S ₃₊)	8 9

pecks within an area of 20 mm of each symbol were accepted as choices and only one peck per trial was registered. If the bird pecked on any of the nonrewarding stimuli, the symbols disappeared while the screen background remained black for 7 s and no reward was given. Nothing happened if the bird pecked on the background. If the bird pecked on any of the rewarding stimuli, the symbols disappeared and the screen turned white for 9 s. The white screen light made it possible for the birds to see the delivered reward, 0.65 g of commercial pellets per correct response. The same rewarding stimulus triplet was shown repeatedly until the bird had pecked on any of the stimuli in that triplet for five separate trials. The five pecks were automatically evaluated. If the majority of pecks had been to S₃₊, that is, the colour most different from the nonrewarding triplet, a rewarding triplet of higher number was displayed on the next trial. Vice versa, a preference for S₁₊ generated a display of a lower triplet. In contrast, a lack of preference for S₁₊ or S₃₊ generated a repetition of the same triplet. In other words, the criterion for the colour to evolve in either direction was the bird's expression of a preference for any of the two extreme colours (S₁₊ or S₃₊) in a triplet. A triplet could never evolve more than one step at a time in either direction; nor could it evolve below triplet number 1 or beyond number 9. **Table 1** shows the calculation rules for evolution of the rewarding stimulus triplets.

EXPERIMENT 1

Methods

Six fowls were randomly divided into two groups, the green group (green as nonrewarding colour) and the cyan group (cyan as nonrewarding colour) with three birds in each. The experiment proceeded over 20 sessions, each session consisting of a series of trials invoking one rewarding and one nonrewarding stimulus triplet (**Fig. 1**). Within a session the colour evolved in response to the bird's choices according to the algorithm in **Table 1**. The colour was reset prior to each daily session. Thus, each session of the experiment always started with rewarding stimulus triplet number 1.

Results

The cyan group and the green group behaved similarly and no significant differences were found between them

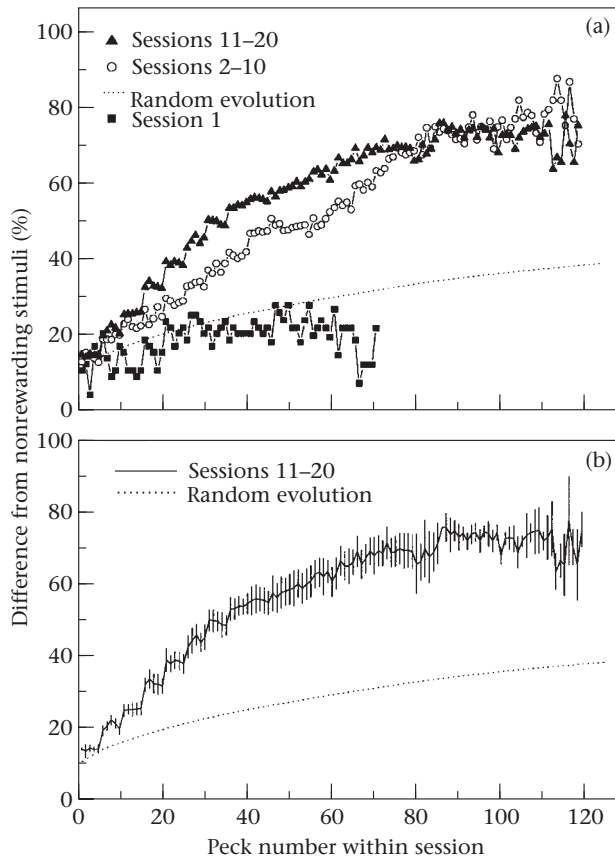


Figure 2. Difference (%) from the nonrewarding stimuli as a function of peck number within a session in experiment 1. Each data point is the average for the six subjects (because of variation between individuals in number of pecks per session N is less than six in the last data points). The expected evolution under random choice is indicated (see text). (a) The development of the result. (b) The standard error of the estimate for sessions 11–20.

(see below). In most analyses given below, data from both groups are combined to simplify the presentation and create larger sample sizes. During the first day the pecking on any rewarding colour was limited and random. Thus, the colour did not evolve in session 1 (Fig. 2a). However, from session 2 onwards the evolution changed directionally and more rapidly, with the colour continuously becoming more distinct from the nonrewarding colour. The average difference from the nonrewarding stimuli during the last 20 pecks in sessions 11–20 \pm SE was $70.7 \pm 3.0\%$ ($N=6$). Means for the two groups separately did not reveal any difference between them (green: $70.1 \pm 4.3\%$, $N=3$; cyan: $71.2 \pm 5.0\%$, $N=3$; two-sample t test: $t_4=0.17$, $P=0.88$). A comparison between random evolution driven by random choice and the evolution driven by the birds shows considerable differences (Fig. 2a).

Since the colour could never evolve beyond the fixed minimum and maximum values of stimulus triplets 1 and 9 (Fig. 1), floor and ceiling effects need to be considered when evaluating this result. To obtain the expected change under random pecking we simulated 100 000 sessions using the same program that normally controlled

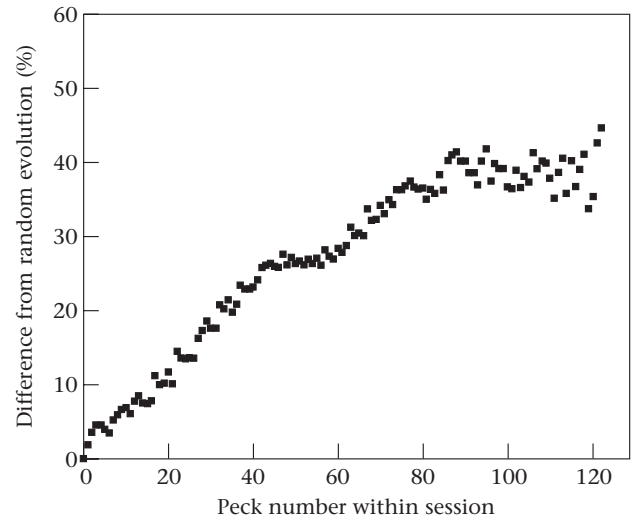


Figure 3. Difference between observed evolution and evolution expected under random choice for sessions 2–20, in experiment 1. Data are the same as in Fig. 2a.

the experimental apparatus but generated random pecks instead of touch screen events (Fig. 2). In Fig. 3 the change expected from random choice is subtracted from the experimental data to allow us to see directly the result of the birds' biases on the evolution of the signal. Random choice could not explain all the evolution away from the nonrewarding stimuli. The average difference from the nonrewarding stimuli during the last 20 pecks in sessions 11–20 \pm SE was $70.7 \pm 3.0\%$ ($N=6$), which is significantly higher than the 36.6% (peck 100–119) expected under random choice (one-sample t test: $t_5=11.5$, $P<0.0001$). Thus, the birds' biases had a significant effect on the evolution of the colour.

The evolution of the colour implies that the birds developed a bias for the hue most different from the nonrewarding colour. Analysis of choices within the colour triplets also revealed such biases (Fig. 4). The bias also grew stronger during the experiment (Spearman rank correlation: $r_s=0.75$, $N=20$, $P<0.00015$). Analysing biases in the green and cyan group separately did not suggest any difference between them.

EXPERIMENT 2

Methods

Three new birds were assigned to an experimental group and three new birds to a control group. Our aim in the second experiment was partly to mimic a more authentic evolutionary course by allowing the colour to evolve continuously throughout the experiment. Thus, we did not reset the evolution of the rewarding stimulus triplet prior to the next session. In contrast, each bird started its daily session with the rewarding triplet displayed at the end of the previous session. Partly, the aim was to assess the effect of the nonrewarding colour. Thus, the control group could choose between any of the stimuli only in the rewarding stimulus triplets, whereas

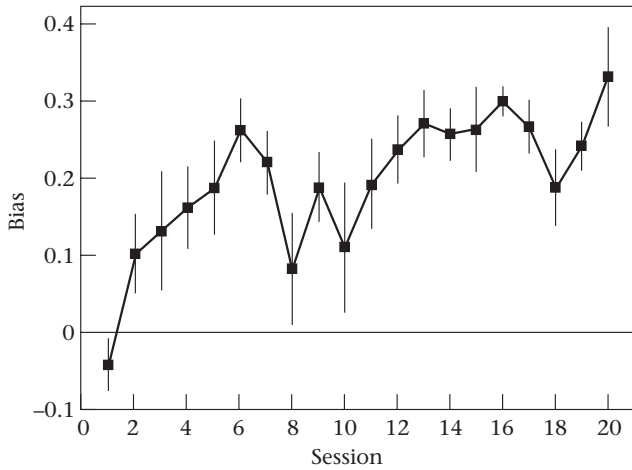


Figure 4. Response bias as a function of session in experiment 1. Each data point is the average for the six subjects. Vertical lines indicate SE. The bias was calculated by the formula $(N_{3+} - N_{1+})/N$ (i.e. pecks on S_{1+} (the stimulus most similar to the nonrewarding stimuli) were subtracted from the pecks on S_{3+} (the stimulus most different from the nonrewarding stimuli) and divided by the total number of pecks). A negative value indicates a tendency to prefer a less different colour and a positive value a preference for a more different colour.

the experimental group could choose between both rewarding and nonrewarding stimulus triplets. The colours evolved from the birds' choices according to the same principle as in experiment 1, and as previously described in the General methods (see also Table 1). A total of 500 pecks on any rewarding stimulus was obtained from each bird. All other procedures were identical with experiment 1.

Results

The amount of blue in the evolving stimuli initially decreased in both groups. However, the evolution soon levelled off in the control group, which did not have any nonrewarding stimuli, whereas it continued to evolve further towards green in the presence of the nonrewarding cyan stimuli (Fig. 5). In the second half of the experiment (pecks 251–500) the levels were roughly constant in the two groups. On average the difference from cyan along the cyan–green dimension for the evolving colour \pm SE was $67.8 \pm 4.7\%$ ($N=3$) in the experimental group and $29.3 \pm 1.3\%$ ($N=3$) in the control group. This difference between the experimental group and control group is statistically significant (two-sample t test: $t_4=7.93$, $P<0.0007$). Since the small sample sizes are a concern we tested whether we can trust the obtained P value. The t test assumes that population distributions are normal and have equal variances but it is also well established that the test is robust towards deviations from these assumptions (e.g. Quinn & Keough 2002). We applied transformations, arcsine and tangent, the first of which is known to normalize proportions, without the magnitude of the P value being affected. Applying the Welch test (e.g. Quinn & Keough 2002), which does not

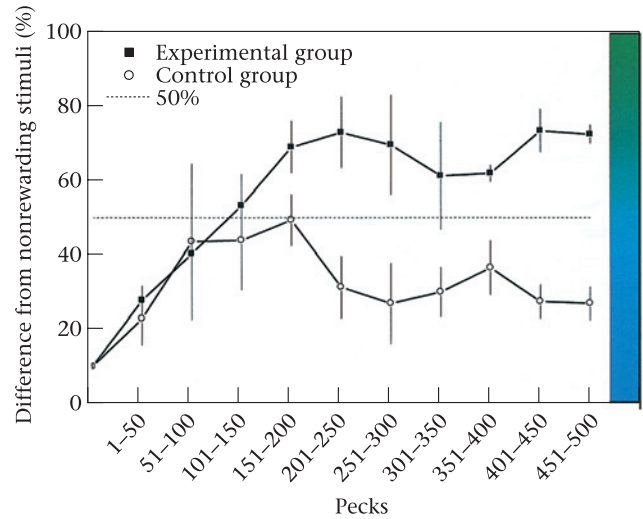


Figure 5. Difference (%) from the nonrewarding stimuli as a function of peck number in experiment 2. Each data point is the average of the three subjects in the control group or in the experimental group. Vertical lines indicate SE.

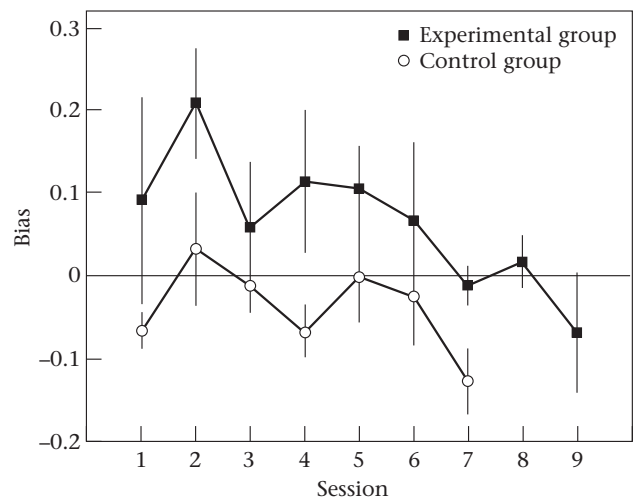


Figure 6. Response biases as a function of rewarding stimulus triplet in experiment 2. Increasing triplet number equals increasing difference from the nonrewarding triplet. Each data point is the average of the three subjects in the control group or in the experimental group. Vertical lines indicate SE. See Fig. 4 for definition of bias.

assume equal variances, we still obtain a strong result ($P<0.0075$). In addition, we studied two similar data sets, collected independently of the present one, without detecting any deviations from normality and the observed variances were similar in all samples.

The observed biases in responding (Fig. 6) are consistent with the result described in Fig. 5. The bias, of both groups, decreased along with the rewarding stimulus triplets and eventually became negative. This shape of the biases explains how a stable colour level was maintained. As long as the bias was positive the colour evolved away from the nonrewarding colour. When the bias eventually became negative the direction of evolution reversed. These dynamics will maintain a given colour level. In the experimental group the bias changed from positive to

negative around triplet 7 corresponding to a difference of 70% (from the nonrewarded colour), which is close to the evolved value of 67.8% (Fig. 5). In the control group the only positive bias was obtained for triplet 2, corresponding to 22% in contrast to the evolved value of 29.3%.

DISCUSSION

In both experiments the birds developed a bias for the colour more distinct or different from the nonrewarding colour. More precisely, among the three rewarding colours of each trial, the birds preferred the colour most different from the nonrewarding colour. This bias decreased when the difference between rewarding and nonrewarding colours became larger. The design of experiment 1 allows us to follow the development of the bias in time. No bias could be detected in the first session; but it clearly existed in the second. Over the remaining 18 sessions the bias continued to develop. There was no tendency for the bias to decrease despite repeated experiences with the same colours. Bias developed in both directions, towards more or less blue, which excludes any important effect from inherited colour preferences. A bias towards more blue occurred when the nonrewarding colour was green (experiment 1) and towards less blue when the nonrewarding colour was cyan (experiments 1 and 2). Thus, the rewarding colours evolved away from the nonrewarding colour. Experiment 2 shows that it was the presence of a nonrewarding colour that caused the development of receiver bias.

The results can be explained as a consequence of the birds' experiences of the different training stimuli requiring opposing responses, peck and not peck. The discrimination generated a response bias in the direction away from the nonrewarding stimulus. The existence of this bias is consistent with the general finding of response biases, such as peak shifts, in experimental studies of discrimination (e.g. Hanson 1959; Mackintosh 1974). When animals are trained to discriminate between rewarding and nonrewarding stimuli the strongest response is usually not achieved for the rewarding training stimulus but for a stimulus located beyond that, in the opposite direction to the negative stimulus (Hanson 1959). The response to familiar and novel test stimuli is usually illustrated by a generalization gradient, with strength of response plotted against the different values within the stimulus dimension. Most generalization gradients are bell shaped with one important exception. When stimuli vary in intensity (amount of receptor stimulation), as in our experiments, the response often yields monotonic gradients (Mackintosh 1974). This means that the response increases as the intensity of the stimulus increases, even substantially beyond the intensity of the rewarding training stimulus. However, reversed monotonic intensity gradients are obtained, that is, higher responses at low intensities, after training on a faint rewarding stimulus and an intense nonrewarding stimulus (Pierrel & Sherman 1960; Huff et al. 1975; Zielinski & Jakubowska 1977). Peculiar to intensity bias is that the bias remains even after substantial training (Bass

1958; Murray & Kohfeld 1965; Birkimer & James 1967; Scavio & Gormezano 1974) which we also found in our experiment.

Our results agree with the findings from computer simulations addressing the same issue. Enquist & Arak (1994) simulated coevolution of signals and receiver preferences using an artificial neural network as a model of the receiver mechanism. After a number of generations, they found that the coevolved signals most likely to provoke a strong response, in addition to symmetries, consisted of the chromatic opponents of those colours present in the nonrewarding stimulus. The evolving signal thus became polarized away from the non-evolving stimulus. Hurd et al.'s (1995) study investigated, with similar methods, intraspecific signalling where the recognition mechanism was required to respond differently to several different stimuli. Also in Hurd et al.'s study the signals evolved away from each other and other stimuli, eventually taking the antithetical forms of each other. These results were caused by the biases emerging in the networks (e.g. Ghirlanda & Enquist 1998). In our experiment, the artificial neural network was replaced with a real animal with a real recognition mechanism. Essentially the same biases emerged in reality as in the networks and, furthermore, they were capable of driving the evolution of the signal form towards distinctiveness. The final outcomes of our experiments were somewhat less extreme; the colours did not become as antithetical as in the simulations and as suggested by intensity generalization gradients (e.g. Mackintosh 1974; Ghirlanda 2002). One difference between our experiment and most studies of intensity generalization is that our range of intensities was small and changed in absolute steps. Others have often used relative steps over a much wider range of intensities where each step, for instance, has doubled the intensity.

In this paper we have explored a new way of investigating signal evolution and its merits and drawbacks should be discussed. It is obvious that signal evolution in reality is much more complex than in our experiment. Two issues seem particularly important: is the situation oversimplified and can one generalize from signal changes caused by one bird to the outcome of evolution from many sender and receiver interactions over many generations? Even if the situation is simplified one can also argue that simplicity is strength. Our controlled experimental design makes it possible to explore the effect of the recognition mechanism in isolation, without any confounding effects. The test stimuli are artificial, but there is no reason to expect that individuals given comparable experiences in nature would develop different biases to signals containing similar features. Receiver bias, for specific kinds of stimuli, develops because of a general reaction pattern of the recognition mechanisms caused by different degrees of stimulation of different receptors. This means that the result may be applied to all sorts of visual signals, such as sexual displays or food. It is also applicable to the avoidance of warning signals. Avoidance of a stimulus is a response just as approaching or pecking on a stimulus is. If our experiment had been designed the other way around, with a fixed rewarding stimulus and an

evolving nonrewarding stimulus, the nonrewarding stimulus would instead have evolved away from the rewarding stimulus. Concerning the evolutionary course, a potentially important difference is that each of our birds experienced a considerable range of colours whereas in real evolution each generation of receivers would probably experience a smaller range. This suggests a development of our method involving series of subjects each engaged in a smaller evolutionary step of the signal.

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References

- Baerends, G. P. & Drent, R. H. 1982. The herring gull and its egg. Part II. *Behaviour*, **82**, 1–416.
- Basolo, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. *Science*, **250**, 808–810.
- Bass, B. 1958. Gradients in response percentage as indices of nonspatial generalization. *Journal of Experimental Psychology*, **56**, 278–281.
- Birkimer, J. C. & James, J. P. 1967. Stimulus intensity dynamism and generalization of inhibition in a discriminated lever press avoidance situation. *Psychonomic Science*, **8**, 377–378.
- Coren, S., Ward, L. M. & Enns, J. T. 1999. *Sensation and Perception*. Orlando, Florida: Harcourt Brace.
- Endler, J. A. & Basolo, A. L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, **13**, 415–420.
- Enquist, M. & Arak, A. 1994. Symmetry, beauty and evolution. *Nature*, **372**, 169–172.
- Enquist, M. & Arak, A. 1998. Neural representation and the evolution of signal form. In: *Cognitive Ecology* (Ed. by R. Dukas), pp. 21–87. Chicago: University of Chicago Press.
- Forkman, B. & Enquist, M. 2000. A method for simulating signal evolution using real animals. *Ethology*, **106**, 887–897.
- Gamberale, G. & Tullberg, B. 1996. Evidence for a peak-shift in predator generalization among aposematic prey. *Proceedings of the Royal Society of London, Series B*, **263**, 1329–1334.
- Gamberale, G. & Tullberg, B. 1999. Experienced chicks show biased avoidance of stronger signals: an experiment with natural colour variation in live aposematic prey. *Evolutionary Ecology*, **13**, 579–589.
- Ghirlanda, S. 2002. Intensity generalization: physiology and modelling of a neglected topic. *Journal of Theoretical Biology*, **214**, 389–404.
- Ghirlanda, S. & Enquist, M. 1998. Artificial neural networks as models of stimulus control. *Animal Behaviour*, **56**, 1383–1389.
- Ghirlanda, S. & Enquist, M. 2003. A century of generalization research. *Animal Behaviour*, **66**, 15–36.
- Hanson, H. 1959. Effects of discrimination training on stimulus generalization. *Journal of Experimental Psychology*, **58**, 321–333.
- Hogan, J., Kruijt, J. & Frijlink, J. 1975. Supernormality in a learning situation. *Zeitschrift für Tierpsychologie*, **38**, 212–218.
- Huff, R. C., Sherman, J. E. & Cohn, M. 1975. Some effects of response-independent reinforcement in auditory generalization gradients. *Journal of the Experimental Analysis of Behavior*, **23**, 81–86.
- Hurd, P. L., Wachtmeister, C. A. & Enquist, M. 1995. Darwin's principle of antithesis revisited: a role for perceptual biases in the evolution of intraspecific signals. *Proceedings of the Royal Society of London, Series B*, **259**, 201–205.
- Leimar, O., Enquist, M. & Sillén-Tullberg, B. 1986. Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *American Naturalist*, **128**, 469–490.
- Mackintosh, N. 1974. *The Psychology of Animal Learning*. Vol. 1. London: Academic Press.
- Murray, H. G. & Kohfeld, D. L. 1965. Role of adaption level stimulus intensity dynamism. *Psychonomic Science*, **3**, 439–440.
- Pierrel, R. & Sherman, J. G. 1960. Generalization of auditory intensity following discrimination training. *Journal of the Experimental Analysis of Behavior*, **3**, 313–322.
- Purtle, R. B. 1973. Peak shift: a review. *Psychological Bulletin*, **80**, 408–421.
- Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- Ryan, M. J. 1998. Sexual selection, receiver biases, and the evolution of sex differences. *Science*, **281**, 1999–2003.
- Ryan, M. J. & Keddy-Hector, A. 1992. Directional patterns of female mate choice and the role of sensory biases. *American Naturalist*, **139**, 4–35.
- Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, S. A. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*, **343**, 66–67.
- Scavio, M. J. J. & Gormezano, I. 1974. CS intensity effects on rabbit nictitating membrane, conditioning, extinction and generalization. *Pavlovian Journal of Biological Science*, **9**, 25–34.
- Spence, K. 1937. The differential response in animals to stimuli varying within a single dimension. *Psychological Review*, **44**, 430–444.
- Tinbergen, N. 1948. Social releasers and the experimental method required for their study. *Wilson Bulletin*, **60**, 6–51.
- Varela, F. J., Palados, A. G. & Goldsmith, T. H. 1993. Color vision in birds. In: *Vision, Brain and Behavior in Birds* (Ed. by H. P. Zeigler & H. J. Bischof), pp. 77–98. Cambridge, Massachusetts: MIT Press.
- Weary, D. M., Guilford, T. C. & Weisman, R. G. 1992. A product of discriminative learning may lead to female preferences for elaborate males. *Evolution*, **47**, 333–336.
- Zeigler, H. P. & Bischof, H. J. (Eds) 1993. *Vision, Brain and Behavior in Birds*. Cambridge, Massachusetts: MIT Press.
- Zielinski, K. & Jakubowska, E. 1977. Auditory intensity generalization after CER differentiation training. *Acta Neurobiologiae Experimentalis*, **37**, 191–205.