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Brightness Dependence of Colour Preferences in Herring Gull Chicks

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With one figure

Introduction

Since the classic study by Tinbergen and Perdeck (1950) of the colour preferences of gull chicks reacting with the begging response to models of the parental beak, much has been published on spontaneous behavioural colour preferences of birds (e. g. Curtius 1954; Hess 1956; Tinbergen et al. 1962; Kear 1964; Quine and Cullen 1964; Hailman 1967; Oppenheim 1968; Delius 1968). Several aspects of this phenomenon are of special interest, including the nature of the filtering mechanism (Marler 1961) that causes the behavioural response to the colour spectrum to be different from the physiological spectral sensitivity recorded at the level of the sensory organs (Thompson, in press) and the question of the adaptive value of the preferences in the animal's normal environment (Hailman 1968).

Colour preferences have been mainly considered as a function of the wavelength composition of the chromatic stimuli; intensity and saturation have received little attention. A note by Kear (1966) however does suggest that intensity can be an important variable, since it markedly affected the spectral preferences of newly-hatched coots (*Fulica atra*) and moorhens (*Gallinula chloropus*).

Previous experiments (Thompson 1970, in prep.) demonstrated that when Herring gull (*Larus argentatus*) chicks had the choice of approaching two surfaces illuminated with narrow band monochromatic light of different wavelengths, their preference pattern was quite similar to that they displayed in the classically studied begging-pecking response, provided that the spectral stimuli were of equal energy at a specific level. They had then a maximal preference for red and blue and a minimal one for green. If, however, the intensities of the stimuli were varied, as happened by error and non-systematically in one experiment, the preference pattern was drastically modified. The experiments reported here explore this phenomenon in a more systematic way.

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Methods

The apparatus consisted of an arena (Fig. 1) painted medium grey, with a sawdust-covered floor and with two ground glass surfaces 20 cm × 16 cm, each illuminated from behind by two independent projection systems, each consisting of a 50 watt bulb, a heat filter, a condensor lens, exchangeable interference and neutral density filters, and a projection lens.

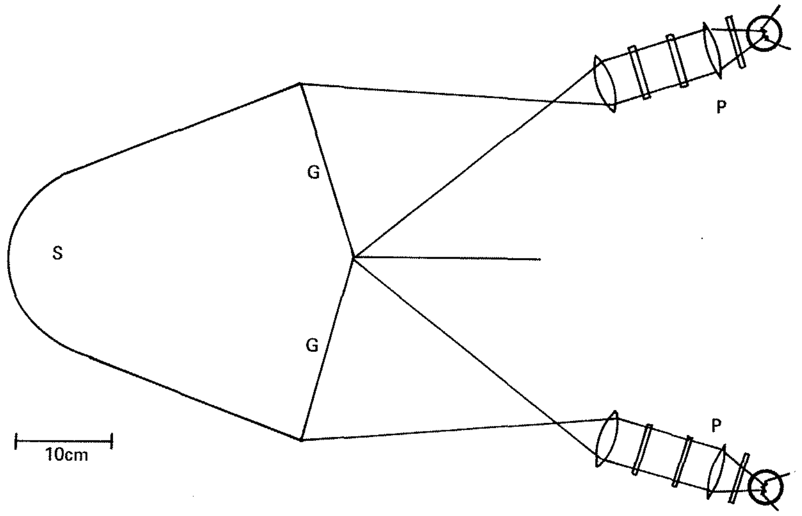

Fig. 1: The arena used in the choice experiments. The walls were 16 cm high. S — starting point, G — ground glass stimulus panels, P — projector systems

Green and red monochromatic lights were obtained by interposing interference filters (Balzer) with 40 % transmittance peaks at 536 and 620 nm respectively, and with halfband widths of 10 nm. The "white" light used had a spectral distribution close to that of a black body radiating at 3100 degrees Kelvin, as checked with a spectrally calibrated photocell. All light intensity adjustments were made with factory calibrated neutral density filters (Kodak).

The intensities of the green and red lights were adjusted to equal, in terms of human subjective brightness (2 observers), a "white" light giving an approximately 1.4 log ft. L luminance to the stimulus pannels as measured with a SEI exposuremeter. All light intensities are given in terms of log unit attenuation of these baseline intensities.

Clearly, the human subjective brightness criterion did not necessarily match the lights to equal gull subjective brightness. The electroretinographic spectral sensitivity of gulls (THOMPSON, in press) does in fact indicate that the baseline red may have appeared to them about 0.4 log units brighter than the green, with the white falling somewhere in between. In terms of radiant energy the red was approximately 0.6 log units more intense than the green, as measured with a spectrally calibrated photocell.

The gull chicks came from incubator-hatched eggs collected at the Newborough (Angelesey) or the Walney (Lancashire) gull colonies. Most were Herring gulls (*Larus argentatus*), with only a few Lesser Black-backed gulls (*L. fuscus*). No behavioural differences were detected between these two closely related species in any of the present experiments. The chicks were kept in infra-red heated, brown hardboard pens with sawdust floors illuminated by two 60 watt bulbs. They were fed about every three hours except at night, and had water ad libitum. No effort was made to maintain them visually naive, but they were not exposed to any strongly chromatic stimuli except in the experimental arena.

For each choice trial a chick was placed at the starting point in the arena and given 5 minutes to make a choice, which was defined as an approach to within 7 cm of one of the stimuli. Mostly they made their choice in a clearcut manner, either by squatting while facing a stimulus panel or by leaning sideways against a panel. Only a few would waver undecidedly at the midline junction between the panels before making a choice. Choice latencies were recorded but their analysis revealed no systematic variations.

In about 10 % of the trials chicks would refuse to make a choice within the 5 minutes, because they either fell asleep or tried to break out away from the stimuli. The trial was then repeated with another chick. An analysis of these refusals failed to indicate any stimulus dependency but they were unfortunate in that they prevented a fully systematic design of the experiment.

For each experiment a new group of between 15 and 25 one to three day old chicks were used. Individual chicks ran in up to 5 trials with intervals of at least one hour between trials. The sequence of stimulus pairs the individuals faced in their trials was random. To allow for possible side preferences each stimulus combination was run in two (or multiple thereof) trials with right-left stimulus exchanges.

Results

Four experiments were done, the first two compared the attractiveness of four intensities of red (620 nm) and four of green (536 nm), the lights which had been respectively the most and the least effective in Thompson's experiments mentioned earlier. In the first experiment all 16 possible red-green stimulus pairs were run four times. Table 1 presents the results.

Table 1: Choice of four red and green intensities by Herring gull chicks

	G - 0.3	G - 0.6	G - 1.0	G - 1.3	N	%
R - 0.3	0 4	0 4	1 3	2 2	16	81
R - 0.6	1 3	0 4	1 3	1 3	16	81
R - 1.0	2 2	0 4	1 3	1 3	16	75
R - 1.3	2 2	1 3	2 2	0 4	16	69
N	16	16	16	16		
%	31	6	31	25		

While the percentages of choices made for the different intensities of red did not vary significantly (χ^2 on homogeneity, $p > 0.95$), there was a marked dip in preference for the green dimmed by a 0.6 neutral density filter, in comparison with the greens both a step dimmer and a step brighter (χ^2, $p < 0.05$). This suggests that the attractiveness of red was relatively unaffected by changes in intensity, while the response to green was quite dependent on intensity.

There was not enough data to examine on whether this held true irrelevantly of which intensity of green the various reds were compared with, and conversely of which intensity of red the various greens were paired with.

The second experiment was essentially a replication of the first, but was motivated by a hypothesis which assumed that preferences depended on relative stimulus intensity differences. This hypothesis proved untenable, but unfortunately the design of the experiment was adjusted to test it, resulting in an unequal number of trials for each of the 16 stimulus combinations. It is difficult to see however, how the design by itself could have brought about the results presented in Table 2.

To compensate for the effect of the design a column with corrected percentages is given in Table 2. The correction consisted in weighting the contribution of each cell proportionally to the number of choices it involved. The difference between the corrected and uncorrected percentages however

Table 2: Choice of four red and green intensities by Herring gull chicks

	G + 0.1	G - 0.2	G - 0.6	G - 0.9	N	%	Corr. %
R 0	4 2	2 6	2 10	11 13	50	62	61
R - 0.3	3 5	2 4	1 7	6 6	34	65	67
R - 0.7	6 6	3 5	0 6	4 4	34	62	66
R - 1.0	12 12	5 7	1 7	3 3	50	58	61
N	50	34	34	50			
%	50	35	8	48			
Corr. %	51	34	10	49			

are minimal. As in the previous experiment the attractiveness of red seemed hardly affected by its intensity (χ^2, $p > 0.95$), while the preference for green again showed a marked dip at the intermediate intensities (χ^2, $p < 0.001$).

It should be noticed that the dip in the green preferences can be detected in every row of the table, i. e. independent of the red intensity the greens were compared with. A suitable analysis of the data did in fact reveal that relative brightness differences between the stimuli did not significantly affect the choice pattern.

The third experiment compared four intensities of each "white" (3100° K) and red (620 nm) lights. The results are shown in Table 3.

Table 3: Choice of four red and white intensity steps by Herring gull chicks

	W 0	W - 0.3	W - 0.7	W - 1.0	N	%	Corr. %
R 0	4 2	4 4	4 8	10 14	50	56	52
R - 0.3	5 3	4 2	3 5	4 8	34	53	52
R - 0.7	9 3	3 5	2 4	4 4	34	47	51
R - 1.0	13 11	9 3	5 3	1 5	50	44	48
N	50	34	34	50			
%	62	58	41	34			
Corr. %	65	57	42	36			

Again the attractiveness of red remains essentially the same over the range of intensities (χ^2, $p > 0.95$). For white light, however there is marked decay in responding from the brightest light to the dimmest white light (χ^2, $p < 0.05$). In the three first rows of the table there is an indication of a dip in the preference for white dimmed by a 0.7 log unit filter, but the last row of the Table, for unknown reasons, cancels out this effect.

A fourth experiment compared an extended range of four intensities of "white" against each other. Only 36 trials were run, yielding a 69 % preference for a W+0.4, 50 % for a W0, 31 % for a W—0.6 and 50 % for a W—2.0. Although this result suggests again that the effectiveness of "white" depends on its intensity, a χ^2 test on homogeneity yields a $p > 0.05$.

Were it not for the previous experiment and for the fact that Thompson (1970, in prep.) showed that in a situation similar to that used here, Herring gull chicks prefer black and white over a graded series of greys, the above result would merit little attention.

Discussion

The conclusion drawn from these experiments is that depending on the spectral composition of the stimuli their effectiveness is modulated in different ways by comparable variations of intensity. The attractiveness of red appears to be virtually impervious to intensity changes, at least over the range explored, while the attractiveness of both green and white varies markedly with intensity changes of similar order. More specifically it is noted that the effect of the latter stimuli seems to be a non-monotonic U shaped function of intensity. This contrasts with the fact that most visual responses are monotonic functions of intensity (Bartley 1951) and that where non monotonic response functions to stimulus intensities are found, these almost invariably follow an inverted U relationship, that is the intermediate intensities are preferred to the extremes (Hebb 1949).

Two issues are raised by these findings, one is that of the adaptiveness of this response pattern, the other concerns the physiological mechanism involved.

The situation used in the experiment would seem similar to that facing the chick when approaching the parents from a distance or seeking cover when frightened (Impekoven 1969). It is interesting to note that the red-blue preference and green avoidance shown in the begging situation (Thompson 1970, in prep.; but see Kear 1964) does also persist in this situation. The red preference seems somewhat puzzling in this context since the parent's red beak spot, which makes this red preference significant in the begging situation, is not very obvious from a distance. The function of the blue preference is mysterious in both situations (Hailman 1968), and in natural settings it could even be maladaptive since the chicks of cliff nesting Herring gulls are exposed to the blue sea. Other mechanisms such as the visual cliff response (Emlen 1963) may however ensure that this preference is of no consequence. The low preference for green, while meaningful as vegetation avoidance in the begging situation, seems irrelevant in the context of cover seeking. The relatively higher responsiveness to darker greens may reflect a compensatory adaptive adjustment but the increased preference for the bright green remains obscure. Seeking for cover may also explain the preference for dim white light while the responsiveness to bright white light could have something to do with approaching the white underside plumage of the adult gulls.

The conclusion must be that although the colour preference patterns must be adaptive in some way, their function is not obvious. This may be due to the overlaying of various preferences meaningful in very specific contexts adequate at various stages in the individual's life (the blue preference for example may be important for the adult gull seeking its marine environment), and to constraints in the capacity of evolving and developing perfectly adapted preference mechanisms, because of inherent system limitations.

Since the spectral preference pattern with a red and blue maximum and a green minimum does not match the spectral sensitivity of the Herring gull eye, which is maximal in the green decreasing slowly towards the blue and steeply towards the deep red (Thompson, in press), some selective "filtering" mechanism must be interposed between the receptors and the response directing systems.

The wavelength-response function would agree well with the predictions of the filter models proposed by Hailman (1964, 1966) to account for the pecking preferences of Laughing gull chicks (*Larus atricilla*); but they generate intensity-response functions which are incompatible with those described in this paper.

A mechanism whose performance conforms with these empirical functions can be proposed on the assumption that trichromatic colour vision operates in birds. This assumption is supported by Donner's (1953) and Galifret's (1961) electrophysiological and Hamilton and Coleman's (1933) behavioural findings in the pigeon (*Columba livia*). The filtering mechanism would consist in the red sensitive and the blue sensitive modulator units having a high gain link and the green sensitive modulator units having a low gain link connecting them with the response mechanism. This would produce a preference pattern with a maximum for red and blue and a minimum for green.

As it stands, however, this model would predict a monotonic response improvement at all the wavelengths with increasing intensity, in contradiction with our results. Additional features are required to cope with this aspect. Some which suggest themselves are the following: firstly, the gain of the red system is such that response saturation occurs even at low red light intensities. This would have the effect that over a wide range of intensities, red's behavioural effect would be constant. Secondly, the green system is subject to inhibition from the rods, the scotopic dominator, that being responsible for the decreasing attractiveness of green with increasing brightness over the lower intensity range. In the higher intensity range the scotopic dominator saturates because of rod pigment overbleaching, self inhibition, or perhaps, inhibition by cones. The green modulator activation takes over and is responsible for the increase of preference for green with increasing intensity in the higher range.

We have no data for an intensity dependence of blue, except for the uncontrolled experiment mentioned in the introduction which seems to suggest such. In view of the contradictory results that have been obtained with blue in the begging situation, some authors finding that it was as good a releaser as red, others finding blue to be mediocre, perhaps because of using blues of various intensities (Hailman 1969), it seems likely that its effectiveness is intensity dependent. Elsewhere one of us has in fact suggested that changes in the light-dark adaptation state of the retina, i. e. in the ratio of cone to rod activity, plays a role in determining the response to blue (Delius 1968). The red system on the other hand cannot of course be affected by the rods because they are not sensitive to this wavelength. Since the response to white light can be expected to be controlled by the sum of the modulator systems, i. e. the photopic dominator, one may assume that it too will be subjected to rod controlled inhibition as green and perhaps blue are.

Clearly this hypothesis needs to be put on a sound quantitative basis, but at present there are not sufficient baseline facts available for this to be feasible. Further experimental data on the effects of intensity on the preference for blue and other hues, including non-monochromatic ones, and the effect of variations in chromatic saturation would be desirable. The physical characteristics of the stimuli should be accurately specified, the intensity on an absolute scale.

Summary

Using a situation in which Herring gull chicks could choose to approach either of two stimulus panels illuminated with coloured lights, it was investigated whether the colour preference pattern they show is affected by the intensity of the stimulus lights. The response to red was found to be little affected by intensity differences, but attractiveness of green and white light depended markedly on its intensity, following a U-shaped function. After a discussion on the adaptiveness of the response mode, a new model is proposed, complying both with the spectral preference pattern and with the intensity dependencies found. Through differential amplification of the photopic modulators it generates the spectral response pattern with red und blue maxima and a green minimum, and through inhibition of the low threshold scotopic dominator on the higher threshold photopic modulators it accounts for intensity dependence of green and white's behavioural effectiveness.

Zusammenfassung

In Experimenten, in denen Silbermöwenküken eine von zwei beleuchteten Flächen zu wählen hatten, wurde untersucht, ob ihre Farbbevorzugungen von der Helligkeit der Farbe abhängen. Rotes Licht wurde unabhängig von der Helligkeit weitgehend gleichmäßig bevorzugt, während sich bei grünem und weißem Licht die Helligkeit stark auswirkte. Die Bevorzugung dieser Farben schien eine nicht monotone, konkave Funktion der Helligkeit zu sein. Der Anpassungswert dieses Reaktionsmusters wird besprochen. Um die Spektral- und Helligkeits-Bevorzugungen zu erklären, wird ein Modell vorgeschlagen, welches durch differenzierte Verstärkung der photopischen Modulatoren eine maximale Reaktion auf Rot und Blau und eine minimale auf Grün hervorruft. Durch Hemmung der höherschwelligen photopischen Modulatoren durch den niedrigschwelligen skotopischen Dominator erzeugt das Modell die gefundene Helligkeitsabhängigkeit der Verhaltensreaktion auf grünes und weißes Licht.

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