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SOURCES OF INDIVIDUAL VARIATIONS IN THE NAIVE APPROACH PREFERENCES OF QUAIL CHICKS: AGE, STIMULUS INTENSITY, AND GENOTYPES

by

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(With 3 Figures)
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When newly hatched chicks or ducklings are first exposed to a conspicuous visual stimulus they orient toward it and approach it. When confronted with two or more such stimuli they show approach preferences which may change with age and be modified by experience. These behaviors are commonly referred to by the term "imprinting". They command one of the most extensive research literatures in the study of early behavioral development (for recent reviews see: RAJECKI, 1973; HESS, 1973). The present report is part of a project in our laboratory which (1) seeks to identify genetic sources of individual variation in the naive color discrimination component of imprinting in the Japanese quail (*C. coturnix japonica*) and (2) hopes to relate such sources to the learning component of imprinting. As were the earlier reports from this project (KOVACH, 1974a, 1974b, 1976; KOVACH & WILSON, 1975; KOVACH, WILSON & O'CONNOR, 1976) the present study is subordinated to an overall aim of examining gene action and gene-environment interaction in the processing and coding of stimulus information in behavior. The Japanese quail is used because this species has an exceptionally short generation time and very high fertility that make it uniquely suited for behavior-genetic and behavior-developmental experimentations (KOVACH, 1974a).

Newly hatched quail chicks show distinct preference for the middle and short wavelengths of the color spectrum (green and yellow over blue and

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red, and blue over red; KOVACH, 1974b). They also prefer the higher intensity stimulus when approaching a pair of stimuli equal in color, size and pattern, but different in intensities by about one log unit (KOVACH & WILSON, 1975). Our earlier investigations indicated large individual variations in color preferences (KOVACH, 1974b, 1976) and we found that the quail responds well to their artificial genetic selection (KOVACH *et al.*, 1976). The present study tested age and stimulus intensity as possible sources of individual variation in the quails' manifest preferences between colors. It examined the possibility that age effects and stimulus intensity effects are involved in the quails' genetic response to selection for naive color preferences.

METHOD

Apparatus and testing procedures.

Approach preferences were tested by the mass-screening procedures described elsewhere (KOVACH, 1974b, 1976). The related apparatus is illustrated in Plate XIV and Figure I. It was built of 28 discrimination compartments arranged in a manner such that a single starting compartment was on top, two compartments were in the second row, three in the third row, and so on terminating in eight collection boxes on the ground floor. Each discrimination compartment offered a binary choice between the same pair of visual stimuli, which were of the type that normally elicit approach responses in quail chicks. A trap door was located in front of each stimulus in each compartment. Approaching the stimulus within 7.5 cm resulted in the opening of a corresponding trap door and exiting through it into the next compartment. This was repeated upon approach of a stimulus in the next compartment, and so on until seven choices were completed and the subject arrived in one of the eight collection boxes. Position of subject in a particular collection box identified the number of choices it made for one over another of two testing stimuli in 7 trials.

Subjects were placed into the starting box in ten minute intervals, in groups of 15 to 25 accumulating to a total of no more than 250 in a single testing session. Each subject was individually identified by a numbered tag, which was attached to the neck with the help of a small rubber band. Upon completion of the first seven trials each subject was removed from its collection box, received a corresponding individual score, and was placed back into the starting box for a second run. Maximum time allowed to complete two runs was 2 hrs and 45 minutes. Data from subjects which did not complete the two runs were not used in the study, but percentages of such subjects in each group are specified.

Subjects and experimental conditions.

Subjects were dark incubated and dark reared in our laboratory. Eggs were obtained from the genetic lines of our bidirectional selection study in which one line was artifically selected for preference of blue over red, another for preference of red over blue, and still another, a genetic control line, was tested and maintained without selection for the same number of generations as the selected lines. Results of this selection experiment are illustrated in Fig. 2.

Procedures for testing color preferences in genetic selection and in the present experiments were identical, except the presently added age and stimulus intensity variables. Subjects received no visual experience prior to testing, except a minimum of 20 minutes adaptation to the background illumination of experimental room (approx.

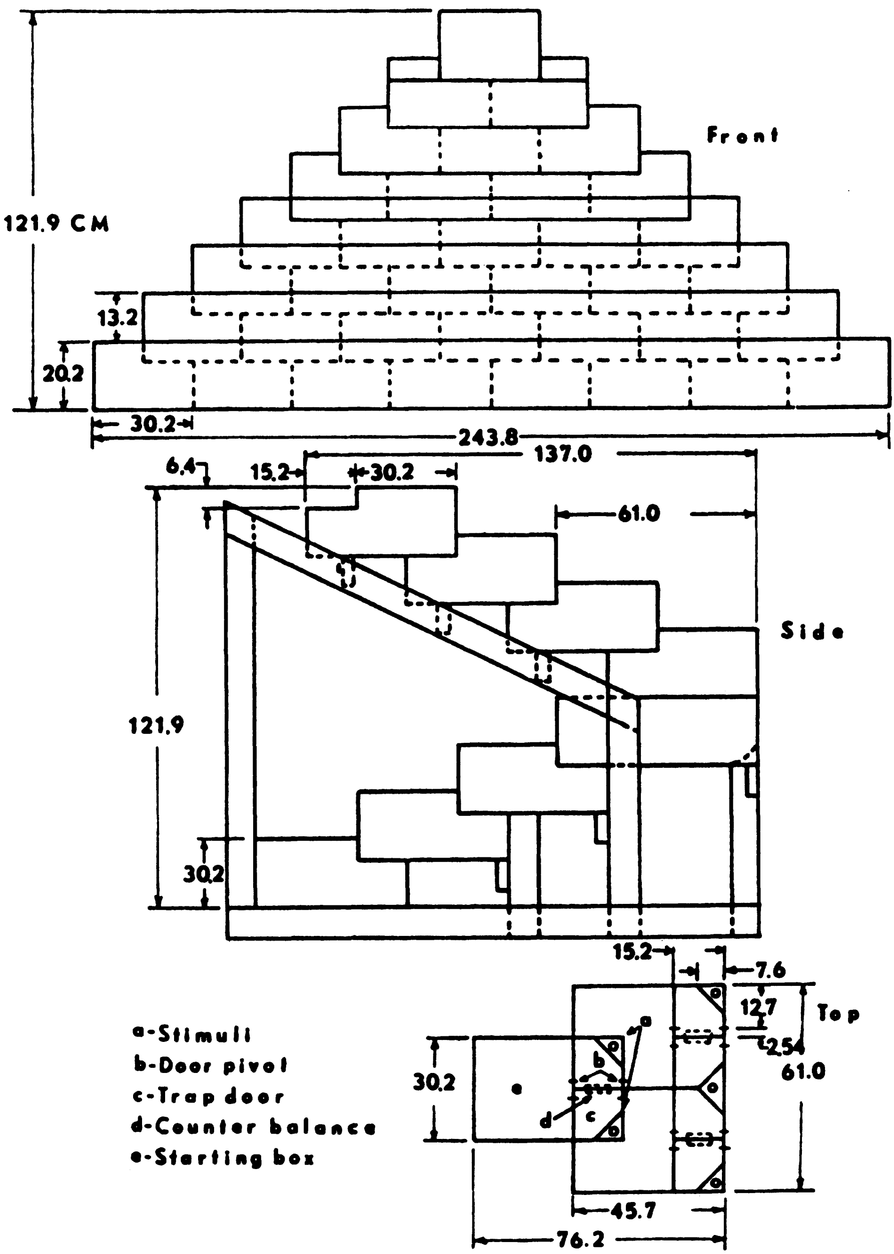


Fig. 1. Schematic drawing of the apparatus for binary mass-screening of approach choices. Measurements are indicated in cm. For further details see earlier reports (KOVACH, 1974b, 1976)

1 lux) and brief exposures to dim light during tagging and transportation to the experimental room.

Average posthatch ages at testing were 7 hrs, 27 hrs, and 47 hrs. Age variations within groups approximated the normal distribution, with *1* SD not exceeding 5 hrs. This was about half the size of age variations allowed in testing for selection. Different groups were tested with the same pair of blue and red stimuli of equal photopic intensities (20.0 lux) that was used in selection, or a pair of white stimuli differing in intensities (20.0 lux *versus* 2.0 lux).

All stimuli were back lighted with flourescent light sources operating intermittently at the rate of 3 flashes/sec of 50% "on" and 50% "off" light. All stimuli were equal in pattern and size (2.54 cm X 2.54 cm). Intensities were measured at each stimulus source of Tektronix J 16 photometer. Wavelength characteristics of colors corresponded to Wratten gelatin filters (No. 29 for red, and No. 45 for blue) placed into stimulus holders in front of the two light sources of each discrimination compartment.

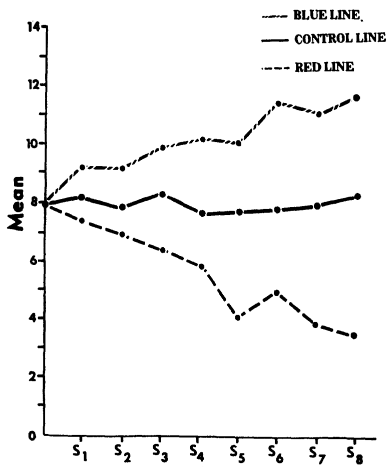


Fig. 2. Results of 8 generations of bidirectional genetic selection for blue and red preferences in the responses to the blue-red color pair. One line was selected for preference of blue over red, another for preference of red over blue. Both lines were mass-screened by the same stimuli at the average posthatch age of 27 hrs, in groups of comparable age variations to the present study. Approximately 3,000 subjects were tested and 320 subjects selected in each generation of each of the two selected lines. Approximately 800 subjects were tested and 160 unselected pairs of quail used in each generation of the genetic control line. This experiment is still in progress. Results of related genetic analyses will be described in a subsequent report. The present study used samples from the two selected lines at generation 3, 5 and 8 and at generation 4 from the control line. Related distribution parameters are given in Tables 1, 2, 3 and 4 below.

Experiment 1 dealt with the question of age effects in the quails' naive approach preferences. Subjects were drawn from the genetic control line and were tested for color and intensity preferences by mass-screening at 7, 27, and 47 hrs of posthatch age. A blue-red stimulus pair and a pair of white stimuli of different intensities were used.

Experiment 2 dealt with possible interaction between age effects and genetic effects in color and intensity preferences. Subjects were drawn from generations 3, 5, and 8 of the two genetically selected lines (see Fig. 2). As before, groups were tested at 7, 27, and 47 hrs of age by the blue-red and white-white stimulus pairs.

In both experiments, each combination of age-versus-stimuli-versus-genetic-condition was tested in a separate group of at least 50 subjects, amounting to a total of 5000. Of these 3990 subjects completed 14 trials and were used for data analysis.

Statistical analysis of data.

In each group probability estimates of preference ($\hat{p}$) were made from the obtained empirical means, and *Chi*-square goodness-of-fit procedures were used to assess deviation of distribution shapes and variances from those of the binomial distributions of $p = \hat{p} = \frac{\overline{X}}{n}$ and $q = \hat{q} = 1 - \hat{p}$. Means and variances of 14 trials and correlations of individual scores on the first and second series of 7 trials were determined within each group. Analysis of variance and *Chi*-square procedures were used to determine between group differences of means and variances.

RESULTS

Experiment 1: Age effects.

This experiment dealt with the question — do color and intensity preferences of naive quail chicks change as a function of age during the first two days of posthatch life? Table 1 describes the results.

TABLE 1

Choices between blue vs *red, yellow* vs *red and a pair of white stimuli of different intensities, by genetic controls (G_4) at 7, 27 and 47 hrs of posthatch age*

Groups	N of *Ss* tested	% of *Ss* completing 14 trials	$\overline{X}$*	S^2	Probability of preference (n = 14) $\hat{p} = \frac{\overline{X}}{n}$	Comparison with binomial of ($p = \hat{p}$) χ^2	$p \leq$	Correlation of individual scores on the 1st and 2nd seven trials r	$p \leq$
Blue vs *red*									
at 7 hrs	154	67.5	9.4	9.1	.66	7174.1	.001	.42	.001
at 27 hrs	499	68.1	7.9	10.1	.56	5220.9	.001	.36	.001
at 47 hrs	133	66.1	6.4	9.8	.46	2758.5	.001	.48	.001
White 20 lux vs *white 2.0 lux*									
at 7 hrs	78	100.0	8.7	5.6	.62	49.6	.001	.23	NS
at 27 hrs	74	100.0	8.1	6.3	.58	59.1	.001	.31	.01
at 47 hrs	154	98.0	8.4	8.1	.60	617.6	.001	.46	.001

* Means ($\overline{X}$) refer to choices of blue and yellow over red, respectively, and to brighter over the dimmer white stimulus in 14 trials.

As can be seen, there was a progressive and significant change from very high and significant ($p \leq .001$) tendency of responding to blue over red at 7 hrs ($\hat{p} = .66$ of choosing blue) through a reduced but still significant

($p \leq .01$) blue preference at 27 hrs ($\hat{p} = .56$ of choosing blue) to a shift over to slight but statistically not reliable red preference by 47 hrs ($\hat{p} = .46$ of choosing blue). Responses to the white-white stimulus pair indicated statistically reliable ($p \leq .05$) tendencies to choose the higher intensity stimulus at all ages. Related probabilities were .62, .58, and .60 for the three age groups. There were no significant changes with age between these probabilities.

All differences between performances with the blue-red pair were statistically reliable ($p \leq .05$). There were no significant differences between the groups tested at different ages with the pair of white stimuli. They all showed about equal preference of the higher intensity stimulus.

These results indicated significant changes with age in the quails' color preference during the first 48 hrs posthatch life. These changes were not due to a uniform maturational trend of decreasing responsiveness to an initially preferred stimulus. Age appeared to be a significant source of change only in the approach preferences between colors, but not in the approach preferences between stimulus intensities.

Experiment 2: Interactions between age effects, stimulus intensity effects, and genetic selection effects.

In this experiment samples were drawn from the 3rd, 5th and 8th generations of two genetically selected lines (see Fig. 2). They were tested for naive preferences between blue and red at 7 hrs, 27 hrs, and 47 hrs of posthatch age. Table 3 describes the results from subjects selected for preference of blue over red, and Table 4 from subjects selected for preference of red over blue. It should be recalled that preferences for selection were tested at 27 hrs of average age, in the same manner as the present groups of the same age, with about twice the range of present age variations.

These results show the familiar decline in the choice of blue over red as subjects grow older (see Table 1). But here the decline started from a higher level of blue preference in the blue line than in controls, and from lower level in the red line. Subjects of the blue line at generations 5 and 8 showed highly significant ($p \leq .001$) preferences of blue over red even at 47 hrs of age. Subjects of the red line showed preferences of red over blue in all but one instance, at 7 hrs of age in generation 3 where there was a slight blue preference that was not statistically reliable. At generations 5 and 8 all the genetic red samples showed highly significant preferences ($p \leq .001$) of red, which increased with age. Differences between the two lines at corresponding ages remained approximately constant within generations but the magnitudes

TABLE 2

Choices of blue over red at 7, 27, and 47 hrs of posthatch ages by subjects drawn from progressive generations of the genetic line selected for preference of blue over red at 27 hrs

Generations and Agegroups	N of *Ss* tested	% of *Ss* completing 14 trials	$\overline{X}$**	S^2	Estimated preference $\hat{p} = \frac{\mid \overline{X} \mid}{n}$ (n = 14)	Goodness of fit with binomial ($p=\hat{p}$) χ^2	$p \leq$	Correlation of individual scores on 1st and 2nd seven trials r	$p \leq$
Blue line S_3*									
at 7 hrs	174	84.5	11.5	6.4	.82	>9999.0	.001	.45	.001
at 27 hrs	586	77.5	10.6	8.0	.76	>9999.0	.001	.52	.001
at 47 hrs	248	51.6	7.0	9.8	.50	611.0	.001	.41	.001
Blue line S_5*									
at 7 hrs	70	99.3	11.1	5.3	.79	360.1	.001	.24	.05
at 27 hrs	143	86.7	11.3	7.7	.81	>9999.0	.001	.58	.001
at 47 hrs	140	79.3	9.4	12.2	.67	>9999.0	.001	.60	.001
Blue line S_8*									
at 7 hrs	54	100.0	12.4	4.0	.89	>9999.0	.001	.46	.001
at 27 hrs	242	96.4	11.6	6.4	.83	>9999.0	.001	.55	.001
at 47 hrs	55	100.0	10.7	9.9	.76	1418.9	.001	.57	.001

* S_3, S_5, and S_8 refer respectively to generation 3, 5 and 8 of selection.

** Means ($\overline{X}$) refer to choices of blue over red in 14 trials.

of changes in preferences with age became diminished with the progress of selection in both lines. At generation 3 all groups within lines were significantly different ($p \leq .05$) from each other. At generations 5 and 8 only the 7 hrs groups were reliably different from older groups. Analysis of variance revealed significant age effects in both lines at each generation ($p \leq .001$ for all exposures, except $p \leq .05$ for the red line at S_5).

These results offer definitive proof that selection did not utilize age effects. Contrary to the hypothesis proposed in the introduction, it appears to have utilized genetic influences pertinent to choices between colors. Age effects and selection effects summated additively in the different lines, and selection reduced age effects about equally in both lines. Table 4 describes the results of testing the two genetic lines with the pair of white stimuli of different intensities at different early ages.

Both lines showed significant preferences of the brighter of two white stimuli at all ages. These effects were somewhat more pronounced in genetic blue than in genetic red subjects. Comparison of the two lines with each other

TABLE 3

Choices of blue over red at 7, 27, and 47 hrs of posthatch ages by subjects drawn from progressive generations of the genetic line selected for preference of red over blue at 27 hrs

Generations and Agegroups	N of *Ss* tested	% of *Ss* completing 14 trials	$\overline{X}$**	S^2	Estimated preference $\hat{p} = \frac{\lvert\overline{X}\rvert}{n}$ (n = 14)	Goodness of fit with binomial ($p=\hat{p}$) χ^2	$p \leq$	Correlation of individual scores on 1st and 2nd seven trials r	$p \leq$
Red line S3 *									
at 7 hrs	230	82.6	7.7	11.4	.54	5648.0	.001	.54	.001
at 27 hrs	427	89.9	6.1	10.5	.43	2435.0	.001	.45	.001
at 47 hrs	53	92.2	4.9	6.3	.34	52.1	.001	.36	.001
Red line S5 *									
at 7 hrs	90	95.6	4.9	8.4	.35	227.2	.001	.59	.001
at 27 hrs	198	86.4	3.5	7.1	.25	2650.1	.001	.49	.001
at 47 hrs	86	75.6	3.8	8.9	.28	1865.4	.001	.67	.001
Red line S8 *									
at 7 hrs	129	100.0	6.2	10.5	.45	1127.0	.001	.53	.001
at 27 hrs	243	96.9	3.4	8.1	.24	>9999.0	.001	.51	.001
at 47 hrs	188	100.0	4.1	8.2	.30	>9999.0	.001	.53	.001

* S3, S5, S8 refers respectively to generations 3, 5, and 8 in selection.

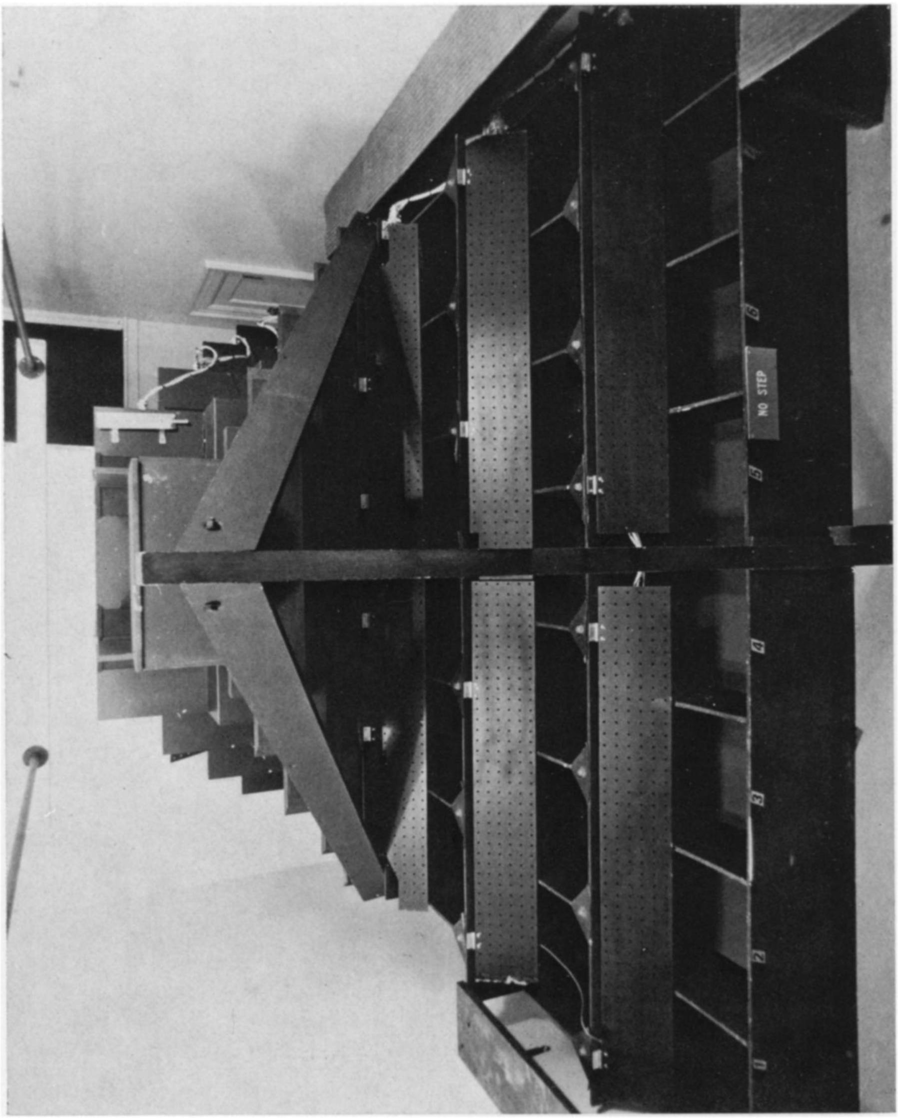
** Means ($\overline{X}$) refer to chices of blue over red in 14 trials.

and with corresponding control performances of *Experiment 1* revealed significant differences ($p \leq .05$) only between the genetic blue and control subjects at 7 and 27 hrs. and the genetic blue and genetic red subjects at 7 hrs.

DISCUSSION

These results show statistically reliable changes in the quails' naive preferences between two colors, blue and red, as a function of change in age during the first two days of posthatch life. But age differences resulted in no statistically reliable changes in the preference of the higher intensity of two otherwise equal white stimuli. Age may thus be viewed as a significant source of individual variations in the quail's approach preferences between colors but not intensities.

The hypotheses that age effects and stimulus intensity effects may have played significant roles in the quails' response to bidirectional genetic selection for preferences between colors were rejected by data. These hypotheses would imply: (1) That genetic selection for naive preferences between



Photographic view of the binary mass-screening apparatus.

TABLE 4

Choices between two white stimuli at different intensities (20.0 lx vs 2.0 lx) at different posthatch ages by subjects drawn from generation 8 of the two lines selected respectively for preferences of blue or red

Generations and Agegroups	N of *Ss* tested	% of *Ss* completing 14 trials	$\overline{X}$**	S^2	Estimated preference $\hat{p} = \frac{\overline{X}}{n}$ (n = 14)	Goodness of fit with binomial ($p=\hat{p}$) χ^2	$p \leq$	Correlation of individual scores on 1st and 2nd seven trials r	$p \leq$
Blue line S8 **									
at 7 hrs	90	95.5	10.0	4.1	.72	16.2	NS	.32	.01
at 27 hrs	77	67.5	10.0	5.3	.71	38.3	.001	.35	.001
at 47 hrs	54	100	8.7	9.9	.62	2391.8	.001	.59	.001
Red line S8 *									
at 7 hrs	124	96.7	8.9	4.0	.63	15.5	NS	.26	.01
at 27 hrs	61	98.3	9.1	4.1	.65	27.2	NS	.33	.01
at 47 hrs	186	99.6	8.6	7.8	.58	696.7	.001	.51	.001

* S8 refers to generation 8 of selection.

** Means ($\overline{X}$) refer to choices of the brighter stimulus in 14 trials.

colors utilized age effects, such that the blue preference of younger and slowly maturing subjects were selected in one line and the red preference of older and more quickly maturing subjects were selected in another line. (2) That selection utilized possible differences in the responses to perceived intensities of colors, such that preference of higher subjective intensity was selected in one line and preference of the lower subjective intensity was selected in another line.

Data revealed that eight generations of bidirectional genetic selection of preferences between blue and red, while resulting in very large and highly significant differentiation of color preferences, did not differentiate age effects in the performances of subjects drawn from the two lines. Age effects and selection effects appeared to summate in a simple additive manner in the two lines. There were increases in the probabilities of choosing blue at 7 hrs of age in both lines, and similar decreases in the probabilities of choosing the blue at 47 hrs of age. However these probabilities did not increase to levels of significant blue preferences in any of the samples tested from the red line, nor decreases to levels of significant red preference in any of the samples tested from the blue line. Within generation differences between the two lines at corresponding ages remained constant. Selection reduced the magnitude of age effects about equally in both lines.

Stimulus intensity effects also appeared at best marginal in genetic responses to selection for color preferences. Selecting responses to subjective intensities of colors would imply responding to subjectively brighter stimulus in one line and subjectively dimmer stimulus in another line. Such responses should be expected to generalize (KOVACH, 1976) to intensity differences between other colors including white, which did not happen. Subjects drawn from both lines preferred the higher intensity white stimulus in a way that was equal to or slightly higher than the similar preference of genetic controls. The only statistically reliable differences between intensity preferences of the two selected lines was at 7 hrs of age, where subjects from the blue line showed slightly greater tendency to approach the brighter stimulus than subjects from the red line.

Apparently, bidirectional genetic selection of quail for the naive choices between colors may result in small modification of age effects in color preferences. Selection effects may also be generalized in marginal ways to intensity preferences. But the present data offer definitive proof that age and stimulus intensity effects do not represent primary targets of selection for color preferences. We may thus conclude that the observed responses to genetic selection of the quails' choices between colors revealed direct genetic influences in the coding and naive processing of the stimulus information of light wavelengths.

SUMMARY

Variations in the early approach choices of naive quail chicks (*C. coturnix japonica*) were studied in relation to stimulus colours, stimulus intensities, age of subjects, and genotypes. Binary choices were tested at 7 hrs, 27 hrs, and 47 hrs of post-hatch age by a pair of coloured stimuli (blue and red) of identical photopic intensities (2.0 lux) and a pair of white stimuli of different intensities (20.0 lux *vs* 2.0 lux). Subjects were drawn from a genetically unmanipulated control population and from two genetic lines that were bidirectionally selected for choices between blue and red. Genetic controls showed very high preference of blue over red at 7 hrs of age, decreased blue preference at 27 hrs, and a slight preference of red over blue by 47 hrs. The two genetic lines showed significant modifications of colour choices by selection without showing corresponding changes in age effects. Both the control and the selected subjects showed preference of the higher intensity white stimulus, but this preference did not change with age. It was concluded that the gene effects in naive colour preferences are not related to age effects, nor to preferences between intensities of stimuli.

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ZUSAMMENFASSUNG

Genetisch bedingte Variationen bei der Farbwahl unerfahrener Wachtelkücken (*Coturnix coturnix japonica*) wurde mittels des Annäherungsverhaltens und in Zusammenhang mit Alter und Stimulusintensität untersucht. Die Tiere wurden von zwei genetischen Linien die mit zweigerichteter Auslese auf Blau und Rot gezüchtet worden waren und von einer genetisch unbehandelten Kontrollgruppe bezogen. Sie wurden im Alter von 7, 27 und 47 Stunden nach dem Ausschlüpfen mit zwei Farben (Blau und Rot) identischer photopischer Intensität (20.0 lux) und mit zwei weissen Stimuli unterschiedlicher Intensität (20.0 lux versus 2.0 lux) getestet. Nach 7 Stunden wurde ein sehr hoher Grad von Blaupräferenz beobachtet, die nach 27 Stunden abgenommen hatte und nach 47 Stunden verschwunden war. Mit zunehmendem Alter ergaben sich keine bedeutenden Veränderungen in beobachteter Präferenz für den helleren der zwei weissen Stimuli. Versuchstiere, die nach 3, 5 und 8 Generationen zweigerichterer genetischer Auslese nach Farbpräferenz getestet wurden, zeigten nur geringe Unterschiede zu nichtausgelesenen Kontrolltieren in Alter und den Auswirkungen der Stimulusintensität. Die beobachteten starken genetischen Reaktionen auf die künstliche Auslese von Wachteln nach Frabpräferenz wurden nicht durch Alter vermittelt und standen in keiner Beziehung zu den Auswirkungen der Stimulusintensität. Diese Daten zeigen, dass die Gene direkten Einfluss auf die nervliche Aufschlüsselung und verhaltensmässige Verarbeitung von Information, insofern sie sich auf die naive Farbwahl der Wachtel bezieht, ausüben.