

The Ontogeny of Auditory Frequency Generalization in the Chicken

Edwin W Rubel and Morton H. Rosenthal
Yale University

To determine if there is an ontogenetic change in stimulus coding, chickens between the day of hatching and 9-10 days old were tested using a habituation-generalization paradigm. Experiment 1 indicated that 1-day-old and 3-4-day-old chicks show similar habituation of an eye-opening response to auditory stimuli in the 800-1,200-Hz range. In Experiment 2 the eye-opening response to a 1,000-Hz stimulus was habituated and then immediately tested using stimuli which varied between 800 and 1,200 Hz. Each age-group (1 day, 3-4 days, and 9-10 days) showed a symmetrical stimulus generalization gradient around the 1,000-Hz stimulus and the 1-day-old chicks displayed a reliably flatter gradient than either of the older groups, which did not differ. In a third experiment, the position of the gradients relative to the baseline was shifted without altering the relative shapes. These results allow general arousal, general auditory responsiveness, overall error rate, and metric characteristics of the independent and dependent variables to be eliminated as possible sources of the age differences in gradient shape. The changes in stimulus generalization, therefore, support the view that during normal development there is a sharpening of perceptual coding processes.

The ontogeny of perception may involve processes whereby an organism becomes progressively more able to distinguish and utilize subtle changes in its environment (Ganz, 1968; Gibson, 1969; Werner, 1948). For example, Gibson (1969) states that perception begins as "crudely differentiated and grossly selective." According to this view, as the organism develops and acquires more experience its perceptual system becomes more "differentiated" by establishing dimensions of association and of differences between stimuli. Thus the organism becomes more capable of extracting critical

cues from the environment and responding with greater specificity. Support for this notion is drawn mainly from studies showing developmental changes in human cognitive abilities and studies comparing deprived animals with normally reared subjects (Ganz, 1968). Furthermore, a number of studies have shown that the number of stimuli evoking species-typical behavioral responses decreases during normal ontogeny (Gottlieb, 1971; Hinde, 1970).

If increased canalization is a general property of perceptual development, it should be reflected in an organism's coding of stimulus differences along a relatively simple physical dimension such as wavelength or frequency. Stimulus generalization gradients reflect the organism's detection and utilization of differences between stimulus configurations. When stimuli differ only along one independently defined physical dimension the gradient represents a functional mapping of perceptual processes onto the physical dimension. An ontogenetic change in generalization gradients would therefore serve as an indication that the functional size of a stimulus class had also changed. Such a

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Requests for reprints should be sent to Edwin W. Rubel, Department of Psychology, Yale University, New Haven, Connecticut 06520.

demonstration would serve several purposes. First, a developmental sharpening of stimulus generalization gradients would provide strong support for the canalization view. Second, further understanding of the normal ontogeny of stimulus coding along a readily quantifiable stimulus dimension will aid in attempts to understand the role of experience in perceptual development. Finally, if increased canalization is indeed a pervasive process in perceptual and cognitive development, its identification using a single physically defined stimulus dimension may provide a "model system" wherein the mechanisms may be investigated in greater detail.

The experiments reported here investigated a developmental change in frequency generalization in the hatchling chicken. The first experiment demonstrates that the eye-opening response to presentation of an auditory stimulus declines over repeated stimulus presentations. In Experiments 2 and 3 the response to tonal stimuli was habituated at one frequency. Generalization tests using surrounding frequencies were then used to determine the extent of stimulus generalization.

EXPERIMENT 1

When a hatchling chicken is placed in a warm, dimly lit chamber, it will quickly assume a relaxed posture with its head down and eyelids closed. Presentation of an auditory stimulus evokes an orienting response which includes eye opening. In this experiment, habituation of the eye-opening response to 800-, 1,000-, and 1,200-Hz stimuli was studied in 1-day-old and 3-4-day-old chickens.

Method

Subjects. Subjects were 12 White Leghorn chicks (*Gallus domesticus*) obtained on the day of hatching from a local breeder (Spafas, Inc., Norwich, Conn.). Subjects were housed communally in a commercial brooder at a temperature of $32 \pm 4^\circ$ C. At the time of training chicks were 1-day (6-24 hr) or 3-4-days (48-96 hr) posthatch. Each age-group consisted of 6 subjects.

Materials. The experimental chamber was $20.32 \times 20.32 \times 20.32$ cm, painted flat black on the interior of three sides and the top. The fourth side was black except for the bottom 3 cm of transparent Plexiglas. The subject was supported

on hardware cloth. The chamber was lit with diffuse light from below, maintained at 32° C and situated in a sound-attenuated room. A television camera (Sony AVC 1400) was situated in front of and below the chamber in order to monitor the bird's behavior, and a background noise of 77 db. (re $20 \mu\text{N}/\text{m}^2$, C scale) was present at all times.

Each stimulus consisted of a 1.5-sec train of tone pulses. Pulses within a train were of 73 msec duration with rise and fall times of 5 and 8 msec, respectively, and delivered at a rate of 4 per sec. Stimuli were generated by a Hewlett-Packard audio oscillator (Model 200 ABR) and delivered through a 20.32-cm speaker mounted on the top of the chamber. Tone production of this system was 90 ± 6 db. (re $20 \mu\text{N}/\text{m}^2$, C scale), 13 db. above background noise.

Procedure. A subject was removed from the brooder and placed in the experimental chamber. Its subsequent behavior was monitored over closed circuit television from an adjoining room. After a minimum adaptation period of 3 min, stimulus presentation was begun when the chick had assumed a relaxed posture with eyelids closed for at least 15 sec. The frequency of each stimulus was 800, 1,000, or 1,200 Hz. Each subject received a total of 12 stimulus presentations, arranged as four blocks of three trials, with one trial at each frequency per block. The order of stimulus presentation was counterbalanced such that one subject in each age-group received each of the six possible orders of the three stimuli. The same order was repeated over the four trial blocks. The intertrial interval was 30 sec. If the chick had not reassumed a relaxed posture with eyes closed at the end of any 30-sec interval, the stimulus was withheld for an additional 30 sec.

A response was arbitrarily defined as eye opening within 2 sec of stimulus onset. Eye opening was behavior easily observed over the video system except when the subject faced directly away from the camera. On such occasions the stimulus was withheld until the subject changed position. Two observers independently scored responses of three subjects. Observer reliability was found to be perfect.

Results and Discussion

Both 1-day-old and 3-4-day-old chicks showed a decrement in responding over the four trial blocks. The mean percentage of trials on which an eye-opening response was elicited, over the four blocks, were 67, 55.5, 55.5, and 22.2 for the 1-day-old subjects; and 88.8, 61.1, 44.4, and 22.2 for the 3-4-day-old birds. The two age-groups also showed similar response functions to the three stimulus frequencies. Mean percent responses to the 800-, 1,000-, and 1,200-Hz tones were, respectively, 41.6, 62.5, and 45.8

for the 1-day-old subjects and 54.1, 66.7, and 41.6 for the 3–4-day-old birds. Statistical analysis yielded a highly significant main effect for trial blocks, $F(3, 30) = 6.24$, $p < .01$, and a marginally significant main effect for frequency, $F(2, 20) = 3.65$, $p < .05$. The comparison between age-groups did not approach statistical reliability, $F < 1.0$, as was the case for the Age \times Trial Blocks interaction, $F = 1.05$, Age \times Frequency interaction, $F < 1.0$, Trial Blocks \times Frequency interaction, $F = 1.05$, and Age \times Trial Blocks \times Frequency interaction, $F < 1.0$.

These results indicate that (a) the eye-opening response showed reliable habituation over repeated presentations of the auditory stimulus, (b) the 1-day-old and 3–4-day-old chicks were similar in overall response rate, (c) habituation to the 800-, 1,000-, and 1,200-Hz stimuli was not reliably different either within or between age-groups, and (d) both age-groups responded slightly more often to the 1,000-Hz stimulus than either the 800-Hz or the 1,200-Hz stimulus.

EXPERIMENT 2

The purpose of this experiment was to determine if there is an ontogenetic change in behavior reflecting an organism's coding of differences in the frequency of auditory stimuli. Hatchling chickens that were 1 day, 3–4 days, and 9–10 days of age were habituated to a 1,000-Hz stimulus. Stimulus generalization gradients were then determined by recording the eye-opening response to a series of stimuli ranging from 800 to 1,200 Hz.

Method

Subjects. Subjects were 40 White Leghorn chicks (*Gallus domesticus*), supplied as fertilized eggs by a local breeder (Spafas, Inc.) and incubated at 37.5° C in the animal care facilities of the psychology department at Yale University. After hatching, subjects were housed in groups, with a minimum of 16 animals housed together. Brooder temperature was maintained at $32 \pm 4^\circ$ C. At the time of training and testing, chicks were 1-day (0–24 hr), 3–4-days (48–96 hr), or 9–10-days (192–210 hr) posthatch. Each age-group consisted of 16 birds, except for the oldest group, in which only 8 birds were included.

Materials. The experimental chamber was 20.32 \times 25.40 \times 20.32 cm, painted flat black on the interior with a 2.54 \times 20.32 cm Plexiglas window on the top of one side. The chamber was situated in a sound-attenuated room, illuminated with diffuse white light and maintained at 32° C. Background noise (77 db.) and stimulus characteristics were the same as in Experiment 1. The stimulus was delivered through a 20.32-cm speaker mounted on one side of the chamber. Tone intensity in this experiment was 90 ± 3 db. (re 20 μ N/m², C scale), 13 db. above background noise, at all frequencies used.

Procedure: Habituation. Chicks were removed from their brooder and placed in the experimental chamber. The experimenter observed the chicks' behavior directly rather than over the closed circuit television system. No stimuli were presented until the chick had assumed a relaxed posture with eyes closed for at least 15 sec. This period, from placement in the chamber to eye closure, was recorded as duration of habituation to box. Subjects were then presented with a 1,000-Hz stimulus every 30 sec. A response was arbitrarily defined as eye opening within 2 sec of stimulus onset. If a chick had not reassumed a relaxed posture with eyes closed at the end of any 30 sec interval, the stimulus was withheld for an additional 30 sec. Habituation training was ended when the subjects had reached criterion.

Two different criteria were used: High criterion was defined as failure to respond for 10 of 10 trials; low criterion was defined as failure to respond for 5 of 10 trials. All three age-groups were run on the high criterion condition, while only the 1-day-old and 3–4-day-old groups were run on the low criterion condition. There were eight birds in each of the resulting five groups. Trials to criterion, defined as the number of trials prior to the first of the trials ultimately achieving the criterion, was recorded.

Procedure: Generalization. The generalization test was begun 30 sec after the final criterion-achieving habituation trial and consisted of blocks of nine stimulus presentations, one at each of the frequencies: 800, 900, 950, 975, 1,000, 1,025, 1,050, 1,100, and 1,200 Hz in random order. These stimuli had the same intensity and duration parameters as the habituation stimulus. Animals in the high criterion group were presented with three randomized blocks while those in the low criterion group were presented with four such blocks. The chick's response or lack of response to each presentation was recorded. All scores were converted to percentages (number of responses to a given frequency/number of presentation of the frequency \times 100) and analyzed as such.

Observer reliability test. In order to test whether the orienting response was reliably observed, an observer reliability test was undertaken. Two unhabituated chicks were individually placed in the chamber. After the chick had assumed a relaxed posture with eyes closed, 15 stimuli at 1,000 Hz were presented. The experimenter and

two observers who had no knowledge of the experimental hypothesis independently recorded each chick's eye-opening behavior. On all but two of the trials, where it was not possible for all three observers to gain a concurrent view of the eyes, the three observers agreed perfectly. During the actual testing the experimenter was able to assume an optimal position for viewing at all times.

Results and Discussion

Habituation. No statistically significant differences in either duration of habituation to the testing chamber or trials to criterion were found between age-groups (see Table 1), suggesting again that neither differences in habituation rate nor general arousal differences which may affect habituation behavior were present at the ages tested. In addition, no differences were found across habituation criteria for the duration of habituation to the chamber.

Generalization test. Results of the generalization test for the high and low criterion groups are shown in Figures 1 and 2, respectively. The unconnected symbols above 1,000 Hz show the response rate averaged over the first four habituation trials. Inspection of the figures reveals that within each criterion condition there was a symmetrical generalization gradient around the 1,000-Hz stimulus. Furthermore, in each criterion condition the 1-day-old chicks had flatter gradients than the older animals.

Separate analyses of each criterion condition yielded similar results and there were no reliable differences between 3-4 and 9-10-day-old animals in the high criterion con-

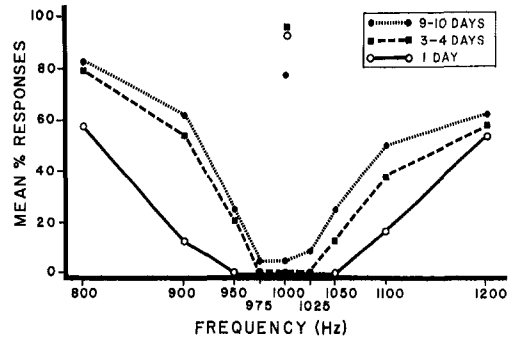


FIGURE 1. Symbols connected by lines indicate mean percentage of stimuli to which subjects in the high criterion groups responded during generalization test; symbols not connected by lines indicate mean percent responses during first four habituation trials. ($n = 8$ for all groups.)

dition. Thus an overall analysis of variance was performed from which the 9-10-day-old animals were eliminated. The overall analysis supported the suggestion that the two criterion conditions essentially replicated each other, as this factor did not approach statistical significance, $F < 1.0$, nor did the Criterion Condition \times Age interaction, $F < 1.0$, Criterion Condition \times Frequency interaction, $F = 1.32$, or Criterion Condition \times Age \times Frequency, $F < 1.0$. On the other hand, the analysis revealed that the differences in response rate due to age and frequency were highly statistically reliable, $F(1, 28) = 11.88, p < .01$, and $F(8, 224) = 56.72, p < .01$, respectively. As expected, the Age \times Frequency interaction was also statistically significant, $F(8, 224) = 2.86, p < .01$.

More detailed analyses of these data utilized the Newman-Keuls method for individual comparisons (Winer, 1962). This analysis indicated that at frequencies $\pm 50, \pm 100$, and ± 200 Hz away from the training stimulus the 1-day-old subjects responded reliably less to test stimuli than 3-4-day-old subjects ($p < .01$ at 800, 900, 950, 1,100, 1,200 Hz; $p < .05$ at 1,050 Hz). At 975, 1,000, and 1,025 Hz the differences between age-groups did not approach statistical significance.

It is noteworthy that the age difference in generalization gradients was apparent during the first block of test trials. At each

TABLE 1

DURATION OF HABITUATION TO THE TEST CHAMBER AND TRIALS TO CRITERION

Chicks	Duration of habituation to test chamber (in min) ($\bar{X} \pm SD$)	Trials to criterion ($\bar{X} \pm SD$)
High criterion condition (10/10)		
1-day-old	28.8 \pm 11.4	14.25 \pm 6.08
3-4-day-old	22.3 \pm 10.3	30.25 \pm 28.75
9-10-day-old	20.6 \pm 11.4	15.75 \pm 20.17
Low criterion condition (5/10)		
1-day-old	28.6 \pm 27.8	6.38 \pm 5.36
3-4-day-old	11.0 \pm 9.77	9.88 \pm 5.59

Note. For all groups $n = 8$.

frequency greater than 50 Hz from the training stimulus a larger percentage of 3-4-day-old than 1-day-old subjects responded to the first presentation of the test stimulus.

The reliability of response differences between each frequency combination within the two age-groups was also analyzed by the Newman-Keuls method. Results of this analysis can be summarized in the following way. The generalization gradients appear symmetrical around the training frequency (1,000 Hz); response levels equidistant from this frequency within either age-group did not differ reliably. At ± 50 Hz from the training stimulus 3-4-day-old chicks showed a reliable increase in responses ($p < .01$ for 950 Hz, $p < .05$ for 1,050 Hz). The 1-day-old subjects, however, did not show a reliable increase in responses until ± 200 Hz from the training stimulus ($p < .01$ for 800 and 1,200 Hz). Therefore, the younger subjects showed a flatter generalization gradient in the area of the habituation frequency. Subjects 3-4 days old were capable of responding differentially to frequencies separated by as little as 25 Hz (950 vs. 975 Hz, $p < .01$), while the younger subjects showed reliable differential responding to frequencies separated by no less than 100 Hz (800 vs. 900 Hz, $p < .01$; 1,100 vs. 1,200 Hz, $p < .01$). Thus, there appear to be age differences in the steepness of the generalization gradients both in the immediate region

of the habituation frequency and at more remote frequencies.

The results, therefore, indicate that 1-day-old chickens show flatter generalization gradients than either 3-4 or 9-10-day-old hatchlings. However, no reliable differences were found between 3-4 and 9-10-day-old subjects, suggesting that any developmental change affecting this behavior occurs prior to the 4th day posthatch. The difference in shapes of the generalization gradients from 1-day-old and 3-4-day-old birds was primarily due to differences in the number of frequency points at which the response rate did not differ from the response rate at the training frequency (1,000 Hz). Since the gradients appear truncated at the baseline, it could be argued that the difference was attributable to an overall response rate difference between the two groups that was unrelated to frequency. Although such a difference was not apparent in Experiment 1 or in this experiment prior to habituation, habituation training possibly produced some type of "state" change leading to age differences in overall responsiveness (Groves & Thompson, 1970). It had been hoped that the low criterion of habituation would leave the response rates above zero for a greater number of central frequencies than in the case of the high criterion; however, no such outcome was observed.

EXPERIMENT 3

This experiment was undertaken in an attempt to raise the overall response rate of subjects during generalization testing. By raising the response rate at the central frequencies it was possible to determine if the age differences in the slopes of the generalization gradients would occur when the gradients were not differentially truncated as in Experiment 2. In this experiment there was no subject-contingent criterion of habituation, but rather, subjects were simply presented with five trials at 1,000 Hz after habituation to the test chamber and prior to the generalization test.

Method

Subjects. Subjects were 24 White Leghorn chicks supplied as fertilized eggs by a local breeder

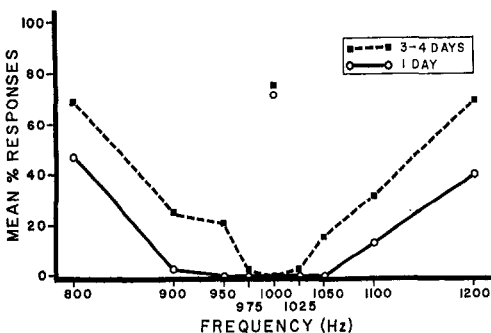


FIGURE 2. Symbols connected by lines indicate mean percentage of stimuli to which subjects in the low criterion groups responded during generalization test; symbols not connected by lines indicate mean percent responses during first four habituation trials. ($n = 8$ for both groups.)

(Spafas, Inc.) and incubated at 37.5° C in the animal care facilities of the psychology department at Yale University. After hatching, chicks were housed in groups of at least 12 birds in a commercial brooder. At the time of testing and training, chicks were 1-day or 3-4-days post-hatch. There were 11 birds in the 1-day-old group and 12 in the 3-4-day-old group, since one bird was dropped from the 1-day-old group because it failed to respond at all during either training or testing.

Procedure. The procedure of Experiment 3 was identical to that of Experiment 2, with the following exceptions: The chamber was maintained at 30° C, only five 1,000-Hz habituation trials were presented prior to the generalization test, and the generalization test consisted of four randomized blocks of the nine test stimuli.

Results and Discussion

Habituation. No significant differences in duration of habituation to box was found between age-groups: The means and standard deviation, respectively, were 6.9 and 7.15 for 1-day-old subjects, and 10.6 and 9.8 for the 3-4-day-old subjects.

Generalization test. The mean percentage of stimuli responded to by 1-day-old and 3-4-day-old subjects at each test frequency are indicated in Figure 3. Fewer training trials with the 1,000-Hz stimulus effectively left the response rate at all frequencies above the baseline for both groups. This procedure, however, did not appear to alter the general shape of the gradients or the differences between age-groups. The younger animals still displayed a markedly flatter generalization gradient than the older birds. Again,

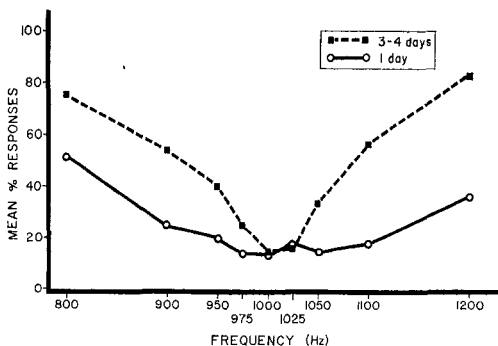


FIGURE 3. Mean percentage of stimuli to which subjects responded during the generalization test. ($n=11$ and 12 for 1-day-old and 3-4-day-old subjects, respectively.)

this pattern was apparent during the first presentation of each test stimulus in that a larger percentage of 3-4-day-old than 1-day-old subjects responded to the 800-, 900-, 950-, 1,050-, 1,100-, and 1,200-Hz stimuli.

Statistical analysis of these data revealed that the younger animals respond less often than older chicks, $F(2, 21) = 6.81$, $p < .05$, a significant frequency effect, $F(8, 168) = 25.32$, $p < .01$, and a significant Age \times Frequency interaction, $F(8, 168) = 5.04$, $p < .01$.

Comparisons between the age-groups at each frequency using the Newman-Keuls method yielded results identical to those obtained in Experiment 2: At ± 50 , ± 100 , and ± 200 Hz from the training stimulus the 1-day-old animals responded reliably fewer times than the 3-4-day-old subjects ($p < .01$ at 800, 900, 950, 1,100, and 1,200 Hz; $p < .05$ at 1,050 Hz); whereas at 975, 1,000, and 1,025 Hz the differences between age-groups did not approach statistical significance.

Comparisons between response rates to the nine test frequencies within each age-group also yielded a pattern similar to that found in Experiment 2. The generalization gradients are largely symmetrical except that the 1-day-old subjects showed reliably more responses to 800 than 1,200 Hz ($p < .05$). As found in Experiment 2, the 1-day-old subjects did not show a reliable increase in response rate until ± 200 Hz from the training frequency (1,000 vs. 800 Hz, $p < .01$; 1,000 vs. 1,200 Hz, $p < .05$), while at ± 50 Hz the 3-4-day-old animals responded significantly more than they did at 1,000 Hz (1,000 vs. 950 Hz, $p < .01$; 1,000 vs. 1,050 Hz, $p < .05$). Finally, the younger animals responded differentially to tones differing by 100 Hz (800 vs. 900 Hz, $p < .01$), while the older subjects responded differentially to frequencies separated by 50 Hz (950 vs. 1,000 and 1,050 vs. 1,100, $p < .01$; 900 vs. 950 and 1,000 vs. 1,050, $p < .05$), although not to lesser differences, as they did in the previous experiment.

GENERAL DISCUSSION

These experiments indicate that over the first 3-4 days of posthatching development

chickens become differentially responsive to progressively smaller stimulus changes. That is, stimulus coding behavior changes toward increasing specificity. Figure 4 presents the gradients from the 1-day-old and 3-4-day-old subjects in Experiment 2, collapsed over the two criterion conditions, along with the gradients from Experiment 3. When the generalization test results from the two experiments are viewed together, conclusions can be drawn which effectively rule out several alternative explanations.

First, the development trend is both robust and dramatic. Figure 4 demonstrates that in both training conditions older animals showed steeper generalization gradients than younger subjects, and in each experiment older animals were consistently more likely than younger animals to respond to a stimulus differing by greater than or equal to 50 Hz from the training stimulus.

Second, the developmental changes in the slopes of generalization gradients observed in Experiment 2 are apparently *not* due to age differences in the subjects' general responsiveness to auditory stimuli. The results of Experiment 1 indicate that the age-groups do not differ in general responsiveness to tones in the 800-1,200-Hz frequency range or in habituation rate across this frequency range. Figure 4 indicates that with fewer habituation trials the response rates to the 975-, 1,000-, and 1,025-Hz stimuli were effectively raised above the baseline for both age-groups while the ontogenetic difference in the slope of the gradients remained stable. Thus the ontogenetic change in gradient shape was not due to age differences in general responsiveness that were induced by the habituation procedure. It is also unlikely that the age differences in gradient shape were due to differential habituation during generalization testing since the difference is apparent in responses to the first presentations of the test stimuli in both Experiments 1 and 2.

Finally, Blough (1965) and Shepard (1965) both point out that the shape of a generalization gradient is a function of the metric characteristics of the response measure and the stimulus measure. The shape of a single gradient and the relative slopes

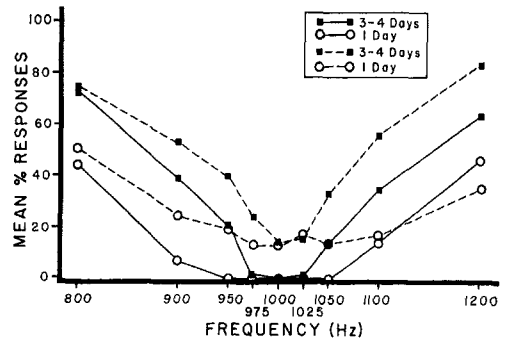


FIGURE 4. Solid lines indicate mean percentage of stimuli to which subjects in Experiment 2 responded during the generalization test, high and low criterion conditions combined; broken lines indicate mean percentage of stimuli to which subjects in Experiment 3 responded during the generalization test.

of any two gradients can be altered by arbitrary transformations of the variables. Thus, the differential gradient shapes observed in either Experiment 1 or 2 could be peculiar to the measures employed. However, the fact that the generalization function from the 1-day-old group in the second experiment transects the function for the 3-4-day-old group in Experiment 1 suggests that this is not the case, since no monotone transform of either or both scales can equalize the slopes of the 1- and 3-4-day gradients seen in Figure 4.

Summarizing the above discussion, the results indicate that following habituation to tone pulses of one frequency, 1-day-old chicks generalize the decrement to a wider frequency band than do older subjects. Since the ontogenetic "sharpening" of generalization gradients does not appear to be a result of changes in general arousal, differential habituation to the training or test frequencies, or nonlinearity of the measurement scales, it appears to represent a developmental change in unidentified perceptual-associative processes which are reflected as a change in sensory coding by the organism.

Habituation and Stimulus Specificity

Thompson and Spencer (1966) state that one of the nine parametric characteristics of habituation is that "habituation of response to a given stimulus exhibits stimulus gen-

eralization to other stimuli." A large number of previous studies have shown that following habituation to one stimulus an intermodal or intramodal change in stimulus characteristics leads to increased responsiveness in adult humans (Allen, Hill, & Wickens, 1963; Badia & Defran, 1970; Coombs, 1938; Hare, 1968; Houck & Mefferd, 1969; Korn & Moyer, 1968; Weisbard & Graham, 1971; Zimmy, Pawlick, & Sour, 1969), human infants (Bornstein, Kessen, & Weiskopf, in press; Bridger, 1961), and other organisms (Bagshaw & Benzie, 1968; Bagshaw, Kimble, & Pribram, 1965; Peeke & Peeke, 1973). Although there is less abundant evidence that the amount of response increment is a function of the amount of difference between training and test stimuli, this relationship has now been demonstrated in several different organisms by using a variety of response measures (Apelbaum, Silva, Frick, & Segundo, 1960; Corman, 1967; Engen & Lipsitt, 1965; Greer, 1969; Sokolov, 1963; Williams, 1963). The present study therefore provide additional quantitative evidence that the habituation process is sufficiently specific (to the stimulus complex present during training), that response probability is significantly altered by small changes in one parameter of the stimulus.

Although the results presented here do not deal directly with the neural basis of habituation, the finding of relatively sensitive and symmetrical stimulus generalization gradients along the frequency dimension may have important implications for future research in this area. The frequency specificity of the response decrement is reminiscent of the frequency specificity of neuronal organization in nuclei of the auditory pathway, where discrete tonotopic organizations are found (Rose, Galambos, & Hughes, 1959). This suggests that neuronal networks responsible for the stimulus generalization gradient may lie within brain regions where receptor specification is most highly maintained, such as the principal sensory pathways. If this is the case, then the parametric characteristic of stimulus generalization may prove crucial for identifying the neural mechanisms underlying the response decrement, since it may be possible to identify

and compare neuronal elements which exhibit a gradient of change due to the habituation procedure. The identification of neuronal systems in which the topographic organization can be quantitatively described may therefore yield excellent preparations for future investigations on the neural basis of habituation.

Stimulus Specificity and Development

Probably the most universal concept in developmental theories is that of progressively increasing canalization. This concept underlies theories ranging from those dealing with the differentiation of specific tissue compartments (Saxen & Toiven, 1962) to those attempting to describe cognitive development in the human (Piaget & Inhelder, 1969; Witkin, Dyk, Faterson, Goodenough, & Karp, 1962) and has met with varying amounts of success (e.g., see Coghill, 1929; Windle, 1944). Theories of perceptual development, likewise, abound with the proposition that organisms become able to detect and/or differentially respond to ever more subtle stimulus differences during development (e.g., Ganz, 1968; Gibson, 1969; Hebb, 1949; James, 1892; Werner, 1948). Implicit in this notion is the proposition that stimulus generalization gradients along a quantitatively defined stimulus dimension should show increasing slope during normal development. Support is usually drawn from a number of experiments (reviewed by Gibson, 1969, and Hinde, 1970) in which complex stimulus configurations have been used to show that young children classify more stimuli as similar than do older children (e.g., Gibson & Gibson, 1955) or to show that a wider range of stimulus configurations will elicit species-typical responses in younger than in older animals (Hailman, 1967; Messmer & Messmer, 1956). Although these studies do suggest an ontogenetic change toward increasing stimulus specificity, the use of complex stimulus configurations has not allowed investigators to determine if the developmental trend is systematically related to a physical or psychological gradient which can be independently assessed. Thus, the results can be interpreted, alternatively, as a change in the rate

of "error responses" unrelated to the physical or psychological differences between stimulus configurations (e.g., Mednick & Lehtinen, 1957). Gottlieb (1968, 1971) has used a similar approach to determine the time at which embryonic ducklings respond differentially to species-typical vocalizations. By showing a developmental change in *differential responsiveness* to species-typical maternal vocalizations versus other natural stimuli, it can be concluded that a perceptual change has occurred. The use of complex stimuli, however, makes it difficult to isolate and quantitatively manipulate the relevant stimulus characteristics. Although some progress has been made along these lines (Gottlieb, 1971, 1974), the exact nature of the developmental changes in stimulus coding behaviors are, as yet, obscure.

The other major line of research relevant to the issue of ontogenetic changes in stimulus coding behavior has employed early deprivation of one or more stimulus dimensions and then compared discrimination or generalization performance of deprived animals to a group of "normally reared" animals (Ganz & Riesen, 1962; Tracy, 1970). These studies are usually interpreted as support for the view expressed by Lashley and Wade (1946) that the slope of a stimulus generalization gradient is related to an organism's differential experience with the stimulus class (Ganz, 1968; Gibson, 1969; Terrace, 1966). However, using this evidence to imply an ontogenetic change in stimulus coding behavior without concomitant knowledge of normal development is tenuous (Solomon & Lessac, 1968).

The approach utilized in the present study differs from those discussed above in several ways. First, by using a relatively simple dimension, frequency, it has been possible to present a series of stimuli which are at least ordinally related, thereby ruling out the possibility that the ontogenetic trend reflects merely a change in overall response level or in "error rate" which is unrelated to the position of the training stimulus. Second, by looking directly at age differences rather than inferring an ontogenetic trend from a deprivation experiment, the interpretive problems of the latter have been avoided.

Finally, the experiments cited above and, indeed, most experiments dealing with stimulus generalization (Mostofsky, 1965) have used a conditioning paradigm and tested generalization during extinction. Results are interpreted as yielding information regarding the "cue control over behavior" exerted by the particular stimulus dimension. However, the use of this paradigm for investigations concerned with perceptual development necessitates determining the differential effects of reinforcement and extinction on age and/or experience as well as equating groups on acquisition level. The use of a habituation-generalization paradigm by no means alleviates these problems entirely, but the task of attempting to equate groups on all but the relevant dimension(s) becomes more feasible. Although neither the present study nor those cited above can make conclusions regarding the absolute perceptual abilities of the subjects, the habituation-generalization paradigm may therefore represent a more useful test of developmental and/or experiential changes in cue utilization than generalization around a reinforced point. In this regard, it is noteworthy that the habituation-generalization paradigm (usually with only one test stimulus, however) has been used for some time to study perceptual behavior of human infants (see Engen & Lipsitt, 1965) and has recently been used to show categorical perception of color (Bornstein et al., in press) and speech signals (Eimas, 1974) in infants.

The present finding of an ontogenetic change reflecting the organism's coding of the frequency of an auditory signal poses two important questions for future research on the ontogeny of perceptual processes. First, what is the locus of the change? At present it is not possible to determine if the changes result from differentiation in the resolving power of the cochlear partition, changes in connectivity within primary or secondary central auditory nuclei or alterations in "higher level" associative networks within the brain. Detailed studies on the development of peripheral and central coding of auditory stimuli, using Mössbauer and cellular electrophysiological methods, may shed light on this problem. The second

problem involves the role of auditory experience. In the present study subjects were incubated and reared communally in order to provide a wide range of auditory experience. Future investigations in which both the amount and frequency range of auditory experience are precisely controlled will provide valuable information regarding the role of an organism's interaction with its environment on the ontogeny of perceptual coding processes.

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