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Development of Responsiveness to Suprathreshold Acoustic Stimulation in Chickens

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Developmental changes in an unconditioned response to acoustic stimulation were observed in young chickens. Specifically, durations of distress call (peep) suppression were measured after the onsets of tones that differed in intensity and frequency in 384 newly hatched and 4-day-old chicks. Resuppression was also measured after a 6% change in the frequency of these tones, once the animals had habituated to the original tone. The data showed that the suppression varied systematically as a function of age, intensity, and frequency: (a) the duration of suppression increased with increasing stimulus intensity, as expected; (b) responsiveness to high frequencies grew more rapidly over the first 4 days than responsiveness to low frequencies, an effect indicating a developmental gradient across frequencies with age; (c) resuppression to the 6% change in frequency increased in duration with age; and (d) young birds suppressed vocalizations longer to loud tones in the range of their species' maternal assembly call than to other frequency-intensity combinations. These developmental trends indicate rapid changes in "perceived loudness" and "perceptual sharpening" over the first few days of postnatal life.

The normally occurring processes that culminate in mature or asymptotic responses to sensory stimulation remain largely undocumented despite the fact that nearly all animals must somehow come to attend to relevant stimuli and stimulus changes in their environment. This gap in our knowledge is understandable, given the difficulties inherent in interpreting animals' responses to different stimuli and the still greater difficulties in measuring rapid developmental changes in these traits. Nevertheless, these problems in "developmental animal psychophysics" (as this area of inquiry might be termed) can be simplified by describing the functions that relate changes in responses to changes in stimulation, and by describing how these functions change over the first few days of life. To this end, this research is an example of how one stereotyped response (peep suppression in young chickens) is affected by pure tones that differ in frequency and intensity and how the effect of those stimuli changes over the first 96 hr of life.

Previous studies on the development of auditory perception have consistently shown an age-related process termed differentiation (Gottlieb, 1977), specificity (Gottlieb, 1976), or sharpening (Rubel & Rosenthal, 1975). In this view, developing organisms become progressively more able to distinguish and utilize subtle differences in their environment (Gans, 1968; E. Gibson, 1969). Rubel and Rosenthal (1975) and Kerr, Ostapoff, and Rubel (1979) showed that 1-day-old chicks, for example, had flatter frequency generalization gradients following habituation to pure-tone stimuli than did 4-day-old chicks. Other animal studies have shown the same age-related sharpening in preferences (Bateson, 1971; Gray & Tardif, 1979; Hailman, 1967; Lehrman & Rosenblatt, 1971), in discrimination (Zolman & Becker, 1968), and possibly in neuronal responses (Aitkin & Moore, 1975; Carlier, Le-

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noir, & Pujol, 1979; Grobstein & Chow, 1976; Mistretta & Bradley, 1978). A similar developmental trend in perceptual and intellectual abilities appears to take place in humans (Bornstein, 1979; Gaines & Little, 1975; J. Gibson & Gibson, 1955; Mednick & Lehtinen, 1957; Wolf, 1973). Thus it seems that discrimination improves, generalization gradients steepen, preferences narrow, and neuronal coding sharpens as humans and other animals mature. All of these changes would allow the organism to respond differentially to progressively smaller changes along a stimulus continuum. These observations of perceptual sharpening suggest that as animals mature, a given amount of stimulus change above threshold would produce progressively greater amounts of response change.

The auditory system seems appropriate for a developmental psychophysical study, and it has not yet been subjected to extensive experimental inquiry (Gottlieb, 1977). The signals are easily controlled, and changes in these stimuli seem to naturally cause changes in some responses, as indicated below.

Certain unconditioned responses may be particularly well suited for psychophysical studies because animals may be "prepared" to associate some cues with a particular response (Blough & Blough, 1977). Such "built-in" responses would be ideal for a developmental analysis because no training is required. Naturalistic observation and imagination often suggest useful responses (Blough & Blough, 1977; Leavitt, Brown, Morse, & Graham, 1976; Rubel & Rosenthal, 1975). Rubel (1970), for example, showed that exposure of young quail to a stimulus on which they had been "imprinted" resulted in cessation of distress vocalizations (peeps). More recently, Kerr et al. (1979) showed that young chickens peep nearly incessantly when alone in a well-lit temperate chamber and that changes in the acoustic environment often cause a momentary suppression of these ongoing peeps. This suppression habituates quickly but can be reinstated by other stimulus changes. D. Miller (1980) showed that young ducks respond to specific features of the maternal call with sustained suppression of their vocalizations and that, in the field, these calls seem correlated with predator presence. Thus, in the present study, peep suppression was used as an unconditioned measure of responsiveness to sounds.

To summarize, the present study assesses the ontogeny of peep suppression produced by changes in acoustic stimulation. The results are first conservatively described as age-related changes in the functions relating responsiveness to stimulus parameters. The discussion is more speculative, suggesting that these data indicate rapid developmental changes in psychophysical scales and perceptual sharpening.

Method

The general strategy was to document the duration of peep suppression following the onset of a tone and after a 6% change in the frequency of that tone. The durations of peep suppression at two ages, to two intensities, in three frequency ranges were observed.

Subjects

Subjects were 384 chicks (*Gallus domesticus*, Hubbard × Hubbard, broiler stock) obtained as fertilized eggs from a commercial farm. They were incubated in a forced-draft incubator and turned four times daily for 19 days. They were then transferred in groups of 12 or more to smaller hatching incubators and finally to communal brooders (≥ 12 birds per brooder) after they hatched. Animals were tested between 6 and 24 hr after hatching (termed "1-day-old chicks"), or between 96 and 120 hr after hatching (termed "4-day-old chicks").

Apparatus and Calibration

The subjects were individually tested in a vertical Plexiglas cylinder (12 cm ID × 11 cm) located inside a double-walled sound-attenuating room (Industrial Acoustic Corp. Model 1204) and were constantly monitored by closed-circuit TV and an audio monitor. The temperature (23.5 ± 2.5 °C), lights (300 W), and a constant background noise (broadband white noise at 55 dB SPL, B scale) were controlled to produce a mild state of arousal, sufficient to induce regular peeping.

Sound was delivered through a speaker under the cylinder. The sound was within ± 2 dB across the cylinder at the level of the animals' ears at all frequencies used. Calibrations were made periodically (by General Radio .5-in [1.27-cm] electret microphone and 1900A wave analyzer) and did not change over the course of the experiment. The electronic equipment to deliver the stimuli and measure the responses was located outside the sound-attenuating room.

The animals' vocalizations were picked up by a microphone (Sony Cardoid F-98) above the cylinder and sent to a specially built "peep discriminator" and an oscilloscope. The peep discriminator utilizes multiple criteria, including fundamental frequency, minimum intensity, and envelope shape, which must be satisfied before sending a logic level pulse to the computer. These variables were set individually for each chick during the 2-5 min acclimation period by comparing the discriminator output with the vocalizations, as heard over the audio monitor and as seen on the oscilloscope trace. On a few occasions when the experimenter estimated the peep discriminator to be in error once or more in 20 pulses, the subject was discarded. In general, comparisons of the computer-tabulated peeps with those counted by a human listener, with the aid of a storage oscilloscope, on more than one hundred 10-sec intervals yielded counts within 1%.

Stimuli

The stimuli were continuously pulsing (2/sec) pure tones (492 msec on, 8 msec off, with 32-msec rise-fall time). This 2/sec pulse rate was used because pilot experiments showed that this stimulus elicited much greater suppression than a constant tone.

The tones differed in intensity, either 70 or 90 dB SPL, and in frequency. Twelve frequencies were selected, four in each of three ranges, a Low range of 500, 531, 558, and 625 Hz, a Mid range of 800, 850, 941, and 1000 Hz, and a High range of 2250, 2391, 2648, and 2813 Hz. The selection of these values was based on previous data (Kerr et al, 1979). The Mid range includes frequencies in the chickens' maternal assembly call and partially replicates the Kerr et al study. The frequencies of High and Low ranges were selected in order that the thresholds of brain stem evoked potentials at these frequencies are roughly equal and noticeably higher than the thresholds of the frequencies in the Mid range (Kerr et al, 1979). Pairs of frequencies differ by 6% because the results of Kerr et al suggested that older chicks would respond to a 6% change and younger chicks would not. The highest and lowest frequencies within each range differ by 25%, primarily for consistency.

The stimuli were controlled by a PDP 11-04 computer: from a digitally switched oscillator, through a Wisconsin (Ludwig) electronic switch, a Charybdis digital attenuator, and a power amplifier, to the speaker inside the sound-attenuating room. The computer switched stimuli only during the few milliseconds when the pulsing tones were off. No switching artifacts were detectable to the human ear or electronically with stimulus levels well above those used in the study (> 110 dB SPL).

Response Measurement

The dependent variable was the duration of suppression of ongoing peeps and was measured in two ways: as the length of time between a change in acoustic stimulation and the next peep (called "suppression time") and as the number of peeps in the 10 sec following the change (called "number of peeps"). To allow time for the chicks to react to the stimulation, we did not count peeps during the first 500 msec after the start or change of a tone. Data were collected in the same way during baseline and control trials (described below) except that there was no change in the stimulus.

The computer started the various trials (baseline, onset, change, and control) only when the birds were peeping to a criterion of at least two peeps in 2 sec. This ensured that the animals were in a particular "state" with respect to the dependent variable when the stimuli were presented. The criterion greatly reduced response variability, especially in very young subjects which often peep in bouts separated by several seconds (see also Leavitt et al, 1976).

Procedure

The automated testing took approximately 10 min per subject and involved three "trials": baseline, onset and change (see Figure 1).

Initially, each chick was acclimated to the testing chamber for 2-5 min. After 2 min, and as soon as the bird was peeping regularly, the computer program was started. The subject was discarded if it did not begin to peep within 5 min or if the peep discriminator did not trigger reliably (36 subjects, or 7%, were so discarded).

Baseline data were collected during the first trial. As soon as the acclimation period was over and the birds were peeping to criterion, the baseline trial was begun. During this period (beginning at "1" in Figure 1), the time until the next peep (suppression time) and the number of peeps during the next 10 sec were measured. No stimulus, other than the background noise, was present during this "trial."

During the second trial, the suppression after the

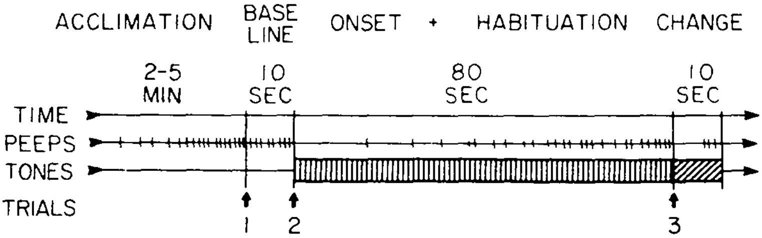

Figure 1 A schematic representation of the automated testing procedure. (The onset and subsequent 6% change in the frequency of a tone are indicated by the wide stripes; those stripes do not accurately represent the tone pulses, although all tones were pulsed at 2/sec. A criterion of two peeps in 2 sec was required to start the three trials as indicated by vertical arrows.)

CHICKS OF TWO AGES	(1 AND 4 DAYS)
HEARD TWO INTENSITIES	(70 AND 90 dB SPL)
IN THREE FREQUENCY RANGES	(500-625, 800-1000, 2250-2813),
IN EIGHT PERMUTATIONS	(OF 4 FREQUENCIES, POOLED),
WITH FOUR REPLICATIONS	(3 WITH 6% CHANGE, 1 CONTROL),
EACH GIVEN TWO ONSETS	(AVERAGED)
AND TWO 6% CHANGES	(AVERAGED),
FOR 12 TREATMENT GROUPS	(2 AGES X 2dB'S X 3 HZ'S),
SO, N=32 PER ONSET GROUP	(ALL BIRDS HEARD THE ONSETS),
AND N=24 PER CHANGE GROUP	(75% HEARD REAL CHANGES),
AND N=8 PER CONTROL GROUP	("MOCK" CHANGES),
FOR 384 TOTAL SUBJECTS	(PLUS 140 DISCARDED)

Figure 2 Summary of experimental design

onset of a tone was measured As soon as the baseline trial was over and the birds were peeping to criterion, a pulsing tone was turned on, and the two response measures were collected The tone pulses continued for at least 80 sec A pilot study determined this to be an optimal period for habituation, by which time the birds' peep rates had returned to near baseline levels

To begin the third trial, the frequency of the tone was changed by 6% After the initial tone had been on for 80 sec and then as soon as the bird had peeped twice in 2 sec, the frequency of the tone was changed by 6% The time period from the onset of the new frequency to the next peep and the number of peeps during the next 10 sec were determined. The tone was then turned off

Finally, the whole process was repeated There were 90 sec of reacclimation to the background noise followed by the same sequence of baseline, onset of a different frequency for 80 sec, and a 6% change in that frequency.

Control Animals

One quarter of the subjects were controls for the response to a change in frequency. At the end of the 80 sec of habituation, the frequency of the tone was *not changed*, but the measurements were taken as before The suppression times to the 6% change were compared with the times for these "mock" changes The baseline measures provided a control for the onset responses

Birds were automatically discarded if they did not peep for 2 min at any time during the experiment, we doubted that a psychophysical analysis of sleeping chicks would be interesting Highly agitated subjects would jump out of the chamber and discard themselves, this also may have provided a convenient control because greatly distressed subjects are not likely to attend to subtle acoustic changes These requirements eliminated 104 birds, or 20% of the total, which were replaced

Design

This experiment has an age by intensity by frequency cross-classified design (summarized in Figure 2): The subjects were either 1 or 4 days old (see Subjects); pulsing tones were either 70 or 90 dB (see Apparatus and Calibration), and in one of three frequency ranges (see Stimuli) Each animal was randomly assigned an intensity and a frequency range. Each subject heard all four frequencies in its assigned range There are eight possible orders of presenting these tones, with a 6% change 1234, 1243, 2134, 2143, 3412, 3421, 4312, 4321 Note that changes to higher and lower frequencies are equally represented. Animals were randomly assigned to one of these permutations, for example, a four-day-old chick might be given 70-dB tones, in the Mid range, in the third permutation Consequently it would be acclimated to the chamber, hear an 850-Hz tone for 80 sec which would then be changed to 800 Hz, be reacclimated, and finally hear a 941-Hz tone which would be changed to 1000 Hz after 80 sec There were 3 birds in every group, for a total of 228 subjects that heard both onsets and 6% changes

For the control subjects, these permutations were the same except the frequency was not changed 1133, 1144, 4422 There was 1 bird in each group, for a total of 96

Analysis of the Data

Separate analyses were performed on the responses to the onsets of the tones and to the 6% changes in frequency. Responses of the control subjects to the mock changes were analyzed separately, although the onset data from these birds were pooled with the other onset data Suppression time was selected a priori as the primary dependent variable, but the same analyses were also performed with the number of peeps as the dependent variable As expected (Kerr et al , 1979), the two measures were highly correlated

There were no reliable differences among responses to the four selected frequencies within each range, so the data in each range were pooled Since each animal heard the onset of two frequencies, both within a given range and each followed by a frequency change, convenient pooled measures were the arithmetic mean of the two onset responses and the mean of the two reactions to the 6% changes. The use of an averaged response from each animal decreases variability, avoids a repeated measure, and normalizes the distribution (MacArthur, 1972)

Three-way cross-classified analyses of variance with equal sample sizes were used to evaluate the effects of age, intensity, frequency, and their interactions

(SPSS-ANOVA, Nie, Hull, Jenkins, Steinbrenner, & Bent, 1970) Subsequent comparisons used the overall error term to locate the significant differences (SPSS-MANOVA, Cohen & Burns, 1977)

Results

Responses to Onsets of Tones

Figure 3 shows the mean suppression times for each age and intensity over the three frequency ranges. All responses are clearly greater than the mean baseline suppression (.52 ± .06 sec), which indicates that there was reliable suppression of vocalizations to the onset of tone pulses in all 12 groups. Several trends are evident in these data; they are discussed below and are confirmed by an analysis of variance shown in the left-hand columns of Table 1.

Intensity. At both ages in all frequency ranges, suppression times following the onsets of 90-dB tones were greater than those following the onsets of 70-dB tones. This main effect of intensity is statistically reliable as shown in Table 1. Thus, peep suppression increases with increasing stimulus intensity, as do several other variables, such as perceived loudness (Robinson & Dadson, 1956) and the reciprocal of reaction time (Moody, 1970; Stebbins, 1966).

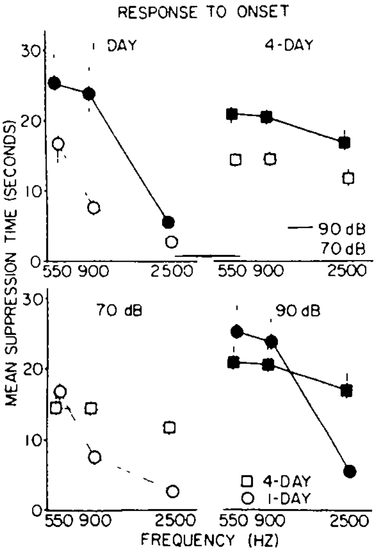

Figure 3 Mean suppression times (± 1 *SE*) for two ages at two intensities over three frequency ranges (The top panel is organized to show the effect of intensity The bottom panel is the same data, rearranged to show the effect of age. Four-day-old chicks are shown as squares, newly-hatched chicks, as circles Solid symbols and lines indicate 90-dB tones Open symbols and dashed lines indicate 70-dB tones The flat trapezoid in the middle of the top panel indicates baseline responses; it is centered on the mean, and the total width equals ± 1 *SE* Where points have no error bars, the standard errors were smaller than the symbols Pairs of points are offset slightly to separate error bars and do not indicate a difference in frequency.)

Frequency and age. The young animals suppressed much less to high-frequency tones than to low frequencies. By 4 days of age, however, the responses were statistically flat across these frequencies; that is, the degree to which responsiveness was affected by frequency depended on the age of the subject, as indicated by the significant age by frequency interaction in Table 1.

There was no overall effect of age, as seen in the bottom panel of Figure 3. In half of the pairs, the 1-day-old chicks suppressed more than the 4-day-olds, and vice versa The short suppression times of the young chicks at high frequencies can account for the significant main effect of frequency in the analysis of variance.

Thus, a second major result of this study is that whereas responsiveness to low frequencies seems relatively mature at birth, responsiveness to high frequencies develops later. Subsequent tests confirmed the leveling of responses over these frequencies with age. There was a significant effect of frequency in the 1-day-old birds alone, $F(2, 372) = 19.2, p < .00001$, but no effect of frequency in the older birds alone, $F(2, 372) = .9, p < .38$. As astutely noted by Gottlieb (1971b), this developmental gradient in acoustic responsiveness—progressive maturation from low to high frequencies with increasing age—is also seen in a large number of other functional responses in all vertebrates thus far examined (see also Rubel, 1978).

Interaction with species-specific signals The 1-day-old chicks responded to the loud tones in the Mid range with much longer suppression times than would be expected from the other data; that is, the differences in suppression times elicited by 90-dB tones compared with 70-dB tones were much greater in this age and frequency combination than the others, as seen in the top panel of Figure 3. The average gain in suppression time that resulted from the 20-dB increase

Table 1
Analyses of Variance

		Onset			Change		
Source	*df*	*M*	*F*	*p*	*M*	*F*	*p*
dB	1	550,703	22.0	.00001	5,760	12.6	.0005
Age	1	79,695	3.2	.08	10,296	22.5	.00001
Hz	2	354,436	14.2	.00001	2,357	5.2	.006
Age × Hz	2	148,885	6.0	.003	1,822	4.0	.02
Age × dB	1	26,800	1.1	.30	2	.1	.95
dB × Hz	2	41,333	1.7	.19	1,573	3.4	.03
Age × dB × Hz	2	32,049	1.3	.28	450	1.0	.37
Error		25,001	(372 *df*)		457	(276 *df*)	

Note. This table shows three-way cross-classified analyses of variance of suppression times to the onsets of the tones and to the 6% changes in frequency. The independent variables were age (1 and 4 days posthatch), decibels (the intensity of the tones which was either 70 or 90 dB SPL), and hertz (the frequency of the tones in three ranges: Low, 500–625; Mid, 800–1000; and High, 2250–2813). There were equal sample sizes in each of the 12 treatment groups, 32 for the onsets and 24 for the changes (see Figure 2).

in intensity was 7.6 sec ($SE = 1.9, n = 6$). The 16.3-sec gain in the 1-day, Mid-range group is clearly an outlier (+ 4.6 *SE* from the mean, $p < .01$; Gill, 1978).

This third trend in the data suggests that the stimuli eliciting extraordinary responses from young birds may be correlated with species-specific signals. Normally, young precocial birds are selectively responsive to the maternal assembly call of their species (Gottlieb, 1971a), and in chickens that call has a fundamental frequency around 800 Hz. This call is uttered soon after the chicks hatch and functions to call them toward the hen. Thus, it is likely that the maternal call will be loud, since the hen and brood remain close together.

Relation between the two dependent measures. Basically, the same results were found when using the number of peeps in the 10 sec following tone onset as the dependent variable. The analysis of variance showed significant main effects of intensity, $F(1, 372) = 7.7, p < .006$, and an Age × Frequency interaction, $F(2, 372) = 8.0, p < .001$, as discussed above. The two variables were closely correlated ($r = -.81$, or $r = -.93$ when the logarithm of suppression time is correlated with the number of peeps, which would be appropriate if the interpeep intervals decreased exponentially from their suppressed levels).

Baseline. As noted above, the baseline suppression times (unstimulated inter-peep intervals) were much less than any of the responses to tone onsets. The 1-day-old birds, however, had slightly longer mean baseline suppression times (.65 ± .1 sec) than did the 4-day-old birds (.40 ± .05 sec; $p < .05$). In contrast, the median suppression times of the two ages were nearly identical, (.27 and .26 sec, respectively), and their modes ($< .1$ sec) were identical. Thus, the difference in mean baseline suppression times was due to the distribution of interpeep intervals; the younger birds peeped in bursts with intervening pauses, while the older birds were more regular. Since the onset responses were averaged and hence approached normality (MacArthur, 1972), the slight difference in distributions of baseline peeping is unlikely to have affected the conclusions. Notice, in addition, that where the age-groups showed marked differences, it was in the opposite direction; the young birds displayed shorter suppression times than the older chicks in response to tone onset, whereas the slightly longer baseline suppression times of the young chicks would be expected to increase suppression times.

Response to Frequency Changes

Figure 4 shows the suppression times in response to the 6% change in frequency. Similar trends as in the onset data, with the notable addition of an overall effect of age, are evident. These trends are discussed below and evaluated in the analysis of vari-

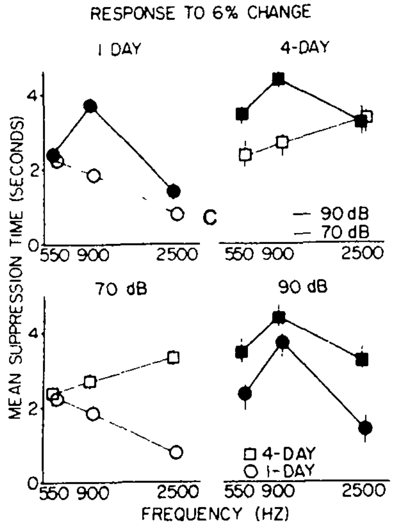

Figure 4 Mean suppression times to a 6% change in frequency. (The top and bottom panels are the same data arranged to show the effects of intensity and age, respectively. The large C in the middle of the top graph indicates the control responses; the letter is centered on the mean, and its top and bottom delineate ±1 *SE* Other symbols are as in Figure 3.)

ance shown in the right-hand columns of Table 1.

Age. In every frequency range at both intensities, the suppression times elicited by a 6% change in frequency were longer in the 4-day-old chicks than in the newly hatched birds (shown in the bottom panel of Figure 4). This main effect of age was statistically reliable as shown in Table 1. This indicates that responsiveness to a constant shift in frequency increases with age, at least across the range of frequencies tested.

Intensity. In all but one pair (4-day, High range), the suppression times were longer to frequency changes at 90 dB than at 70 dB, as shown in the top panel of Figure 4. This main effect of intensity is also highly significant as shown in Table 1. Thus, chicks suppressed more at higher intensities in response to frequency changes as well as to tone onsets.

Frequency. The young animals responded very little to the changes in the high-frequency range, as indicated by a significant effect of frequency in the 1-day-old animals alone, $F(2, 276) = 8.06, p < .0005$. They suppressed no more to the high-frequency changes at 70 dB than did the controls, $t(118) = .26, p > .5$; they did, however, show marginally reliable suppression of peeping in response to the high-frequency changes at 90 dB, $t(118) = 1.96, p \sim .05$. All other suppression is clearly greater than that of the controls.

By 4 days of age, the suppression times were statistically flat across frequencies, as indicated by a nonsignificant effect of frequency in the 4-day-old birds alone, $F(2, 276) = 1.1, p > .33$. Thus, at the same time that responsiveness to frequency shifts is increasing with age across all frequencies, that response grows relatively faster at high frequencies. This is demonstrated by the significant age by frequency interaction and the resulting effect of frequency in the three-way analysis shown in Table 1. In other words, a gradient of maturation in responsiveness from low to high frequencies is seen in these data as well as in the onset data.

Interaction with species-specific signals Chicks of both ages responded with longer suppression times to loud changes in the frequency range of their maternal assembly call than to the lower intensity or to other frequency ranges. This consistent nonlinearity in both ages produced the significant intensity by frequency interaction seen in Table 1. The effect was greater in the younger birds, as was this effect in the onset responses.

Controls. One fourth of the animals were controls and heard no change in frequency after their 80 sec of habituation. Analyses of variance of suppression times and numbers of peeps (not shown) revealed no significant effect of any independent variable; not age, frequency, intensity, or any interaction was significant. Accordingly, all of the control data were pooled, and the mean (± 1 *SE*) suppression time is shown in Figure 4. There were, therefore, no differences in the peep rate after 80 sec of habituation despite the large differences shown above in the initial suppression times (supporting an expectation, mentioned above, that interpeep intervals decreased exponentially from their suppressed level to a consistent asymptote).

Relation between dependent variables. Similar trends were found when using the number of peeps in the 5 sec following the frequency shift. (The period of time was halved from the 10 sec used previously in order to monitor these more subtle responses.) The main effects of age, $F(1, 276) = 16.3$, $p < .001$, and the Age × Frequency interaction, $F(2, 276) = 4.8$, $p < .01$, were significant. The measures were highly correlated ($r = -.93$; or $-.94$ assuming a log-linear relation discussed previously).

Summary of Results

The responses of chicks of two ages to the onsets and changes of tones that differed in intensity and frequency showed four major trends. First, responses were uniformly greater to 90-dB stimuli than to 70-dB stimuli. Second, responsiveness to high-frequency tones increased rapidly over early postnatal development, whereas the responses to low frequencies increased only slightly or not at all. That is to say, there was a developmental gradient over frequencies with age. Third, there was a consistent increase across all frequencies tested in responsiveness to the 6% frequency changes over the 96 hr after hatching but no consistent developmental trend in responsiveness to tone onsets. Finally, young chicks responded with disproportionately long suppression to loud stimuli in the range of their maternal assembly call.

The initial tone onsets could, of course, be viewed as changes in the acoustic environment, although the parameters of that change are difficult to specify. The "onset" responses were elicited by the addition of a pulsing pure tone to a 55-dB white noise; the "changes" were 6% shifts in frequency. The two suppression times might, therefore, be related. The data confirm this hypothesis ($r = .34$, $p < .001$, evaluated by correlating each onset with the subsequent 6% change, $N = 576$). This relation, however, explains only a small percentage of the observed variance ($r^2 = .12$). This echoes the above summary and suggests that some of the relations between age and acoustic responsiveness are the same for onsets and changes but that others are different.

More specifically, the relation between the responses to onsets and to changes is tighter in the young chicks ($r = .46$) than in the older ones ($r = .21$), and the two coefficients are significantly different ($z = 3.4$, $p < .0001$). This provides further support for the summary above, suggesting that at 1 day of age the functions relating the stimulation to the suppression are similar for both onsets and changes (dominated by low responsiveness to high frequencies and long suppression to loud Mid frequencies) but that by 4 days of age these extreme responses have leveled out.

Discussion

"Stimulus Control"

Stimulus control is observed when a change in a particular property of a stimulus produces a change in some response (Rilling, 1977). Typically, stimulus control is defined only after animals are trained to respond differentially to two stimuli (Guttman & Kalish, 1956; Herrnstein & VanSommers, 1962; Schusterman & Balliet, 1970; Terrace, 1966), but this training is not always necessary (Stebbins, 1970a). Certain response features tend to covary naturally with parameters of external stimulation (Moody, 1970); these orderly relations raise the interesting question of what laws describe the control of the stimulus over the response (Malott & Malott, 1970). In particular, these responses have been interpreted as psychophysical scales of suprathreshold stimulation (Blough & Blough, 1977; Malott & Malott, 1970; Moody, 1970); that is, since there has been no training imposed by the experimenter, differences in the responses may indicate the animals' "perception" of the stimulus changes.

The present study shows that peep suppression varies systematically with the intensity and frequency of acoustic stimulation and with the age of the subjects. Since this response shows orderly variation with the parameters of stimulation, peep suppression can be used as an indication of stimulus control; for example, the laws of stimulus control over peep suppression are similar to those of other variables (Moody, 1970; Robinson & Dadson, 1956; Stebbins, 1966) in that the responses increase with increasing stimulus intensity. Given this interpretation, the developmental differences reported in this article can be viewed as an indication that the laws of stimulus control change rapidly over age: There is a developmental gradient in stimulus control across frequencies with age; stimuli in the range of species-specific signals exert far more control over the responses of young animals than do other sounds; and the stimulus control provided by a constant shift in frequency increases with age. Finally, since these subjects were never trained to respond in any way to the stimuli, the ontogenetic changes in stimulus control may indicate changing "perceptions" of the acoustic environment, as discussed below.

"Perceived Loudness"

There is some precedence for interpreting unconditioned responses to the onset of tones as "perceived loudness" in both humans and animals (Bartoshuk, 1962; Blough & Blough, 1977; Leavitt et al., 1976; Malott & Malott, 1970; J. Miller, Kimm, Clopton, & Fetz, 1970; Moody, 1970; Robinson & Dadson, 1956; Scharf, 1978; Stebbins, 1966, 1970a, 1970b; Stevens, 1975). The conditions for this interpretation seem to be some *intuitive* satisfaction that the response might reflect "loudness," and an orderly covariance of the response with parameters of stimulation, specifically increasing responses with increasing intensity and a roll-off at extreme frequencies. With respect to the data reported here, it seems reasonable that chicks might orient more strongly and hence suppress peeping longer to tones that they perceive as louder. More important, these responses vary with frequency and intensity in ways that are similar to other measures of perceived loudness. Consequently, we believe it is not unreasonable to interpret the onset data as reflecting developmental changes in perceived loudness.

We realize that all inferences about psychophysical scales in nonverbal subjects are highly speculative and, as yet, are not open to objective analysis. Nevertheless, the cautious interpretation of the onset data as perceived loudness provides a useful framework. Loudness at high frequencies increases quickly with age, whereas loudness at low frequencies does not appear to change. "Ethologically relevant" sounds are especially salient, but only during the early postnatal period. As a consequence of all these developmental trends, perception of loudness rapidly levels off across frequencies, at least in the middle of the chicken's audible range. This, then, is one indication of perceptual maturity.

"Perceptual Sharpening"

Older animals responded more to a given change along one stimulus dimension (6% in hertz) than did younger animals. Developing chickens, therefore, become progressively more able to utilize small stimulus changes along a single dimension, as predicted by a widely held tenet of perceptual development (Bornstein, 1979; Gans, 1968; E. Gibson, 1969; Gottlieb, 1971a, 1976; Gray & Tardif, 1979; Mistretta & Bradley. 1978; Rubel, 1978; Rubel & Rosenthal, 1975).

The relative equivalence, at the older age, of responses to a 6% change in frequency suggests that Weber's law ($\Delta F/F$ is a constant, or constant stimulus ratios produce equal differences in responses; Geldard, 1972) holds fairly well for the perception of differences in frequency in 4-day-old chicks. However, the rapid roll-off of responsiveness to frequency changes at higher frequencies in newly hatched chicks suggests that Weber's law may not hold for neonates. Thus, as in perceived loudness, there is a developmental gradient across frequency with age, leveling the responses to frequency changes.

Finally, the two developmental trends in stimulus control suggested by this study, changes in perceived loudness and in perceptual sharpening, appear to diverge from each other with age. This divergence is shown by the reliable decrease over age in correlations between the responses to tone onsets (a simultaneous change along many dimensions) and to tone changes (a change along a single dimension, frequency); that is, young chicks responded to onsets and to changes in roughly the same way, whereas older chicks did not. One interpretation of these data is that the animals become progressively more able to distinguish changes along a single perceptual dimension from general changes in acoustic stimulation. The role of early experience in this "learning" is, at present, unknown, but the work of many investigators predicts that experiences with frequency shifts are necessary for the animals to separate this dimension from other dimensions (Gans, 1968; Gottlieb, 1971a, 1976; Kerr et al., 1979; Lashley & Wade, 1946; Peterson, 1962; Tees, 1976; Tracy, 1970).

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