

THE UNIVERSITY OF MANITOBA

INDIVIDUAL PARENTAL CALLS AND AUDITORY  
DISCRIMINATION LEARNING BY YOUNG  
GALLUS GALLUS AND BRANTA CANADENSIS

by

P. J. COWAN

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the University of Manitoba in partial fulfillment of the requirements  
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ABSTRACT

Observations of the stable family groups of Domestic Chickens and Canada Geese have suggested the ability of the young to recognize their own parents by voice. Laboratory experiments conducted with Domestic Chickens and Canada Geese demonstrated that after training with a parental call paired with visual movement (simulating the adult's gait), the familiar call can produce a greater number of approach responses relative to the parental calls of other individuals. Distress vocalization is similarly affected in Domestic Chicks. This process of auditory discrimination learning involving the presence of visual movement may be a basis of individual recognition of the parent's voice by the young.

Investigation of the parameters of chick behavior and parental sound in auditory discrimination learning showed that a familiar parental call can cause a much earlier but otherwise slower approach response than a novel parental call from a second individual hen. A familiar call can also

produce an approach response which at onset is more directly oriented towards the sound stimulus. An additional series of experiments using synthetic calls demonstrated that call frequency appears to be the most important call parameter facilitating auditory discrimination learning of individual calls. Such learning was not shown for intensity and duration which appear, rather, to allow fine control over chick behavior.

## ACKNOWLEDGEMENTS

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GENERAL INTRODUCTION

Precocial and semiprecocial young birds (Nice, 1962) have often been observed approaching and following their parents, for example, when initially leaving the nest, when swimming and when walking around the breeding grounds (Collias, 1962: 578-581). The majority of studies of approach and following behavior have concentrated on the responses made to visual stimuli (Bateson, 1966; Sluckin, 1965; Smith, 1969). However, parents of most precocial and semiprecocial species also utter 'parental' calls when near their young, when leading young and when on the nest before and during hatching (Collias and Collias, 1956; Hess, 1972; Impekoven, 1973). This thesis is primarily concerned with the effects such auditory stimuli have on the approach behavior of young Domestic Chickens (Gallus gallus) and young Canada Geese (Branta canadensis).

Parental calls can differ in structure between species. Gottlieb (1968a, 1971, 1973) described the parental calls of various duck species while Evans (1970a, b, 1973) and Beer (1970a) have presented spectrograms of the parental calls of four species of gulls. Species differences in parental calls can produce differential effects on embryonic behavior and may facilitate species recognition by young on hatching (Gottlieb, 1971, 1973). In Wood

Ducklings (Aix sponsa), posthatch exposure to parental calls enhances following of the species-typical call relative to the calls of other waterfowl (Klopfer, 1959). Parental calls also appear to influence the development of species recognition by visual properties (Klopfer, and Gottlieb, 1962).

Different individuals of the same species may also possess distinctive parental calls. Evans (1970a, b) has published spectrograms of the Black-billed Gull (Larus bulleri) and the Ring-billed Gull (Larus delawarensis) demonstrating the individual distinctiveness of parental calls. Individual distinctiveness of the 'fish' call of the Sandwich Tern (Sterna sandvicensis) has also been shown (Hutchison, et al, 1968). Other examples were reviewed by Beer (1970a). Individual differences in parental calls provide a 'physical' basis for individual recognition of parents by their young (Thorpe, 1968).

Individual recognition of parents by voice has been experimentally demonstrated for young of several species, including the Common Guillemot (Uria aalge) (Tschanz, 1965, 1968), Laughing Gull (Larus atricilla) (Beer, 1969, 1970b), Ring-billed Gull (Evans, 1970b), Black-billed Gull (Evans, 1970a), Common Tern (Sterna hirundo) (Stevenson et al, 1970) and the Domestic Chicken (Ramsay, 1951). Observations consistent with individual recognition of parents by voice have also been reported

for the King Penguin (Aptenodytes patagonica) (Stonehouse, 1960), Canada Goose (Collias and Jahn, 1959) and several other waterfowl species (Ramsay, 1951).

Klopfer (1959) found that selective responses to particular auditory stimuli in young ground-nesting waterfowl develop when posthatch auditory exposure is accompanied by the simultaneous movement of a human investigator in front of the young bird (cf. Sluckin, 1965: 107). On the basis of this report, Evans (1972) carried out a laboratory experiment with Domestic Chicks which demonstrated that pairing a swinging pendulum (the visual movement of which resembles to some extent the locomotory gait of the parent) with a simulated parental call can subsequently enhance the number of approach responses given to the familiar call relative to a second call that was not previously paired with the visual stimulus. Such auditory discrimination learning, involving actual parental calls, was subsequently demonstrated by Evans and Mattson (1972). Young chicks can give a higher number of approach responses to a familiar parental call previously paired with a visual stimulus, compared to a parental call from a different individual hen. Visual stimuli may therefore be especially effective in influencing the development of individual recognition by voice in young precocial birds (cf. Evans, 1972).

There are many aspects of individual recognition of the parental voice which remain to be elucidated. Part I of this thesis presents three experiments to investigate further the significant variables of auditory discrimination learning in Domestic Chickens. Section 1 tests whether a more 'naturalistic' training procedure than that used by Evans and Mattson (1972) can result in chicks selectively approaching and distress calling to individual parental calls. Distress vocalization is a new dependent variable in the study of auditory discrimination learning of individual calls. The second section of part I examines whether selective responsiveness to individual calls can occur by simple exposure in the absence of a visual stimulus i.e. by auditory imprinting. The third section of part I presents an experiment to test whether auditory discrimination learning can occur in the classic revolving-wheel apparatus, an adaptation of which has recently (Bateson and Wainwright, 1972) been found useful in studies of visual imprinting.

Although the Domestic Chicken is ideal biological material for the testing and development of hypotheses derived originally from field studies (cf. Wood-Gush, 1971: 1), it is important to determine if results obtained with this species are applicable to other precocial species. Part II of this thesis extends research on the auditory basis of individual recognition to a second precocial species, the Canada Goose. Families of Canada Geese can survive over more than one season and appear highly stable (Raveling,

1970) which suggests that individual recognition of voice may be well-developed in this species under a variety of social and ecological conditions. Section 1 of part II describes a laboratory study to test the extent to which goslings can selectively respond to a familiar parental call previously paired with the movement of a pendulum. Section 2 then presents an investigation to discover if the calls of different individual Canada Geese are individually distinctive under alarm conditions, and therefore potentially able to provide a basis for individual recognition by goslings in the presence of predators and intruders.

From the experiments in parts I and II of this thesis, it became evident that results obtained with the Domestic Chicken were similar to those <sup>obtained</sup> with the Canada Goose. The more readily available Domestic Chickens were therefore used for experiments in part III to investigate the actual parameters of chick behavior and parental sound involved in auditory discrimination learning.

An experiment to investigate the effect of individual parental calls on the instantaneous speed, orientation, direction of movement and latency of an approach response is presented in section 1 of part III. It should be noted that instantaneous speed, although a standard measurement in studies of animal mechanics (Gray, 1968; Tricker and Tricker, 1966; Alexander, 1968), has apparently not

been used previously to study discrimination learning in young precocial birds. Section 2 of part III presents four experiments to determine the possible call parameters involved in auditory discrimination learning and the individual recognition of parents by voice.

Each section of this thesis is presented in the format of a self-contained manuscript to aid future dissemination of findings. These sections are followed by a general discussion and the literature cited.

PART I

AUDITORY DISCRIMINATION LEARNING OF INDIVIDUAL PARENTAL  
CALLS BY YOUNG DOMESTIC CHICKENS

## SECTION ONE

PARENTAL CALLS AND THE APPROACH BEHAVIOR AND DISTRESS  
VOCALIZATION OF YOUNG DOMESTIC CHICKENS

## Introduction

Evans (1972) has suggested that visual stimuli may be an important influence on the development of individual recognition by voice in young precocial birds. Evans and Mattson (1972) subsequently demonstrated that pairing a parental call with a conspicuous visual stimulus during training can result in one-day-old Domestic Chickens responding selectively to the individual parental call.

In the experiments on approach behavior reported by Evans (1972) and Evans and Mattson (1972), all chicks during training received identical durations of exposure to the two test calls, the difference being that one call was paired with a familiar visual stimulus while the other was not. This procedure appears somewhat unnatural as nesting in this species is secretive (McBride et al, 1969). 'Training' probably usually involves pairing of maternal calls with the visual movement of the mother alternating with more or less silent periods rather than with equal intensity sounds of another hen. The present study investigated whether parental calls recorded from different

individuals affect the approach behavior and distress vocalization of young Domestic Chickens after training with either a parental call paired with movement alternating with silent periods ('naturalistic' regime), or movement alone alternating with silent periods. The distress vocalization of chicks, which previously has not been studied in investigations of selective responses to individual parental calls, consists of relatively loud 'cheeps' descending in frequency in contrast with the quieter, rather higher, rapid twittering notes called contentment or pleasure calls (Sluckin, 1965; Hoffman, 1968).

## Methods

### Apparatus

Two tape loops of Domestic Chicken maternal calls were used. Each loop was made from 9 repetitions of a single call recorded from two different individual white rock X cornish hens, as described by Evans and Mattson (1972). The higher call, call A, contains sound up to at least 1700 Hz compared to only 1200 Hz for the lower call, call B. The rate of call presentation, 110 calls per min, was the same for both calls. Each call was played at about 65 decibels (db) scale C slow, as measured with a General Radio Co. type 1565-A sound level meter. A background of white noise, at about 60 db (C), was produced by Grason-Stadler model 901 B noise generators. The movement of a pendulum was

used as the visual stimulus.

Auditory training and testing were carried out in a modified version of the tip-floor apparatus described by Evans (1972: 79), which basically consists of a pen with a tipping floor. To avoid the possibility that clicks of the microswitches or movement of the tipping floor in the earlier version might lead to spurious results, a photocell apparatus was used equipped with a stationary, immovable floor and silent photocells.

The photocell apparatus consisted of a grey plywood pen (117 x 40 x 28 cm) containing a 57 cm-long runway. A loudspeaker and pendulum were placed in compartments at either end of the run and separated from the runway by a 1.26 cm-mesh screen. The loudspeakers were wired to Fanon model 3512 amplifiers which were connected in turn to the output of Sony model Tc 800 Solid State tape recorders. The pendulums were controlled via electric motors and swung to and fro at 35 cycles per min. A white disc 15 cm in diameter with 12 red discs, 1.8 cm in diameter attached in a polkadot pattern (illustrated in Evans, 1972), was fixed at the base of each pendulum. A fine light beam and concealed photocell were set up in the runway parallel to and 15 cm from each screen, 3.8 cm above the runway floor. The photocells were wired to a Hunter model 335S photo relay and a self-holding relay, such that as a chick approached the activated loudspeaker and pendulum at one end of the runway, the chick

cut the light beam, thereby deactivating this loudspeaker and pendulum and simultaneously activating the loudspeaker and pendulum at the opposite end of the runway. In this way a chick could continuously run to and fro the length of the runway, at all times approaching the active loudspeaker. The photo relay was wired to an Esterline Angus event recorder to provide an automatic record of the number of times a chick moved the length of the runway, i.e. the number of approach responses.

The number of distress calls given by a chick was automatically recorded by means of a Hunter model 320S sound-operated relay connected to the event recorder. Sensitivity of the relay was set so as to be activated by the high intensity distress calls but not by weaker chick calls or the parental call. Owing to the often rapid emission of distress calls, calls were counted in terms of the number of 1 s periods in which at least some distress vocalization occurred.

Two photocell apparatuses were set up, each in a separate sound-proofed room maintained under identical conditions, thereby allowing two chicks to be trained or tested simultaneously. Use of rooms was balanced within experimental groups. Temperature in all the experimental and holding rooms was maintained at  $25.6^{\circ}$  C. Chicks were briefly handled when being placed in, and during removal from, the covered cardboard box used to move chicks

between incubator and holding pens, and between holding pens and experimental apparatus.

Initial visual training (Evans, 1972) was carried out in separate grey plywood pens (38 x 52 x 20 cm). Each pen was fitted with an overhead 15-w light and a single, continuously moving pendulum identical to that described above. The pendulum was situated in an end compartment behind a wire mesh screen.

### Subjects

Incubated eggs were collected from a commercial hatchery about one day before pipping and hatched in the laboratory. After hatching the chicks were group reared in holding pens equipped with a wire floor and 25-w light bulb. No food or water were provided. A total of twenty-four white rock X cornish Domestic Chickens were used as subjects.

### Procedure

After hatching, chicks were randomly allocated into two groups of twelve. All chicks of both groups were individually given the initial visual training with a swinging pendulum beginning at 6  $\pm$  3 h posthatch. At this time chicks were exposed to the pendulum for an initial 2 h, returned to the holding pen for 2 h and then brought back for a final 2 h of visual training. Training in photocell pens began at 27  $\pm$  3 h posthatch. Group 1 chicks were individually exposed to call A paired with an active pendulum for 5 min,

followed by 5 min of silence and no pendulum activity. This 10 min period was immediately repeated 8 times for a total of 80 min. Group 2 chicks, the controls, had identical treatments to group 1 birds except that no parental calls were played during training. Three min after training, the chicks were tested. Testing consisted of presenting each chick singly and successively with 5 min each of call A and call B. The test sequence was carried out twice and in a balanced order. In testing, the pendulums remained immobile for both groups of chicks.

Selected a priori comparisons were statistically analyzed using the one-tailed t test or the one-tailed paired t test (Goldstein, 1964) unless otherwise indicated.

#### Results and conclusions

The mean number of approach responses and the mean number of 1 s periods with distress vocalization in training and testing are shown in Fig. 1. During the first test period, chicks trained with call A gave significantly more approach responses to call A than the parental call-naive chicks and approached call A significantly more frequently than call B (Table 1, Fig. 1, comparisons 1>3, 1>2). The lack of a statistically significant difference between calls in test period 2 agrees with Evans and Mattson's (1972) suggestion that response selectivity may not be particularly stable when repeated testing is done in the absence of additional

## FIGURE 1

The mean number of approach responses and distress calls to Domestic Chicken calls A and B during training and testing. A = parental call A; B = parental call B; A+V = call A and visual movement of pendulum; V = visual movement of pendulum; No Stim = no experimental stimuli. Numbers in brackets aid identification of statistical comparisons (see text and Tables 1 and 4).

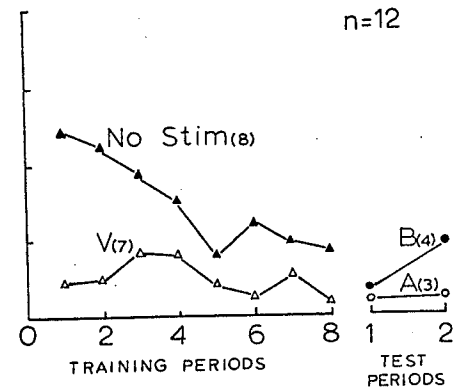
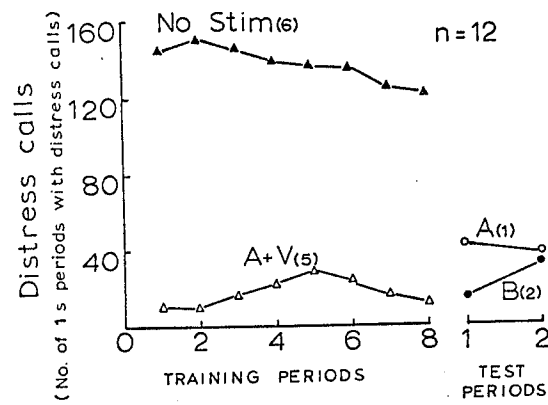
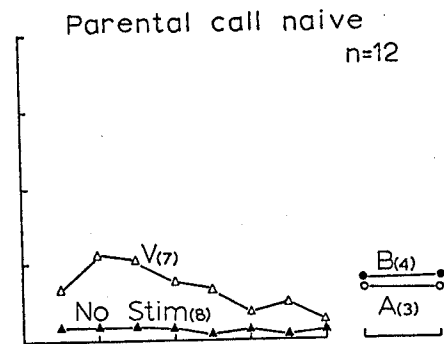
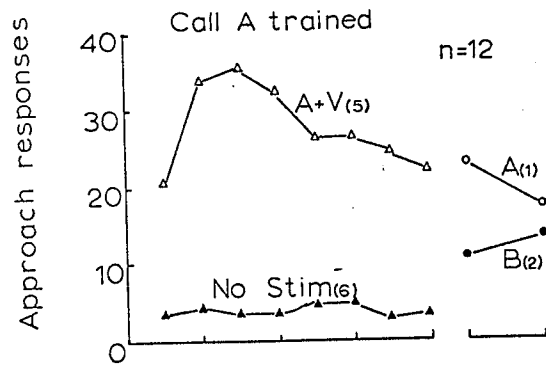


TABLE 1

(1)  
 Statistical comparisons of approach responses and  
 distress calls during testing

---

Statistical comparisons (see Fig. 1)	Approach responses		Distress calls	
	Test period		Test period	
	1	2	1	2
1 > 2	2.97**	ns	2.64*	ns
3 vs 4	ns	ns	ns	ns
1 > 3	1.97*	1.86*	1.97*	ns
2 vs 4	ns	ns	ns	ns

---

1 t test or paired t test where appropriate

\* $p < 0.05$ ; \*\* $p < 0.01$

training. Similarly, chicks trained with call A gave significantly more distress calls to call A than the parental call-naive birds during the first test period, and also gave significantly more distress calls to call A than to call B (Table 1, Fig. 1,  $1 > 3$ ,  $1 > 2$ ). Clearly, after training the familiar call A has a distinct effect on both approach behavior and distress vocalization producing a greater number of approach responses and distress calls than the novel call B. In all except one comparison there was a significant positive correlation between the number of approach responses and the number of distress calls given by a chick in testing (Table 2) which suggests the influence of a relatively individual chick-specific factor.

Correlations between the total number of approach responses made during the 5-min auditory training periods and the number of approach responses during testing were significant for the call A trained birds (Table 3). These correlations also suggest the influence of a relatively individual-specific factor, perhaps anatomical or physiological, on approach behavior (see Sluckin, 1965: 32). Only one comparison was significant for the correlation of the number of distress calls in the training periods with no stimulation and the number of distress calls in testing (Table 3).

TABLE 2

(1)  
Rank correlations . . . between approach responses and  
distress calls during testing

	Test period	To test call A	To test call B
Call A experienced (n=12)	1	ns	+0.55*
	2	+0.52*	+0.75**
Parental call naive (n=12)	1	+0.56*	+0.57*
	2	+0.75**	+0.85**

1 Spearman's coefficient of rank correlation

\*p < 0.05; \*\*p < 0.01

(1) TABLE 3  
 Rank correlations of approach responses and distress calls  
 between training and testing

	Test period	APPROACH RESPONSES <sup>(2)</sup>		DISTRESS CALLS <sup>(3)</sup>	
		To test call A	To test call B	To test call A	To test call B
Call A experienced (n=12)	1	+0.88**	+0.58*	+0.55*	ns
	2	+0.79**	+0.53*	ns	ns
Parental call naive (n=12)	1	ns	ns	ns	ns
	2	ns	ns	ns	ns

1 Spearman's coefficient of rank correlation  
 2 Based on total number of 5-min periods with experimental stimulation  
 3 Based on total number of 5-min periods with no experimental stimulation  
 \*p < 0.05; \*\*p < 0.01

Statistical comparisons of the training results are given in Table 4. The presence of call A not only increased the number of approach responses in the 5-min periods with call A and visual movement (Table 4, Fig. 1, comparisons 5 > 7, also 5 > 6) but it also increased the number of approach responses in the 5-min periods with no stimulation (6 > 8). Exposure to call A resulted in an increase in the number of distress calls in the periods with no stimulation (6 > 8) but the comparisons (5 > 7) for the periods with call A present were not significant. Significantly fewer distress calls were given to call A when it was paired with a visual stimulus than in the periods with no stimulation (5 < 6). Comparisons 7 vs 8 demonstrate that visual pendulum movement also enhanced the approach behavior and inhibited the distress vocalization of parental call-naive chicks.

#### Discussion

This experiment demonstrates that auditory discrimination learning can occur under the more naturalistic training regime of pairing maternal calls with visual movement alternating with silent periods rather than alternating with the same intensity call of a different hen. The call of the second hen in training does not appear essential for auditory discrimination learning.

TABLE 4  
(1)  
Statistical comparisons of approach responses and  
distress calls during training

---

Statistical comparisons (see Fig. 1)

Training period	Approach responses				Distress calls			
	5 > 6	7 > 8	5 > 7	6 > 8	5 < 6	7 < 8	5 > 7	6 > 8
1	6.41**	3.62**	3.77**	ns	7.22**	3.69**	ns	ns
2	5.22**	4.43**	3.36**	2.10*	7.86**	3.09**	ns	1.97*
3	4.18**	3.87**	2.94**	1.86*	7.14**	1.85*	ns	2.14*
4	3.72**	3.55**	2.74**	1.75*	6.55**	ns	ns	2.34*
5	3.01**	3.20**	2.35*	2.75**	4.77**	ns	ns	3.16**
6	3.20**	ns	2.85**	2.17*	5.50**	1.90*	ns	2.41*
7	2.98**	2.62**	2.49*	1.75*	4.76**	ns	ns	2.48*
8	2.74**	ns	2.47*	ns	4.51**	ns	ns	2.53**

---

1 test or paired t test where appropriate

\*p < 0.05; \*\*p < 0.01

The learning of individual parental calls can clearly involve both distress vocalization and approach behavior. The finding that the number of approach responses and distress calls in testing were highly correlated suggests further experiments involving physiological recordings, to relate these factors (cf. Rajecki, 1973).

## SECTION TWO

SELECTIVE RESPONSES TO THE PARENTAL CALLS OF DIFFERENT  
INDIVIDUAL HENS BY YOUNG DOMESTIC CHICKENS: AUDITORY  
DISCRIMINATION LEARNING VERSUS AUDITORY IMPRINTING

## Introduction

Laboratory studies have suggested that experience with a parental call paired with movement of the adult results in individual recognition of the parent's voice by young precocial birds (Evans and Mattson, 1972; Part I, sect. 1). Selective responsiveness to individual calls might also develop as a result of auditory imprinting (Klopfer, 1959; see also Beer, 1970a: 29; Bateson, 1972: 310).

An experiment was carried out to investigate whether posthatch exposure to a parental call in the absence of a visual stimulus in training is sufficient for the development of selective responsiveness by chicks to the parental calls of different individual hens. The first experimental group of chicks received the parental call paired with the visual stimulus in training while the second group received the parental call alone. The experiment also investigated whether

training with a parental call and visual movement, interspersed with periods of no stimulation have a different effect on test behavior than training with the experimental stimuli continuously and whether the presence of the call of a second hen in training, as used by Evans and Mattson (1972) (see also Part I, sect. 1), has any effect on test behavior.

## Methods

### Apparatus

Details of the experimental stimuli and apparatus were as described elsewhere (Part I, sect. 1; see also Evans and Mattson, 1972), except that training and testing were carried out in the standard tip-floor apparatus (Evans, 1972). A photocell apparatus (Part I, sect. 1) converts to a tip-floor apparatus simply by releasing the tip-floor and removing photocells. Both apparatuses, which differ solely in the count transducer, produce equally valid counts of the number of approach responses (eg. compare data in Part I, sect. 1 and in Evans and Mattson, 1972).

### Subjects

Incubated eggs were collected from a commercial hatchery about one day before pipping and hatched in the laboratory. After hatching, chicks were group-reared in lighted holding pens with no food or water. A total of

sixty white rock X cornish Domestic Chicks were used as subjects.

### Procedure

After hatching chicks were randomly allocated into four groups of 15. The first 50 min of training for all groups commenced at 23  $\pm$  3 h posthatch while a second 20 min of training started at 47  $\pm$  3 h posthatch. Group 1 chicks received call A paired with an active pendulum for 5 min, followed by 5 min of silence and no pendulum activity (procedure I). This 10 min period was repeated successively throughout training. The 10 min periods for groups 2 to 4 differed as follows. Group 2 chicks received call A with no pendulum movement for 5 min followed by 5 min of silence and no pendulum movement (procedure II). Group 3 chicks received 5 min of call A paired with pendulum movement followed by 5 min of call B with no pendulum movement (procedure III), whilst group 4 were presented with call A and the moving pendulum throughout training (procedure IV).

Testing, which started about 5 min after the final training session, consisted of presenting each chick singly and successively with 5 min each of call A and call B. The test sequence was carried out three times and in a balanced order. Pendulums remained immobile during testing.

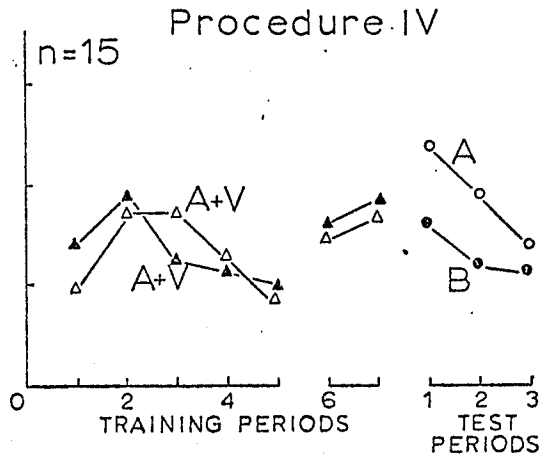
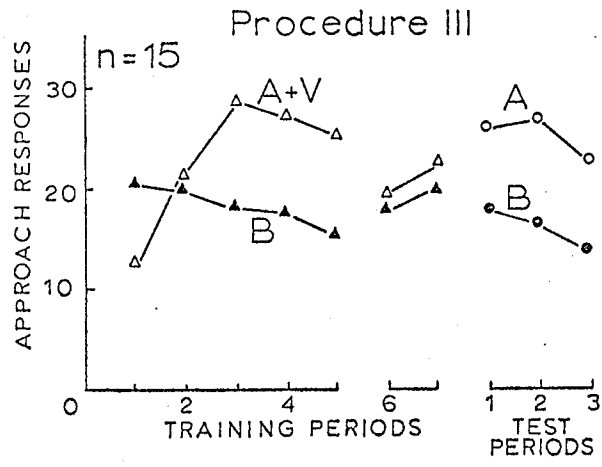
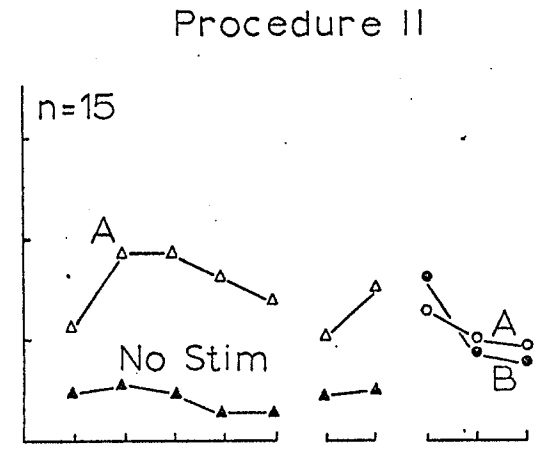
Unless otherwise stated, selected a priori comparisons were statistically analysed using the one-tailed t test or one-tailed paired t test, where appropriate.

#### Results and conclusions

The mean number of approach responses are shown in Fig. 2. For procedure I call A elicited significantly more approach responses than call B in each test period ( $t=2.51, 2.34, p<0.05$ ;  $t=2.77, p<0.01$ , respectively). In contrast, differences in the number of approach responses in testing for procedure II between call A and call B was not significant in any test period. The number of responses to call A was significantly greater for chicks trained with procedure I than procedure II, in each test period ( $t=3.72, 3.10, 2.87, p<0.01$ , respectively). Clearly, after training with visual movement the familiar call A has a distinct effect on approach behavior producing a higher number of approach responses than call B. Chicks which receive call A alone in training do not appear to respond selectively to the familiar call. Simple posthatch exposure to adult calls appears insufficient for the development of selective responsiveness by chicks to the parental call of different individuals.

## FIGURE 2

The mean number of approach responses given during training and testing for training procedures I-IV. A = parental call A; B = parental call B; A+V = call A and visual movement; V = visual movement; No Stim = no experimental stimuli.



Chicks trained with procedure III approached call A significantly more often than call B in each test period ( $t=2.08, 2.38, 2.17, p<0.05$ , respectively). Differences in the number of responses between chicks trained with procedures I and III were not significant for either call in any test period (two-tailed comparison). The presence of a call of a second hen in training does not appear to affect the selective responsiveness to calls in testing. Comparison between call A and call B for procedure IV was significant for test periods 1 and 2 ( $t=2.08, 2.27, p<0.05$ ) but not test period 3. Differences in the number of responses to call A and call B between procedures I and IV were not significant (two-tailed comparison).

The mean number of responses in training are also shown in Fig. 2. Comparison between procedure I and II for periods with experimental stimuli was significant for periods 6 and 7 only ( $p<0.01$ ). Corresponding comparisons between the periods with no experimental stimulation were significant for periods 3, 6 ( $p<0.05$ ), and 4 and 7 ( $p<0.01$ ). Differences in the number of responses between periods with and without experimental stimuli for both procedures I and II were significant in each period ( $p<0.01$ ). The comparison between call B in procedure III and the no stimulation periods for procedure I were also highly significant ( $p<0.01$ ).

Comparisons for procedure III between responses to call A plus visual movement and responses to call B were significant for periods 1 ( $p < 0.01$ ), 3, 4, 5 ( $p < 0.05$ ). The training results indicate that responses are greater during periods of stimulation and that visual stimuli can enhance responsiveness during training.

### Discussion

Posthatch auditory imprinting to individual parental vocalizations was not demonstrated and would not appear to be involved in the development of individual recognition of parents by voice/ <sup>in chicks.</sup> The role of visual movement in the development of selective responsiveness to these calls was confirmed. Auditory discrimination learning, involving training with visual stimuli which are known to have reinforcing properties (Bateson and Reese, 1969), may therefore be the basis of individual recognition by voice of parents by young. It is of interest that although call B affects training behavior, an effect of call B in training on test behavior was not demonstrated even though it was presented in equal amounts to call A in training. This suggests that calls of other adults either on nearby nests or, for example, feeding nearby will not affect the young bird's development of individual recognition of its parent.

In the present experiment, call A paired with visual movement was used in training. Evans and Mattson (1972) found that both call A and call B, when paired with visual movement, can produce selective responsiveness to the familiar call. There were no significant differences due to call type per se (Evans and Mattson, 1972). It would be of interest to test whether auditory imprinting is sufficient for individual recognition of parents by voice in the very different biological situation where both familiar and novel calls are present simultaneously (cf. Gottlieb, 1973: 367; Beer, 1970a: 38). The possible role of prehatch auditory imprinting in the development of posthatch selective responsiveness to individual calls also requires investigation (see General Discussion).

## SECTION THREE

PARENTAL CALLS AND THE LOCOMOTOR BEHAVIOR OF YOUNG  
DOMESTIC CHICKENS IN A REVOLVING-WHEEL APPARATUS

## Introduction

The experiments presented in sections 1 and 2 of Part I investigated effects on approach behavior. Many experiments designed to study visual imprinting in young precocial birds have been concerned with following behavior (see Sluckin, 1965). The Hess-type, circular-runway imprinting apparatus (Schaefer and Hess, 1959; see also Shapiro, 1970) has commonly been used to facilitate the recording of following behavior. More recently, specially adapted running wheels have been employed in visual imprinting research (Bateson and Wainwright, 1972). I carried out an experiment to investigate whether parental calls recorded from two different individual hens can differentially affect the locomotor behavior of parental call-experienced and parental call-naive Domestic Chicks in the classic revolving-wheel apparatus (Munn, 1950: 53-55).

## Methods

Apparatus

The experimental stimuli, call A, call B and the movement of a pendulum were described in Part I, sect. 1. Calls were played at about 72 db (C) and at a rate of 78 calls per min.

Training and testing were carried out in revolving-wheel apparatuses (wheel diameter 35.5 cm). For training, wheels without a one-way attachment were used. Two wheels were set up side by side at one end of the runway of the large goose photocell apparatus (described in Part II, sect. 2). The direction of movement of the wheels was perpendicular to that of the pendulum in the end compartment so that chicks could run towards the experimental stimuli. A wire was attached to each wheel such that an electric circuit was closed once every wheel revolution. The circuit was connected to an Esterline Angus event recorder to provide an automatic record of the number of wheel revolutions. With two wheels facing the pendulum and with two more wheels facing a pendulum in a second sound-proofed room under identical conditions, four chicks could be trained simultaneously. The two chicks facing a pendulum were not allowed visual contact between the wheels. The wheels were quiet running. Auditory testing was carried out in a

revolving-wheel apparatus with a one-way cog attachment. Although chicks in training only very rarely moved away from the experimental stimuli, the one-way attachment ensured that all recorded locomotion in testing was towards the loudspeaker and pendulum.

### Subjects

Incubated eggs were collected from a commercial hatchery about one day prior to pipping and hatched in the laboratory. After hatching, the chicks were group-reared in holding pens equipped with a wire floor and a 25-w light bulb. No food or water were provided. A total of thirty white rock X cornish chicks were used as subjects.

### Procedure

After hatching chicks were randomly allocated into two groups of 15. Group 1 chicks received 50 min of training with call A and a swinging pendulum according to a 5 min on, 5 min off schedule, beginning at about 22 h posthatch. Starting at approximately 46 h posthatch group 1 chicks received this treatment for another 30 min. Group 2 chicks received identical treatment except that no call was presented during either training session. After training all the chicks were given auditory testing which consisted of 2 min of call A and call B successively, twice over, in a balanced order. The pendulum was immobile throughout testing.

## Results and conclusions

The mean number of wheel revolutions in training and testing are shown in Fig. 3. Chicks trained with call A gave significantly more revolutions to call A than the parental call-naive chicks (Table 5, Fig. 3,  $1 > 3$ ). Call A, however, did not produce significantly more revolutions in testing than call B for the call A trained birds (Table 5, Fig. 3, comparison  $1 > 2$ ). In fact, call B produced significantly more revolutions than call A in the second test period for parental call-naive chicks (Table 5, Fig. 3,  $3$  vs  $4$ ). Clearly, call A in training affects later test behavior but a preferential response to the familiar call in testing could not be demonstrated. Rank correlations between the number of wheel revolutions in training and testing were highly significant for the call A trained birds (Table 6).

Statistical comparisons of the number of revolutions in training are given in Table 7. Call A affects following behavior in training both during the periods with experimental stimuli (Table 7, Fig. 3,  $i > iii$ , also  $i > ii$ ), and the periods with no stimulation ( $ii > iv$ ). There was no significant difference between periods with visual movement and with no stimulation for the parental call-naive birds ( $iii > iv$ ).

## FIGURE 3

The mean number of revolutions during training and testing for Domestic Chickens in a revolving wheel. A = parental call A; B = parental call B; A+V = call A and visual movement; No Stim = no experimental stimuli. Numbers in brackets aid identification of statistical comparisons (see text and Tables 5 and 7).

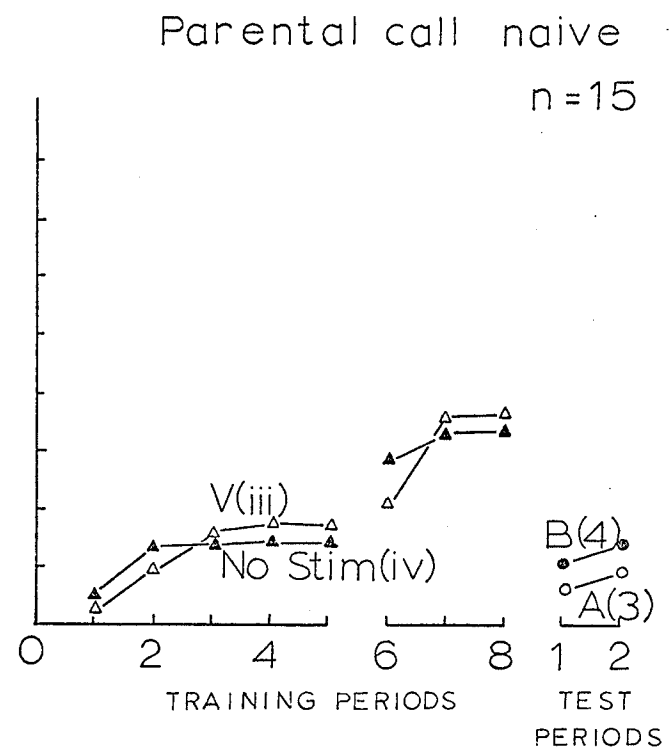
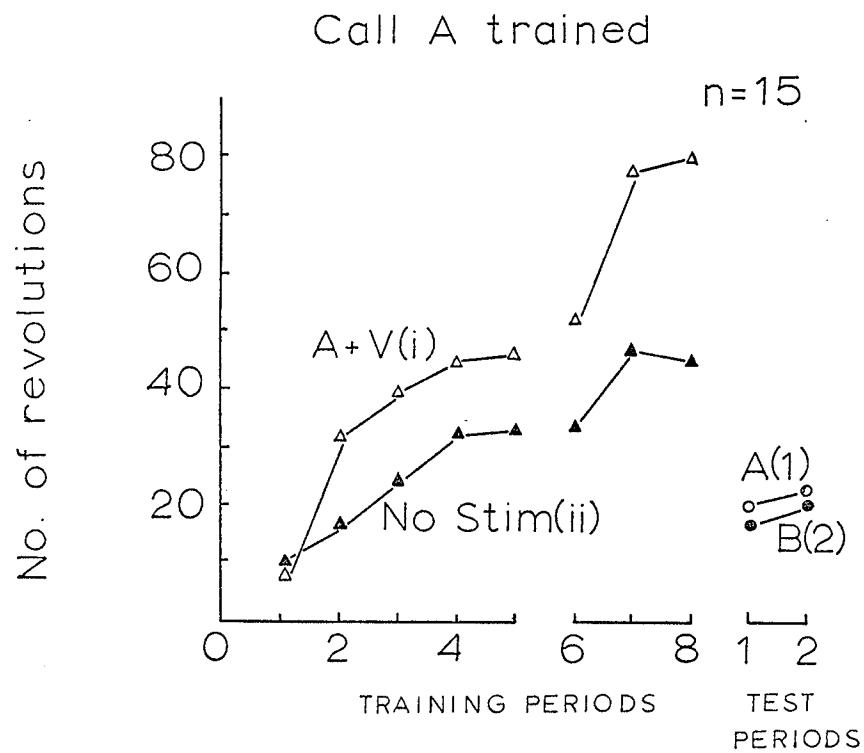


TABLE 5

(1)  
 Statistical comparisons of the number of  
 wheel revolutions in testing

Statistical comparisons (see Fig. 3)	Revolutions	
	Test period	
	1	2
1 > 2	ns	ns
3 vs 4	ns	2.16*
1 > 3	2.56**	2.10*
2 vs 4	ns	ns

1 t test or paired t test where appropriate

\* $p < 0.05$ ; \*\* $p < 0.01$

TABLE 6

Rank correlations<sup>(1)</sup> between the number of wheel revolutions in training and testing

Test period	Training periods <u>with</u> experimental stimulation		Training periods <u>without</u> experimental stimulation		
	To test call A	To test call B	To test call A	To test call B	
Call A experienced (n=15)	1	+0.63**	+0.79**	+0.63**	+0.70**
	2	+0.60*	+0.63**	+0.63**	+0.65**
Parental call naive (n=15)	1	ns	ns	ns	ns
	2	ns	ns	ns	ns

1 Spearman's coefficient of rank correlation  
\*p < 0.05; \*\*p < 0.01

TABLE 7

Statistical comparisons<sup>(1)</sup> of the number of wheel revolutions during training

---

Training period	Revolutions			
	Statistical comparisons (see Fig. 3)			
	i > ii	iii > iv	i > iii	ii > iv
1	ns	ns	2.22*	ns
2	4.19**	ns	3.64**	ns
3	2.37*	ns	3.69**	1.81*
4	5.96**	ns	3.63**	2.54**
5	4.22**	ns	3.57**	2.61**
6	2.78**	ns	3.11**	ns
7	4.22**	ns	2.81**	ns
8	4.30**	ns	2.71**	ns

---

1 t test or paired t test where appropriate

\*p < 0.05; \*\*p < 0.01

## Discussion

An obvious difference between the results reported here and the results for approach behavior (Part I, sect. 1 and 2) is the lack of an apparent habituation effect in training. The number of revolutions in each period with stimulation continually increased up to and including the final training period. This was paralleled by the results for periods with no stimulation. The lack of a significant effect of visual movement in training for the parental call-naive birds suggests that the presence of the rapidly rotating wire mesh 'floor' of the wheel, between the chick and the swinging pendulum, to some extent negates an effect of visual movement ('obscures the chick's view of the pendulum').

There is a possibility that operant reinforcement from the revolving wheel may have been a relevant factor. Kavanau (1966) suggested that kinesthetic feedback is involved in the reinforcing effectiveness of wheel running. Deermice (Peromyscus maniculatus) preferred to run in a large round wheel containing hurdles or in a square 'wheel', rather than in simple round wheels, which suggested that one of the reinforcing aspects of wheel running is the requirement for split-second timing, co-ordination of movements and quick reflex action (Kavanau, 1966).

Another feature of the 'number of wheel revolutions' which detracts from its being a perfect index of locomotor behavior, is that a small portion of this total is accumulated by the chick riding for short distances. The chick partially ascends the wheel then stops. The wheel returns the chick to its starting position adding to the chick's recorded score.

In summary, the classic revolving-wheel apparatus would appear to be an inadequate count transducer for the recording of locomotor behavior as it clearly influences, in an unnatural manner, the young chick's ongoing behavior.

## SUMMARY OF PART I

Studies of selective responsiveness to familiar auditory stimuli were conducted with young Gallus gallus to elucidate aspects of individual recognition of parents by voice. When Domestic Chicks are trained with a parental call paired with visual movement, the familiar call can have a distinct effect on approach behavior, producing a greater number of approach responses relative to the number produced by the parental call of a different individual hen. Distress vocalization is similarly affected. The addition of a call from a second hen in training, as present in the regime used by Evans and Mattson (1972), has no apparent effect on test behavior. Auditory training in which the visual stimulus was withheld, showed that posthatch auditory imprinting appears insufficient for the development of selective responses to individual parental calls. Selective responsiveness was not shown for birds trained and tested in the classic revolving-wheel apparatus.

The results of the experiments presented in Part I suggest that the process of auditory discrimination learning, involving both auditory and visual elements, may be a basis of individual recognition of the parental voice by young Domestic Chicken.

PART II

AUDITORY DISCRIMINATION LEARNING OF INDIVIDUAL PARENTAL  
CALLS BY YOUNG CANADA GEESE

## SECTION ONE

INDIVIDUAL PARENTAL CALLS AND THE APPROACH BEHAVIOR  
OF YOUNG CANADA GEESE

## Introduction

Parents of many precocial bird species vocalize when near their young, when leading their young and when sitting on eggs in the nest before and during hatching (Collias and Collias, 1956; Hess, 1972). Parental calls typically differ between species and appear to facilitate species recognition (Gottlieb, 1971; General Introduction). Parental calls can also differ between individual adults (General Introduction). Laboratory studies have suggested that experience with the parental call paired with a visual stimulus, movement of the adult, results in individual recognition of the parental voice by young Domestic Chickens (Evans and Mattson, 1972; Part I, sect. 1 and 2). However, relatively little attention has been paid to the effects of variations in parental calls between individuals of other precocial species such as the waterfowl.

A laboratory experiment was carried out to test whether various individual parental calls of the Canada Goose have different effects on the approach behavior of

parental call-experienced (pre- and posthatch exposure) and parental call-naive young Canada Geese. Such differential responsiveness, if present, could be the basis of individual recognition in Canada Geese which are characterised by highly stable, interacting, family groups (Raveling, 1970). This experiment also investigated the effect of the parental call of a different species, the Ring-billed Gull, on goslings. The Canada Goose sometimes nests adjacent to breeding colonies of the Ring-billed Gull (Klopman, 1958).

## Methods

### Apparatus

Parental calls were tape recorded at the nests of five Canada Geese at Island Park, Portage La Prairie, Manitoba. The calls were recorded using a microphone placed at the edge of the nest connected by an extension cord to a concealed Uher 4000 Report L tape recorder several hundred feet away. The recordings were of calls by females brooding hatchlings, or incubating pipped or about to pip eggs. Over the microphone goose embryos could sometimes be heard vocalizing, apparently in response to the low intensity parental calls.

From the large number of recordings a selection of spectrograms was produced for each goose using a model 675 Kay Electric Missilyzer. Individual

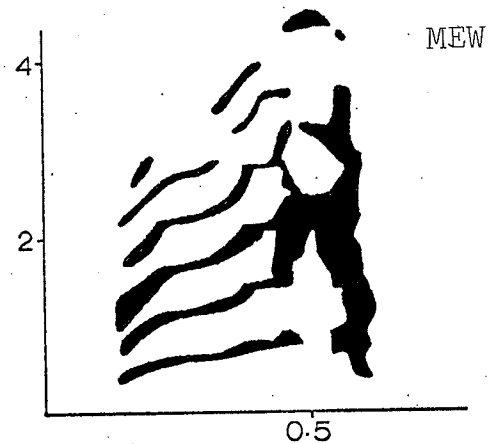
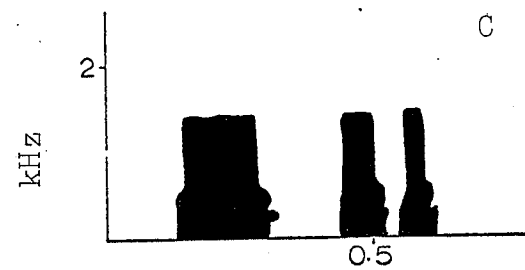
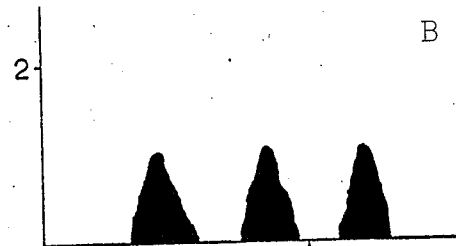
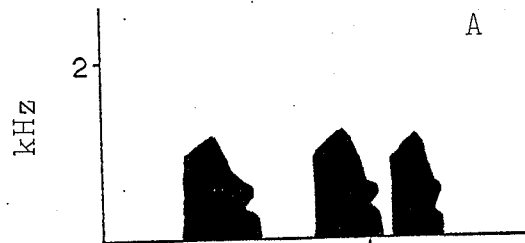
distinctiveness was suggested by visual inspection of the spectrograms (see Beer, 1970a: 36). In particular, the shape of notes, maximum frequency and distribution of sound intensity were relatively stable between calls of the same individual. Tape recordings of three different calls, A, B and C, were selected, each from a different female goose sitting on unhatched eggs. Narrow band spectrograms of these calls are reproduced in simplified form in Fig. 4. The parental mew call of the Ring-billed Gull used in the experiment (Fig. 4) was recorded at a colony near Rogers City, Michigan.

A tape loop was made for each call. Since calls with the same duration were selected and the lengths of the tape loops were identical, the duration of the intercall interval, 1.86 s, and the rate of call presentation, 26 calls per min, were the same for each call. The calls were played at approximately 68 db (C) with a background of white noise at about 63 db (C).

Auditory training and testing were carried out in a giant photocell apparatus. This apparatus consisted of a grey plywood pen (3.05 x 0.76 x 0.46 m) containing a 2.28 m-long runway. A fine light beam and concealed photocell were set up in the runway, parallel to and 12.7 cm from each end screen, 3.8 cm above the runway floor. Other details of the photocell apparatus including pendulums were as described in Part I, sect. 1.

## FIGURE 4

Canada Goose parental call A, call B, call C and Ring-billed Gull mew parental call. The duration of each call is 0.4 s while the maximum frequency of each call is 1220 Hz, 1040 Hz, 1400 Hz and 4760 Hz, respectively.



SECONDS

SECONDS

An Industrial Acoustics Co. model AC-1 sound attenuated chamber was used when playing calls to the egg. The training session at 12 h posthatch took place in a standard tip-floor apparatus (0.57 m-long tip-floor) similarly equipped with pendulums and loudspeakers (Evans, 1972; Part I, sect. 2).

### Subjects

Fresh or slightly incubated Canada Goose eggs were collected at the Delta Waterfowl Research Station and the East Meadow Ranch, Lake Manitoba. A few eggs were also obtained from the Canada Cement Co. Reserve, Fort Whyte, Manitoba. The birds nesting at these sites and at Island Park are Giant Canada Geese (B. c. maxima) (Hanson, 1965). The eggs were artificially incubated at the Delta Waterfowl Research Station. After 20 to 27 days of incubation the eggs were transferred to and incubated at the behavior laboratories, Department of Zoology, University of Manitoba. After hatching, goslings were group reared in pens (56 x 56 x 56 cm). Each pen was equipped with a wire floor, 25-w light bulb, food and water. A total of thirty goslings were used as subjects.

### Procedure

At the onset of pipping, the goose eggs were randomly assigned to two groups. Group 1 eggs were played call A for 10 min soon after pipping. At 12  $\pm$  3 h posthatch

group 1 goslings (n=15) received call A paired with an active pendulum continuously, for 50 min. At 24, 48, 72 and 96 h (each  $\pm 3$  h) posthatch these goslings received call A paired with an active pendulum for 5 min followed by 5 min of silence and no pendulum activity. This 10 min period was immediately repeated five times, for a total of 50 min at each age. On reaching 120  $\pm 3$  h posthatch, the group 1 birds were given two further 10 min training periods as above and then tested immediately. Testing consisted of presenting each gosling with 5 min each of calls A, B, C and the mew call. The test sequence was carried out twice and balanced according to a Latin square. Group 2 goslings (n=15), the controls, had identical treatments to the group 1 birds except that no parental calls were played during training. In testing the pendulums remained immobile for both groups of goslings.

#### Results and conclusions

The median number of approach responses made to each call during testing is shown in Table 8. Comparison of the number of approach responses made in testing showed that goslings trained with call A approached this call more frequently than call C (Wilcoxon matched pairs, signed-ranks test,  $T=16$ ,  $p < 0.05$ ). Comparison between call A and the mew call and call B and the mew call was also significant ( $T=20$ ,  $21$  respectively,  $p < 0.05$ ). There were significantly

TABLE 8

The median number of approach responses during testing to Canada Goose and Ring-billed Gull parental calls

---

Group	Parental call*			
	A	B	C	Mew
Call A experienced (n=15)	45	33	13	16
Parental call-naive (n=15)	23	26	20	20

---

\* A, B and C refer to individual maternal calls of the Canada Goose. Mew refers to a parental call of the Ring-billed Gull.

fewer responses to the mew call in both cases. The number of responses made to call A in testing was significantly greater for goslings trained with call A than those with no prior experience with parental calls (t test,  $t=2.16$ ,  $p<0.05$ ). Other comparisons were not significant.

Inspection of Table 8 suggests that, after training with call A, this call has a greater effect than call B but the corresponding statistical comparison ( $T=26.5$ ) was not significant. However, the significant differences between call A and call C, and call A and the Ring-billed Gull mew call clearly demonstrate that, after training, the parental calls of different individual geese and the Ring-billed Gull can have distinct effects on goslings.

The remainder of the analysis consisted of correlating performance during training with performance during testing. For birds trained with call A, Spearman's rank correlations between the total number of approach responses made during training with call A and the number of approach responses during testing were significant for the responses to call A ( $r=+0.62$ ,  $p<0.05$ ), call B ( $r=+0.58$ ,  $p<0.05$ ) and the mew call ( $r=+0.45$ ,  $p<0.05$ ). Rank correlations between the total number of approach responses in the 5 min silent periods in each photocell pen training session and the number of approach

responses during testing were significant for call A ( $r=+0.57$ ,  $p < 0.05$ ), call B ( $r=+0.54$ ,  $p < 0.05$ ), call C ( $r=+0.48$ ,  $p < 0.05$ ) and the mew call ( $r=+0.53$ ,  $p < 0.05$ ). Clearly, the performance of a gosling during training is a good indicator of test performance and suggests that variation in the number of responses between goslings was the result of factors, perhaps anatomical or physiological, which were relatively individual gosling-specific (see Sluckin, 1965: 32). None of the performance correlations was significant for the goslings which did not receive the parental call in training.

#### Discussion

The results of this experiment, though not designed to test for effects of visual movement in training, are consistent with those of Evans and Mattson (1972) and Part I on the Domestic Chicken. After training with a Canada Goose parental call (in the experiment paired with visual movement), young goslings can respond selectively to the familiar call. This mechanism, probably involving both visual and auditory elements, may be a basis of individual recognition by Canada Geese.

The reason for the relatively high response level to call B is unclear. Perhaps, after training with a call, some unfamiliar calls are more 'attractive' than others.

Certainly, just as the familiar call A, call B has a different effect from the Ring-billed Gull mew call on gosling behavior.

The goslings in this study were tested at approximately 120 h posthatch. A preliminary experiment using four goslings only, showed no apparent selective responsiveness at 24 h posthatch. Individual recognition by young Canada Geese would appear to develop at a later age than in the Domestic Chicken (cf. Kear, in Scott, 1972; Collias and Jahn, 1959).

In the experiment proper, rate of call presentation and intercall interval were held constant and therefore properties of the calls themselves rather than the patterning of call presentation must affect approach behavior. Collias and Joos (1953) suggested that frequency is an important factor influencing approach behavior of Domestic Chicken and the results of this experiment suggest that even seemingly slight differences in sound frequency may affect gosling behavior.

## SECTION TWO

INDIVIDUAL DIFFERENCES IN THE PARENTAL ALARM CALLS  
OF CANADA GEESE LEADING BROODS

The Canada Goose is characterised by highly stable, interacting family groups (Raveling, 1970). Observations of family group behavior suggest that goslings selectively respond to their own parents (Collias and Jahn, 1959: 496). In undisturbed situations, one basis of individual recognition of parents by goslings appears to be the low-pitched call given by the parents when leading young (Part II, sect. 1). In an alarm situation, as when the family party or group of family parties is approached on the breeding grounds by an intruder, adult geese give high-pitched loud 'alarm' calls that also appear to elicit approach and following by the young (pers. obs.). Goslings may therefore respond selectively to the alarm calls of their own parents. If so, the calls of parents must be individually distinctive (White and White, 1970; Beer, 1970a). This possibility was examined by analysing a large sample of alarm calls obtained from B. c. interior in the Churchill region, Manitoba, in 1971.

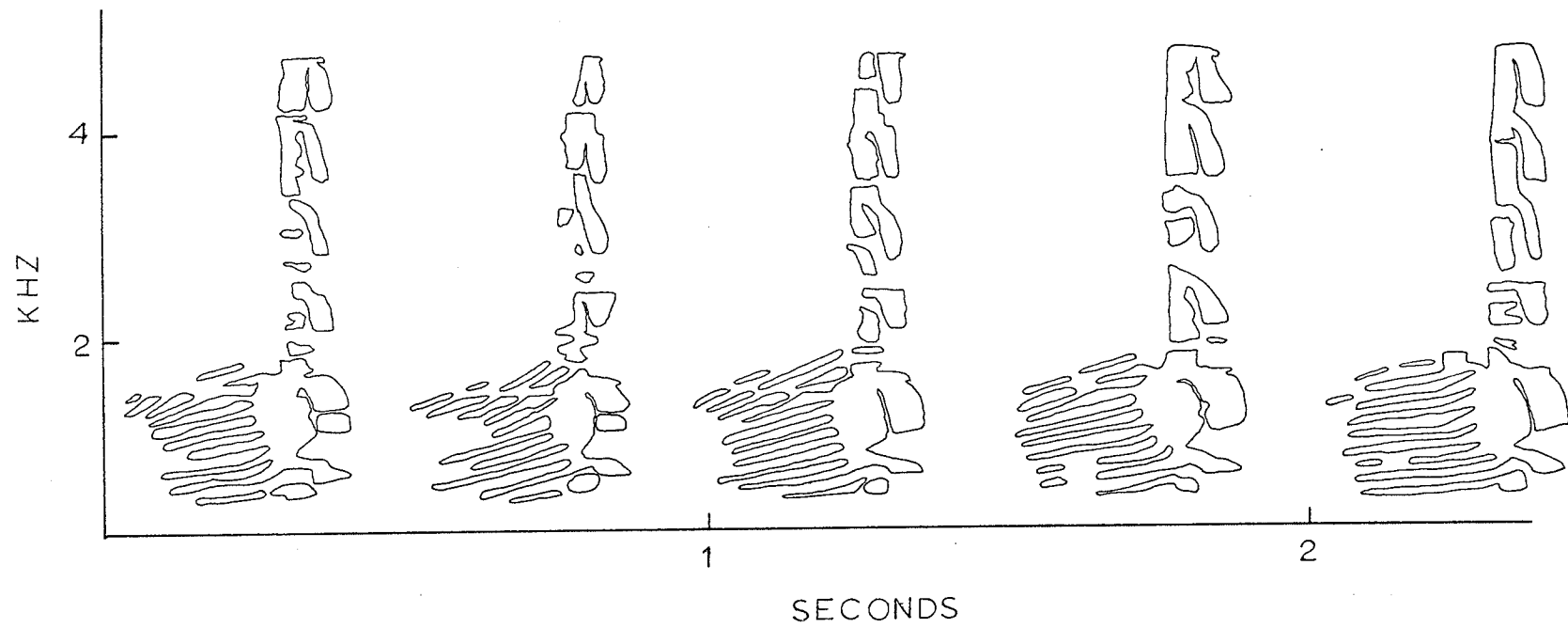
At Churchill, after the young hatch, the geese desert their nesting grounds along the treeline and

move toward the coast where they congregate in large flocks (Jehl and Smith, 1970: 24). The flocks I studied were composed of one or more family parties and probable non-breeders. By approaching and following individual family parties, I was able to record alarm calls from eleven different geese, each leading a brood of young goslings. The second parent, which by behavior and voice was apparently the male, nearly always separated early from the family party in a distraction attempt, and its calls were not recorded. From 6 to 190 calls, a mean of 70 calls, were recorded for each brood-leading goose. All records were made with a Uher 4000 Report L tape recorder and Uher M 539 microphone. For analysis, six calls for each goose were selected randomly and converted to spectrograms using a model 675 Kay Electric Missilyzer (narrow band; flat shape). Visual inspection of spectrograms for shape difference was used to detect call variation (see Beer, 1970a: 36; Thompson, 1970).

Figure 5 shows 5 alarm calls from a single goose selected at random. The results in Fig. 5 are typical of all the geese analysed in that the shape of each call, and in particular the second half of each call was relatively stable between calls of the same individual. Spectrograms of one alarm call from each of the other ten geese are shown in Fig. 6. The marked differences between these calls of different individuals (Fig. 6)

FIGURE 5

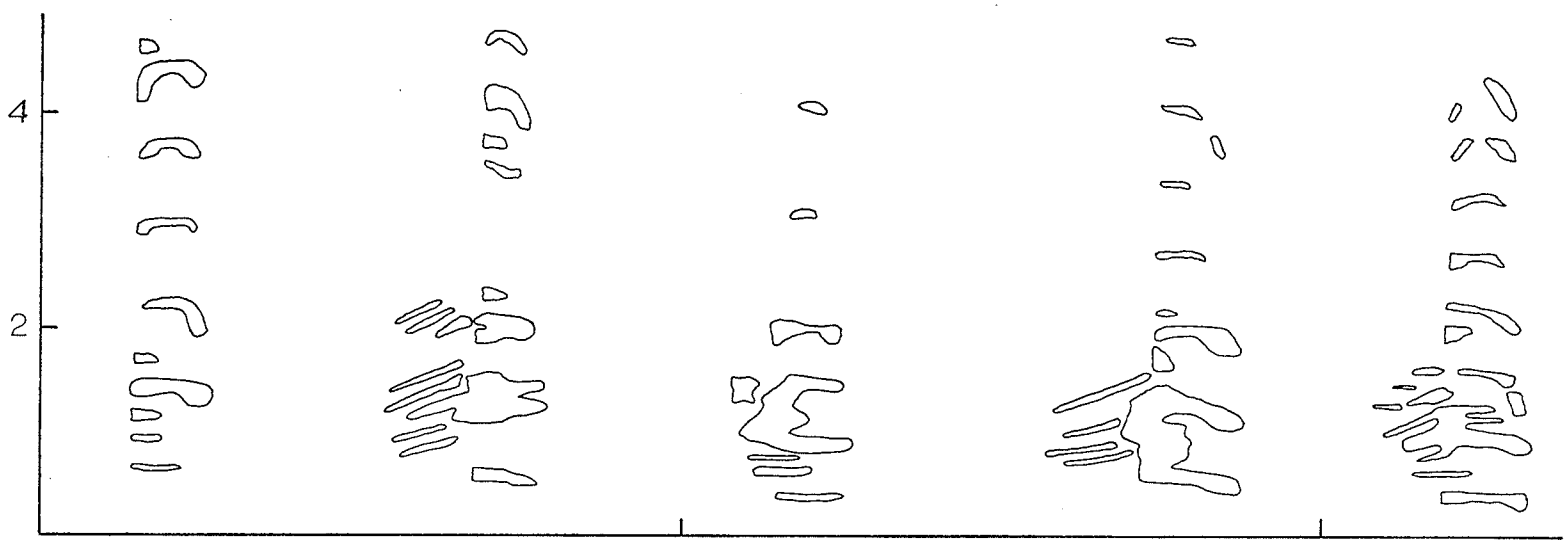
Five alarm calls of a Canada Goose with brood.



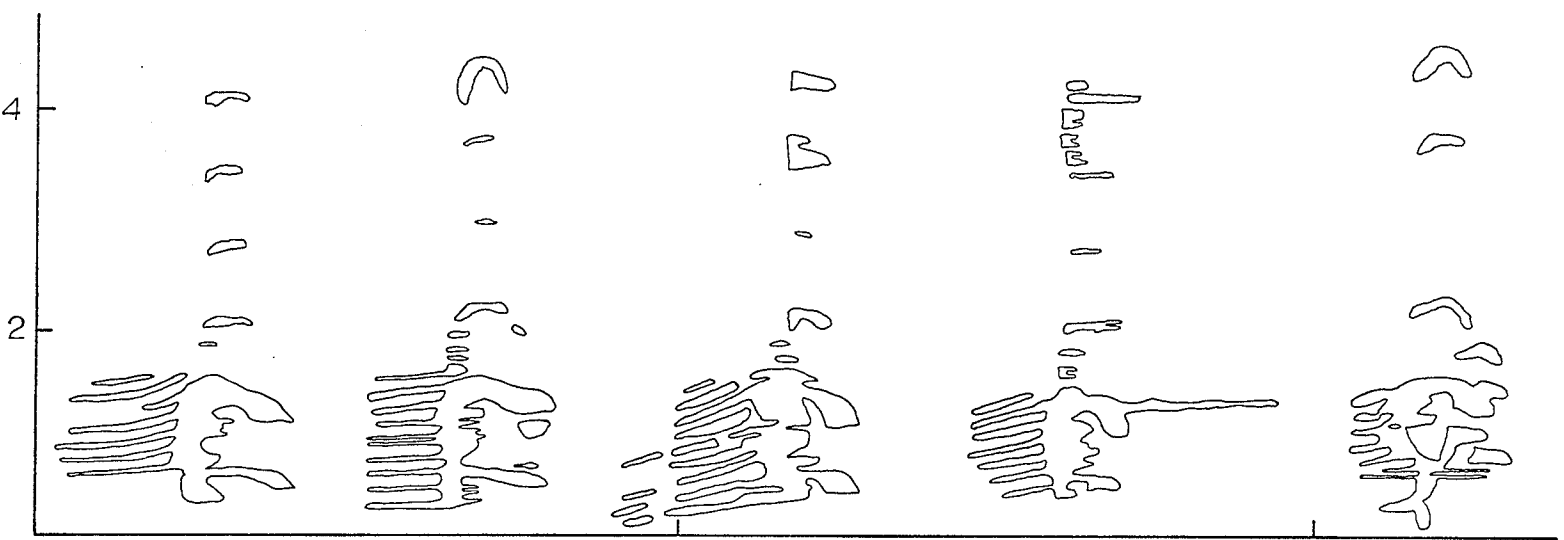
## FIGURE 6

Alarm calls of ten Canada Geese each leading a brood.

kHz



kHz



SECONDS

compared to the relatively slight intra-bird variation (Fig. 5) indicate that alarm calls are individually distinctive, and hence could provide a basis for individual recognition of parents by goslings during alarm situations.

## SUMMARY OF PART II

When young Canada Geese are trained with a parental call, the familiar call can have a distinct effect on approach behavior producing a greater number of approach responses to the familiar call than to calls of other individual geese and the parental call of another species, the Ring-billed Gull. In this experiment the parental call in training was paired with visual movement. The results, compared with those of Part I, sect. 1 and 2, suggest that auditory discrimination learning occurs in a similar manner in both the Canada Goose and the Domestic Chicken.

In an alarm situation, adult Canada Geese with broods give high-pitched alarm calls rather than the low-pitched 'broody' call. For young to be able to respond selectively to the alarm calls of their parents, the calls must be individually distinctive. Analysis of sound spectrograms of alarm calls recorded from female Canada Geese leading broods demonstrated marked differences between the call structure of different individual females and relatively slight intra-bird variation.

PART III

PARAMETERS OF CHICK BEHAVIOR AND PARENTAL SOUND IN  
AUDITORY DISCRIMINATION LEARNING BY YOUNG DOMESTIC CHICKENS

## SECTION ONE

INDIVIDUAL PARENTAL CALLS AND THE PARAMETERS OF  
AN APPROACH RESPONSE

## Introduction

The investigations of auditory discrimination learning reported in Part I, sect. 1 and 2, Part II, sect. 1 and by Evans (1972) and Evans and Mattson (1972) involved using either a tip-floor apparatus or a photocell apparatus to record approach behavior. Both types of apparatus produce a record of the number of approach responses over a period of time and, therefore, allow conclusions about approach behavior per se. It is not known from these studies whether parental calls affect the instantaneous speed (Tricker and Tricker, 1966), orientation and direction of movement of the young bird during, or the latency of, an approach response. An experiment was carried out to detect, by cinematography, which of these approach variables are affected by individual parental vocalizations.

## Methods

Apparatus

The experimental stimuli and training apparatus (photocell apparatus) are fully described in Part I, sect. 1.

Testing was carried out in a pen identical in dimensions to the standard photocell pen (Part I, sect. 1). For testing, a loudspeaker and pendulum were placed in the compartment at one end of the pen only. A small black mark was located on the runway floor, 53.4 cm from the speaker compartment at the opposite end of the runway, to indicate the chick's starting position. A Nikon Super Zoom-8 cine camera with a Cine-Nikkor Zoom lens fixed at the wide angle setting (8.8 mm) was firmly supported 122 cm above the runway such that the whole runway entered the field of view. Kodak Ektachrome 160 Super 8 film was used and shot at 12 frames per sec. A cable release allowed the camera to be electrically triggered at a distance. In order to record the instant when each parental call occurred, a Kyoritsu VU meter was placed at the edge of the runway in the field of view of the camera. The meter was connected to a sound-operated relay. The relay microphone was located next to a loudspeaker in parallel with the loudspeaker in the test apparatus but located in a separate soundproof room. This arrangement allowed parental calls but not chick vocalizations to individually deflect the needle along the meter's scale. A small black spot was marked on each chick's back adjacent to the nape and a second spot marked on the rump to facilitate film analysis.

Developed film was analysed by projection (Tricker and Tricker, 1966). The instantaneous speed, direction of movement and orientation of a chick during an approach response were measured at every twelfth of a second for a period of just over one and one half seconds from the start of the approach response. During this period chicks reached positions varying from the middle to the end of the runway adjacent to the speaker. The chick's speed at a particular frame (x) was measured by recording the straight-line distance from its position on the previous frame (x-1) to that on the subsequent frame (x+1) i.e. over 1/6th s. The chick's position was located by the black spot on the chick's back. The direction of movement of the chick (0 deg to 180 deg) at a particular frame (x) was recorded by measuring the angle between the straight line connecting the positions of the chick used for speed measurement and a direction perpendicular to the loudspeaker end of the pen. A reading of 0 deg thus indicated movement directly towards the loudspeaker compartment while 180 deg would indicate movement directly away. The orientation of the chick was ascertained at a frame (x) by measuring the angle between the chick's axis, taken as the line connecting back spot to rump spot, and the direction perpendicular to the loudspeaker end of the pen.

The latency of response was measured by counting the number of frames from the first call to the start of approach. The number of frames from the onset of approach and its finish when the chick reached the opposite end of the pen, was the measure of the duration of the response.

### Subjects

Incubated eggs were collected from a commercial hatchery about one day before pipping and hatched in the laboratory. After hatching, the chicks were group-reared in holding pens equipped with a wire floor and 25-w light bulb. No food or water were provided. A total of twelve white rock X cornish Domestic Chickens were used as subjects.

### Procedure

All chicks received parental call A, paired with visual movement, in training. This training procedure is fully described in Part I, sect. 1. Three min after completion of auditory training, the chicks were given 60 s of either call A followed by 60 s of call B or vice versa in balanced order. The pendulum was immobile throughout the test. Test procedure involved placing the chick at the start position, triggering the camera from a distance and then playing the appropriate tape loop. The chick was filmed for 60 s from the first call. The chick was then

placed in a holding box for a few seconds, then returned to the start position and the film procedure repeated using the second call.

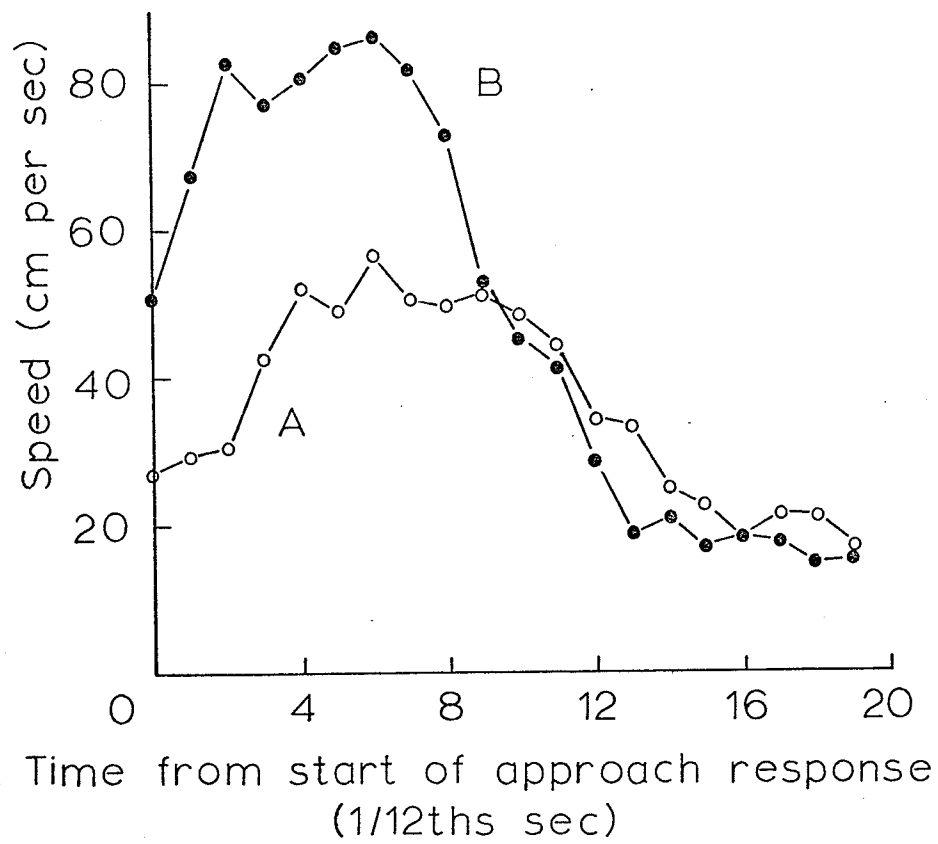
#### Results and conclusions

Of the twelve chicks tested, ten approached call A, eight approached call B and two did not approach either call, in the 60 s of filming. The median latency of the approach responses to call A and call B was 10.04 s and 19.75 s respectively. Chicks started to approach the familiar call A significantly earlier than call B (paired t test,  $t=1.97$ ,  $p < 0.05$ ). The median duration of the approach responses to call A and call B was 3.12 s and 3.87 s respectively. There was no significant difference in approach response duration to the two calls.

The mean speed of the approach response to each call at successive  $1/12$ th s intervals after the onset of approach locomotion is shown in Fig. 7. The distribution of the mean instantaneous speeds during approach responses suggests that call B elicited faster approach response speeds than call A for at least the first  $1/2$  s after the start of locomotion. Using the two-tailed paired t test,  $t=1.60$  (0 s), 2.81 (after  $1/12$ th s), 2.61 ( $2/12$ th s), 1.94 ( $3/12$ th s), 1.66 ( $4/12$ th s), 1.92 ( $5/12$ th s) and 2.01 ( $6/12$ th s). The comparisons at  $1/12$ th s and  $2/12$ th s were statistically significant ( $p < 0.05$ ). Comparisons at

## FIGURE 7

Mean speed of the approach response to Domestic Chicken calls A and B during testing.



3/12th s, 5/12th s and 6/12th s were only significant using one-tailed criteria whilst comparisons at 0 and 4/12th s were not statistically significant on either basis. The familiar call causes an earlier but initially slower approach response than call B.

The median direction of movement and orientation of chicks during the approach response are shown in Fig. 8. Chicks oriented significantly more directly towards the speaker compartment to call A than call B at the onset of the approach response (two-tailed, paired t test,  $t=3.09$ ,  $p<0.05$ ) and after 1/12th s ( $t=2.91$ ,  $p<0.05$ ). Other comparisons for orientation and the direction of movement were not significant. The direction of movement and orientation of a chick appear restricted to within narrow limits during an approach response.

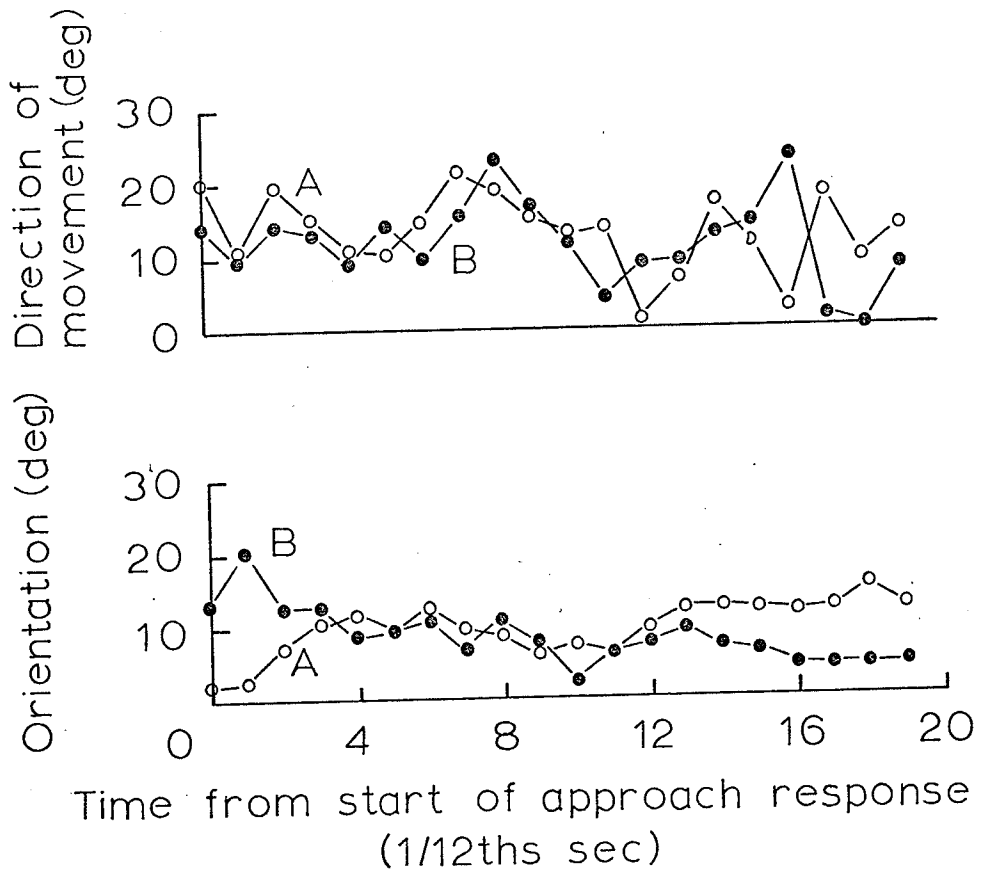
Spearman's rank correlations between the total number of approach responses in training periods with call A and approach response latency in testing were significant for responses to call A ( $r=-0.67$ ,  $p<0.05$ ) and call B ( $r=-0.92$ ,  $p<0.01$ ). The more approach responses in training, the shorter the approach response latency in testing. Other rank correlations between number of responses in training and test variables were not significant.

### Discussion

The results of the present experiment are consistent with those presented earlier (Part I, sect. 1 and 2; Part II,

## FIGURE 8

Median direction of movement and orientation of the approach response to Domestic Chicken parental calls A and B during testing.



sect. 1). Even though chicks initially approach at a slower speed, they reach the loudspeaker compartment, from call onset, earlier to the familiar call A than to call B because of the much shorter latency to call A. In a photocell or tip-floor apparatus this process, when repeated, would lead to a higher number of approach responses to the familiar call over a fixed period of time as found for the Domestic Chicken (Part I, sect. 1 and 2) and young Canada Geese (Part II, sect. 1).

Prior to the approach response, as observed by cinematography, the chicks appeared to show behavioral characteristics of the orientation reaction (Lynn, 1966). The latency measures, therefore, probably reflect the duration of an orientation reaction prior to approach. If, under approach conditions, duration of the orientation reaction and performance (i.e. speed) are indirect measures of physiological arousal (Hokanson, 1969) then the experimental results are consistent with what is known of the effects of 'novelty' and the habituation of arousal (Lynn, 1966). The onset of familiar call A is followed by lower arousal (shorter orientation reaction) than the novel call B. The initial more direct orientation during an approach to call A is also consistent with this interpretation. Even after the termination of the simple orientation reaction, the chick's arousal is apparently

still higher to call B (higher initial approach speed) than call A. A completely satisfactory model relating neurophysiology to approach behavior has yet to be devised though a neuronal model hypothesis involving arousal habituation appears a good prospect (Rajecki, 1973).

## SECTION TWO

SYNTHETIC PARENTAL CALLS AND AUDITORY DISCRIMINATION  
LEARNING BY YOUNG DOMESTIC CHICKENS:  
FREQUENCY, INTENSITY AND DURATION

## Introduction

Individual recognition of parents by voice has been demonstrated in the young of several species of precocial and semiprecocial birds, e.g. the Domestic Chicken, Laughing Gull, Black-billed Gull, Ring-billed Gull, Common Tern and the Common Guillemot (reviewed in Beer, 1970a; General Introduction). Observations consistent with individual recognition of parents by young on the basis of voice have been reported for the King Penguin, Canada Goose and other waterfowl species (see General Introduction). Individual distinctiveness of parental calls given in the parent-young situation has also been described for the alarm call of Canada Geese leading broods (Part II, sect. 2) and the fish-call of Sandwich Terns (Hutchison et al, 1968). Laboratory studies suggest that experience with the parental call paired with a visual stimulus, movement of the adult, results in individual recognition of the parental voice

by young precocial birds (Evans and Mattson, 1972; Part I, sect. 1 and 2; Part II, sect. 1). The properties of parental calls which provide the basis for such auditory discrimination learning in young precocial birds, however, have not been experimentally demonstrated (cf. Thorpe, 1968).

Owing to the relatively complex structure of parental calls, it is technically difficult, if not impossible at the present, to identify natural calls that could serve as suitable controls to discover directly the properties of parental calls which are important for auditory discrimination learning. In the present study, simple synthetic 'calls' were used to investigate the effects of training and testing with various call properties on the approach behavior and distress vocalization of young. Approach behavior and distress calls (peeps) are important factors in individual parent-young interactions (McBride et al, 1969).

Simple calls, containing properties found in parental calls, were synthesized from basic components (Busnel, 1968: 37). The first experiment used pure tones to investigate the effects of training with a sound frequency on the subsequent responsiveness of young Domestic Chickens to the training frequency and to a series of novel frequencies. Experiments 2 to 4 used sounds composed of two tones played simultaneously, referred to as 'double tones'. Experiment 2 tested whether chicks respond

more often to a familiar combination of frequencies than to other frequency combinations. The experiment was controlled to determine whether varying either frequency in the double tone would affect approach behavior and distress vocalization. Experiment 3 investigated whether chicks respond more frequently to combinations of sound intensities used in training, while experiment 4 tested whether chicks respond more often to familiar tone durations.

## Methods

### Apparatus

An RCA audio generator WA-44C was used to produce pure tones (sine wave). For experiment 1, tones were tape recorded and then spliced with silent gaps between. Each tone had a duration of 0.12 s and was played at about 110 tones per min. The intertone interval was constant. Tape loops were constructed for 200 Hz, 500 Hz, 600 Hz and 1300 Hz tones for experiment 1. Tape loops for experiment 2 consisted of 500 Hz/600 Hz, 500 Hz/800 Hz and 600 Hz/800 Hz double tones, obtained by re-recording two tones simultaneously. Each double tone had a duration of 0.12 s and was played at about 110 tones per min with a constant intertone interval. Tape loops for experiment 3 were made as for experiment 2 except that

the intensity of the component tones was varied. Tapes of 600 Hz/400 Hz double tones with 65 db/60 db, 65 db/65 db, 60 db/60 db and 60 db/65 db intensity combinations were produced. Each double tone had a duration of 0.07 s and was played at about 96 calls per min. To ensure that the appropriate volumes were occurring during playback, their calculated combination products (Peterson and Gross, 1967: 208) were produced as measured with the sound level meter. For experiment 4, tape loops of 600 Hz/400 Hz double tones were also used. Tones had durations of 0.07 s, 0.1 s, 0.2 s and 0.4 s respectively and each was spaced equally on its own loop. The rate of presentation was about 96 tones per min. The tones in experiments 1, 2 and 4 were played at about 65 db (C), each component having identical intensities. In all experiments a background of white noise was produced at 59 db (C). The movement of a pendulum was used as the visual stimulus.

Auditory training and testing were carried out in a photocell apparatus (Part I, sect. 1). Owing to a relay failure, half of the chicks in each experimental group in experiments 2 to 4 received their auditory training and testing in a tip-floor apparatus (Evans, 1972; Part I, sect. 2).

The number of distress calls given by a chick was automatically recorded by means of a sound-operated relay (Part I, sect. 1).

Initial visual training was carried out in grey plywood pens, one chick per pen, each fitted with an overhead 15-w light and a single, continuously moving pendulum (Part I, sect. 1).

### Subjects

Each experiment used 24 white rock X cornish Domestic Chickens. Incubated eggs were collected from a commercial hatchery about one day before pipping and hatched and raised in the laboratory as described in Part I, sect. 1.

### Procedure

After hatching, the chicks for a given experiment were randomly assigned to two groups of 12. Both groups of chicks, in all the experiments, received initial visual training with a swinging pendulum at 6  $\pm$  3 h posthatch. Chicks were exposed to the pendulum for an initial 2 h, returned to the holding pen for 2 h and then brought back for a final 2 h of visual training.

At 27  $\pm$  3 h posthatch the group 1 chicks in experiment 1 received the 600 Hz tone paired with an active pendulum for 5 min, followed by 5 min of silence and no pendulum activity. This 10 min period was immediately repeated 8 times for a total of 80 min. Group 2 chicks had identical treatments to the group 1 birds except that a 1300 Hz tone was played during auditory training. Three min after training the chicks were

tested. Testing consisted of presenting each chick singly and successively with 5 min each of the 200 Hz, 500 Hz, 600 Hz and 1300 Hz tones in a Latin square balanced order.

In experiment 2, group 1 chicks were trained with the 500 Hz/600 Hz tone while group 2 chicks received the 500 Hz/800 Hz tone. Testing consisted of presenting each bird with 5 min of the 500 Hz/600 Hz, 500 Hz/800 Hz and 600 Hz/800 Hz tones in balanced order. In experiment 3, group 1 chicks were trained with the 60 db/65 db tone while group 2 chicks received the 65 db/60 db tone. Testing consisted of presenting each chick with the 60 db/65 db, 65 db/65 db, 60 db/60 db and 65 db/60 db tones for 5 min each in a balanced order.

Chicks in experiment 4 were trained with either the 0.07 s duration tone (group 1) or the 0.1 s tone (group 2). Testing consisted of presenting each chick with 5 min of the 0.07 s, 0.1 s, 0.2 s and 0.4 s tones in balanced order.

In experiments 2 to 4 chicks, after auditory training, were returned to their holding pens for 100 min in anticipation of enhancing any discrimination. They were then brought back and given auditory training for an extra 5 min period, and then immediately tested. The procedures in all experiments were otherwise identical. Throughout testing pendulums remained immobile in all experiments. Statistical analysis of selected a priori comparisons was carried out

using the one-tailed t test or the one-tailed paired t test unless otherwise stated.

## Results and conclusions

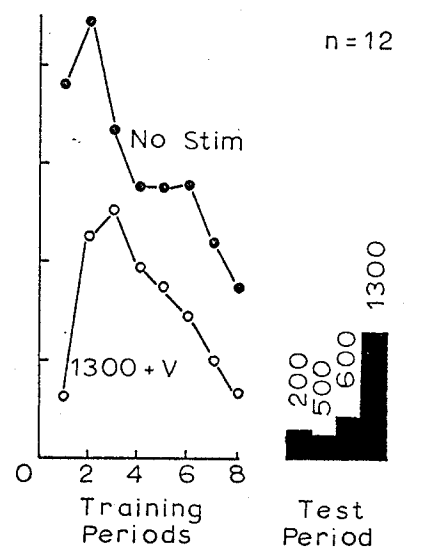
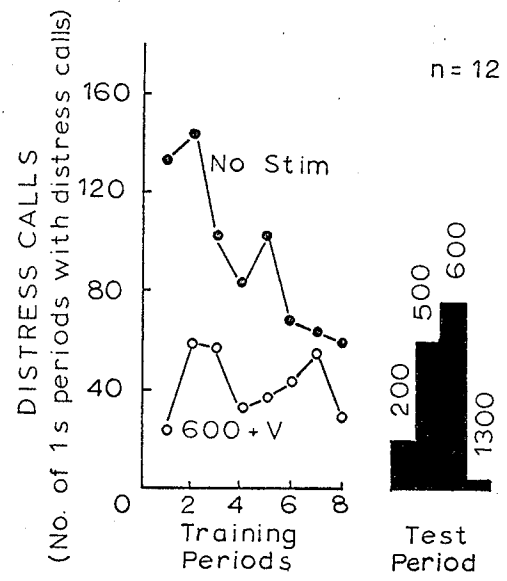
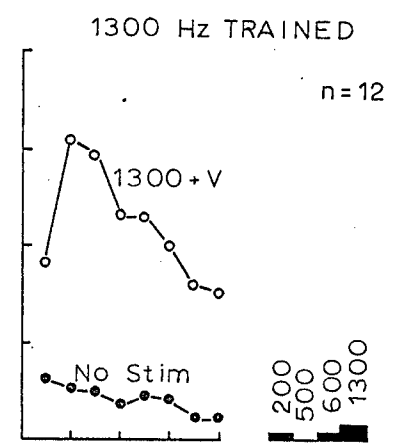
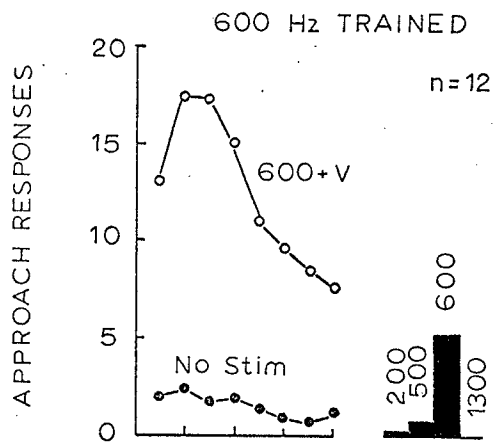
### Experiment 1

The mean number of approach responses and the mean number of 1 s periods with distress vocalization, in testing, are shown in Fig. 9. Comparison of the number of approach responses showed that chicks trained with the 600 Hz tone approached this tone significantly more often than the 200 Hz, 500 Hz and 1300 Hz tones ( $t=2.62$ ,  $2.58$ ,  $2.67$ ,  $p<0.05$ , respectively). Chicks trained with the 1300 Hz tone approached this tone significantly more often than the 500 Hz tone only ( $t=1.97$ ,  $p<0.05$ ). The number of approach responses to the 600 Hz tone was significantly greater for chicks trained with 600 Hz than for those trained with 1300 Hz ( $t=2.53$ ,  $p<0.01$ ). Similarly, the number of approach responses to the 1300 Hz tone was significantly greater for chicks trained with 1300 Hz ( $t=2.03$ ,  $p<0.05$ ).

Comparison of the number of distress calls showed that chicks trained with the 600 Hz tone gave significantly more distress calls to this tone than to the 200 Hz, 500 Hz and 1300 Hz tones ( $t=2.49$ ,  $2.13$ ,  $p<0.05$ ;  $t=2.79$ ,  $p<0.01$ , respectively). Chicks trained with the 1300 Hz

## FIGURE 9

The mean number of approach responses and distress calls to pure tones of different frequency in training and testing (experiment 1). 600+V = 600 Hz and visual movement; 1300+V = 1300 Hz and visual movement; 200, 500, 600, 1300 = test frequencies (in Hz). No Stim = no experimental stimuli.



tone gave significantly more distress calls to this tone than the 200 Hz and 600 Hz tones ( $t=2.43, 2.22, p<0.05$ ). The number of distress calls given to the 600 Hz tone was significantly greater for chicks trained with 600 Hz compared with chicks trained with 1300 Hz ( $t=1.86, p<0.05$ ). The number of distress calls to the 1300 Hz tone was significantly greater for chicks trained with 1300 Hz than for chicks trained with the 600 Hz tone ( $t=2.08, p<0.05$ ). Clearly, after training both 600 Hz and 1300 Hz have distinct effects on the approach behavior and distress vocalization of young Domestic Chickens compared to various novel frequencies.

There was a significant positive correlation (Spearman's rank) between the number of approach responses and the number of distress calls given in testing for responses to 600 Hz and 500 Hz for birds trained with 600 Hz ( $r=+0.75, p<0.01; r=+0.52, p<0.05$ , respectively). Other correlations between the two responses were not significant.

The mean number of approach responses and distress calls in training are shown in Fig. 9. The periods with experimental stimuli produced significantly more approach responses than the periods without stimulation for 600 Hz trained chicks ( $p<0.01$ ) and for chicks trained with 1300 Hz ( $p<0.01$ ). In many cases the periods with experimental stimuli produced significantly fewer distress calls than the periods with no stimulation for 600 Hz

trained chicks (periods 1, 2, 4, 5,  $p < 0.05$  or better) and for chicks trained with 1300 Hz (periods 1, 2, 6 to 8,  $p < 0.05$  or better). A differential effect of 600 Hz and 1300 Hz in training on approach responses or distress vocalization was not demonstrated.

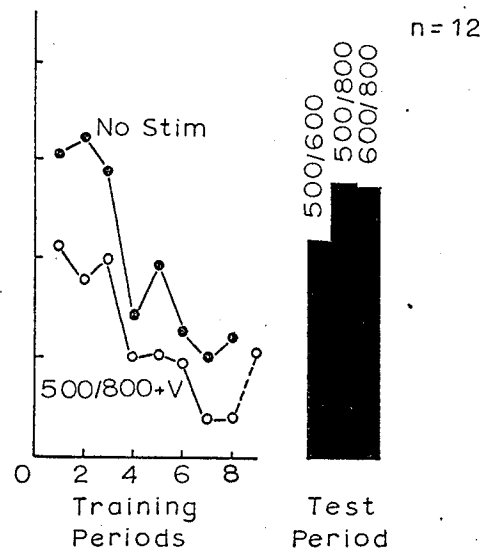
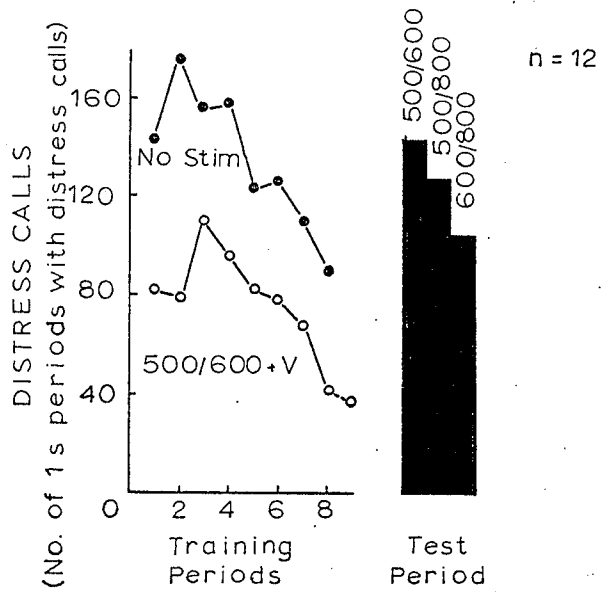
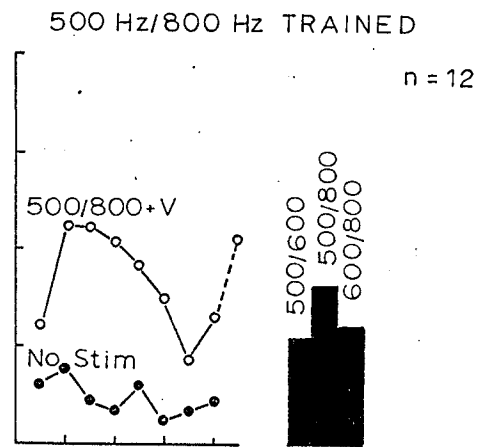
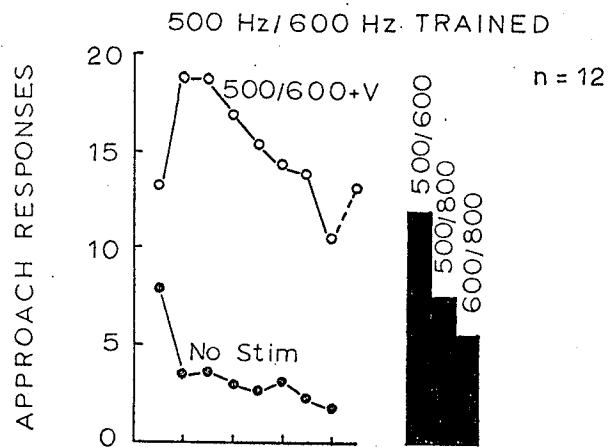
### Experiment 2

The mean number of approach responses and the mean number of 1 s periods with distress vocalization in testing are shown in Fig. 10. Comparison of the number of approach responses in testing showed that chicks trained with the 500 Hz/600 Hz tone approached this tone significantly more often than either the 500 Hz/800 Hz ( $t=2.46$ ,  $p < 0.05$ ) or 600 Hz/800 Hz tone ( $t=2.38$ ,  $p < 0.05$ ). The number of approach responses to the 500 Hz/600 Hz tone was significantly greater for chicks trained with this tone than for those trained with the 500 Hz/800 Hz tone ( $t=1.82$ ,  $p < 0.05$ ). Clearly, after training the familiar 500 Hz/600 Hz combination has a distinct effect on approach behavior such that if either component frequency of the combination is changed, a smaller number of approach responses is elicited. Both frequencies of the double tone affect approach behavior.

The results for birds trained with 500 Hz/800 Hz were less consistent. Statistical comparison of the number of approach responses in testing showed that chicks

## FIGURE 10

The mean number of approach responses and distress calls to double tones of different frequencies in training and testing (experiment 2). 500/600+V = 500 Hz/600 Hz and visual movement; 500/800+V = 500 Hz/800 Hz and visual movement; 500/600, 500/800, 600/800 = test frequency combinations (in Hz). No Stim = no experimental stimuli.



trained with this tone approached it significantly more often than the 500 Hz/600 Hz tone only ( $t=2.07$ ,  $p < 0.05$ ). The birds trained with the 500 Hz/800 Hz tone did not respond significantly more to this tone than those trained with the 500 Hz/600 Hz tone.

Although the distribution of means in Fig. 10 suggests otherwise, differences in the number of distress calls given to the familiar and novel test stimuli were not statistically significant except for the 500 Hz/800 Hz and 500 Hz/600 Hz comparison for birds trained with the 500 Hz/800 Hz tone ( $t=1.91$ ,  $p < 0.05$ ). Spearman's rank correlations of the numbers of approach responses and distress calls in testing for both groups of chicks were, however, significant ( $p < 0.05$  or better). The more approach responses given by a chick to a frequency combination in testing, the more distress calls are uttered at the same time.

The mean number of approach responses and distress calls in training are shown in Fig. 10. The training periods with experimental stimuli produced significantly more approach responses than the periods with no stimulation for both the 500 Hz/600 Hz trained birds (periods 2 to 8,  $p < 0.01$ ) and birds trained with 500 Hz/800 Hz (periods 2 to 8,  $p < 0.05$  or better). A differential effect between 500 Hz/600 Hz and 500 Hz/800 Hz

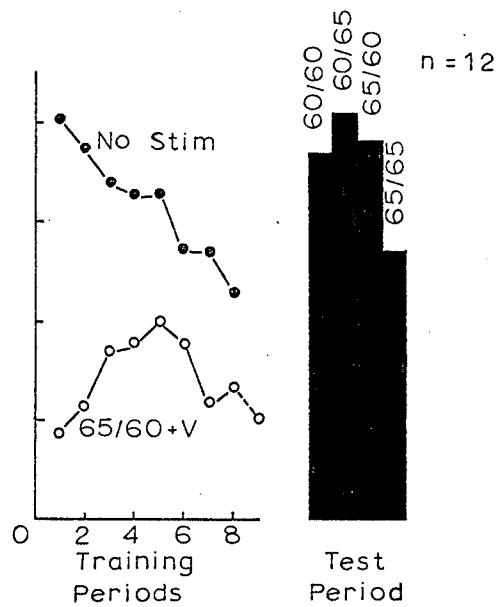
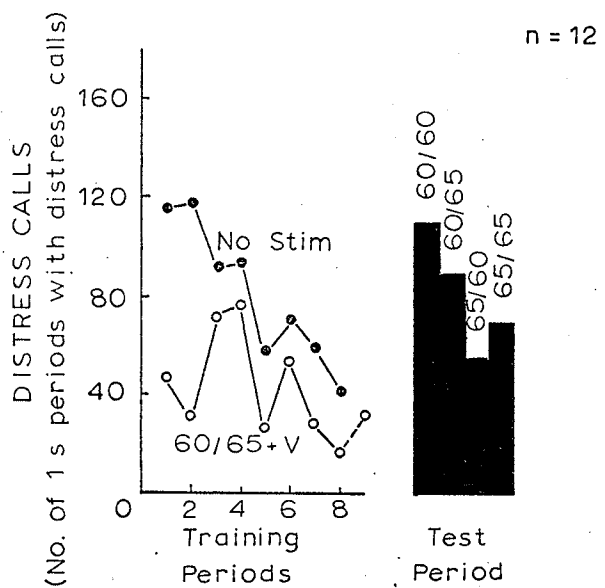
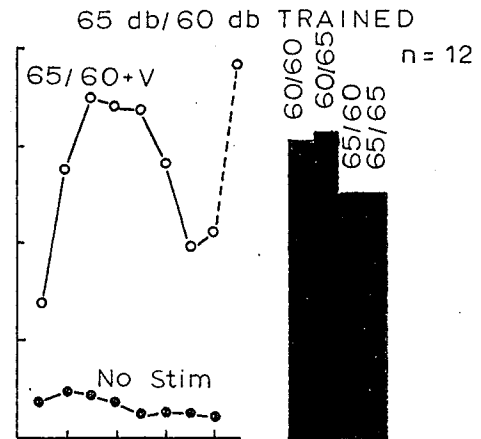
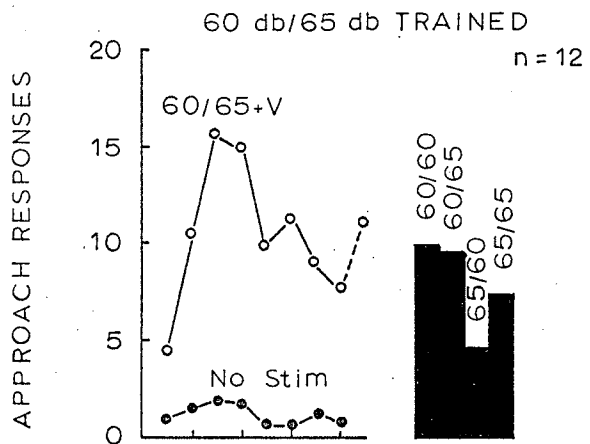
in training, though statistically significant in a few comparisons (two-tailed t test), was not conclusively demonstrated for either approach behavior or distress vocalization.

### Experiment 3

Figure 11 presents the mean number of approach responses and the mean number of 1 s periods with distress vocalization during testing. Comparison of the mean number of approach responses in testing between tones was significant for a single comparison only, between the number of responses to the 60 db/65 db tone and the 65 db/60 db tone for 60 db/65 db trained birds ( $t=1.92$ ,  $p<0.05$ ). None of the corresponding a priori comparisons for distress calls was significant. However, the 65 db/60 db combination did produce significantly more approach responses and distress calls for chicks trained with this combination than for chicks trained with 60 db/65 db ( $t=1.75$ ,  $p<0.05$ ;  $t=3.03$ ,  $p<0.01$ , respectively). This comparison, and inspection of the mean number of responses to tones in testing between the two groups of chicks (Fig. 11), suggests that training with the 65 db/60 db combination enhances the general response level to both familiar and novel double tones in testing, compared to chicks trained with the 60 db/65 db combination. Rank correlations of the number of approach responses and the number of distress calls given by chicks in testing

## FIGURE 11

The mean number of approach responses and distress calls to double tones of different intensities in training and testing (experiment 3). 60/65+V = 60 db/65 db and visual movement; 65/60+V = 65 db/60 db and visual movement; 60/60, 60/65, 65/65, 65/60 = test intensity combinations (in db). No Stim = no experimental stimuli.



were significant for both groups of chicks ( $p < 0.05$  or better) except for the 65 db/60 db tone comparison for chicks trained with that combination.

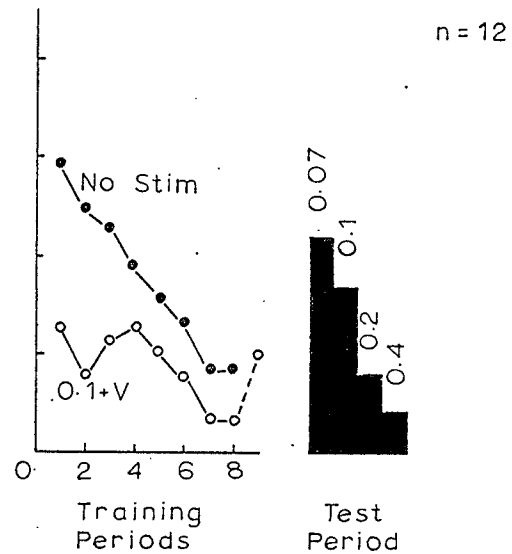
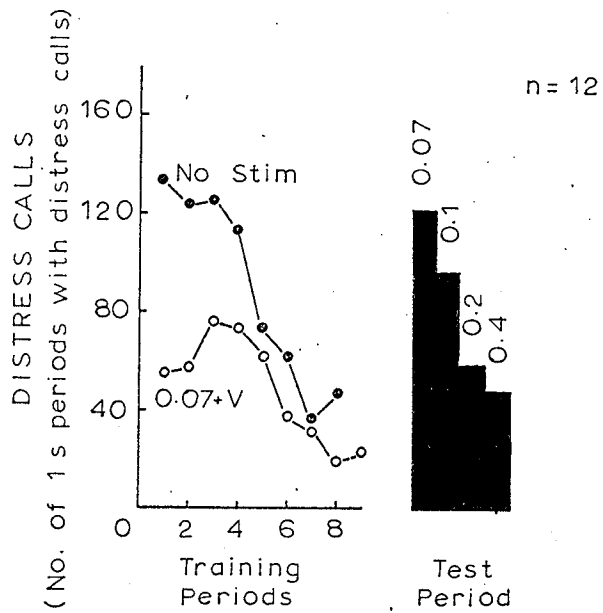
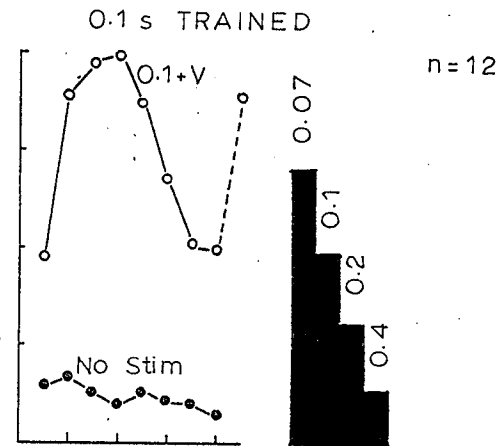
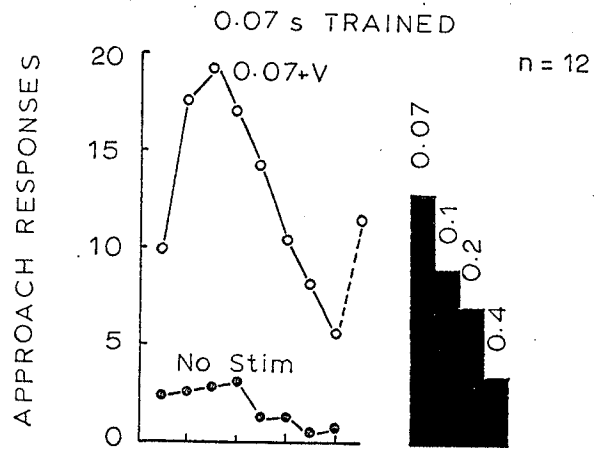
The mean number of approach responses and distress calls in training are shown in Fig. 11. The periods with experimental stimuli initially produced significantly more approach responses but significantly fewer distress calls than periods with no stimulation for birds trained with 60 db/65 db (approach responses: periods 1 to 4,  $p < 0.05$  or better; distress calls: periods 1, 2,  $p < 0.01$ ). Periods with experimental stimuli also produced significantly more approach responses but significantly fewer distress calls than periods with no stimulation for the birds trained with 65 db/60 db (approach responses: periods 1 to 8,  $p < 0.01$ ; distress calls: periods 1 to 4, 7,  $p < 0.05$  or better). Although the distribution of means shown in Fig. 11 suggests that 65 db/60 db elicits more approach responses and distress calls than 60 db/65 db in training, the statistical comparisons (two-tailed t test) were not significant.

#### Experiment 4

There were no significant differences in the number of approach responses or distress calls to the 0.07 s or 0.1 s tones between chicks trained with 0.07 s and 0.1 s (see Fig. 12). In the absence of such training effects, the data were further analysed on the basis of Fischer's

## FIGURE 12

The mean number of approach responses and distress calls to double tones each of a different duration in training and testing (experiment 4). 0.07+V = 0.07 s and visual movement; 0.1+V = 0.1 s and visual movement; 0.07, 0.1, 0.2, 0.4 = test durations (in s). No Stim = no experimental stimuli.



(1972) results for tone-naive chicks, to determine whether decreasing the tone duration increases the number of approach responses and distress calls regardless of the training tone. The data were consequently combined ( $n=24$ ).

Chicks gave significantly more approach responses to the 0.07 s tone than the 0.1 s tone ( $t=2.02$ ,  $p<0.05$ ). They also gave significantly more approach responses to the 0.1 s tone than the 0.2 s tone ( $t=2.76$ ,  $p<0.01$ ). Although the comparison between 0.2 s and 0.4 s was not significant, the difference between 0.1 s and 0.4 s was significant ( $t=2.95$ ,  $p<0.01$ ). The shorter the tone duration, the more approach responses are produced.

Chicks gave significantly more distress calls to the 0.1 s tone than the 0.2 s tone ( $t=3.42$ ,  $p<0.01$ ). Comparisons between 0.07 s and 0.1 s and between 0.2 s and 0.4 s for distress calls were not significant but comparisons were significant for distress calls between 0.07 s and 0.2 s and between 0.1 s and 0.4 s ( $t=3.68$ ,  $3.58$ ,  $p<0.01$ , respectively). Tones of 0.07 s and 0.1 s duration produce more distress calls than tones of 0.2 s and 0.4 s duration. Spearman's rank correlations were significant for correlations between the number of approach responses and distress calls in testing ( $p<0.01$ ).

The mean number of approach responses and distress calls in training are shown in Fig. 12. Periods with experimental stimuli produced significantly more approach responses than the periods without stimulation for both the 0.07 s trained birds ( $p < 0.05$  or better) and the birds trained with 0.1 s ( $p < 0.05$  or better). Periods with experimental stimuli initially produced significantly fewer distress calls than periods with no stimulation for both the 0.07 s trained birds (periods 1 to 4,  $p < 0.01$ ) and the birds trained with 0.1 s (periods 1 to 3,  $p < 0.01$ ). No differential effect during training between 0.07 s and 0.1 s could be shown (two-tailed t test).

#### Discussion

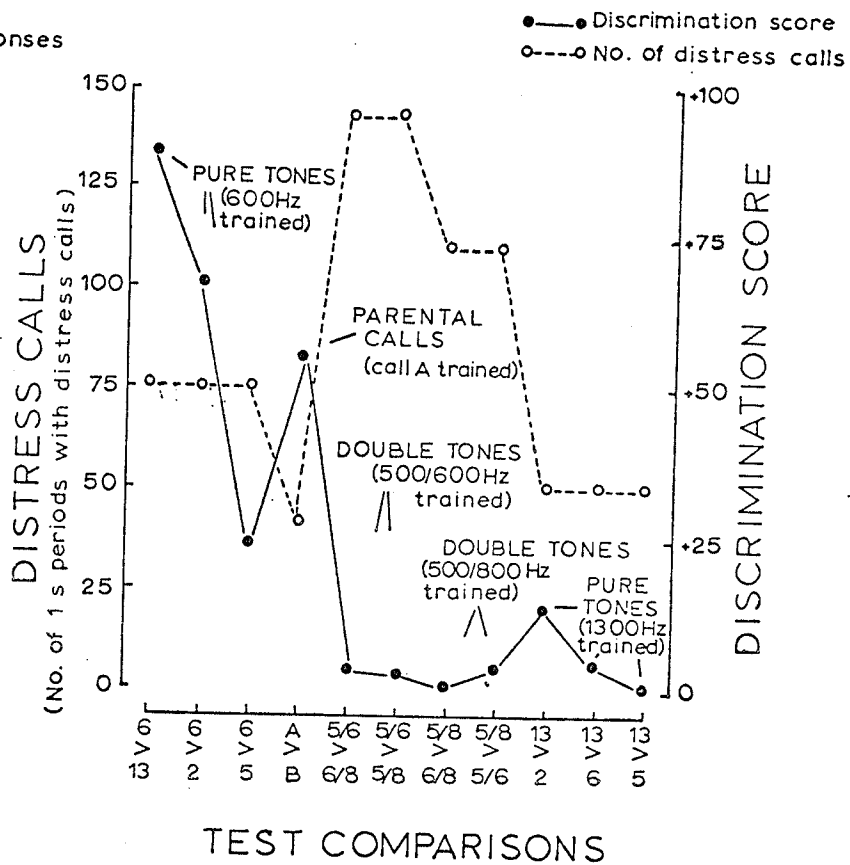
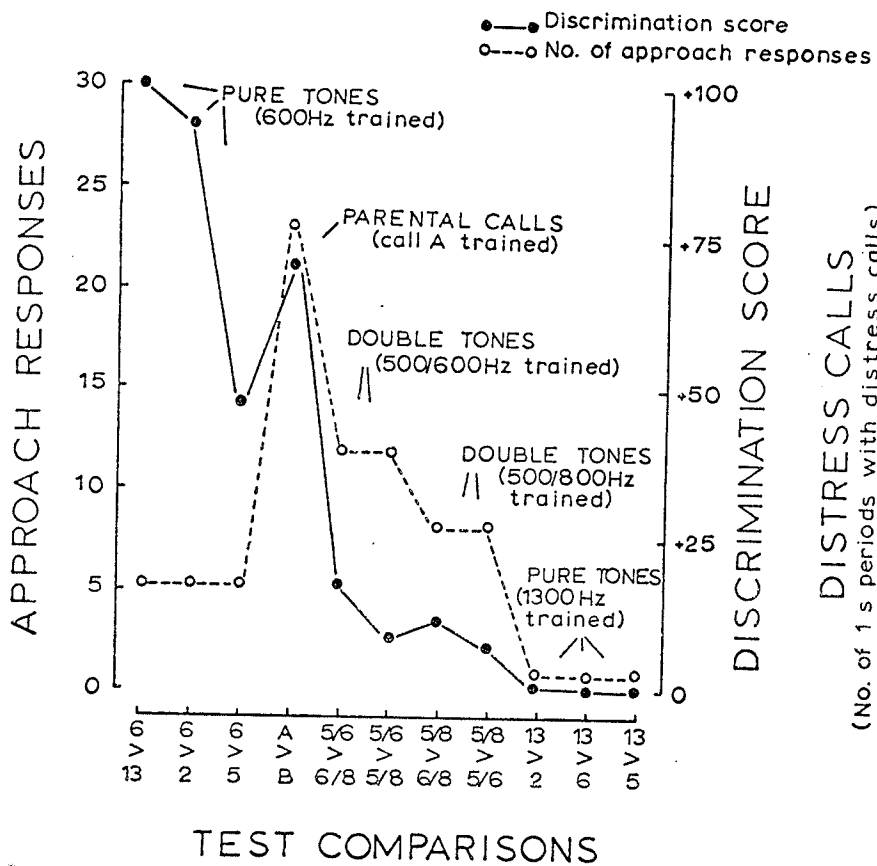
Experiment 1 demonstrated that, after training, a familiar frequency can affect approach behavior and distress vocalization producing more approach responses and distress calls than other, novel frequencies. Experiment 2 showed that a familiar frequency combination can produce a higher number of approach responses than other, novel combinations. Alter either frequency, and the response level is lowered. In a comparable experiment (Part I, sect. 1), it was demonstrated that chicks trained with a parental call can approach and distress call more frequently to this call compared with a parental call tape recorded from a different individual hen. Comparison

of the number of responses to the familiar sound shows, however, that the parental call used in the experiment described in Part I, sect. 1 elicited more approach responses and fewer distress calls than the familiar tones of experiments 1 and 2 (Fig. 13). Not only did the absolute number of responses consistently differ but also the relative difference between the number of responses to familiar and novel stimuli was distinct (see Fig. 13). In terms of this 'discrimination' score (Fig. 13), the results for pure tones (600 Hz trained chicks) and natural parental calls were similar. Scores for the chicks trained with a 1300 Hz pure tone and for the chicks trained and tested with double tones were considerably smaller (Fig. 13). The low discrimination scores for the 1300 Hz tone may simply mean that this frequency is not particularly suitable for discrimination learning, though as the training data show, it does appear as effective as 600 Hz on training behavior. Fischer (1972) has found that pure tones of 375 Hz to 625 Hz produce considerably more following by tone-naive chicks than higher or lower tones.

Unlike the single tone experiment in which different frequencies were used for each test tone, each double tone test 'call' contained a frequency in common with each other test call. This overlap of frequencies

## FIGURE 13

Median 'discrimination' scores and the mean absolute response level to the familiar sound for young Domestic Chicks to pure and double tone frequencies and parental calls in testing. The discrimination score (%) is calculated by dividing the numerical difference between responses to the familiar and novel calls by their sum and multiplying by 100 (cf. Evans, 1972). Data for responses to parental calls are taken from a comparable experiment described in Part I (sect. 1). Test comparisons listed along the abscissa are in Hertz divided by 100 except for A and B which refer to parental calls. > = greater than.



may have contributed to their low discrimination scores. The lower scores for double tones suggest that the voices of different individual hens would be most easily discriminated if they possessed combinations of frequencies with no, or few, shared or common components.

Inspection of spectrograms of parental calls indicates that the calls of different individuals probably share at least several frequencies, although the frequency range and maximum frequency can be quite different (e.g. Evans and Mattson, 1972; Part II, sect. 1). A possible call structure which could both facilitate individual recognition and contain shared frequencies, involves variation in the presence of frequencies with time. For example, a call might possess only a few, individually distinctive, frequencies in the beginning section or segment, have a central 'body' composed of a range of frequencies that are not individually distinctive and have a final section which perhaps again is individually distinctive. Clearly, many other variations are also possible. Detailed inspection of spectrograms of parental calls suggests that particular temporal segments of a call may indeed have individually distinctive frequencies (see spectrograms in Part II, sect. 2; Evans, 1970b; Beer, 1970a; Hutchison et al, 1968).

The lowest frequency of the central segment of the fish call of the Sandwich Tern, which usually only possess a fundamental and two harmonics, appears individually distinctive (Hutchison et al, 1968). Similarly, White and White, (1970) have demonstrated that the beginning section of the 'landing call' of male Gannets (Sula bassana) is individually distinctive in terms of amplitude.

Parental calls usually possess more than two component tones. The greater the stimulus complexity perhaps the greater attraction (cf. Matthews and Hemmings, 1963). Clearly, the double tones of experiment 2 elicited more approach responses than the pure tones. The results of experiment 3 suggest that the distribution of intensity in a call may also, after training, enhance overall response levels. Call amplitude allows fine control over the young chick's behavior (see Fischer and Gilman, 1969) and hence, as found here (experiment 3) might not be expected to be involved in discrimination learning per se.

Effects of training with different tone durations on test behavior were not demonstrated. This contrasts with Tschanz's (1968) work on guillemots in which call duration was thought to be an essential factor for recognition by the young.

Although tone duration does not appear to provide a basis for auditory discrimination learning in chicks, the results of experiment 4 are of interest. The shorter the duration of the tone presented to chicks, the more approach responses and to some extent distress calls elicited. Variation in the duration of a parent's call may result in young approaching faster or slower, sooner or later, thereby allowing further fine control of the chick's behavior.

In studies of tone-naive chicks Fischer and Gilman (1969) and Fischer (1972) found the optimal pure tone intensity and duration to be most effective in producing following. Frequency, by comparison, was less relevant. In contrast, on the basis of the experiments presented here, it appears that sound frequency, whether singly or in combination with other frequencies, may be the most important call parameter facilitating auditory discrimination learning as involved in individual recognition of the parental voice by young.

## SUMMARY OF PART III

Investigation of the parameters of chick behavior in auditory discrimination learning showed that a familiar parental call can cause a much earlier but initially slower approach response than a parental call from a second individual hen. A familiar call can also produce an approach response which, at onset, is more directly oriented towards the sound stimulus. These results were discussed in terms of arousal habituation.

A series of four experiments using synthetic calls were carried out to investigate the parameters of parental sound in auditory discrimination learning. Call frequency appears to be the most important call parameter facilitating auditory discrimination learning of individual calls. Such learning was not shown for intensity or duration which appear, rather, to allow fine control over chick behavior. The relevance of these parameters for individual recognition of the parental voice by young precocial birds was discussed.

GENERAL DISCUSSION

The experimental findings have been fully discussed in the appropriate sections of Parts I to III. Some more general points arising from these findings are presented and discussed below.

A model of parent-young interaction

The results of the experiments reported in this thesis suggest the following model of parent-young interaction in precocial birds.

- 1) In the absence of relevant stimulation from the parent, e.g. a lost chick in high grass some distance from its mother, a chick utters a stream of distress calls and remains relatively still.
- 2) A stream of distress calls cause the mother to return to the chick.
- 3) On making contact with the mother again, distress calls give way to contentment chirps and the young bird approaches and follows the mother.
- 4) In the absence of relevant visual but not auditory stimulation from the mother, e.g.

a chick in high grass but close enough to hear its mother's call, the chick increases its rate of distress calling somewhat and locomotes toward the sound source, its parent.

- 5) An increased rate of distress calling causes the mother to halt, slow down or approach the chick allowing reunion.
- 6) Parental calls from a strange adult conspecific in the absence of relevant stimulation from a chick's own parent, cause the chick to reduce its rate of distress calling and to remain relatively still.
- 7) A low level of distress calling and movement reduces the likelihood that a lost chick will be approached, attacked or adopted by a strange adult.
- 8) If a strange parental call persists for some time in the absence of stimulation from the lost chick's own parent, the young bird will gradually increase its rate of distress calling and will locomote toward the strange adult thereby enhancing chances of adoption.

When young chicks and ducklings become separated from their parent and are lost, they emit a stream of distress calls (Sluckin, 1965; 16; Hoffman, 1968). Distress

calls terminate with the parent's return (Hoffman et al, 1970: 230). When separated from the remainder of the brood, young Canvasback ducklings (Aythya valisneria) also give distress calls; on rejoining the brood they give contentment notes (Collias and Collias, 1956; see also Kear, 1968). These findings are consistent with hypotheses 1 and 3 of the present model. Observations recorded in the literature also demonstrate the effect of distress vocalization on parents (hypotheses 2, 5 and 7). Bruckner (as described by Smith, 1969) demonstrated that a Domestic Chicken hen would fail to come to the rescue of her chick visibly struggling under a glass bell. When the bell was raised slightly, permitting the chick's distress calls to be heard, the hen responded immediately. In ducks, "the normal functions of distress cries are to attract the mother who goes to the duckling if it is lost, broods it if it is cold, leads it to safety if it is frightened, or perhaps leads it to food if it is hungry" (Collias, 1962: 579; see also Hoffman et al, 1966a, b). McBride et al (1969) observed hens retrieving lost, distress-calling chicks. Hens return with the whole brood before moving off again.

McBride et al (1969) observed that of the members of a brood following their parent, those furthest from the mother gave the loudest chirps. This might explain

why, even when auditory and visual contact are made with the 'parent' in the laboratory experiment, a low level of distress vocalization at a rate of about 3 calls per min is still present. Each time the parent moves to the opposite end of the photocell pen, the parent-young distance is automatically increased.

Although hypotheses 4 and 6 are supported by the results of experiments in this thesis, no relevant 'natural' observations appear to have been recorded in the literature. Hypothesis 8 was suggested by the increased responsiveness of chicks to novel calls in the second test period of the experiment presented in Part I, sect. 1 and by the comparable findings by Evans and Mattson (1972) and Evans (pers. comm.).

What is the response of adults to strange young? Alley and Boyd (1950) observed adult Coots (Fulica atra) attacking and driving away chicks conspicuously older or younger than their own. These attacks were often extremely vigorous, adults returning again and again to attack, sometimes persisting until the death of the strange chick. Adult gulls attack and injure, often critically, strange young that trespass on their territories (Tinbergen, 1953; Emlen, 1956). However, adoptions of young can also occur. Where wandering Coot chicks resemble very closely the offspring of the pair

into whose territory they have strayed, the strange chicks may be not only accepted but adopted (Alley and Boyd, 1950). Fostering of young is apparently quite common in Common Guillemot colonies (Pickup, 1973 -- this author described in detail the adoption of a guillemot chick by an adult Gannet). In the Canada Goose, brood mixing has been recorded especially for geese nesting under confined seminatural conditions (Collias and Jahn, 1959; Sherwood, 1967). Ryder (1967) noted that hunting pressure may break up family groups of Ross's Geese (Anser rossii). Dzubin (1965) suggested that, in Saskatchewan late hatching geese are not physiologically capable of migration at the time their parents depart but are adopted by families that leave later.

Evans (1970b) has pointed out that, in gulls, if a chick has lost its parent its only hope of survival may lie in the chance that it can get itself fostered and fed by other adults. Since young gulls rely on adults for food it would not be in the chick's 'interest' to persist in discriminating against strange adults. Presumably, in precocial species the need for direction to food and predator protection would similarly favour adoption for survival (hypothesis 8).

In relation to these observations, the parent-young interaction model presented above at least appears plausible. However, the effects of distress vocalization

on both familiar and strange adults requires much further experimental investigation. Similarly, much detail is missing from the model. Consider hypothesis 3. Parental calls do not just simply cause approach or following. The parental call is also able to exert finer control over the chick's behavior. Variations in duration of the call may cause chicks to approach sooner or later, faster or slower (Part III, sect. 2). Variations in overall amplitude may have similar effects (Part III, sect. 2; Fischer and Gilman, 1969).

The classification of auditory discrimination learning  
in young precocial birds

Learning may be defined as a change in the strength of an act through training procedures as distinguished from changes in the strength of the act by factors not attributable to training (Hilgard and Marquis, 1940). Clearly, many of the conclusions reached in this thesis refer to 'learning'.

According to several conventional treatments (e.g. Kimble, 1961; Thorpe, 1963; Hinde, 1970) most forms of learning can be referred to one of three classes: habituation, classical conditioning and operant conditioning. Can the auditory discrimination learning described here be classified as one of these types? Visual reinforcement

is probably involved (Part I, sect. 1 and 2), hence habituation, which involves a waning of response in the absence of reinforcement, is not sufficient to account for the results. The number of responses to parental calls previously paired with visual movement was consistently higher than to those not previously associated with visual movement in training (e.g., Part I, sect. 2).

Call A and visual movement were presented according to a classical conditioning paradigm. They were not response contingent as required for operant conditioning. Can the results be classified as classical conditioning? In this form of conditioning, the conditioned response resembles the unconditioned response. The number of responses given to the familiar call A in testing, after prior training paired with visual movement, differs considerably from the number given to call A and visual movement in training in periods of the same duration, although this may reflect latency differences rather than speed or 'form' differences (Part I, sect. 1 and 2; Part III, sect. 1). However, in classical conditioning, as in operant conditioning, the conditioned stimulus is usually neutral before conditioning takes place. Call A, even at the onset of auditory training, is clearly not a neutral stimulus vis-a-vis approach behavior or distress vocalization (see especially Part I, sect. 2).

Although the learning shown in the experiments reported in this thesis resembles classical conditioning more than the other forms, it is evident that it cannot be neatly pigeon-holed as one of the simple learning types outlined above. The attempt to fit particular examples of learning into a classificatory scheme may, in the long run, be detrimental in that a majority of workers may tend to investigate classified forms to the exclusion of other, perhaps biologically more important variations.

Embryonic exposure and the development of individual  
recognition of parents by voice

Goose embryos used in the experiment described in Part II, sect. 1 received a short period of prehatch exposure to a parental call of the Canada Goose. The remainder of the experiments in this thesis did not employ prehatch exposure to parental calls. The experimental results clearly indicate that prehatch exposure to the familiar call is not essential for the development of selective responsiveness to individual parental calls.

There are four main sources of sound which might affect the developing embryo -- namely, the parent(s), other embryos in the nest (see Vince, 1964, 1969), the embryo itself (Gottlieb, 1965,<sup>1968b</sup>/Gottlieb and Vandenberg,

1968), and the general environment (e.g. wind noise, thunderclaps). Parent birds have often been observed calling quietly over unhatched eggs both before and after pipping (Collias and Collias, 1956; Gottlieb, 1963; Hess, 1972; Part II, sect. 2). Parental calls can affect embryonic responsiveness (Gottlieb, 1965; Impekoven, 1973). For the pekin duck there is evidence that perinatal exposure to auditory stimuli can enhance posthatch responsiveness to species-typical calls (Gottlieb, 1966).

The Common Guillemot nests in crowded colonies on cliff ledges. As would be expected, the development of individual recognition of parents by voice, by young guillemots, occurs particularly early -- prehatch exposure to calls of the parent appears sufficient for posthatch individual recognition (Tschanz, 1965, 1968). However, the results of a series of experiments in which individual parental calls (calls A, B) were played for considerable periods to Domestic Chicken embryos were inconclusive (Evans, pers. comm.). Posthatch, the chicks did not selectively approach or vocalize to the familiar individual calls. Prehatch exposure to the parental 'mew' call of the Herring Gull (Larus argentatus) does not selectively facilitate responses to this call by young Herring Gulls. They prefer the mew call of the Ring-billed Gull (Evans, 1973). An effect of prehatch exposure to the familiar parental call on the test behavior

of chicks to individual calls, after one or more days posthatch, remains to be demonstrated.

Presumably, sounds due to the embryo itself and incubator-sharing embryos occurred during all the experiments carried out for this thesis. A possible effect of these sounds on test behavior was not investigated.

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