THE ROLE OF PRENATAL AUDITORY STIMULATION IN THE DEVELOPMENT OF FILIAL BEHAVIOUR IN THE DOMESTIC DUCKLING

by

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ABSTRACT

The aim of the first three experiments was to delineate the physical characteristics of an artifical call for which naive Peking X Aylesbury ducklings show the greatest natural preference. In each experiment 50 ducklings were tested at 20 ± 2 hrs. posthatching, for following and approach responses to one of four auditory stimulus conditions or a silent model. The responsiveness of subjects was greatest when the call contained tone frequencies of 500, 800, and 1600Hz and was presented at a repetition rate of 4/second with a note duration of 50 milliseconds (Optimal call).

In Experiment 4 Peking X Aylesbury eggs were exposed to intermittent prenatal stimulation with the optimal call and the hatchlings were tested for responsiveness to this call at 20 ± 2 hrs. posthatching. Subjects with prenatal auditory experience of the optimal call showed significantly greater responsiveness to this call than non-stimulated control subjects.

The aim of the final experiment was to determine whether the natural auditory stimulus preferences of ducklings could be overriden through sheer prenatal experience of a non-preferred call. Ducklings with prenatal experience of the non-preferred call continued to show as strong a preference for the optimal call as non stimulated control subjects. The responses of both stimulated and non-stimulated subjects to the optimal call were significantly stronger than the responses of stimulated and non stimulated subjects to the non-preferred call. The responses of stimulated subjects to the non-preferred call were only slightly stronger than responses of non stimulated subjects to the same call. These results indicate that responsiveness to calls for which naive birds show the greatest preference is enhanced by prenatal experience of the preferred call. This effect is not evident, however, when subjects are stimulated prenatally with a non-preferred call.

SUMMARY

Chapter 1 : Introduction

The main issues examined in this study all stem from Lorenz's (1935, 1937) original conceptualization of imprinting. He maintained that:

1. The predispostion to follow moving objects soon after hatching is innate, but recognition of adults of the species is not.
2. Rather young birds acquire recognition of the imprinting object during a specific period in their posthatching life.

Before attention is given to these specific problems the sources of disagreement in the imprinting literature and the semantic confusion surrounding the term "imprinting" is examined. It is proposed that a circular definition of imprinting should be avoided and that the terms "following response" and "approach response" should not be used synonymously with "imprinting".

Having defined the place of the present study in the context of the field of imprinting literature relating to the issues listed above is reviewed. Attention is drawn to the fact that precocial birds do not necessarily respond indiscriminately to the first moving ojbect. Gottlieb (1965) has shown that young birds respond selectively to the conspecific maternal call. The maternal call was more effective in eliciting following and approach responses (the traditional indices of imprinting) than the calls of other species. A distinction is drawn between the processes and mechanisms involved in the "acquisition of recognition" of imprinting and species identification which is not dependent on prior exposure to the object of attachment. Evidence indicating that both processes may operate in determining the strength of filial responses is discussed i.e. there is evidence for the existence of natural preferences for the species specific maternal call and

acquired preferences for the call of the parent with its individual characteristics.

After a discussion of evidence showing that both extra specific and species specific auditory stimuli are prepotent over visual stimuli in eliciting filial responses, two main sets of questions to be examined in this study are posed:

1. Can the physical characteristics of a call attractive to birds be specified and, if so, can an effective artifical call be synthesized?

These questions are examined in chapter 3.

2. The second set of questions concerns the development of selective responsiveness in birds. Does parent/embryo interaction affect postnatal filial behaviour? Can specific events be isolated in the prenatal ontogeny of a species specific auditory mechanism?

These and related questions, and research designed to answer them, is the topic of chapter 4.

Chapter 2: Methodological details.

In this chapter the methodological details common to all experimental research described in chapters 3 and 4 are presented. It is observed that the source of much of the conflicting data in the literature can be traced to differences in methodology. Consequently considerable attention is devoted to precise specification of details and identification of sources of extraneous variability.

This chapter provides details of subjects, incubation conditions, brooding, prenatal and postnatal experimental apparatus, tests and testing procedures. In the final section the rationale for employing statistical procedures is given. The tendency for previous workers to exclude non responders in computation of means and statistical analyses is examined critically. Arguments in favour of using the scores of all subjects (both responders and non-responders) are presented.

Chapter 3: Auditory Stimulus Preference in Birds: The Analysis of the Physical Properties of Preferred Sounds.

Literature describing prior attempts to delineate the critical acoustic characteristics of artificial calls attractive to ducklings and chicks is reviewed. The more systematic analyses of Heaton (1971) and Fischer (1972) receive the greatest attention. Heaton found that parentally naive Peking ducklings possess a highly attuned predisposition to respond to calls with frequencies of 780, 1125 and 2250Hz, presented at a repetition rate of 4/second. An artificial call with these features proved as effective as the actual maternal call in eliciting approach responses. In a similar study performed with domestic chicks Fischer (1972) was able to identify optimal frequencies repetition rates and tone durations. A combination of the optimal elements in each parameter resulted in a highly effective synthetic call.

The object of the three experiments described in this chapter was to specify the critical elements in a call attractive to naive Peking X Aylesbury ducklings. The ultimate aim was to produce an effective artificial call, the elements of which could be manipulated in subsequent experiments. In each experiment 50 Peking X Aylesbury ducklings were tested for following and approach responses to artificial calls in which the elements in a given parameter were varied. In Experiment 1 subjects were tested with calls in which the tone frequency varied on both sides of the frequencies found to be optimal for Pekings. The results indicated that the combination of frequencies at 500, 800, and 1600Hz produced the greatest mean scores (shortest latency, longest duration). There was, however, a lack of consistently significant statistical difference in responsiveness to the different frequency combinations. Nevertheless a comparison of mean response scores to the optimal frequency combination with response scores reported by previous workers indicated that this was an effective call. Possible explanations for the absence of clear cut differential responding are discussed.

In Experiment 2 frequency and note duration were kept constant while repetition rate values were varied. In this case there were definite indications of repetition rate dependent differential responding. The results indicated that the call with the repetition rate of 4/second was most effective in eliciting following and approach responses. In some response measures, however, there was no significant difference between the 4/sec. and 8/sec. calls, suggesting that the 8/sec. rate lies at the upper limits of a generally attractive repetition rate range.

In Experiment 3 the optimal frequencies and repetition rate obtained in Experiment 1 and 2 were kept constant while the note duration was varied. Evidence of duration dependent differential responding was found. Calls with note durations of 50 msec or less were significantly more effective than longer durations. Although a call with 50msec. durations elicited the strong mean responses the results indicate that the 25msec duration falls into a generally attractive note duration range. A comparison of mean response scores of subjects tested with the 500, 800 and 1600Hz, 4/second,50msec call (optimal call) with mean scores reported by other workers indicated that this was an attractive call. The optimal call was thus considered to be suitable for use in subsequent experiments.

Chapter 4: The Development of Species Specific Auditory Perception in Birds

The use of concepts such as "instincts" and "genetic programmes" as explanatory concepts is criticized on the grounds that they create a conceptual barrier to the further analysis of developmental factors. It is argued that the existence of natural stimulus preferences should not automatically lead to the supposition that they are responses resulting from the passive translation of genetic programmes into behaviour.

It is proposed that a full understanding of species typical behaviour patterns will only be achieved after a complete analysis of the ontogeny of instinctive behaviour. Behaviour is viewed as the functional product of the dynamic relationship between the organism and its environment from the moment of conception.

The viewpoints of the proponents of the predetermined and probabalistic epigenesis of behaviour are reviewed. Research by Gottlieb (1971) has provided experimental evidence for the theoretically important notion that stimulative events occurring normally before birth play a role in the perfection of species specific perception. That is, that species specific auditory perception is a probabalistic phenomenon, the threshold, timing and perfection of such perception being regulated jointly by organismic and sensory stimulative factors. It is observed that not sufficient attention has been given in imprinting research to the role of parental behaviour directed towards the embryo or hatchling. Research indicating that parent/embryo interaction affects postnatal behaviour is reviewed. Greatest attention is devoted to the research which has been done on: (i) the prenatal origins of personal recognition in birds (ii) the influence of prenatal stimulation with the conspecific maternal call on postnatal filial responses. Tschanz (1965, 1969) and Beer (1970 a & b) have shown that Guillemot and Laughing gull chicks acquire recognition of the individual characteristics of their parents calls while still in the egg. The basis for such recognition is discussed.

Impekoven (1973) was successful in her attempt to achieve prenatal auditory imprinting by means of prenatal stimulation with the conspecific maternal call. The possible reasons for Hess' (1959) failure in a similar attempt are discussed.

Experiment 4 was designed to ascertain whether prenatal experience of the optimal artificial call will affect the strength of responsiveness to that call. Results indicated that those subjects which had experience of the call from the 18th day of incubation responded more quickly to that call and for a greater length of time than control subjects incubated in

silence. Implications of these findings for imprinting theory and research are discussed. It is proposed that greater cognisance be taken of the natural and acquired preferences which birds bring to the postnatal imprinting situation. The "critical period" concept and the problems of using locomotor responses as the sole behavioural criteria of imprinting are discussed in the light of present findings.

Attention is then directed towards the question whether it is possible to alter the natural preferences of birds through prenatal stimulation with non-preferred calls. Will prenatal stimulation with a non-preferred call result in a bird showing a greater preference for that call than for one which naive ducklings show the greatest natural preference? Will experience of a non preferred call weaken responsiveness to an optimal call?

Previous research related to these questions is reviewed. Gottlieb (1965) found that neonatal birds continue to show preference for the maternal call of the species in spite of prior experience of another species call after hatching. Simner (1971), however, succeeded in enhancing responsiveness of chicks to a non-preferred visual flicker through perinatal stimulation with the non-preferred stimulus. Grier, Counter & Shearer (1967) found greater responding in chicks which had been exposed prenatally to an artificial call with features differing from the natural maternal call. Rajecki (1972) has shown, however, that it is not possible to enhance responsiveness to all kinds of calls. Prenatal stimulation with calls differing markedly from the natural maternal call resulted in no strengthening of postnatal responsiveness to such calls.

In an attempt to answer the questions posed earlier, a completely randomized block design was employed in Experiment 5. Groups of ducklings were exposed prenatally to a call in which the repetition rate had been altered from the optimum. These subjects and non-stimulated control subjects were tested with either the optimal or altered calls. The results indicated that there was no marked alteration in responsiveness to calls as a result of prenatal stimulation with the altered call. Both stimulated and non stimulated subjects continued to show a preference for the optimal call. There was only a slight increase in responsiveness to the altered call as a result of prenatal stimulation and no weakening of responsiveness to the optimal call.

Chapter 5: Conclusions and Suggestions for Future Research.

It is concluded that the results of this series of experiments indicate that Peking X Aylesbury ducklings possess a highly attuned response predisposition to react to specific stimulus complexes. The ability to react selectively occurs without the benefit of known forms of learning. The biological significance of this ability is discussed. Differential responding, however, does not represent the passive translation of genetic material into behaviour. The actual strength of response to the preferred auditory stimulus complex is influenced by prenatal stimulation with the preferred call. It would appear that in natural situations, parent/embryo interaction has an affect on later filial behaviour.

The results of the final experiment indicate that the predisposition to react to certain classes of stimuli only reduces the likelihood of birds becoming attached to species other than their own before hatching.

Two areas requiring attention in future research are examined. Firstly, it is observed that the close temporal correlation of stimulative events in the nest may have an effect on postnatal behaviour. Suggestions on how to determine the most natural way of presenting experimental stimuli are given. Secondly, observations made during the present study suggested that vocalization patterns might prove to be sensitive indicants of social attachment. Running spectrum analyses of duckling vocalizations emitted in relation to stimulus presentation are presented as evidence of the existence of characteristic vocalization patterns. The need to establish the relationship between characteristic vocalization patterns and other indicants of long term attachment on more objective grounds, is emphasized.

Chapter I

INTRODUCTION

> "Those Ducks that haue bene brought up under a
> henne, the Drakes of that broode will desire to
> tread the hennes"
>
> Mascall, 1581.

The observation that newly hatched precocial birds approach and follow the first moving object to which they have been exposed, has led, in recent years, to an extremely active area of behavioural research. Although interest in this phenomenon has only recently expanded it was not unnoticed through centuries of time. Indeed, it was observed by the Ancient Greeks, described by Sir Thomas More in "Utopia" (1516) and studied more extensively by the English naturalist, Douglas Spalding (1873).

Experimenting with wild pigeon, Craig (1908) discovered that, in order to cross two different species, it was necessary to rear the young of one species under the adult of the other. Upon reaching maturity the birds so reared preferred mates of the same species as their foster parents. Shortly aferwards Heinroth reported that Greylag geese would respond to humans in a filial fashion in preference to adults of their own species, if they are exposed to humans rather than geese immediately after hatching.

It was not until 1935, however, that a term was coined for this phenomenon. Konrad Lorenz, an Austrian zoologist, used the term Prägung, later translated as "imprinting", to describe the process whereby certain species of precocial bird become imprinted on, or show filial attachment to, a wide variety of animate or inanimate objects.

While Lorenz certainly has evolved his conceptualizations regarding the nature of imprinting since his pioneering 1935 paper, his earliest theories have had a marked influence on subsequent conceptualizations and the directions that experimental investigations have taken. Those aspects of Lorenz's theory which are of the greatest relevance to, and which will be examined in the present study are succinctly stated in the following quotations from his 1935 and 1937 writings:

"We have seen that in many cases the object appropriate to innately determined instinctive behaviour patterns is not instinctively recognized as such but that recognition of the object is acquired through a quite specific process which has nothing to do with learning. With many instinctive behaviour patterns oriented towards conspecifics, the motor component is itself innate but the recognition of the object of the pattern is not"

(Lorenz, 1937. Translation by R. Martin, in Lorenz 1970, Vol. 1. p.245)

And further ...." the recognition of the object is acquired during the individual's life time by means of a process which is so peculiar that it merits detailed consideration" (Lorenz, 1935. Translation by R. Martin, in Lorenz, 1970, Vol 1, p. 124)

To summarize Lorenz's theory then:

(a) Certain species of bird have an innate predisposition to follow moving objects soon after hatching. According to Lorenz the motor component is innate but the recognition of the object is not.

(b) It follows, therefore, that birds do not instinctively recognise adult members of their own species.

(c) Recognition of the object is acquired during a quite definite period in the post hatching life of the bird - the critical period.

(d) Recognition is acquired by means of a process which has nothing to do with learning. Imprinting, Lorenz believed, is an instance of behaviour which does not conform to the classical characteristics of learning through conventional association or conditioning processes.

Other distinctive properties that Lorenz attributed to imprinting, but which are not investigated in the present study, include:

(e) Imprinting is irreversible. Once imprinted on an object the bird will always respond in preference to that object even when confronted with the adult of its own species.

(f) The first object to elicit a social response on the part of the young bird, such as following, later releases not only that response but also related responses such as sexual behaviour.

This conceptualization was a direct challenge to the behaviourists' attempts to explain all behaviour acquisition on the basis of learning principles. However, it was not until many years later that this challenge was taken up by experimental psychologists. Lorenz was working in Europe and writing in German. It is unlikely that many American and British psychologists had read or were even aware of his publications. As a result 20 years were to pass before the experimental investigation of imprinting came into prominence. Much of the credit for the pioneering of laboratory analysis of imprinting can go to Eckhard Hess. It was certainly his efforts that attracted the attention of experimental and comparative psychologists to a topic which had, for so long, remained of interest solely to the ethologists.

The last 20 years has seen an explosive increase in interest shown in the experimental investigation of imprinting. A comprehensive review of experimental findings at this stage is neither practical nor necessary. The growing body of knowledge of the imprinting phenomenon has been adequately reviewed by Moltz (1960, 1963), Bateson (1966) and Hinde (1970). The most recent and comprehensive review of imprinting research may be found in Hess' book entitled "Imprinting: Early experience and the developmental psychobiology of attachment" (1973). The review of literature which is to follow later in this section will be concerned only with that material which is relevant to the present study.

The advent of the phase of laboratory experimentation in imprinting research has led, surprisingly, more to confusion and controversy than to clarity and unanimity. It is pertinent for any researcher in this field to examine the reasons for this lack of unanimity. An examination of this kind will not only indicate the difficulties encountered by a researcher entering this field but may also reveal possible ways of resolving our present problems.

The sources of disagreement may be classified as follows:

(i) Differences in interpretation of collected data. This problem is inevitable and not easily solved because of the widely divergent theoretical starting points of the many workers in this field. Rajecki (1973), in a recent review, has discussed at least six interpretations of imprinting: the contextual, ethological, conditioning, epigenetic, information-processing and neuronal model interpretations of imprinting. It is hoped that the present study will contribute to the development of a widely accepted theory of imprinting.

(ii) Conflicting or variable research findings is another major source of disagreement. Closer examination reveals that this, in turn, is due to:

(a) The use of different species of bird. Researchers have incautiously compared, for example, the results of studies of chicks with those of ducks. It should be recognized that even within the same genus there are marked differences in behaviour patterns. For example, Vantress broiler chicks have proved to be good followers whereas White Leghorn chicks have not (Hess, 1959).

(b) The wide variety of different apparatus and behaviour measures used in imprinting research. For example, imprinting apparatus may have an enclosed walkway (Hess, 1973) or be of the open field kind (Gottlieb, 1965, 1971). In addition to the more traditional designs some workers have constructed their own unique apparatus. Grier, Counter and Shearer (1967) measured the tendency of chicks to approach, through a series of concentric circles, the imprinting object at the centre of a flat table. In spite of proposals by writers such as Shapiro (1970), to reduce variance by standardizing equipment and recording measures, little attention has been given to this problem. In the present study apparatus was constructed following closely as possible the design used by a major worker in this field - Gilbert Gottlieb. Those procedural changes that were made were considered improvements and are justified by supporting arguments.

(c) Differences in prenatal and neonatal rearing conditions prior to testing of subjects. The need for, and the means of, controlling for as many extraneous variables as possible are discussed in greater length in the section dealing with methodological details.

A further source of disagreement, and one which requires immediate attention, is the semantic confusion surrounding "imprinting". Unfortunately the term has taken on almost as many shades of meaning as there are researchers in the field. At the one extreme the usage is still tied tightly to Lorenz's original ideas about imprinting. Although some researchers have adjusted Lorenz's original conceptualization to accomodate experimental findings, the overwhelming trend has been to go to the other extreme in defining imprinting. In the research reports of the last few decades there has been an unfortunate tendency to define imprinting solely in terms of approach and following responses, even if only implicitly. This is largely due to the fact that so-called "imprinting research" has not been concerned with the questions about imprinting at large, but rather with approach and following responses of certain species of precocial bird during a limited neonatal period. Most important contributors in this field use the approach and following response as the sole behavioural criteria of imprinting. Consequently we have arrived at the untenable situation in which we have a circular definition of imprinting. That is, imprinting is being defined in terms of the operations used to measure it. In his review of imprinting, Moltz (1960) admits to having to use the term imprinting "... to denote a particular experimental operation and not a process or mechanism (p.294)."

It is proposed here that the term "imprinting" be reserved for the still incompletely conceptualized process or mechanism which encompasses the generalized social responses traditionally associated with the concept. Furthermore it is proposed that the terms "following response" and "approach response" should not be used synonymously with "imprinting". It should be recognized that these responses are, at the most indicants of initial attachment and do not necessarily provide evidence that long standing bonds have been established. It is unfortunate that economic considerations (both time and funds) discourage researchers from using such measures of long term preferences as those employed by Schein (1963) and Shultz (1965). These investigators studied mate selection as a function of early experience - surely a more biologically meaningful measure of imprinting?

It is emphasized that the present study, although related to the larger field of imprinting, is concerned with only one aspect of the field ie. with the initial responsiveness of ducklings to auditory stimuli during a limited period in the bird's life (20 ± 2 hrs post-hatching), responsiveness being measured in terms of following and approach responses. At the most it may be inferred that socialization with the stimulus is taking place when the subjects approach or follow the stimulus to any appreciable extent.

Having defined the place of this study in the context of the field of imprinting it is now time to turn attention to the issues which are to be examined and to review the literature relating to them.

On the basis of his original observations Lorenz (1935 Translation by R. Martin in Lorenz, 1970, Vol I) concluded that " ... a bird does not recognise conspecifics innately and purely "instinctively" in all situations and respond accordingly (p.124)". Indeed ..."young birds of most species will direct the instinctive behaviour patterns adapted to conspecifics towards a human being if they are reared in human care isolated from their own kind (p.124)."

These statements should not be interpreted to mean that birds indiscriminately follow the first moving object they are exposed to and show no preference for members of their own species. Recent research has shown that, while birds will approach and follow a wide variety of animate and inanimate objects soon after hatching, they often show a greater preference for some objects than for others. The observation that birds respond selectively to different classes of stimuli has been most apparent in studies involving the auditory modality. Gottlieb (1965) has shown that parentally naive ducklings and chicks greatly prefer the call of their own species to those of other species. That is, there appears to exist a highly attuned response predisposition directed towards species specific maternal calls. The parental calls of each species of bird studied by Gottlieb were more effective in inducing and maintaining the following response by naive hatchings than were the parental calls of other species. Furthermore, ducklings of one species (Peking) which had previously been exposed to the parental call of another species (Wood duck), favoured the parental call of their own kind in a choice test. These observations led Gottlieb (1965) to conclude that parentally naive ducklings and chicks possess an auditory perceptual mechanism allowing them to identify their own species on the basis of species typical auditory stimulation emanating from the parent. This general identification of conspecifics appeared to occur without the benefit of any known forms of learning. Ninety two years before Spalding (1873) had also observed that " ... chickens follow the call of their mother before they have had any opportunity of associating that sound with pleasurable feelings (p.5)".

Since imprinting is traditionally conceived of as involving acquisition of recognition of the imprinting object during the birds life time, there is clearly a need to distinguish between the processes and mechanisms involved in imprinting and those involved in species identification. Species identification, and resulting filial behaviour, is not dependent on prior experience of the adults of the species (the object of filial attachment). Imprinting, on the other hand, is dependent on exposure to auditory and visual stimuli emanating from the imprinting object. On subsequent occasions only these stimuli evoke filial behaviour. Viewing the imprinting concept more broadly than mere "Acquisition of recognition" it is clear that species identification is not in opposition to long term social attachment which is usually implied by "imprinting". Indeed the ability to identify conspecifics is likely to facilitate the hatchlings being "imprinted" on the biologically appropriate object.

The distinction between the initial processes involved in imprinting and species identification might become clearer by examining the behaviour of young birds exposed to either species specific or extra specific stimulus objects. Given the choice, young birds will show species specific preferences. However this does not mean that extra specific preferences cannot be established through imprinting. Imprinting can operate in establishing filial contact with species other than the neonates own (i.e. extra-specific filial attachment). However, as Gottlieb (1965) has shown, these extra specific preferences can only be readily established when the species specific parental call is not available.

Furthermore there is evidence that neonatal birds are able to discriminate the call of its own parent from the call of another parent of the same species (Gottlieb, 1963, Tschanz, 1964, 1968 Beer, 1970 (a), 1970 (b)). Auditory imprinting is clearly requisite to the development of this ability ie. the bird learns, or acquires recognition of, the individual characteristics of the call of the parent. There is thus evidence for the existence of a natural preference for the species specific call and an acquired preference for the call of the parent with its individual characteristics. Evidence indicating that such auditory imprinting can occur while the bird is still in the egg (prenatal auditory imprinting) will be examined in greater detail later in this report.

Although a number of different sensory modalities may be involved in the initial attraction of young birds to a stimulus complex, the auditory component appears to play the dominant role. Investigations of the sensory preferences of young birds have revealed that auditory stimuli are prepotent over visual stimuli in the young of all precocial avian species tested. This finding holds for both species specific and non species specific stimulation. A number of workers, using a variety of extra specific stimuli, found auditory stimuli to be prepotent over visual stimuli (Boyd & Fabricius, 1965, Fischer, 1966, Gottlieb & Simner, 1969). In a study designed to determine the respective potencies of species specific maternal auditory and visual stimulation,Gottlieb (1971) found that species specific maternal auditory stimulation was more effective in eliciting the following response in maternally naīve chicks and ducklings than the visual attributes of the conspecific adult. These findings provide compelling evidence that, in the initial stages, species identification is based primarily on auditory perception. In natural situations, of course, the parent is not only a source of auditory stimulation but also provides visual, tactile, and thermal stimulation. However, as Gottlieb and Simner (1969) point out, under field conditions ducklings frequently lose sight of their parents because of the terrain and rely on the parental call to direct them away from predators and towards sources of food. The biological significance of this auditory perceptual mechanism is evident.

Now that it is established that auditory stimuli (both conspecific and non specific) are prepotent over visual stimuli and that certain calls are prepotent over others, two question complexes require examination:

1. What are the physical characteristics of a call that makes it more attractive than others? Can certain critical parameters and elements within these parameters be specified? Is it possible to synthesize an artificial call which is as attractive to a bird as the maternal call?

   Experiments 1 to 3 were designed to answer some of these questions about the species of bird used in this study.

2. The second group of related questions concerns the development of selective responsiveness in birds.

   Why are neonatal birds more responsive to calls with certain characteristics than to others? Is this an instinctive ability independent of prenatal stimulation or can specific events be isolated in the prenatal ontogeny of a species specific auditory perceptual mechanism? What role, if any, does the parent play in the development of the discriminative response to the conspecific maternal call? Finally, will a non-preferred call become more attractive than the preferred call by virtue of early (prenatal) exposure to the non-preferred call? In other words, is it possible to alter a bird's natural preferences via prenatal stimulation?

   The object of Experiments 4 and 5 is to answer, even if only partially, some of these questions.

Chapter 2

METHODOLOGICAL DETAILS

For the sake of convenience those methodological details common to all experiments will be described collectively in this chapter. Details specific to each experiment and any departures from procedures described here will be mentioned in the presentation of the experiments.

As mentioned earlier, the source of much conflicting data in the literature can be traced to (a) differences in species of birds used. (b) differences in prenatal and postnatal rearing conditions (c) the large variety of procedures and measures used. Keeping this in mind great care has been excercised in providing precise details of subjects, rearing conditions, etc. In each sub-section sources of extraneous variability will be identified and discussed.

Subjects:

The same species of domestic duck, bred from a single flock, were used throughout the present series of experiments. Partially incubated Peking X Aylesbury duck eggs were collected from the suppliers, Clearsprings Farm, Klipheuwel and transferred to the laboratory incubators. Although the cross breeding was done for commercial reasons it resulted in a very suitable experimental subject since the easy mobility of the Peking was combined with the hardiness of the Aylesbury.

On the twelth day of incubation eggs were transferred from the commercial hatchery to the laboratory incubators in an insulated and buffered carrier designed for the purpose. This practice of transporting 12 day old embryos had no detrimental affect on hatchability, nor any noticeable effect on postnatal behaviour. The possibility that visual and auditory stimulation, uncontrolled for during the first 12 days might influence postnatal behaviour seemed remote since neither the auditory nor the optical systems are sufficiently differentiated by that stage to be sensitive to stimulation. (Gottlieb, 1968). Even in the event of some unknown influence it was assumed that such influence would be found equally in all birds.

Since no attempts were made to delineate exact critical periods the pre-incubation refrigeration technique to determine the exact developmental age (Gottlieb, 1963) was not considered necessary.

Since hatchability was high in all batches, always greater than 60%, all hatchlings were considered suitable for testing. Gottlieb (1971) has suggested that groups in which hatchability is less than 50% be excluded as a safeguard against introducing extraneous variability or unreliability into the results of behavioural experiments.

Incubation:

> "Environment has its effect on living embryo,
> its doom ...
> Through changing forces or neglect -
> From heat to noxious gases' fume."
>
> Romanoff, 1972.

As Gottlieb (1968) observes, most investigators do not report any details of incubation. Since temperature, humidity, position of eggs, turning of eggs and type of incubator all influence development, it seems certain that some differences in results among investigators, especially the time of first appearance of a given response can be attributed to incubator differences. In the present study considerable care was taken to maintain constant incubation conditions and to exclude all forms of uncontrolled stimulation.

Incubators

Two makes of still-air incubators, housed in seperate air-conditioned, sound attenuated rooms, were used.

In the first three experiments all eggs were incubated in an incubator designed and constructed in the Psychology Department, U.C.T. This incubator, which was designed by the experimenter for the purposes of manipulating the sensory environment, was equipped with (i) a thermostatically controlled heating system utilizing heating elements in the roof of the apparatus (ii) a hygrometer for humidity regulation (iii) double walls packed in between with sound proofing material (iv) a double walled glass observation window in the roof. When not in use the window was covered by a close fitting lid. (v) a fixed 6,5 cm permanent magnet speaker with voice coil impedence of 4 ohms and a maximum output of 0.3 watts. For the purposes of application the frequency range was within specifications. This speaker was connected via an external lead to a Hitachi Levelmatic TRQ220 type-recorder. In experiments 4 and 5 this incubator housed those eggs which were subjected to prenatal auditory stimulation. A diagram of this apparatus is provided in Appendix 1.

The incubator used to hatch control subjects in Experiments 4 and 5 was an "Ovo warm water incubator (obtainable from Autrex Industrial, Parow). This incubator was equipped with an electrically powered heating system, regulated by means of a wafer thermostat, and operating through the circulation of warm water through pipes in the roof.

Temperature:

According to Romanoff (1972) temperature during incubation is the single most significant environmental factor in the development of the avian embryo. All deviations from the optimum temperature of incubation greatly affect the rate of growth and development of physiological structures. Since the development of physiological structures, in turn, influences function, the importance for behavioural research of maintaining optimal incubation temperatures cannot be over emphasized.

In this study the ducklings were incubated and hatched at $38 \pm 1^{o}C$, which is regarded as the optimum for still air incubators. All temperature readings were taken level with the upper surface of the eggs. Maximum-minimum thermometers were permanently kept in the incubators to determine the range of variability.

Humidity

For duck a high degree of humidity is required. However, maintaining an optimal level is critical as either too fast or too slow evaporation of water from the egg seriously affects the development of the embryo. (Hurd, 1956).

During the early stages of incubation the moisture pans below the eggs were constantly full and the relative humidity was maintained in the range of 70 - 80%. According to Romanoff (1972) embryonic mortality of ducklings is lowest when the relative humidity is maintained at 80%.

Over the last four days of incubation the relative humidity was increased by 5 - 10%. The aim here was to keep the membranes of the shells soft so that the ducklings could easily break through. As an extra precautionary measure to prevent a loss of moisture through the ventilation holes, the incubator rooms were kept warm and humid.

Ventilation

The embryos were ensured of a fresh supply of air and oxygen entering through the ventilation holes positioned in both the roof and the floor of the incubators. The carbon dioxide given off by the eggs was expelled via the same route.

The ventilation holes in the floor of the still air incubators were kept fully open while the upper holes were kept one third to one half open to prevent excessive loss of warm air and moisture. Fresh, clean and odourless air was provided by air conditioning plants which ensured regular circulation of air without causing draughts.

Turning of eggs

Like other routine procedures involved in incubating duck eggs, variation from the optimum frequency and manner of turning the eggs can have a profound effect on embryonal development and postnatal behaviour.

All eggs were incubated horizontally (i.e. long axes parallel to the ground) and turned 4 times a day by hand by rotating them individually

90° around the long axis. New (1966) reports that turning 90° around the long axis gives a better hatchability than turning through 30°. The eggs were turned alternatively clockwise and anti-clockwise until the 25th day. Thereafter movement of the eggs was kept to a minimum.

Turning was performed with a smooth motion of the hand avoiding irregular movements. Gold (1971) found that irregular, jerky egg turning resulted in a decrease in embryonic weight and later hatch times (measures of growth and maturation) as compared with normal controls.

Candling

All eggs were candled on arrival (12th day) and again on the 21st day. Infertile eggs and those with dead germs were removed from the incubator.

Hatching

The progress of hatching was checked frequently with the time of each hatching being recorded. The ducklings were removed from the incubator when they were dry and "fluffed out", usually within 3 - 4 hours.

On removal from the incubator each duckling was individually housed in a separate cardboard carton with a floor area of 130 sq. cms. Each compartment was labelled with a slip identifying the bird according to its group and hatching. The ducklings were then transferred to the brooder.

Additional control measures

Light:

For the purpose of excluding extraneous variables the eggs were exposed to no more than brief spells of illumination. Turning of the eggs and all observations were performed in a dark room illuminated by a red tungsten bulb (dark-room light) emitting 0.11 lumens/square metre at the level of the eggs. (Light intensity measured with a Salford Illumination Meter, M904).

This precaution was necessitated by the fact that the visual systems of duck embryos one to two days before hatching are morphologically, biochemically and physiologically prepared for their role as receptor of light. (See Oppenheim, 1968 for review of literature). In addition it has been found that duck and chick embryos are behaviourally responsive to light stimulation during the last two days of incubation. Adam & Dimond (1971a) have shown that chicks that receive illumination (8.61 - 9.58 lumens/sq. metre) after the functional development of vision, appear less fearful and show a stronger approach response than chicks that receive stimulation before, or at the time of functional development of vision. In another study Adam & Dimond (1971 b) found that illumination at or after the time of the functional development of vision resulted in earlier hatching of chicks as compared with a control group incubated in darkness.

Sound:

The incubators were housed in separate sound attenuated rooms with air conditioners providing a constant level of background noise of 50 ± 2 db inside the incubators (as measured by a General Radio Sound Level Meter, Type 1551A.

To the extent that the ducklings' vocalizations penetrated the background noise level of the airconditioner, the embryos and hatchlings could hear themselves and their siblings. Apart from this there was no uncontrolled auditory stimulation.

Brooding

Until testing, each duckling was kept in separate ventilated compartments in the brooder. The temperature in the brooder was maintained within the optimum range for the first week, 32.2 - 35°C. (Marais & Joubert, 1964). The brooding room was kept dark at all times except for brief spells of low level illumination when birds were collected for testing. The absence of lighting and the separation of subjects thus prevented birds from seeing the interior of their brooding pens and their siblings. A number of studies have indicated that such precautions are necessary. Bateson (1964 a), for example, has shown that aves can be "imprinted" on their brooding pens. Furthermore a number of studies have demonstrated differences in following and approach responses as a function of social or isolated brooding. Guilton (1959) James (1960), Hess (1964), Graves & Siegal (1968) and Keenan (1972) have found that prior socialization lowers imprinting strength in chicks. In a similar study with Peking ducks Gottlieb & Klopfer (1962) found that ducklings with social experience followed less than ducklings raised in isolation.

Since all testing was done within 24 hours of hatching neither food nor water were supplied until after testing. Young aves have an adequate store from their yolk sac for atleast 48 hours after hatching.

Auditory stimulus tapes

Preparation

In the preparation of the auditory stimulus tapes elements were varied within three parameters.

1. Tone frequency.
2. Repetition rate: the number of bursts of sound per second.
3. Duration of each burst in milliseconds.

All tapes were prepared with an on:off time ratio of 12:6 seconds. Thus various combinations of tone frequency were presented repetitively for specific durations for a period of 12 seconds. This was followed by a period of 6 seconds silence and, in turn, by the next 12 seconds of on-time. A schematic representation of a stimulus tape with a repetition rate of 4/sec. and duration of 50 msec is given as an example in Figure I on page 18.

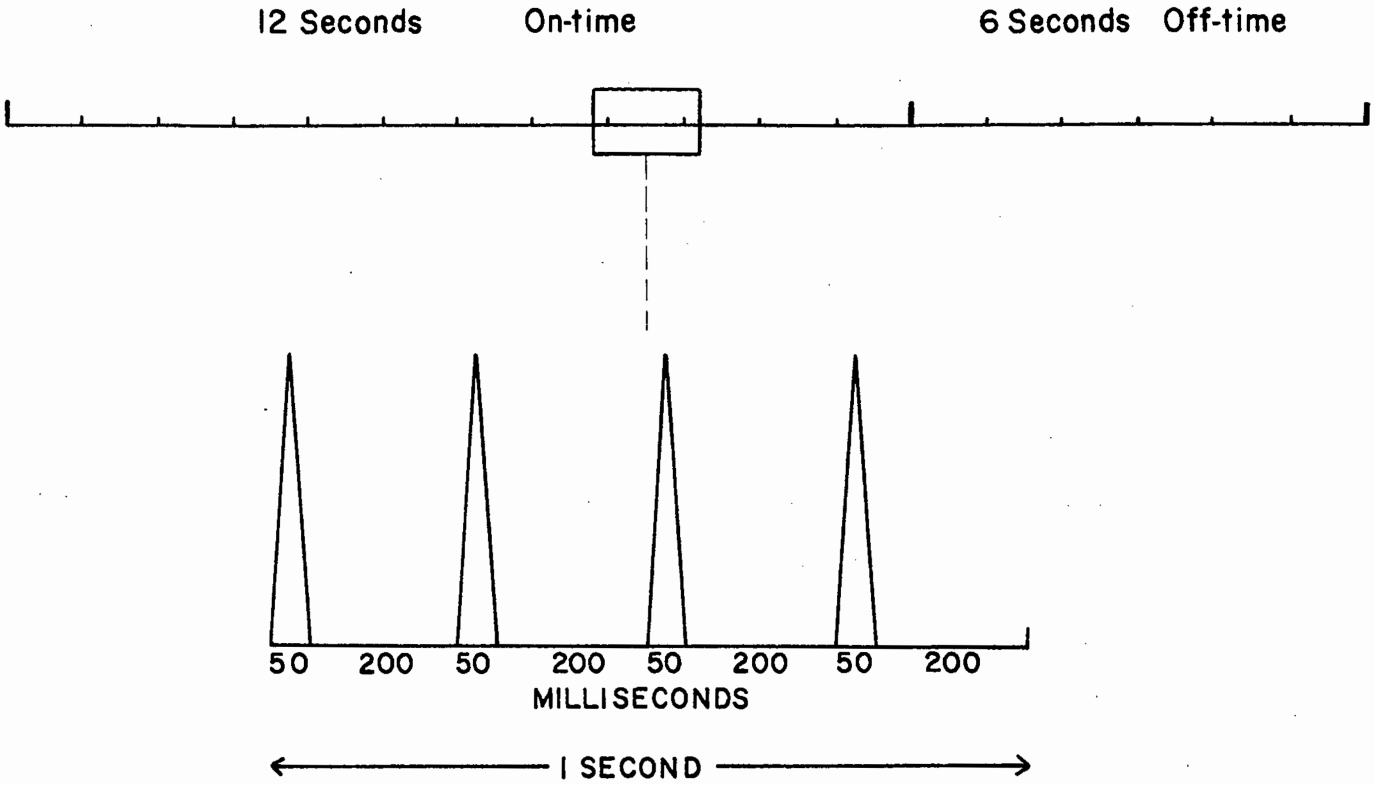


Fig. 1 Diagrammatic representation of section of stimulus tape with repetition rate of 4/second and note duration of 50 milliseconds.

The following apparatus was used in the preparation of auditory stimulus tapes

(i) Hitachi Levelmatic TRQ220 tape recorder with low - noise B.A.S.F. tape.

(ii) Three separate tone generators of the following makes: Advance HI, Krohn-Lite Model 5770, and Heathkit IG 72.

(iii) A tone mixer constructed in the Psychology Department, U.C.T.

(iv) Phillips oscilloscope.

(v) Hewlard Packard 2114B computer.
This was used for the manipulation of repetition rate and on-off times (duration).

The tone signals originating from the tone generators were adjusted to equal levels using the oscilloscope for this purpose. Each input into the tone mixing circuit had its own Mullard silicon planar epitaxial transistor (type BC109) and a gain control. Turning down of this control resulted in a decrease in noise from the input transistor as well as the signal. Current biassing was achieved by returning the single high valve base resistor to the collector, resulting in a measure of negative feed back which was further increased by leaving emittor resistor unbypassed. Overall frequency response was well within the requirements proving to be flat from 20KHz to 10KHz with a gradual drop near the upper end of the spectrum.

A diagram of the tone mixing circuit may be found in Appendix 2.

The computer programme to present various sequences of time intervals was written in "Assembler" language. Using the "Assembler" language compiler an absolute punched tape was produced. Parameters such as the number of tone presentations, time on, and time off, were entered on-line through the front panel switch register of the computer. Interfacing with the tone source employed a "slot-in" 16 bit relay out register and a series of contact closures for the actual switching.

A printed version of the absolute tape is provided in Appendix 3.

Presentation

Prenatal stimulation

In experiments 4 and 5 the experimental group embryos were exposed to controlled prenatal auditory stimulation with "optimal" and "repetition rate altered optimal" calls respectively. Auditory stimulation commenced on the 18th day of incubation and was continued intermittently up until the time of hatching. Stimulation thus commenced well before the 23rd day of incubation when, as Heaton (1971) has shown, duck embryos are first consistently responsive to an optimal artificial call.

Presentation of the auditory stimulus was not continuous but intermittent. Six half hour spells of the tape playback were presented daily. The intensity of auditory stimulation at the level of the eggs was kept constant at 70 db. (General Radio Co. Sound Level meter Type No. 1551A). This intensity level lies in the normal range for ducks.

To a certain extent stimulation in different sensory modalities was temporally correlated in the way it happens in nature. Egg turning went hand in hand with slight decreases in temperature (when the trays were drawn from the incubator for turning) and auditory stimulation (calling) followed turning. The need to consider possible summation of effect of different sensory modalities is discussed in Chapter 5.

Presentation during postnatal testing:

The auditory stimulus intensity was maintained at the same level during both prenatal and postnatal presentations. The decibel level reading, 30 cms from the model, on the floor of the apparatus was kept at 70 db. The importance of keeping the auditory stimulus intensity constant and at an optimal level has been established by Fischer & Gilman (1969). Following in day old chicks was found to relate to sound intensity in an approximately normal manner, with moderate intensities (55 to 75 db) producing substantially more following than either lower or higher intensities.

Further details of postnatal testing are given later in this chapter.

Postnatal test apparatus

Circular "imprinting" apparatus

The circular apparatus was constructed after the design described by Gottlieb (1971). It consisted of a circular table 3,8 metres in circumference with a black floor and an enclosing black wall 33 cms in height.

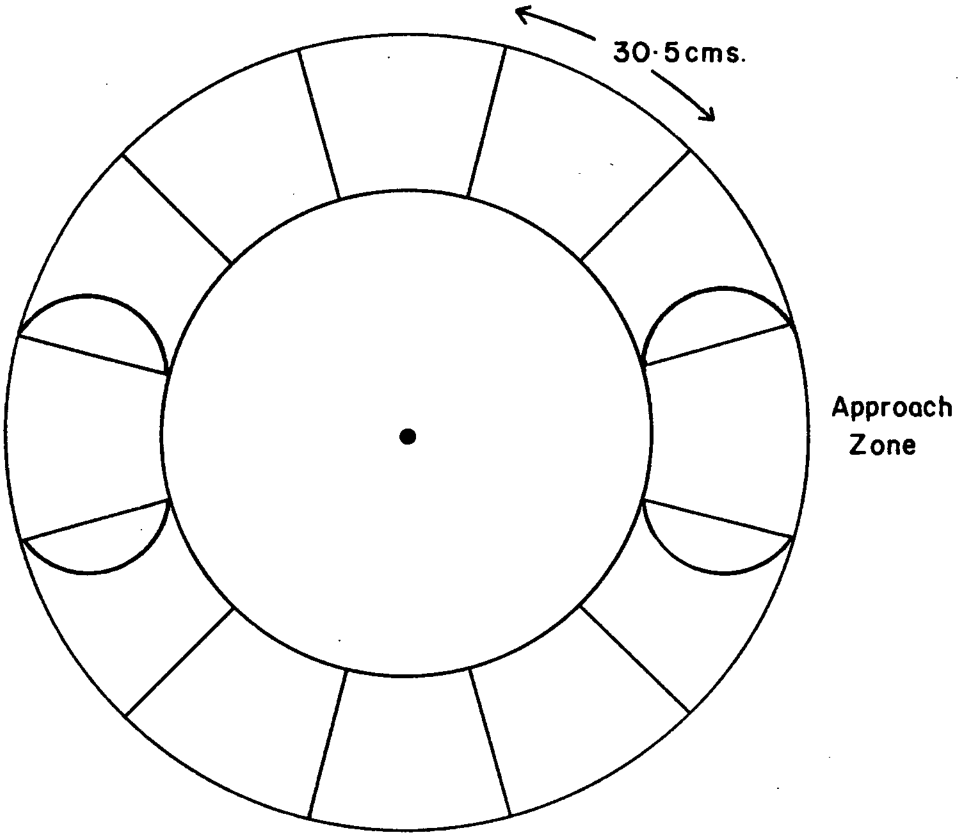


Fig. 2 The plan view of the circular test apparatus.

As shown in Figure 2 radial white strips 1cm wide, were painted at 30,5cm intervals on the floor so that the observer could accurately guage whether the subjects were meeting the criteria for a following response (described below). Partial ellipses denoting a 10cm zone were added so that the ducklings approach response to the stationary object within the zone could be objectively scored (described below). The merits of the open field design over the Ramsay and Hess apparatus are discussed by Gottlieb (1971, p.28).

Stimulus object

The stimulus object (model) used in this series of experiments was suspended from one extremity of a T-shaped pole rising from the centre of the circular apparatus. The model was equipped internally with a 6,5cm permanent magnet speaker with a frequency range suitable for its application. The speaker was mounted on the underside of the object and faced the floor. A lead from the speaker led back to the Hitachi Levelmatic TRQ220 tape recorder via the T-shaped pole and the underside of the apparatus.

The object was suspended 1,5cms above the floor of the apparatus and followed a 3,8 metre path around the apparatus. This was driven by an A.C. constant speed motor (1 revolution per minute) which, in turn, was operated by a timer with an on-time duration of 20 seconds and a time out of 5 seconds. The model thus completed one revolution in 75 seconds (20 sec. run - 5 sec. pause - 20 sec. run - 5 sec. pause - 20 sec. run - 5 sec. pause).

Imprinting studies generally employ an inanimate object as the imprinting stimulus so that "behaviour" of the surrogate parent may be controlled. The types of objects and stimuli used have ranged from electric trains (Fabricius & Boyd, 1954), footballs (Ramsay, 1951), green cubes and cylinders (Jaynes, 1956, 1957), light flicker (James, 1959) to red cubes (Fischer, 1966).

The model used in the present study consisted of a white polystyrene oval object with maximum dimensions: 15cms x 12cms x 11cms. It was designed to correspond to the size of the adult duck of its species. Schulman, Hale & Graves (1970) have demonstrated that models corresponding in size to the biologically appropriate object are more effective in eliciting initial social responses than other sizes of models. Apart from this no attempts were made to invest the model with the visual characteristics of the adult duck. Since the primary aim of this study was to investigate the effect of auditory stimuli on the elicitation of following and approach responses, a model which would, at least, not inhibit responses, was considered sufficient.

Although brightly coloured models have been shown to elicit stronger following responses than plain models on second exposure, on initial testing both models prove equally effective (Klopfer & Hailman, 1964). Since all ducklings were tested only once a plain white colour was used in the present study.

Testing procedure:

The postnatal tests were performed in a sound attenuated room with a window unit airconditioner providing a constant ambient noise level of 50 ± 2 db.

The temperature in the testing room was maintained in the region of 31 ± 1°C. Maintenance of a constant temperature is an important factor to consider in research of this kind. Variations in reported research findings and differences in test scores within the same study, may be traced to variations in temperature in the testing room. Fischer (1970) found neglibible following by chicks tested at a warmer temperature or the same temperature as the one at which they had been brooded. Following was very substantial however, if chicks were tested at a temperature colder than the one to which they had been adapted. Consequently subjects in the present study were tested at the same temperature of 31 ± 1°C. Thus all subjects were tested in room which was 3 - 4°C colder than their brooding compartments.

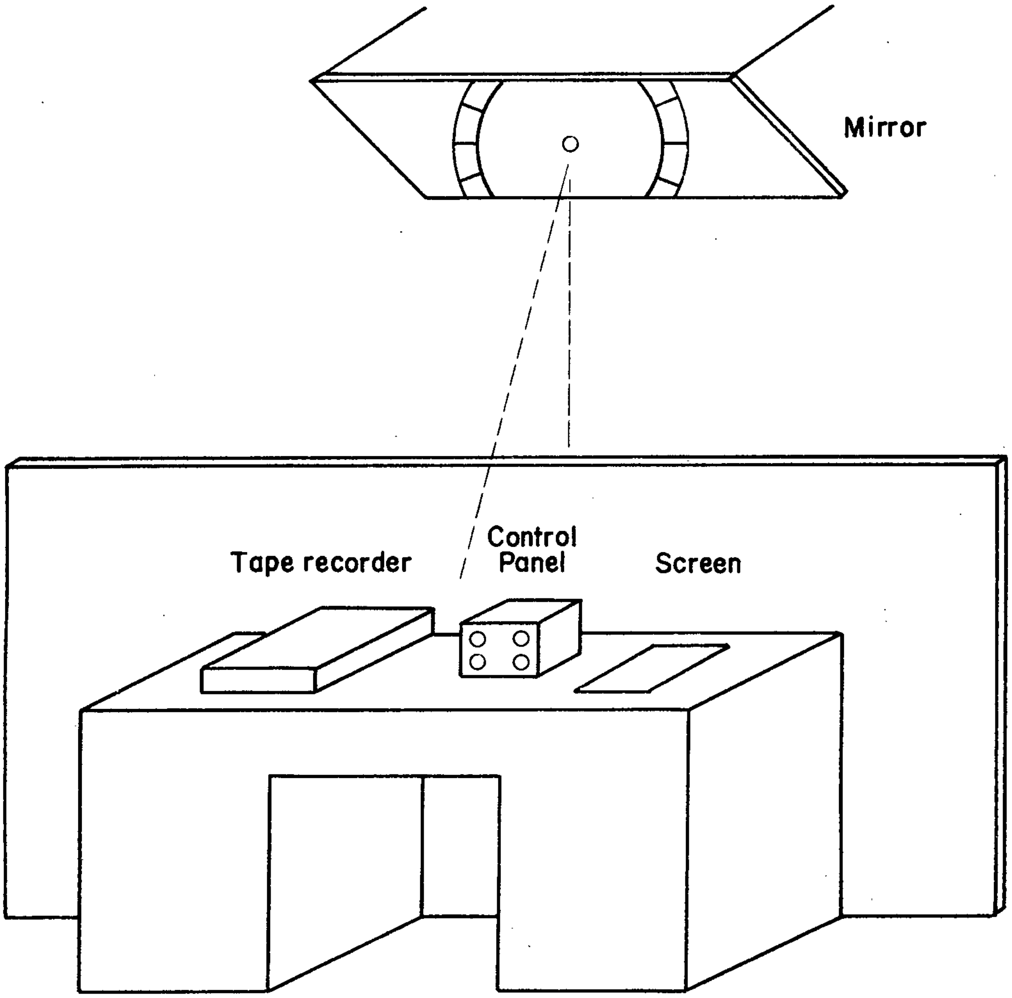


Fig. 3 The arrangement of the experimental apparatus in the testing room.

As shown in Figure 3 the circular apparatus was separated from the observer by a 1,5 metre high screen and observed through a mirror suspended 2,5 metres above the test apparatus. The observation desk was equipped with (a) a Hitachi Levelmatic TRQ220 tape recorder (b) a control panel for operation of the moving object (c) a light switch for the lamp illuminating the circular apparatus (d) and stopwatches for recording: total time, latency of response, and duration of response.

The circular apparatus was illuminated by an incandescent lamp, at a height of 1,4 metres above the apparatus, providing 0,96 lumens/square meter at floor level of the apparatus.

The ducklings were transferred from the dark brooder to the testing apparatus in a 10cm cube box with a hinged lid. Before releasing the duckling on to the apparatus the lights were extinguished. At no stage during the transfer was the bird exposed to light or visual contact with the experimenter. In a study of the influence of tactile and visual stimulation on approach responses in chicks, Graves & Siegal (1968), found that handling in darkness had no effect on the number of responses, while handling in the light decreased the number of responses. It was concluded that tactile plus visual stimulation inhibited the tendency of chicks to respond and approach an imprinting object.

The duckling was placed at a routine starting point on the apparatus and on returning to the observation desk the experimenter triggered the light switch. The 5 minute pre-test period commenced immediately, to be followed by a 12 minute following test and 5 minute approach test.

Postnatal behavioural tests

The two main tests used to measure the strength of attraction to auditory stimuli were the following and approach response tests. In each test the incidence, latency and duration of response were recorded.

It was initially planned, however, to supplement and compare these tests with others used and described by Beer (1970a) and Schulman, Hale & Graves (1970). A score sheet was drawn up in which each test period was divided into 15 second intervals. In each 15 second interval subjects would be scored with regard to (a) orientation: either towards or away from the model (b) posture: sitting and crouching, standing or walking. (c) defaecation (d) calls: pleasure, distress or silence (e) position change: stationary, approaching, or withdrawal. (f) contact with the object. See Appendix 4.

In practice, however, it proved impossible for a single scorer to record all these behaviours simultaneously. A solution to this problem would have been to record the behaviour in each test on television video tape and to score the responses at leisure. Unfortunately the cost of obtaining sufficient tapes for this purpose prevented this solution from being implemented. An alternative solution to this problem in the future would be to construct a response console somewhat similar to a laboratory counter so that the experimenter could record responses without moving his eyes from the viewing mirror.

Although a strictly quantitative analysis of the vocalizations of all subjects was not done, samples of characteristic call patterns were recorded and analysed. The results and implications of these analyses are discussed in Chapter 5.

Before defining the behavioural tests the age of subjects at testing requires attention. Many writers (Bateson, 1964, Jaynes, 1956, 1957, Moltz, 1960) have objected to the term "critical period" on the grounds that it is misleading, implying an "all-or-nothing" effect. It is recognised, however, that there are "sensitive periods" during which time the strongest responses are elicited. It was thus considered expedient to test all birds at approximately the same age (20 ± 2 hrs post-hatching) and prevent possible variations due to age differences.

<u>Pre-test period</u>:

Before being tested for following and approach responses to the model emitting the auditory stimuli or the silent model, each subject was given a 5 minute period in which to acclimatize to the strange environment and the sudden light. In a previous study done by the author it was observed that birds seemed very unsteady on their feet, some more than others. This unsteadiness disappeared with time and practice. It was thus felt that subjects should be allowed to perfect their walking abilities before being tested.

It was originally planned to use the battery of test measures described above to ascertain the basic activity rate of the subjects before testing. A comparison between pre-test activity and activity in the testing situation might help to explain the finding of considerable differences in responses by different subjects in the same situation. Differences in test responses might be due to physiological differences in subjects.

For the reasons mentioned above, full pre-test activity could unfortunately not be measured and compared with activity during testing. The pre-test approach response did not prove to be a reliable index of pretest activity; consequently no pretest scores were compared with test scores in this study.

Following test:

In this test, lasting 12 minutes the following response to the moving object, either silent or emitting the appropriate auditory stimulus, was measured. After the 5 min. pretest period the object began to move. Except in the case when the model was silent the appropriate recording was started to coincide with the start of the objects' moving.

The painted sectors on the circular apparatus permit the observer to objectively determine whether the subject is within 30,5cms of the rear or 10cms to the side of the moving object. A following score (time in seconds) was earned only when the subject was within 30,5cms of the rear or 10cms to the side of the moving object with its head oriented towards and its body moving in the same direction as the object.

Fig. 4 A Peking X Aylesbury duckling fulfilling the criteria of a following response.

A duckling fulfilling the criteria of a following response is shown in Figure 4. Scoring began only after the duckling had taken three steps under these conditions. If the bird's entire body was in front of the object no following time was awarded. If the duckling was fulfilling the criteria of following prior to the 5 second pause in the objects' motion, it continued to accumulate time provided it stayed within 10 cms of the object during the pause.

Both the latency and duration of the following response was recorded. The time taken from the beginning of the test until the duckling first fulfilled the criteria of a following response was recorded as "Latency of following" (in seconds). The total time (in seconds) spent following the object was recorded as "Duration of following". The time spent following was not necessarily continuous. In most cases the duration of following represents an accumulated score.

Approach test

On completion of the following test, a 5 minute test measuring the approach response to the stationary object, either silent or emitting the appropriate call, was performed.

The object was moved into the centre of the ellipsical zone, the lights were extinguished and the subject was placed at least 60 cms from the object. The lights, tape recorder and stop watches were then activated. When the duckling entered the 10 cm approach zone it began accumulating a score. A duckling fulfilling the criteria of an approach response is shown in Figure 5.

Fig. 5 A Peking X Aylesbury duckling fulfilling the criteria of an approach response.

Timing was stopped when the subject left the zone and re-started on re-entry. The total time, in seconds, spent within the approach zone, was recorded as "Duration of Approach". The time taken from the start of the test to the ducklings first entry into the approach zone was recorded as "Latency of approach" (in seconds).

Rationale for statistical procedures and tabular presentation

As far as possible non parametric techniques of hypothesis testing were used. The indications for this choice of statistical procedure were the usual ones. That is, it could not be assumed that scores were drawn from a normally distributed population and, secondly, parametric analyses of variance could not be used on non transformed data because of the extreme heterogeneity of variance of the sub groups. In experiment 5 where no non parametric analogue of the two way analysis of variance for 4 subgroups is available, scores were transformed and parametric techniques were employed.

In experiments 1 to 3 the latency and duration measures of groups subjected to calls were evaluated statistically by the Kruskal-Wallis one way analysis of variance applying the correction for ties (Siegal, 1956). Where significant differences were indicated the Kruskal-Wallis was followed by pairwise comparisons utilizing the Mann Whitney U test (Siegal, 1956). For the purpose of comparing all the auditory stimulus groups with the silent control a non-parametric analogue of Dunnett's procedure developed by Steel (1959) was employed.

In experiment 4 where only two groups were compared, the Mann Whitney U test was used to evaluate the latency and duration measures. All p-values reported are for two tailed tests.

The nature of experiment 5 indicated the need for a two way classification analysis of variance. Since a non parametric technique for this purpose is not available $\sqrt{X + .5}$ transformation was used for transforming the scores and a parametric two way analysis of variance technique was utilized. As Kirk (1968) points out, in most behavioural situations, inferences based on root transformations are just as meaningful as inferences based on untransformed scores.

Hartley's F max. test of homogeneity of variance (Winer, 1962) was employed with the transformed scores before carrying out the two-way classification analysis of variance. Following the F-test pairwise comparisons among means were performed utilizing Turkey's HSD (honestly significant difference) test. (Kirk, 1968).

In all experiments the chi square test was used to determine the reliability of differences in the proportion (incidence) of ducklings which approached or followed in each condition.

An important departure from procedures adopted by Gottlieb (1971) and Heaton (1971), concerns the inclusion of non responders in statistical analyses. Without indicating why they do so, both Gottlieb and Heaton only considered those birds that had accumulated a following or an approach score in computing mean latency and duration measures and in comparisons of these measures i.e. non responders were excluded from these analyses.

It is possible that Gottlieb and Heaton excluded non-responders because of the problem of assigning non-responders a latency score. If there is no response, it follows that there can, strictly speaking, be no latency measure at all. For the purposes of present statistical analysis, however, it was considered admissable and, in fact, desirable to allot non-responders the maximum score of each test i.e. 720 seconds for latency of following and 300 seconds for latency of approach. In the case of both following and approach duration measures all non responders were given a score of 0 seconds.

This procedure was necessitated by the logical requirement to consider all the members of a group when comparing the responsiveness of the groups to the various stimulus conditions. It is logically necessary to compare the effects of experiment treatments on whole, intact groups not just on responders in each group. If a group of birds are exposed to a particular experimental treatment then the results of this treatment should be apparent in all the birds in a group to a greater or lesser extent. Exclusion of non responders would be exclusion of subjects in which the effects of experimental treatment occured to a lesser extent. By excluding non responders from calculations one obtains a false picture of the effect of the experimental treatment on the group of subjects as a whole. Thus, in the present study, statistical analyses utilized the scores of all subjects, both responders and non responders.

There is, however, a disadvantage in including non-responders when computing mean latency and mean duration scores. Means computed in this way do not reflect the actual strength of response of those subjects that do respond. For example, a group which has a low incidence of response will have a very high mean latency because of the large numbers of subjects with maximum scores and a very low mean duration because the majority of subjects have 0 second score.

It was considered appropriate to provide additional tables of means and standard deviations computed after non-responders had been excluded. This allows the reader to guage the actual strength and variability of response of those that responded and at the same time to compare results with other studies in which non-responders have been excluded from computations.

Chapter 3

AUDITORY STIMULUS PREFERENCES IN BIRDS : THE ANALYSIS OF THE PHYSICAL PROPERTIES OF PREFERRED SOUNDS.

In this chapter earlier attempts by investigators to delineate and specify critical acoustic features of effective calls will be examined. This will be followed by a description of a series of experiment designed with the aim of specifying the critical features in a call attractive to neonatal Peking X Aylesbury ducklings.

One of the earliest studies suggesting that parameters such as tone frequency, note duration and repetition rate are related to responsiveness to calls was carried out by Collias & Collias (1956). They found that Mallard ducklings would, on the day of hatching, more readily approach low pitched (below 800Hz), brief notes than high pitched, long notes. Using the popular low pitched short notes they then varied the rate of repetition and found that the ducklings more readily approached high rates (3/sec.) rather than low rates (1/sec., 1 every 3 sec.) of artificial sound repetition.

Until recently, however, no systematic analyses of the physical characteristics of attractive auditory stimuli were carried. Since the beginning of the present decade two workers Heaton (1971) and Fischer (1972), have turned their attention to this field of investigation.

Heaton (1971) has raised the question whether essential information for the selective response of parentally naive Peking ducklings to the conspecific maternal call is encoded in the maternal call. An acoustic analysis of bird calls revealed that the call of a given species tended to have a distinctive and consistent repetition rate and usually one or two fundamental overriding frequencies. This suggested to Heaton that discrimination is due to one or both of these parameters.

The idea that repetition rate is a critical parameter, which in part accounts for the intrinsic appeal of the maternal call, was confirmed by Heaton by measuring the responsiveness of birds to the maternal call and to calls in which the repetition rate had been altered from the normal. She found that a general attractive rate range existed. The best rates were those between 3 and 4/sec and 7 and 8/sec. with an optimum at 4/sec, at 24 hours posthatching. Outside this range responsiveness to rate altered calls declined radically.

That rate alone is not sufficient to account for discrimination was indicated by the ability of ducklings to distinguish between the duckling (sibling) brooding call and the maternal call. Both calls have a repetition rate of 4/sec. but different fundamental frequencies. This pointed to the possibility that frequency cues might also be important in the selective responsiveness of naive Peking ducklings. An investigation by Heaton revealed that there were three critical frequencies in the Peking maternal: 780Hz, 1125Hz and a harmonic at 2250Hz. When these two fundamental frequencies were combined with the harmonic at 2250Hz and presented at 4/sec. they proved a highly effective synthetic call in inducing approach responses by naive Peking ducklings. Heaton records that the synthetic call proved as attractive to the Peking ducklings as the Peking maternal call in a simultaneous auditory choice test.

An important difference between Heaton's study with Pekings and a similar study conducted by Fischer (1972) with domestic chicks, is the difference in success each researcher had in inducing responses with single pure tones. Whereas Heaton found that single pure tones at 780Hz and 1125Hz were ineffective in eliciting approach responses, Fischer reports that substantial following was elicited by pure tone frequencies in the range between 375Hz and 625Hz. These conflicting findings are possibly due to species differences. It is possible that the critical element in the chicken domestic call is a single low frequency cue and not a combination of frequencies. If this is indeed the case it is further indication of the need to be wary of generalizations across species.

Like Heaton, Fischer found that an attractive repetition rate range exists with optimal following at 2/sec. and 4/sec. These rates correspond to the rates of the natural broody hen cluck (2/sec.) and the food call. Rates as slow as 1 tone every 4 seconds and as rapid as 16 tones/sec. were equally ineffective.

It is interesting to observe that the preference for repetition rates in the 3 - 4/sec. range is found in a number of different birds as well as in different sensory modalities. A number of workers (e.g. Simner, 1971) have reported that chicks react optimally to visual light flicker presented at 4/second. In a fascinating series of experiments Vince (1966, 1968, 1970, 1972) has demonstrated that hatching is accelerated in Japanese quail by stimulation with sound or vibration at a rate of 3/sec. Future research might reveal that the ubiquity of this sensitivity to rates at ± 4/sec. is due to common genetic elements or even prenatal ontogenetic factors. Simner (1966) suggests that the embryonic heart rate of 3 - 4 beats/sec. in the chick might be instrumental in establishing a rate preference of 3 - 4/sec.

In addition to delineating certain critical elements in the repetition rate and frequency parameters, Fischer examined the effects of varying tone durations on the following response to a call with the optimal frequency and optimal repetition rate. She found that only very short tones, of less than 100 msec. duration, were effective in eliciting following, with tones of 24 msec. and shorter being most effective. The results of further experiments, in which frequency, rate and duration were varied simultaneously, led Fischer to conclude that frequency is the least critical parameter while tone duration may be more important than repetition rate in eliciting following behaviour in domestic chickens. The importance attributed to tone duration by Fischer pointed to the need to ascertain whether this parameter, like frequency and repetition rate is critical in eliciting approach and following responses in ducklings.

To summarize: Heaton (1971) and Fischer (1972) have isolated critical elements in a number of parameters and have used this information in synthesizing artificial calls which are highly effective in eliciting approach and following responses in parentally naive Peking ducklings and domestic chickens.

The object of the first three experiments in this study was to perform a similar analysis of the critical elements of a call for which parentally naive Peking X Aylesbury ducklings show the greatest preference. The aim of these experiments was partly to replicate the research done by Heaton (1971) and Fischer (1972) with a different species and partly to produce an effective synthetic call, the elements of which could be manipulated in subsequent experiments.

Experiment 1: Specification of the Critical Frequencies in an Artificial Call Attractive to Peking X Aylesbury Ducklings.

The aim of the present experiment was to delineate the critical frequency or frequencies in an attractive synthetic call.

The problem of whether to use single pure tones, as Fischer (1972) had done, or to follow Heaton (1971) and use complex sounds, was of immediate concern. Since the bird used in the present study was of a different species to that used by previous researchers a satisfactory decision could only be made after observing the responsiveness of subjects to both types of stimulus. Consequently a pilot study was carried out and the results indicated that Peking X Aylesbury ducklings are more responsive to complex auditory stimuli than to single pure tones. Since subjects used in this study are closely related to subjects used in Heaton's research this finding was not unexpected. It must be pointed out, however, that this find does not provide evidence negating Fischer's observation that single pure tones at optimal frequencies are effective in eliciting following responses in domestic chicks.

The probable limiting range of attractive frequencies were indicated from reports on the acoustic characteristics of maternal calls of related species. It was unfortunately impossible for the experimenter to obtain a recording of the maternal call of the Peking X Aylesbury duck. In spite of considerable effort, attempts to locate birds of this species together with their brood failed. All incubation and hatching in the Western Cape is carried out in commercial incubators.

A frequency analysis of the Peking maternal call carried out by Heaton (1971) revealed a frequency range of 50Hz to 12KHz. This call, however, has several dominant frequencies, those with the greatest relative amplitude lying at 780, 1125 and 1600Hz. There is, as well, considerable energy around 2250Hz probably constituting a harmonic generated by the 1125Hz fundamental. Of these fundamental frequencies

Heaton found the 780, 1125 and 2250Hz frequencies to be the critical ones.

Using the procedure described in Chapter 2, four combinations of frequencies were prepared. These combinations contained frequencies lower than, the same as, and higher than those found to be critical by Heaton. The frequency combinations used in this experiment were:

(i) 500, 800, and 1600 Hz (complex call 1).
(ii) 780, 1125, and 2250 Hz (" " 2).
(iii) 1000, 1400, and 2800 Hz (" " 3).
(iv) 1300, 1600, and 3200 Hz (" " 4).

The choice of repetition rate and duration to be used while specifying critical frequencies was, by necessity, arbitrary. However the probable range of attractive repetition rates and duration could be predicted from published data. The repetition rate of 4/sec. used while specifying critical frequencies was found to be the optimal rate by both Heaton (1971) and Fischer (1972). It is also the natural rate of the Peking maternal call.

Since note duration was not investigated by Heaton no information about ducklings was available. However it seemed most likely that short durations would be more attractive than long ones. It was reasoned that, at the rate of 4/sec., the longer the duration the less repetitive the stimulus would be perceived. That is, as the duration approaches 250 msec the stimulus would more closely resemble a continuous sound than a repetitive one. The choice of 25msec duration was based on Fischer's finding that this was the optimal duration for chickens.

The aim of experiment 1 was to determine whether the responsiveness of Peking X Aylesbury ducklings to calls with various frequency combinations would differ significantly (5% level of confidence), responsiveness being measured in terms of the incidence, latency and duration of following and approach responses.

Method:

The subjects for Experiment 1 were 50 Peking X Aylesbury ducklings incubated and hatched in a sound attenuated room. (See chapter 2). Each subject was randomly assigned to one of five groups and tested for responsiveness to one of five stimulus conditions - 4 complex calls and a silent model. In this and the following two experiments control groups were tested for responsivness to silent models. The purpose of these controls was to ascertain to what extent ducklings respond, without any form of auditory stimulation, to a moving or stationary object.

At 20 ± 2 hrs. posthatching each duckling was individually subjected to a 12 minute following test and a 5 minute approach test with one of the stimulus conditions. In all cases the following test was preceded by a 5 minute pre-test period of acclimatization during which time the tendency for the duckling to approach the stationary and silent object was recorded.

Responsiveness to each stimulus condition was measured in terms of the incidence, latency (in seconds) and duration (in seconds) of following and approach responses. The latency and duration measures of groups exposed to calls were evaluated statistically by the Kruskal-Wallis one way analysis of variance with correction for ties (Siegal, 1956). Where significant differences were obtained the analysis of variance was followed by pairwise comparisons utilizing the Mann Whitney U test (Siegal, 1956). The latency and duration measures of the four auditory stimulus groups were compared with the latency and duration measures of the silent control group using Steel's (1959) procedure developed for this purpose. Comparisons of the incidence of approach and following responses utilized the Chi square test. All statistical analyses were performed using scores of both responders and non responders. The rationale for, and discussion of these statistical procedures will be found in Chapter 2.

Results

The mean number of seconds taken to respond (latency) and the mean duration (in seconds) of following and approaches responses to the silent model or to the model emitting one of the complex calls is shown in Table 1 and Figs. 6 - 9.

It will be observed that mean latency and mean duration scores are inversely related. It was an almost invariable finding in this research that groups with the shortest latency scores had the longest duration scores and vice versa.

Since the auditory stimulus variable was too complex to be represented on a single axis it was not possible to illustrate the relation between tone frequency and responses. Consequently mean scores are compared by means of histograms in this experiment.

In Table 1 the upper portion contains mean scores and standard deviations of all subjects in each group while the lower portion represents scores of responders only. The reasons for computing two sets of means are discussed in chapter 2.

That the general trend is the same when means are computed in different ways is shown in Figs. 6 - 9. Indeed, if line graphs had been drawn, essentially the same shaped curves would have been obtained with both sets of data.

As shown in Table 1 and Figs. 6 - 9 Complex call 1 elicited the strongest mean responses (shortest latency, longest duration) with regard to both mean latency and mean duration of approach and following responses. A single classification analysis of variance revealed, however, that the difference in the means shown in Table 1 did not reach statistical significance except in the case of following duration (Table 2). Individual comparisons revealed further that the difference in following duration

TABLE 1

Experiment 1: Response Measures of Peking X Aylesbury Ducklings in Following and Approach Tests to Four Complex Calls and a Silent Model.

Test Call	N	Following Response					Approach Response				
		Incidence %	Latency, Sec Mean	Latency, Sec S.D.	Duration, Sec Mean	Duration, Sec S.D.	Incidence %	Latency, Sec Mean	Latency, Sec S.D.	Duration, Sec. Mean	Duration, Sec. S.D.
Response Measures of All Subjects											
Complex call 1	10	80	264.0	259.6	118.9	91.4	80	94.6	113.9	104.0	89.3
Complex call 2	10	60	453.8	246.6	29.9	32.7	60	200.2	103.4	50.2	56.9
Complex call 3	10	50	521.2	227.4	15.7	24.9	70	177.4	102.6	51.6	60.7
Complex call 4	10	60	428.6	280.9	46.5	60.3	60	181.8	115.9	51.4	71.7
Silent Model	10	20	652.2	143.9	2.4	5.1	10	292.3	24.3	0.7	2.2
Response Measures of Responders Only											
Complex call 1	10	80	150.0	111.4	148.6	75.5	80	43.2	40.3	130.0	80.0
Complex call 2	10	60	276.3	122.5	48.8	27.8	60	133.7	77.1	83.7	49.9
Complex call 3	10	50	322.4	132.6	31.4	27.8	70	124.9	71.1	73.7	60.2
Complex call 4	10	60	234.3	169.9	77.5	60.4	60	103.0	74.5	85.67	75.6
Silent Model	10	20	381.0	49.5	12.0	1.4	10	223(a)	-	7.0(a)	-

Notes (a) One Responder only.

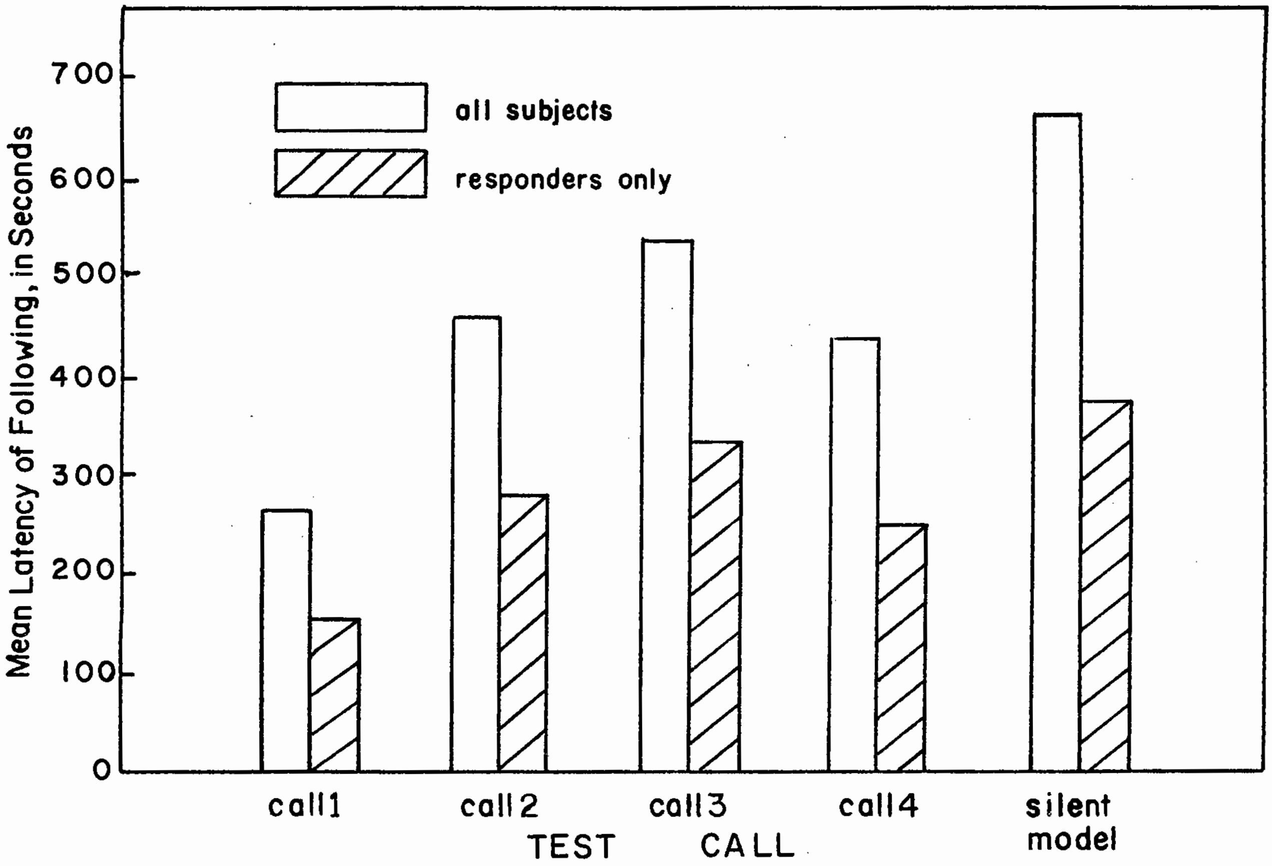


Fig. 6 Mean latency of following of ducklings tested with four complex and a silent model.

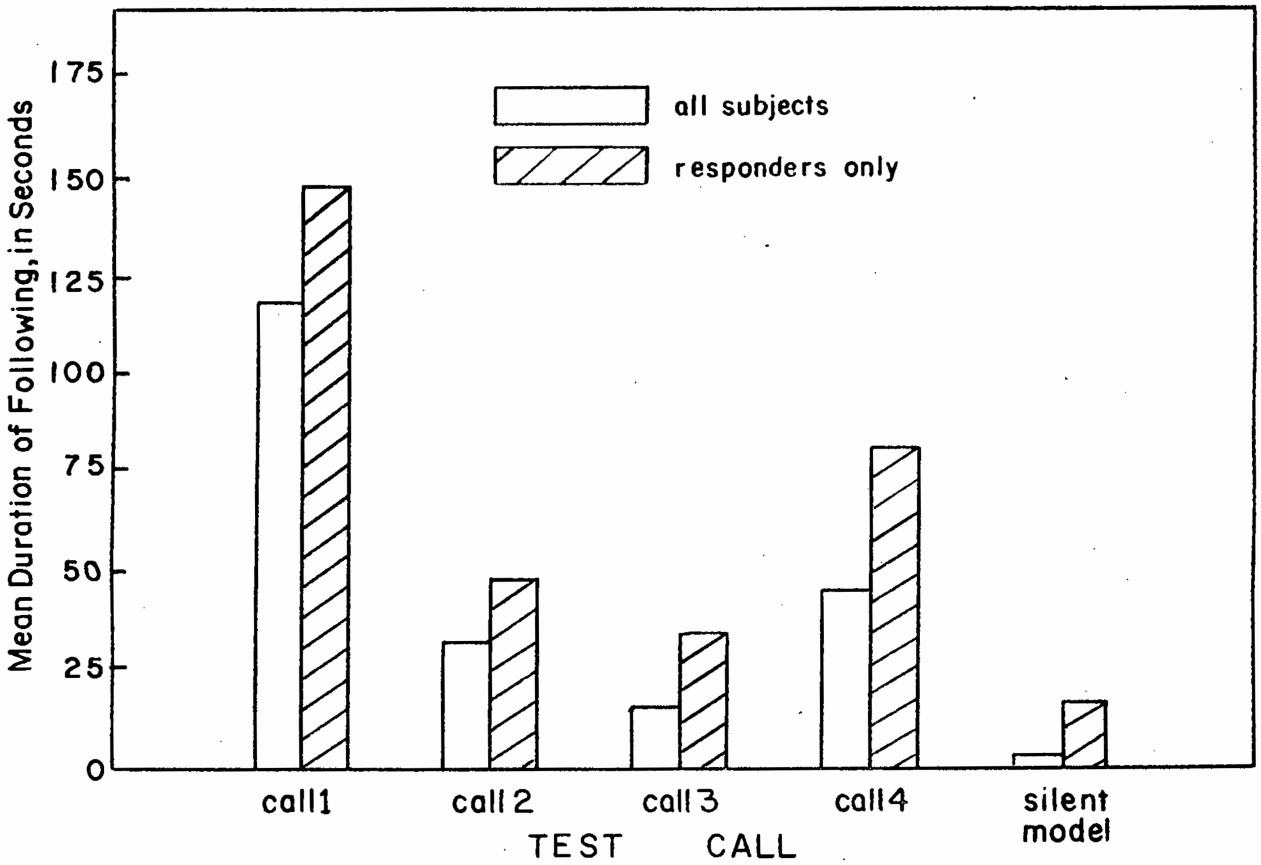


Fig. 7 Mean duration of following of ducklings tested with four complex calls and a silent model.

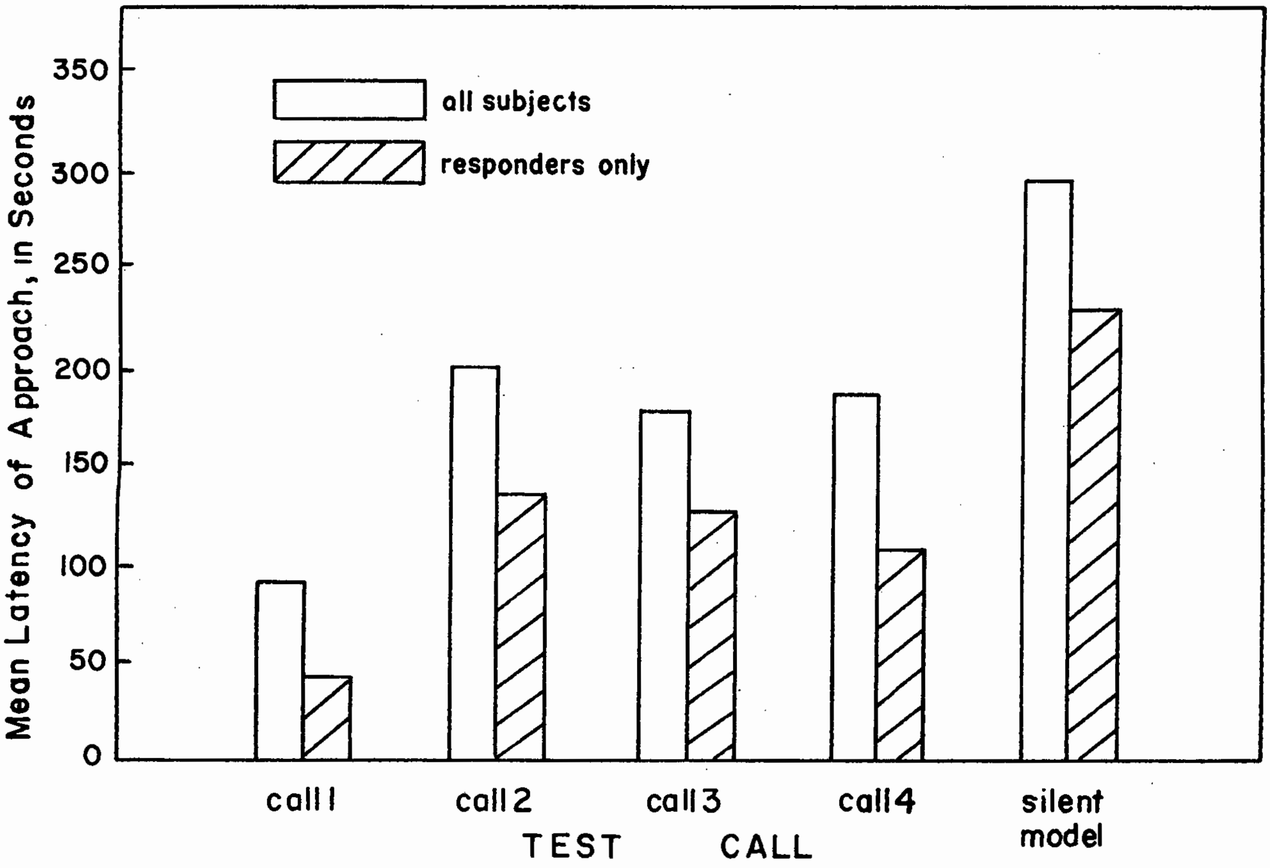


Fig. 8 Mean latency of approach of ducklings tested with four complex calls and a silent model.

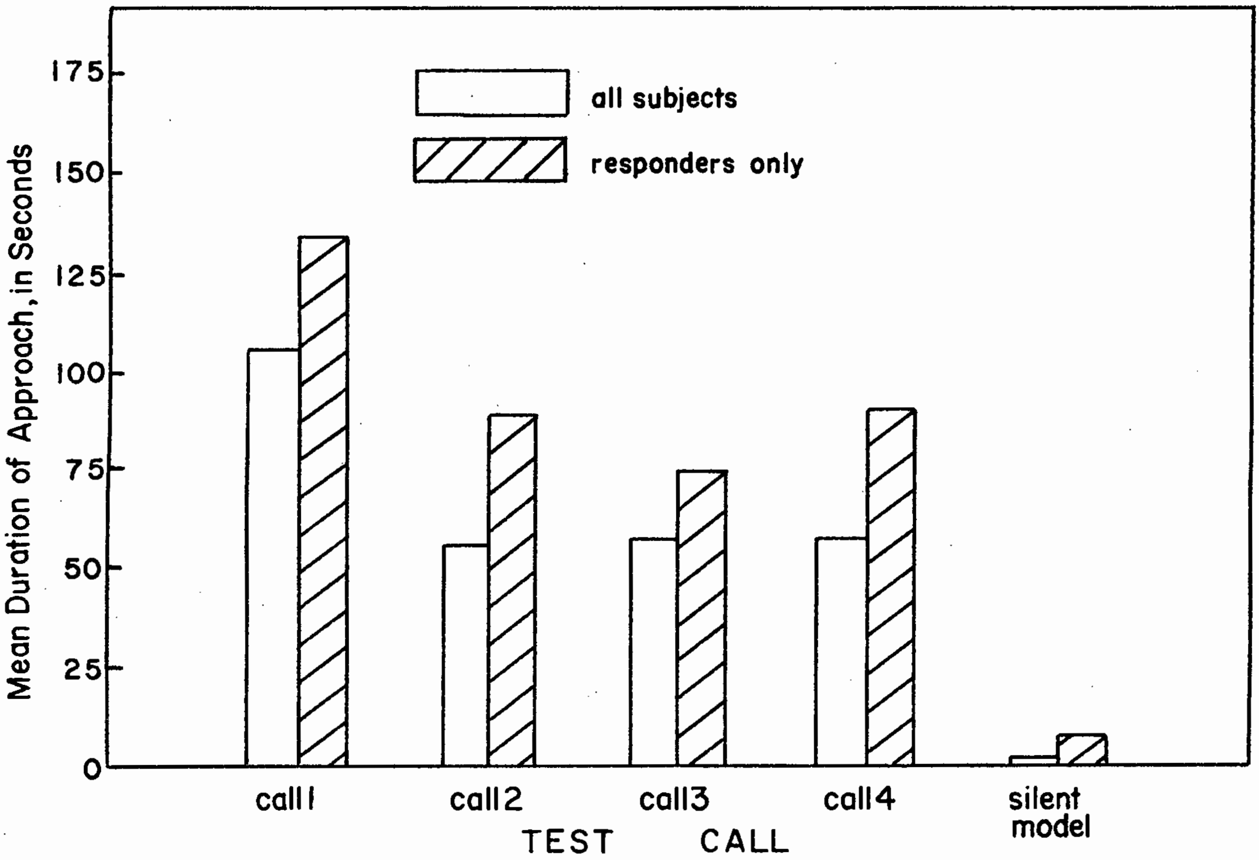


Fig. 9 Mean duration of approach of ducklings tested with four complex calls and a silent model.

STATISTICAL ANALYSES : EXPERIMENT 1

TABLE 2

Summary of Kruskal-Wallis One Way Analysis of Variance By Ranks for Responses of Subjects to One of Four Complex Calls.

Response Measure	df	H	p - value
Following Latency	3	6.18	NS
Following Duration	3	9.95	$<.02$
Approach Latency	3	5.97	NS
Approach Duration	3	3.35	NS

Note: NS = non significant statistical difference $(p > .05)$

TABLE 3

Summary of Mann-Whitney U Tests on Differences Between Pairs of Complex Call Treatment Groups: Experiment 1

Following Duration

	1 ($\bar{x}$ = 118.9)	2 ($\bar{x}$ = 29.3)	3 ($\bar{x}$ = 15.7)	4 ($\bar{x}$ = 46.5
1	-			
2	u = 17.5 $p < .02$	-		
3	u = 16 $p < .02$	u = 39 ns	-	
4	u = 24 ns	u = 45 ns	u = 35 ns	-

Note: 1. Key: 1 = Group responding to complex call 1.
2 = " " " " " 2.
3 = " " " " " 3.
4 = " " " " " 4.
2. In all cases N_1, N_2 = 10.
3. NS = non significant statistical difference.
4. p-values are for two-tailed tests.

TABLE 4

Summary of Comparisons of Complex Call Treatment Groups
With the Control (Steel) : Experiment 1

Response Measure	Treatment Groups							
	Call 1		Call 2		Call 3		Call 4	
	min T	p	min T	p	min T	p	min T	p
Following Latency	67	<.05	89	ns	81	ns	82	ns
Following Duration	67	<.05	85	ns	81	ns	82	ns
Approach Latency	66	<.05	78	ns	71.5	<.05	77	ns
Approach Duration	66	<.05	77	ns	71.5	<.05	77	ns

Note: ns = non significant statistical difference (two tailed $p > .05$)

p-values are for two tailed tests.

scores of groups tested with complex calls 1 and 4 was not statistically significant. The group of subjects tested with complex call 1 did, however, display reliably more following than groups tested with complex calls 2 and 3 (Table 3). Group 1 was also the only group to differ reliably and consistently with the silent control group (Table 4).

An analysis of the proportions of subjects which followed the model emitting one of the four complex calls of the silent model revealed no statistical difference ($x^2 = 7.73$, df = 4, $p > .05$). The incidence of approach responses to the silent model, however, was significantly lower than the proportions of birds that approached the auditory conditions. ($x^2 = 8.5$, df = 1, $p < .01$).

Although it is impossible to describe all the behaviour patterns observed in this experiment it is nevertheless possible to give a general description of the behaviour patterns of strong and weak responders.

The behaviour of those birds which responded most quickly and for the longest period was similar in many ways. Shortly after the model started moving and the playing of an attractive artificial call commenced the high pitched high intensity distress calling, so frequent during the pretest period, was replaced largely by lower pitched, lower intensity "churping" sounds. During testing distress calling occurred most during the short periods of silence spaced every 12 seconds on the tape. A more detailed description of vocalization patterns is given in Chapter 5. At the beginning of the following test the ducklings tended to remain relatively still but with their heads oriented towards the source of the sound as it moved around the apparatus. Within a few minutes the ducklings would start following, most frequently to the rear, but sometimes to the side of the model. In both instances their heads would be oriented towards the source of sound.

An interesting observation, one not made by the author in earlier research with chicks, was the tendency for many of the ducklings to attempt to mount the model. And indeed, some succeeded in jumping the ± 12 cms to land on top of the model. Although many fell off immediately others managed to maintain their balance for a few seconds. Failure to succeed in staying on top was no deterrent. Gottlieb (1974 pers comm.) reports that he has observed similar behaviour patterns in other species of duck.

When the object stopped for the compulsory 5 second pause those duckling which had been following tended to circle the object, pecking it lightly and churping softly.

Following was rarely maintained for more than one minute at a time. It was more usual for the birds to follow for 20 - 30 seconds and then stop, peck the ground, venture to the centre of the apparatus for brief spells and then scurry back to the model emitting the call. As shown in Table 1 the extent to which birds followed a single call varied considerably. Even those birds with similar following scores displayed different patterns of accumulating tune. Some would take longer to respond, but follow for long spells. Others would respond quickly but accumulated a following score in short bursts of following.

The behaviour during the approach test was more consistent. Those ducklings that were awarded strong approach scores proceeded with little delay to the approach zone, and once the area was secured they tended to stay in it. Excursions from the approach zone were few and usually brief.

The behaviour pattern exhibited by poor or non-responders was radically different. The ducklings paid little attention to the model. They were either very still or frantically active. Distress vocalization was frequent, irrespective of whether the call was playing or not. Violent pecking of the floor and walls and defecation was common.

Discussion

In spite of the lack of consistent statistical differences between the various groups some conclusions could be drawn from the results of this experiment.

A comparison of response measures indicated that complex call 1 (500, 800, 1600Hz) elicited the strongest mean scores (shortest latency, longest duration) in both the following and approach tests. However, because of the absence of strong evidence of clear cut differential responsiveness it could not be concluded that a single critical frequency combination had been specified. Yet it could not be concluded that complex call 1 was ineffective in eliciting following and approach responses. A comparison of mean response scores elicited by complex call 1 with mean response scores elicited by recordings of natural and synthetic calls (Gottlieb, 1971, Heaton, 1971) revealed that they compared favourably with the results of previous research.

How do we account for the absence of clear differential responding that other researchers have reported? It is possible that the range of components used in synthesizing the calls was too limited and that all frequencies used fell into a generally attractive range. Although the frequencies used in preparing the calls ranged from 500 to 3200Hz all may be encountered in the natural call.

Furthermore it is possible that the frequencies used in this experiment did not differ widely enough from each other to elicit consistent differential responses. An examination of the frequency structure of each call revealed that most calls contained at least one frequency which was similar to a frequency in other calls. For example, call 1 contained a frequency of 800Hz which is only 20Hz higher than the 780Hz component in call 2. Further evidence suggesting that sharing of related frequencies might be implicated comes from a comparison of frequency characteristics of calls 1 and 4. Call 1, which did not differ significantly with call 4 in any response measures, contained a frequency of 1600Hz as did call 4.

To conclude, this experiment failed to specify a single critical combination of frequencies. A comparison of mean scores indicate, however, that complex call 1 was the most effective of a generally attractive range of complex calls in eliciting following and approach responses. Because call 1 elicited the strongest mean responses the frequency combination of this call was selected as the most suitable one to be used in the following experiments.

Experiment 2: Specification of the Critical Repetition Rates in an Artificial Call Attractive to Peking X Aylesbury Ducklings.

Experiment 2 was designed in an attempt to delineate a critical repetition rate or range of optimal rates. For this purpose an optimal frequency combination (500, 800, 1600Hz) obtained from Experiment 1 was presented at four different repetition rates with a constant duration of 25 msec.

Previous research findings suggested that the range of rates to be used should include rates slower and faster than 4/second, a rate both Heaton (1971) and Fischer (1972) found to elicit the greatest mean approach and following scores with Peking ducklings and domestic chickens. The results of previous research indicate that very slow rates (one every 3 - 4 seconds) and very fast rates (greater than 16/second) are equally ineffective in inducing following and approach responses (Collias & Collias, 1956, Heaton, 1971, Fischer, 1972). With the aim of delineating the critical repetition rate or a narrow range of optimal rates the extremes were avoided when preparing the calls. The rates of 1, 4, 8 and 16/second, used in this experiment represent a range from moderately slow to moderately fast rates.

While Heaton and Fischer both found that the strongest mean scores were obtained with the optimum rate of 4/second they also discovered that this was only one of a generally attractive range of rates. In the case of Peking ducklings tested at 24 hrs. posthatching Heaton found the best rates to be between 3 and 4/second and 7 and 8/second with an optimum at 4/second.

The aim of experiment 2 was to determine whether the responsiveness of Peking X Aylesbury ducklings to artificial calls presented at rates of 1, 4, 8 and 16/second would differ significantly (5% level of confidence), responsiveness being measured in terms of the incidence, latency and duration of following and approach responses.

Method:

The subjects for experiment 2 were 50 Peking X Aylesbury ducklings incubated and hatched in a sound attenuated room. (See chapter 2). Each duckling was randomly assigned to one of five groups and tested individually with one of the rate calls (1, 4, 8 or 16/second) or the silent model. At 20 ± 2 hrs. posthatching each duckling was subjected to a 12 minute following test and a 5 minute approach test. In all cases the following test was preceded by a 5 minute pre-test period of acclimatization.

Responsiveness to each call and the silent model was measured in terms of the incidence, latency and duration of approach and following responses. The statistical procedures used to evaluate the response measures were the same as those used in Experiment 1 and discussed in the section on methodological details.

Results:

The incidence of responses and mean response scores of subjects are shown in Table 5. The relation between repetition rate and latency and duration of following and approach responses is shown in Figures 10 - 13.

As shown in Table 5 and Figures 10 - 13 quite definite indications of differential rate dependent responding were found in the subjects in this experiment. A single classification analysis of variance indicated that the differences between means of all response measures shown in Table 5 were statistically significant (Table 6). Individual comparisons revealed further that the call with a repetition rate of 4/second elicited approach responses reliably more quickly (latency) and for a longer time (duration) than any of the other calls (Table 8). In the case of the following response the 4/sec. rate call induced quicker and more following than either the 1/sec. or the 16/sec. call. The difference in latency and duration of following at 4/sec. and 8/sec. was not significant however. (Table 8). Further evidence for the attractiveness of the 4/second rate

TABLE 5

Experiment 2: Response Measures of Peking X Aylesbury Ducklings in Following and Approach Tests to Calls with Repetition Rates of 1/sec, 4/sec, 8/sec and 16/sec and a Silent Model.

Test Call	N	Following Response					Approach Response				
		Incidence %	Latency, Sec Mean	Latency, Sec S.D.	Duration, Sec Mean	Duration, Sec S.D.	Incidence %	Latency, Sec Mean	Latency, Sec S.D.	Duration, Sec Mean	Duration, Sec S.D.
Response Measures of All Subjects											
Rate 1/sec	10	50	519.0	227.4	12.4	14.9	50	228.0	96.3	31.3	56.3
Rate 4/sec	10	80	260.6	252.2	91.3	54.9	90	78.5	84.4	175.0	87.9
Rate 8/sec	10	70	392.1	246.8	42.1	49.5	60	183.4	104.4	70.0	82.4
Rate 16/sec	10	20	658.9	137.7	2.2	5.0	20	278.4	46.4	3.4	7.7
Silent Model	10	10	689.6	96.1	2.2	6.9	0	300.0	0	0	0
Response Measures of Responders Only											
Rate 1/sec	10	50	318.0	123.8	24.8	10.9	50	156.0	88.9	62.6	68.4
Rate 4/sec	10	80	145.8	79.8	114.1	30.0	90	53.9	34.7	194.4	66.6
Rate 8/sec	10	70	251.6	120.7	60.1	49.0	60	105.7	38.4	116.7	75.4
Rate 16/sec	10	20	414.5	146.4	11.0	5.7	20	192.0	26.9	17.0	8.5
Silent Model	10	10	416.0(a)	-	22.0	-	0	-	-	-	-

(a) One responder only.

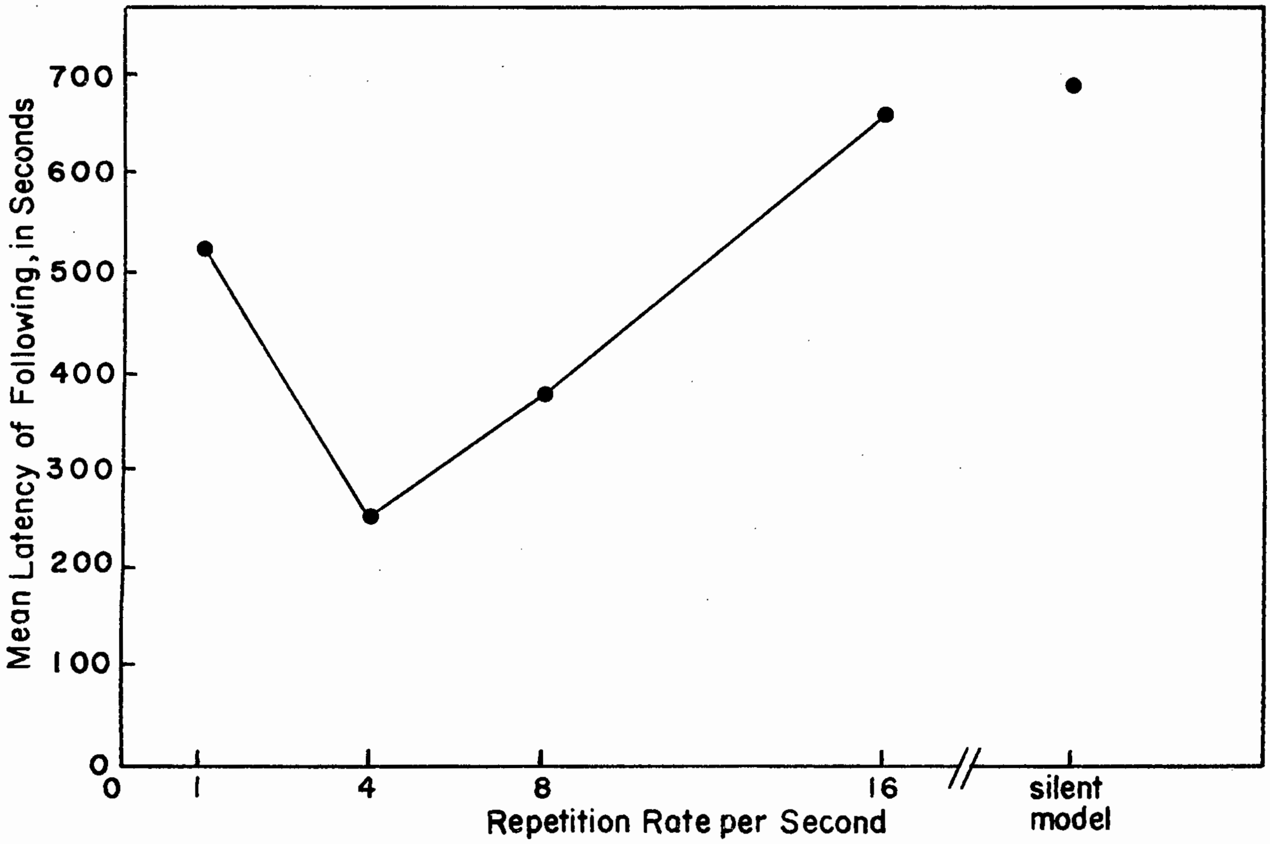


Fig. 10 The relation between repetition rate and latency of following.

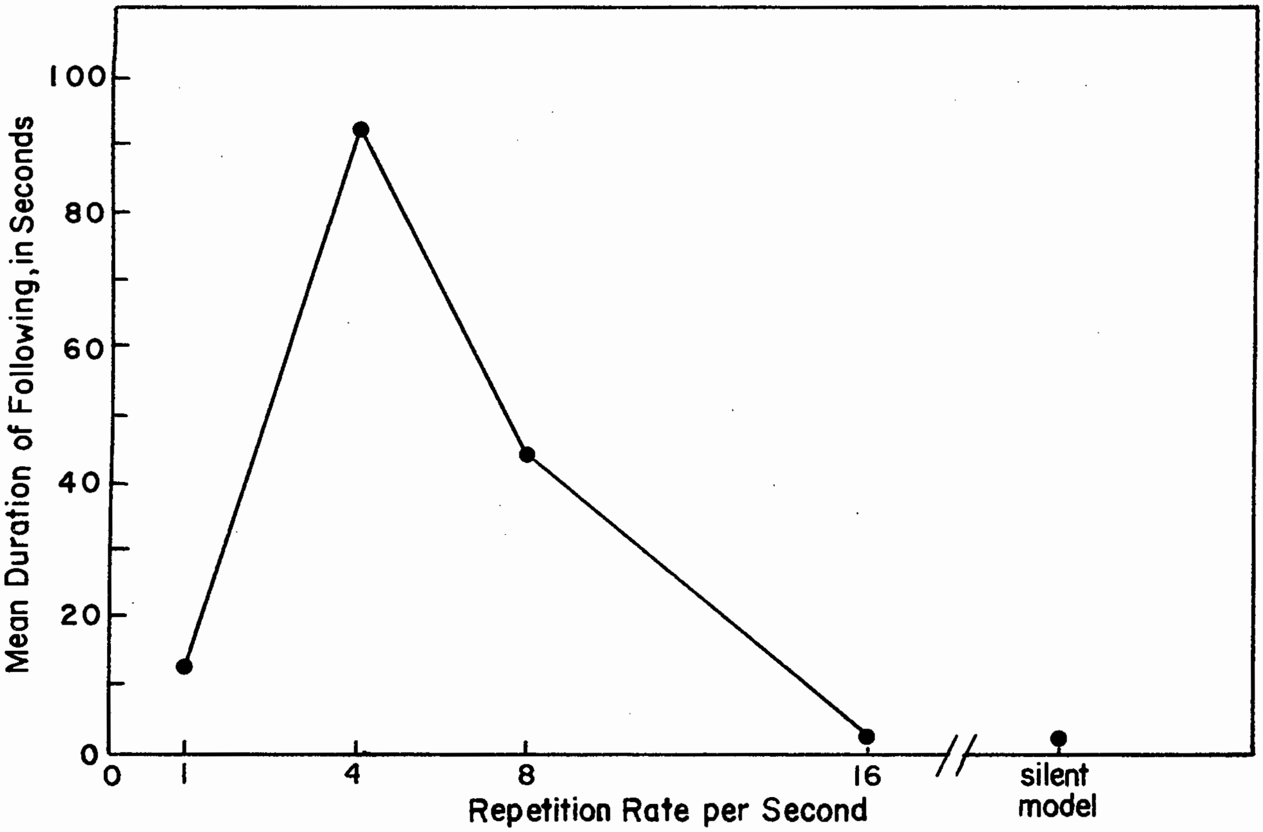


Fig. 11 The relation between repetition rate and duration of following.

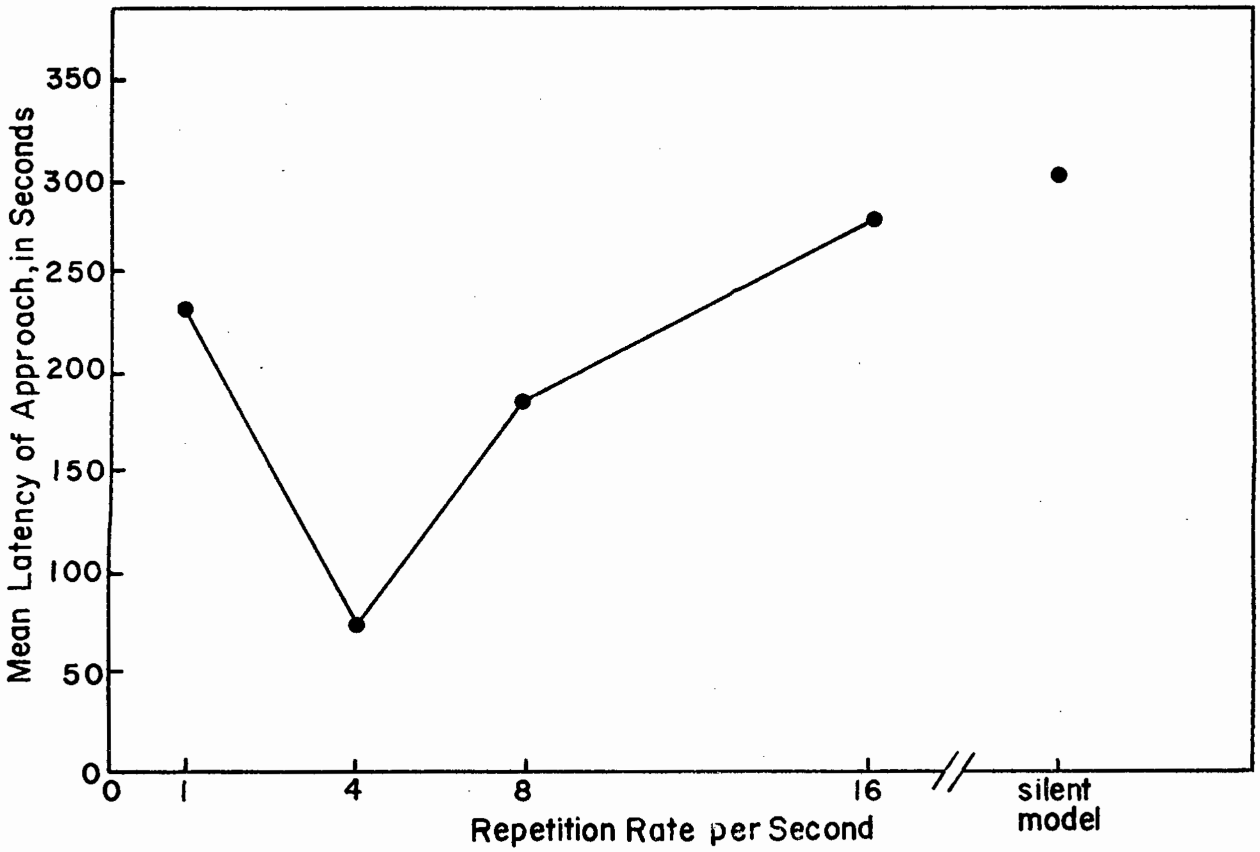


Fig. 12 The relation between repetition rate and latency of approach.

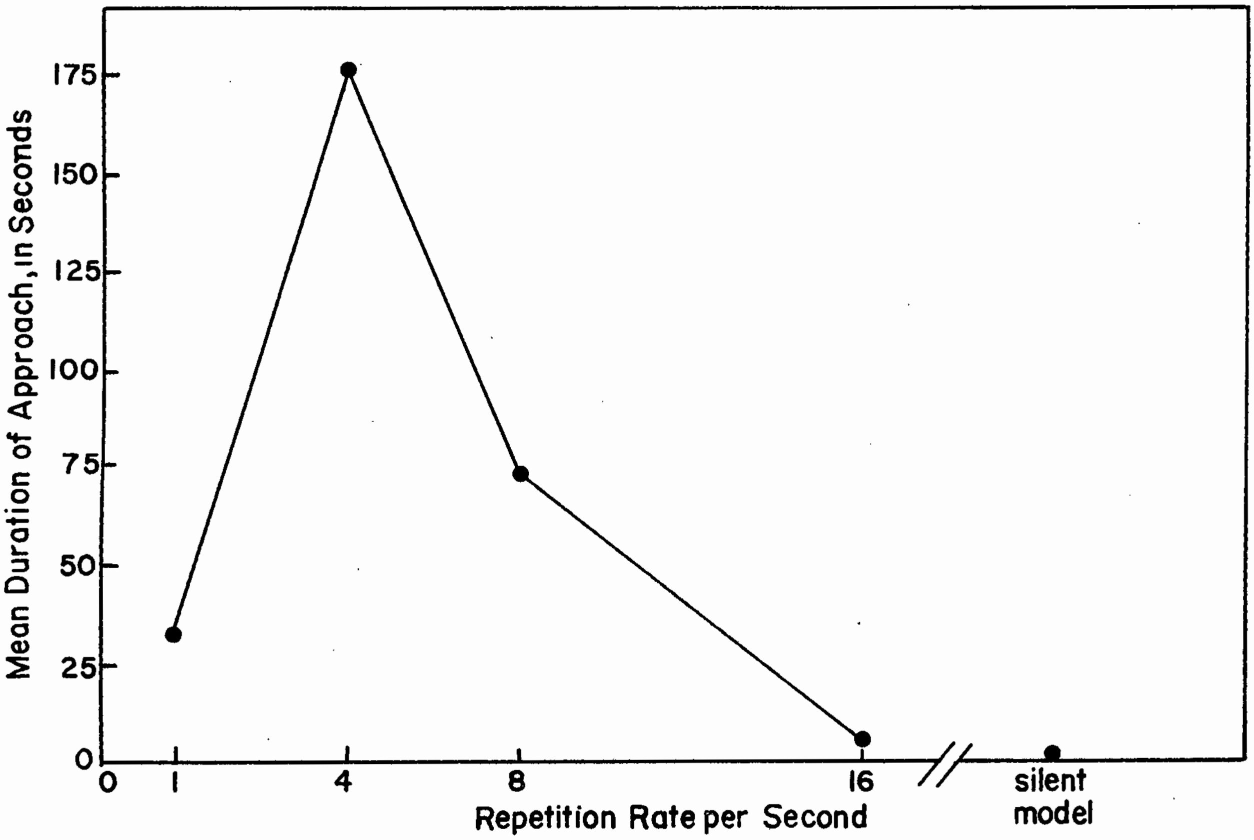


Fig. 13 The relation between repetition rate and duration of approach

STATISTICAL ANALYSES : EXPERIMENT 2

TABLE 6

Summary of Kruskal-Wallis One Way Analysis of Variance by Ranks for Responses of Subjects to Repetition Rate Calls: 1/sec., 4/sec., 8/sec. or 16/sec.

Response Measure	df	H	p-value
Following Latency	3	13.8	$<.01$
Following Duration	3	15.2	$<.01$
Approach Latency	3	17.1	$<.001$
Approach Duration	3	17.6	$<.001$

TABLE 7

Summary of Comparisons of Repetition Rate Treatment Groups With the Control (Steel) : Experiment 2

Response Measure	Treatment Groups							
	1(1/sec)		2(4/sec)		3(8/sec)		4(16/sec)	
	min T	p	min T	p	min T	p	min T	p
Following Latency	83.5	ns	66	$<.05$	72.5	ns	100	ns
Following Duration	84.5	ns	66	$<.05$	72.5	ns	101	ns
Approach Latency	80	ns	60	$<.01$	75	ns	95	ns
Approach Duration	80	ns	60	$<.01$	75	ns	95	ns

Note: ns = non-significant statistical difference (two tailed $p > .05$)

TABLE 8

Summary of Mann-Whitney U Tests on Differences Between Pairs of Repetition Rate Treatment Groups: Experiment 2.

Following Latency

	1 ($\bar{x}$ = 519.0)	2 ($\bar{x}$ = 260.6)	3 ($\bar{x}$ = 392.1)	4($\bar{x}$ = 658.9
1	-			
2	u = 17 $p<.02$	-		
3	u = 36.5 ns	u = 28 ns	-	
4	u = 33 ns	u = 12 $p<.02$	u = 20 $p<.05$	-

Following Duration

	1 ($\bar{x}$ = 12.4)	2 ($\bar{x}$ = 93.1	3 ($\bar{x}$ = 42.1	4 ($\bar{x}$ = 2.2)
1	-			
2	u = 15 $p<.02$	-		
3	u = 27.5 ns	u = 28 ns	-	
4	u = 31 ns	u = 12 $p<.02$	u = 20 $p<.05$	-

Approach Latency

	1 ($\bar{x}$ = 228.0)	2 ($\bar{x}$ = 78.5	3 ($\bar{x}$ = 183.4)	4 ($\bar{x}$ = 278.4)
1	-			
2	u = 13.5 $p<.02$	-		
3	u = 41 ns	u = 16 $p<.02$	-	
4	u = 35 ns	u = 6 $p<.002$	u = 24 ns	-

Approach Duration

	1 ($\bar{x}$ = 31.3)	2 ($\bar{x}$ = 175.0)	3 ($\bar{x}$ = 70.0	4 ($\bar{x}$ = 3.4)
1	-			
2	u = 11 $p<.02$	-		
3	u = 39 ns	u = 18 $P<.02$	-	
4	u = 31 ns	u = 6 $p<.004$	u = 25 ns	-

Notes: 1. Key : 1 = Group responding to call with Rate 1/sec.
2 = " " " " " " 4/sec.
3 = " " " " " " 8/sec.
4 = " " " " " " 16/sec.

2. In all cases N_1 N_2 = 10.

3. ns = non significant statistical difference (two tailed $p>.05$).

call is provided by the results of the analysis of the incidence of following and approach responses. Significantly more subjects followed (x^2 = 4.65, df = 1, $p < .05$) and approached(x^2 = 8.9, df = 1, $p < .01$) the 4/sec. rate call than any other call. Furthermore a comparison of auditory stimulus groups with the silent control group indicated that the 4/sec. rate group was the only one to differ significantly from the silent control with regard to latency and duration of following and approach responses.

In terms of incidence of response, however, all rate calls were significantly more effective than the silent model in eliciting following (x^2 = 5.22, df = 1, $p < .05$) and approach (x^2 = 7.86, df = 1, $p < .01$) responses. The typical behaviour patterns of strong and poor responders, described in Experiment 1, were again observed. In this experiment, however, there was a difference in the activity levels of the birds tested with the unattractive slow rate and the fast rate. Whereas birds tested with the 1/second call tended to be fairly vocal and active, those tested with the 16/second call were very still and quiet. The inhibition of movement and vocalization during the playing of the 16/second call was reminiscent of "freezing".

Discussion:

Indications of rate dependent differential responding were found in this experiment. The results indicated that the 4/sec. repetition rate call elicited significantly stronger responses than all other rate calls and the silent model, except in the case of the following response. The latency and duration of following scores of subjects tested with the 4/sec. rate call did not differ statistically from scores of subjects exposed to the 8/sec. call. This finding suggested that the 8/sec. rate call was relatively effective when responsiveness was measured in terms of latency and duration of following. The generally lower mean scores suggested however, that, if the 8/sec. rate falls into an attractive rate range, then it lies at the upper limits of this range.

The clear superiority of the 4/sec. rate in eliciting and maintaining following and approach responses led to the conclusion that this was the optimal rate, and suitable for use in following experiments. Although not substantial there was some evidence that the 8/sec. rate lies at the upper limits of an attractive rate range for Peking X Aylesbury ducklings. This finding is consistent with Heaton's (1971) observations with Peking ducklings.

Experiment 3: Specification of Critical Note Durations in an Artificial Call Attractive to Peking X Aylesbury Ducklings.

The object of Experiment 3 was to delineate a critical note duration or a range of optimal durations. For this purpose tapes were prepared in which the optimal frequency combination of 500, 800, 1600Hz and the optimal repetition rate of 4/second were kept constant while note durations were varied.

Estimates of probable limiting note durations to which ducklings will respond were obtained from previous research reports. Collias & Collias (1956) reported that brief notes were more effective in inducing following responses in Mallard ducklings than long ones. In a more systematic analysis of duration preferences in domestic chicks Fischer (1972) found that only very short tones of less than 100 msec were effective in eliciting following responses, with tones of 25 msec. or less being most effective. Furthermore, the repetition rate of 4/second placed a maximum limit of just less than 250 msec, since at this duration the call becomes continuous and no longer repetitive. With these considerations in mind the following note durations were employed:

1. 25 msec
2. 50 msec
3. 100 msec
4. 150 msec

The aim of Experiment 3 was to determine whether the responsiveness of Peking X Aylesbury ducklings to artificial calls with note durations of 25, 50, 100 or 150 msec would differ significantly (5% level of confidence), responsiveness being measured in terms of the incidence, latency and duration of following and approach responses.

Method:

The subjects for Experiment 3 were 50 Peking X Aylesbury ducklings incubated and hatched in a sound attenuated room (see chapter 2). Each duckling was randomly assigned to one of five groups and tested individually with one of the duration calls (25, 50, 100 or 150 msec durations) or the silent model. At 20 ± 2 hrs. posthatching each subject was subjected to a 12 minute following test and a 5 minute approach test. In all cases the following response was preceded by a 5 minute pre-test period of acclimatization.

Responsiveness to each call and the silent model was measured in terms of the incidence, latency and duration of following and approach responses. The statistical procedures used to evaluate the response measures were the same as those used in Experiments 1 and 2.

Results:

The incidence of response and mean response scores of subjects are shown in Table 9. The relation between note duration and latency and duration of following and approach responses is shown in Figures 14 - 17. That the various duration calls differed in effectiveness in eliciting and maintaining following and approach responses is shown in Table 9 and Figures 14 - 17. A single classification analysis of variance indicated that the differences between means of all response measures shown in Table 9 were statistically significant (Table 10). Individual comparisons revealed further that the 50 msec call elicited approach and following responses more rapidly and for a longer time than the 100 msec and 150 msec duration calls (Table 12). Differences between the 25 msec group and the 50 msec group did not reach statistical significance. The responses to the 25 msec call, in turn, differed reliably with the 150 msec call in three measures but not with the 100 msec call (Table 12).

A comparison of responses to duration calls with responses to the silent model revealed that only the 25 msec and 50 msec calls differed significantly with the silent control. However an analysis of the incidence of responses indicated that a significantly smaller number of

TABLE 9

Experiment 3: Response Measures of Peking X Aylesbury Ducklings in Following and Approach Tests to Calls With Note Durations of 25, 50, 100 or 150 msec. and a Silent Model.

Test Call	N	Following Response					Approach Response				
		Incidence %	Latency, Sec. Mean	Latency, Sec. S.D.	Duration, Sec. Mean	Duration, Sec. S.D.	Incidence %	Latency, Sec. Mean	Latency, Sec. S.D.	Duration Mean	Duration S.D.
Response Measures of All Subjects											
Duration 25msec	10	70	376.2	249.7	80.5	74.2	80	124.0	109.6	95.8	84.9
Duration 50msec	10	80	241.0	258.7	161.1	125.9	90	57.8	90.3	194.4	106.2
Duration 100msec	10	60	498.0	219.3	34.0	36.9	60	200.2	90.1	38.2	50.8
Duration 150msec	10	30	609.0	181.3	4.0	6.8	40	254.4	66.4	11.0	16.7
Silent Model	10	20	676.4	92.0	3.0	6.5	10	290.9	28.8	1.3	4.1
Response Measures of Responders Only											
Duration 25msec	10	70	228.9	95.5	115.0	60.2	80	80.0	66.2	132.3	89.1
Duration 50msec	10	80	121.3	64.3	201.4	105.4	90	30.9	32.2	216.0	86.2
Duration 100msec	10	60	360.0	144.5	56.7	30.1	60	138.7	36.5	63.7	51.9
Duration 150msec	10	30	350.0	65.1	13.3	4.5	40	186.0	53.3	27.5	15.1
Silent Model	10	20	502.0	12.7	15.0	4.2	10	290.9(a)	-	13 (a)	-

(a) One responder only.

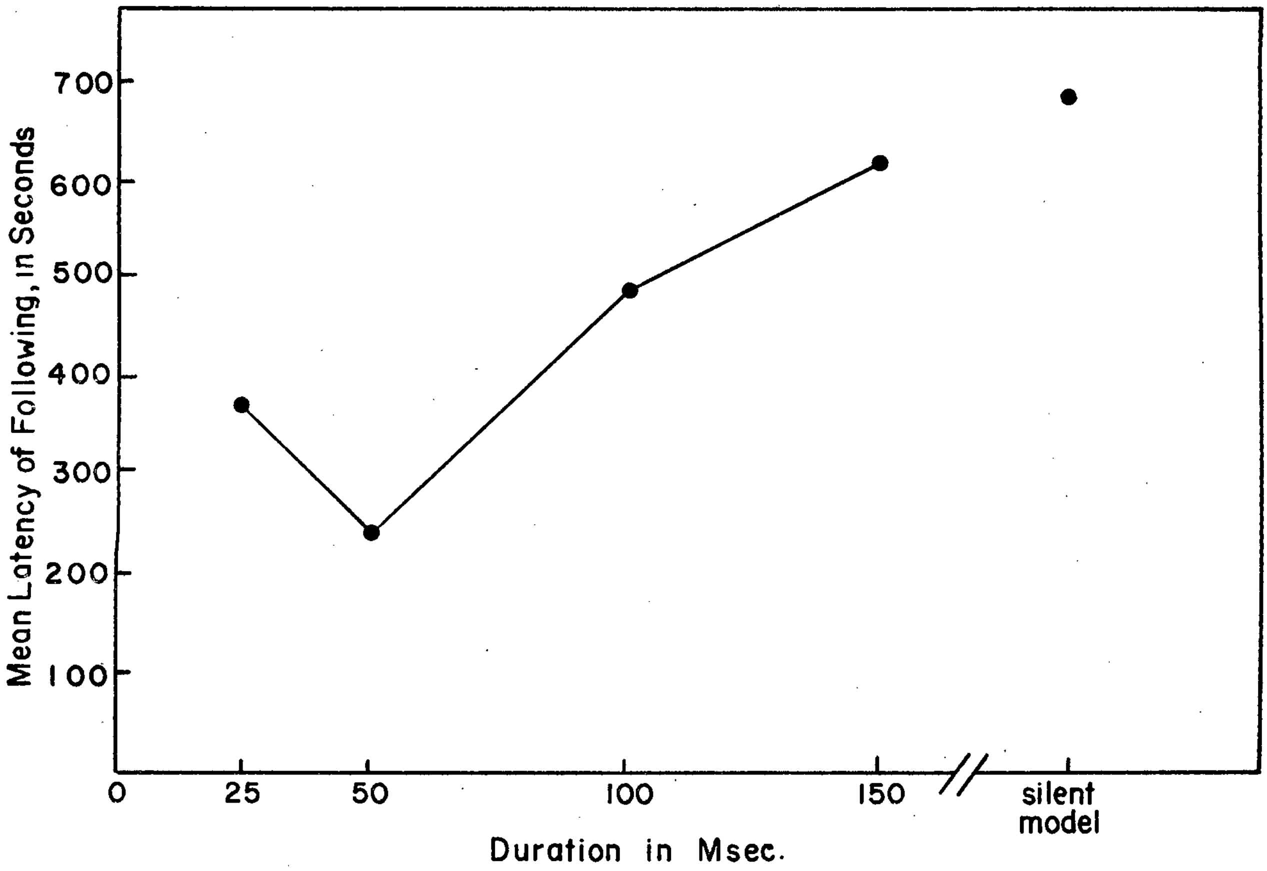


Fig. 14 The relation between note duration and latency of following.

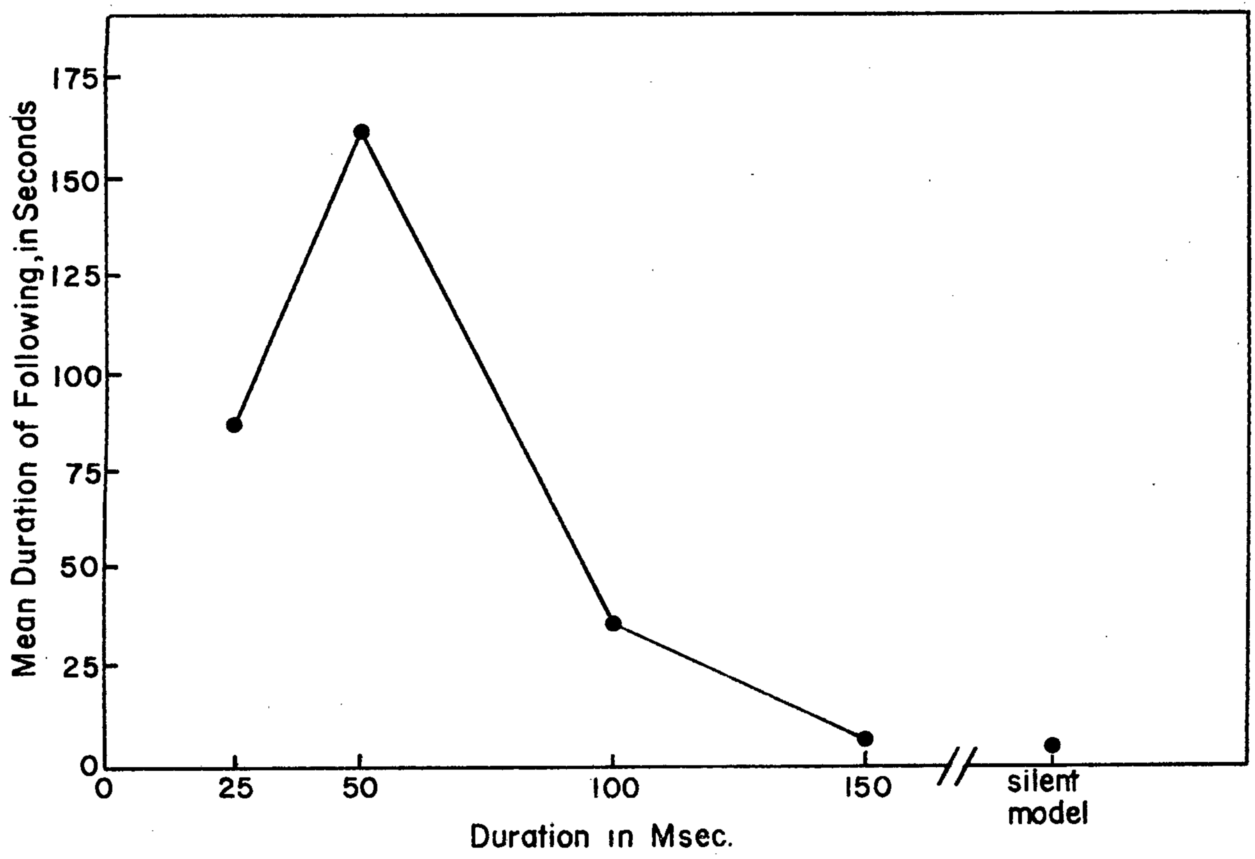


Fig. 15 The relation between note duration and duration of following.

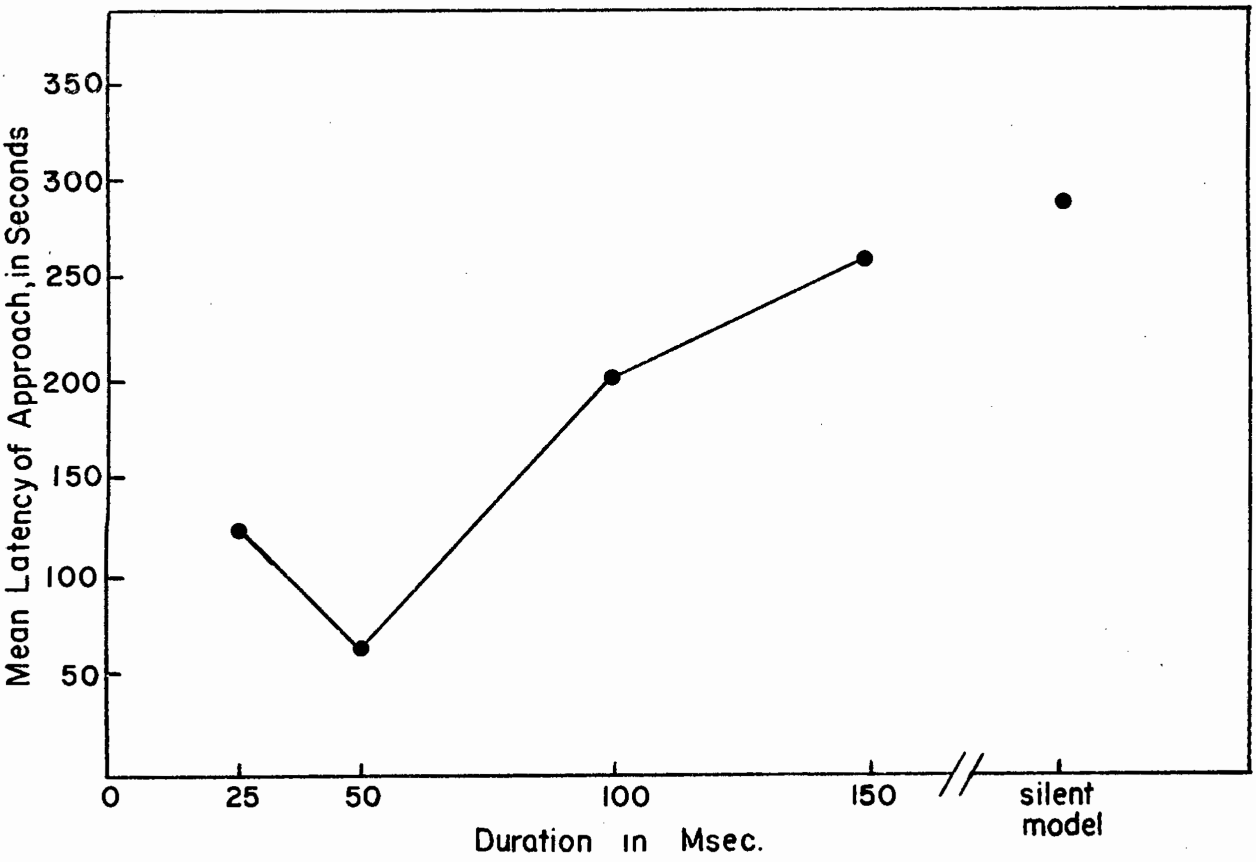


Fig. 16 The relation between note duration and latency of approach.

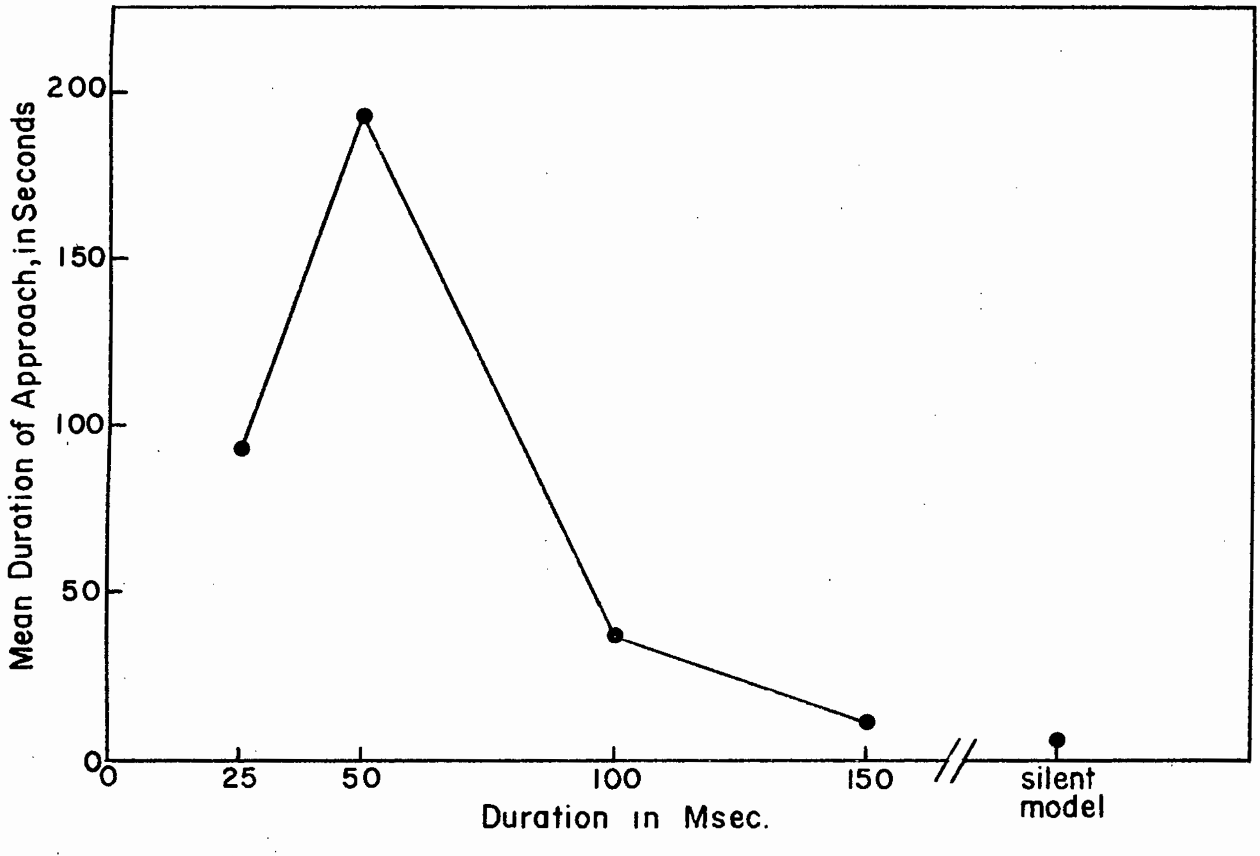


Fig. 17 The relation between note duration and duration of approach.

TABLE 10

Summary of Kruskal-Wallis One Way Analysis of Variance by Ranks for Responses of Subjects to Note Duration Calls: 25, 50, 100 or 150 msec.

Response Measure	df	H	p-value
Following Latency	3	12.8	<.01
Following Duration	3	13.9	<.01
Approach Latency	3	13.9	<.01
Approach Duration	3	16.1	<.01

TABLE 11

Summary of Comparisons of Note Duration Treatment Groups With the Control (Steel) : Experiment 3.

Response Measure	Treatment Groups							
	1 (25msec)		2 (50msec)		3 (100msec)		4 (150msec)	
	min T	p	min T	p	min T	p	min T	p
Following Latency	71	<.05	67	<.05	81	ns	97	ns
Following Duration	71.5	<.05	66	<.05	77	ns	95	ns
Approach Latency	66	<.05	60.5	<.01	77	ns	89	ns
Approach Duration	67	<.05	60.5	<.01	78	ns	89	ns

Note: ns = non-significant statistical difference (two-tailed $p>.05$)

TABLE 12

Summary of Mann-Whitney U Tests on Differences Between Pairs of Note Duration Treatment Groups : Experiment 3.

Following Latency

	1 ($\bar{x}$ = 376.2)	2 ($\bar{x}$ = 241.0)	3 ($\bar{x}$ = 498.0)	4($\bar{x}$ = 609.0
1	-			
2	u = 26.5 ns	-		
3	u = 35 ns	u = 17 $p<.02$	-	
4	u = 23.5 ns	u = 13 $p<.02$	u = 34 ns	-

Following Duration

	1 ($\bar{x}$ = 80.5)	2 ($\bar{x}$ = 161.1)	3 ($\bar{x}$ = 34.0)	4($\bar{x}$ = 4.0)
1	-			
2	u = 30 ns	-		
3	u = 31 ns	u = 18 $p<.02$	-	
4	u = 19.1 $p<.05$	u = 13 $p<.02$	u = 26 ns	-

Approach Latency

	1 ($\bar{x}$ = 124.0)	2 ($\bar{x}$ = 57.8)	3 ($\bar{x}$ = 200.2)	4($\bar{x}$ = 254.4)
1	-			
2	u = 25 ns	-		
3	u = 71 ns	u = 9 $p<.002$	-	
4	u = 17 $p<.02$	u = 7 $p<.002$	u = 32 ns	-

Approach Duration

	1 ($\bar{x}$ = 95.8)	2 ($\bar{x}$ = 194.4)	3 ($\bar{x}$ = 38.2)	4 ($\bar{x}$ = 11.0)
1	-			
2	u = 25	-		
3	u = 30 ns	u = 12 $p<.02$	-	
4	u = 21 $p<.05$	u = 7 $p<.002$	u = 34 ns	-

Notes: 1 Key : 1 = Group tested with call with note duration 25msec.
2 = " " " " " " " 50msec.
3 = " " " " " " " 100msec.
4 = " " " " " " " 150msec.

2 In all cases n_1, n_2 = 10

3 ns = non-significant statistical difference (two tailed $p>.05$)

birds followed ($x^2 = 4.1$, df = 1, $p < .05$) and approached the silent model ($x^2 = 8.59$, df = 1, $p < .01$).

Discussion:

Evidence of duration dependent differential responding was found in Experiment 3. The results of statistical analyses indicate that the 50 msec duration was more effective than the longer note duration in eliciting and maintaining responses. The differences between response measures of the 50 msec and 25 msec duration call groups were not significant, indicating that an attractive range of note durations existsinto which both the 25 msec and 5 msec durations fall.

The difference in mean scores, although unreliable, but taken together with the finding that the 50 msec duration call group did show a significantly higher incidence of approaching ($x^2 = 4.69$, df = 1, $p < .05$) suggested that the 50 msec duration was the optimal one used in this experiment. These findings are consistent with Fischer's (1972) observation that only very short durations of less than 100 msec are effective in eliciting responses. However, the present findings suggest that in the case of ducklings the optimal duration is closer to 50 msec than to 25 msec.

General Discussion:

The choice of the 4/sec. repetition rate and 25 msec. durations in Experiment 1 and the choice of the 25 msec. duration in Experiment 2 proved to be fortunate since these elements fall into the optimal range for each parameter. In the event of it having been discovered that the 25 msec duration and 4/sec. repetition rate were not in the attractive ranges, it would have been necessary to repeat the experiments varying the elements in the parameters simultaneously to ascertain whether the critical elements in each parameter changes as a function of changing elements in other parameters. Fortunately the probable attractive ranges were indicated by previous research and additional experiments, requiring vast numbers of subjects to be tested within a limited time period, were not required.

The series of experiments described above were performed with the following aims:

1. To delineate and specify critical parameters and elements within these parameters that render a call attractive to Peking X Aylesbury ducklings.
2. To produce an effective artificial call the elements of which could be manipulated in further experiments.

With regard to the first aim, these experiments have succeeded in delineating specific ranges of critical elements in the repetition rate and note duration parameters. It thus appears that some essential information is encoded in these parameters which accounts for selective responsiveness in ducklings.

The absence of clear cut differential responding in Experiment 1 may indicate that frequency is a less important parameter in eliciting and maintaining following and approach responses by Peking X Aylesbury ducklings. Although Fischer's (1972) findings with chickens support this interpretation, it is more likely that the range of frequencies attractive to Peking X Aylesbury ducklings is wider than expected and that the lack of consistently reliable differential responding was due to the absence of wholly unattractive frequencies in the calls. Further research will throw more light on this question.

While it is possible to conclude that the repetition rate and note duration parameters are critical parameters in the Peking X Aylesbury call it cannot be concluded that they are the only ones. Research carried out very recently by Gottlieb (1974 in press) indicates that parameters, other than those examined in the present study and by Heaton (1971) and Fischer (1972) might be critical in an attractive call. Specifically, Gottlieb has found that frequency modulation is the basis on which Wood ducklings identify the maternal call of the species.

Furthermore it cannot be assumed that a critical parameter in one species will also be critical in another. Gottlieb reports that Wood ducklings did not respond differentially to calls in which the repetition rate had been altered. It is thus apparent that repetition rate is not a critical parameter in the Wood duck maternal call as it is in the Peking duck and domestic chick calls. (Heaton, 1971, Fischer, 1972). The significance of Gottlieb's recent research is that it points to the need to examine more parameters in future research.

Has the second aim of this series of experiments - to produce an effective synthetic all - been achieved? There are two possible ways of determining whether an artificial call is effective in eliciting following and approach responses. The first, and best way, is to compare the effectiveness of the artificial call with the effectiveness of the actual maternal call by testing ducklings in a simultaneous call choice test. Unfortunately, however, because no Peking X Aylesbury ducks rearing their young could be located, such a test could not be performed. (Note: although ducks emit a wide range of calls e.g. feeding, distress, contentment, etc., none of these resemble the maternal "exodus" call sufficiently to be a satisfactory alternative). Since this is the first time this species of duckling has been used in experiments of this nature it was not possible to obtain the recordings of other workers.

An alternative way of judging the effectiveness of a synthetic call is to compare the strength of response of ducklings exposed to the artificial call with the strength of response of other birds to natural and artificial calls as reported by other researchers. It must be conceded that comparisons of this kind are never completely satisfactory because of differences in responsiveness in different species, different experimental conditions, experimenter differences, etc. Nevertheless they do provide a rough guide for the researcher wishing to ascertain the efficacy of an artificial call. With this in mind, the mean response strength of Peking X Aylesbury ducklings to the optimal artificial call (500, 800, 1600Hz, 4/second, 50 msec) was compared with the mean response strength of Peking ducklings to recordings of the natural maternal call, as reported by Gottlieb (1971). It was found that ducklings used in Experiment 3 followed the optimal artificial call more quickly and for a longer time in a 12 minute following test than Pekings did in a 20 minute following test (Gottlieb 1971). Even allowing for species differences, etc. there can be little doubt that the optimal call used in Experiment 3 was highly effective in eliciting filial responses and thus suitable for use in the next experiments.

Chapter 4

THE DEVELOPMENT OF SPECIES-SPECIFIC AUDITORY PERCEPTION IN BIRDS

> "And surely we are all out of the computation of our age, and every man is some months elder than he bethinks him; for we live, move, have a being, and are subject to the actions of the elements and the malice of disease, in that other world, the truest Microcosm, the Womb of our Mother"
>
> Sir Thomas Brown, Religio Medici, 1642.

It was observed earlier in this report that Gottlieb (1965) has demonstrated that parentally naive ducklings and chicks are able to identify their own species on the basis of species typical auditory stimulation emanating from the parent and that this general identification occurs without the benefit of known forms of learning. Furthermore the results of experiments discussed in chapter 2 have indicated that ducklings respond selectively to artificial calls with specific acoustic characteristics.

The question now posed is: How in the course of previous individual development does this selective process of perception come about?

To resort to such concepts as "instinct", "innate schema" etc. to explain this phenomenon is tempting; a temptation to which Hess has succumbed. In accordance with Lorenz's original formulation it was, until recently, believed that the innate features in imprinting are limited to an inborn predisposition to become rapidly attached to any parental object. A study by Hess & Hess (1969) which revealed that imprinting of neonatal ducklings to a duck decoy was much stronger than to human beings, led them to conclude that the ducklings possess ".. specific innate knowledge of the visual characteristics of the species as the parental object to be learned (p.129)" and that the innate schema of the parental object is rather stronger than that postulated by Lorenz (1935, 1937). There has been they suggest ".. an evolutionary pressure for the young chick or duck to learn the natural parent during the first day of life. This learning they call "genetically programmed" (Hess & Hess, 1969, p.p.129 - 130)". In short, Hess has "explained" the phenomenon and answered the question posed earlier without investigating the development of this ability.

The existence of natural stimulus preferences should not automatically lead to the supposition that these are species typical response patterns resulting from the passive translation of genetic programmes into behaviour. The existence of such preferences does not preclude that they have arizen through developmental processes in interaction with the environment and that they can be modified by further experience. Development involves a nexus of causal relations with action, reaction and interaction both within the organism and between the organism and environment, at every stage.

The elegant investigation by Gottlieb (1971) of the development of species identification has provided experimental evidence for the theoretically important notion that stimulative events occurring normally before birth (hatching) play a role in the perfection of species specific perception. However before reviewing this important research certain metatheoretical issues merit consideration.

One of the main objections to classifying behaviour patterns into simple categories such as "innate", "instinct" or "learned" is that it creates a barrier to the further analysis of the factors and processes involved in their development. The use of such concepts as explanatory concepts simply renders the analysis of development superfluous. By observing or studying only the immediate causation of a behaviour pattern we are viewing the behaviour in an artificially limited span of time. If we are ever to achieve a complete understanding of species specific behaviour patterns it is axiomatic that we analyse the ontogeny of "instinctive" behaviour.

The view that the embryo is completely formed at the moment of conception and that development merely involves the growth of pre-existing structures (preformism) has been discarded by many workers in favour of epigenesis. As Gottlieb (1973) puts it, the term epigenetic, when applied to behavioural development, "... denotes the fact that all patterns of activity and sensitivity are not immediately evident in the initial stages of development and that the various behavioural capabilities of the organism become manifest only during the course of development (p.8)".

While there is general unanimity on the epigenetic character of behavioural development there is disagreement on the character of behavioural epigenesis itself: some theorists assume that epigenesis of behaviour is predetermined while others hold that it is probabilistic. The essential point of difference between the two groups of theorists hinges on the issue of whether normally occurring motor development and sensory stimulation play a regulative role in the development of behaviour or whether behavioural development is a result of an invariant maturational sequence independent of prior motor movements and sensory stimulation. According to the predetermined epigenesis of behaviour, maturation gives rise to function and behaviour in a non-reciprocal fashion, whereas the probabilistic viewpoint holds that there are bidirectional (reciprocal) relationships between maturation, function and behaviour.

There is experimental evidence that during prehatching stages normally occurring sensory stimulation influences the embryo's behaviour and perception and that some of these effects express themselves in later prenatal and early postnatal behaviour. This evidence will be offered in support of the notion that species typical response patterns do not result from the <u>passive</u> translation of genetic factors into behaviour through the medium of tissue growth and differentiation i.e. support will be offered for the viewpoint of a probabalistic epigenesis of behaviour.

This should not be interpreted as an emphasis on all environmentalistic interpretation of behaviour. It should rather be seen as an attempt to uphold the idea that behaviour is a functional product of the dynamic relationship between the organism and its environment from the moment of conception.

The results of Gottlieb's (1971) investigation of the development of species identification in birds indicate that the epigenesis of species specific auditory perception is a probabalistic phenomenon, the threshold, timing and ultimate perfection of such perfection being regulated jointly by organismic and sensory stimulative factors. The capability of parentally naive ducklings to respond behaviourally to the maternal call of the species, Gottlieb discovered, has its antecendents in the embryo. From day 22 of incubation (5 days before hatching) the duck embryos responded behaviourally to the maternal call of the species; firstly with an inhibition of bill clapping and later with an increased rate of bill-clapping and leg movements. At all stages tested the embryos were behaviourally unresponsive to the maternal call of other species.

Further investigation revealed that the amount of bill-clapping in response to the maternal call was not an invariable predetermined response entirely the function of organic maturation. The amount of bill clapping activity during the five days before hatching was intimately related to the amount of auditory stimulation provided by communal incubation.

With the aim of determining the effect of normally occurring auditory stimulation on the ducklings postnatal discrimination of its maternal call, Gottlieb deprived embroyos of hearing their own vocalizations (by devocalizing them) and the vocalizations of their siblings (by isolating them). Ducklings thus deprived of such normally occurring prenatal auditory stimulation showed a delay in the perfection of their postnatal discriminative response to the species specific maternal call. It is thus apparent that species specific auditory perception is not simply the unfolding of a fixed genetic programme that occurs independently of normally occurring sensory stimulation. Exposure to such stimulation helps to regulate the time of appearance of perfected responses as well as the latency of the perfected response.

Although the discriminative response of devocalized - isolated ducklings to the species maternal call did eventually reach a high degree of perfection with time, it was never completely perfect. The devocalized - isolated ducklings at a later stage, could discriminate the maternal call of its species from many other species calls, but not all. This inability, however, could be reversed by exposing the ducklings to normally occurring auditory stimulation before hatching.

Although Gottlieb's (1971) study is one of the most elegant and convincing demonstrations of the influence of prenatal sensory stimulation on prenatal and postnatal behaviour in birds it is not the only one. Numerous other studies (e.g. Adam & Dimond, 1971 a & b; Gold, 1971, etc.) involving the manipulation of the prenatal environment have demonstrated a variety effects on postnatal attachment behaviour (more specifically following and approach responses). Since many such effects are regarded as extraneous variables in the present study, they have been discussed in the chapter dealing with methodological details. In this chapter emphasis will be placed on the auditory modality and further studies on the effects of prenatal sound stimulation on later prenatal and early postnatal behaviour will be examined.

Apart from the stimulation provided by self and siblings, embryos may be exposed to naturally occurring sounds emanating from the parent. It is surprising that parental behaviour towards the embryo and the neonate has received so little attention in imprinting research. It is amazing that it was felt that such a dynamic process like imprinting could be understood adequately by studying only one of the two classes of participants. This lack of insight is possibly the result of the over emphasis placed on laboratory investigations without the perspective gained from naturalistic studies.

Until recently very little attention has been given to the notion that the behaviour of avian embryos is affected by parental calls and that this parent/embryo interaction can affect later behaviour. Incubating birds do not sit passively on their eggs. The parents of many species of bird are extremely active, both vocally and otherwise, during the last few days of hatching; much of this activity is directed towards the eggs.

A number of studies have supplied evidence supporting the idea that prenatal experience of parent calls is a necessary prerequisite for their later effectiveness in eliciting filial responses. In one such study Impekoven (1969, 1973) found that if crooning calls are played to Laughing Gull eggs hatching in an incubator, such calls will increase the rate of pecking at a red rod (a feeding response) by the hatched chicks. Crooning does not have this effect on the pecking response of chicks with no experience of this call prior to hatching. Impekoven has observed that the incidence of crooning by incubating Laughing Gulls increases markedly when the eggs become pipped and during hatching and is associated with times when the young in the eggs are active, vocally and otherwise.

Of greater significance for the present study is the work which has been done on:

1. the prenatal origin of personal recognition in birds.
2. the influence of prenatal exposure to conspecific maternal calls on the responsiveness of neonates to those calls after hatching.

All these studies indicate how important it is to consider the influence that prenatal auditory stimulation has on the strength of approach and following responses after hatching. That we do so is particularly important when one considers that imprinting is frequently defined in quantitative terms i.e. in terms of the strength of responsivenss to the parental object.

Individual recognition of the voices of the parents has been demonstrated in Guillemots (Tschanz, 1965, 1968), Black-Billed and Ring-billed Gulls (Evans, 1970 a & b) and Laughing Gulls (Beer, 1969, 1970 a & b). Tschanz (1965, 1968) found, by playing recordings of calls of adult Guillemots to newly hatched Guillemot chicks raised in the wild, that the chicks could recognise the voices of their parents by individual characteristics in the luring call. The fact that the bird could recognise the parent call at hatching indicated that it acquired this ability to recognise the parent call while still in the egg. This finding led Tschanz to investigate the developmental origins of this selective responsiveness.

Tschanz incubator-hatched nearly 100 Guillemot chicks, some of which were subjected to recordings of natural or simulated luring calls while still in the egg. Shortly after hatching these chicks were tested with either simultaneous or successive presentations of two recordings one of which was the same as that used for prenatal stimulation. Those chicks which had had prenatal experience of a call showed preference for that call. In those cases in which chicks had no prior experience of either call they showed no preference and approached both calls with about the same frequency and speed as experienced chicks approached unfamiliar calls. Some chicks were exposed to two different calls prior to hatching. When tested after hatching they showed equal response to the two calls and preferred them both to unfamiliar calls. The results of these experiments thus confirmed the idea that the Guillemot chicks learn (not necessarily in the traditional sense) the individual characteristics of the luring calls of both of its parents while still in the egg.

In a similar study Beer (1970 a & b) presented recordings of parental calls and calls of parents from a neighbouring nest to parent-raised Laughing Gull chicks. These chicks moved towards the sound and called when the calls of their own parents were played. They tended to withdraw from the sound and sit quietly when the calls of neighbouring parents were played. Hand raised chicks, and therefore deprived of prenatal experience of parental calls, fled from the sound and crouched in silence in response to both calls of their parents and calls of neighbours. The fact that chicks do not recognise, and respond to, the calls of their parents without experience of them indicates that such recognition is not innate. Rather, it has been acquired during prenatal life.

How do birds recognise the calls of their parents apart from other species specific calls? Such recognition is clearly based on individual differences in the acoustic characteristics of vocalizations of members of the same species. So for example, it has been shown that in the case of Guillemots the durations of the pulses and the durations of the intervals between pulses vary within a call in a pattern that is characteristic of an individual and distinct from that of other individuals. (Tschanz, 1965, 1968). The parameter along which individual differences are found are not the same in all species. Whereas the individual differences in the Guillemot are differences in the length of components of the call individual differences in the calls of other species are differences in frequency, amplitude, etc. It would appear that the characteristics of individual calls can only vary within a certain range and maintain their appeal; at least in some species. The results of experiments discussed in chapter 3 and those of Heaton (1971) and Fischer (1972) indicate that marked deviations from the optimal in some parameters render the calls unattractive to ducklings and domestic chicks.

Although Gottlieb (1971) has demonstrated that the selectivity of the response in Peking ducklings is not dependent upon exposure to the maternal call this does not preclude the possibility that prenatal exposure to that call might have an effect on the strength of responsiveness to the maternal call after hatching. Indeed, Impekoven (1973) found that prenatal exposure to the Peking maternal call resulted in a significant increase in the strength of responsiveness to that call after hatching, as measured by the distance travelled towards the sound source. It is likely that an acquisition process similar to that at the basis of the development of personal recognition in birds is involved here. Such a process could be seen as akin to prenatal auditory imprinting i.e. acquisition of recognition before hatching. In this case both natural preference for the maternal call (species identification) and acquired recognition (imprinting) are working together to determine the strength of the filial response.

An earlier attempt by Hess (1959) to achieve prenatal auditory imprinting failed. For 48 hours before hatching 30 Mallard eggs were exposed to a constantly played tape recording of a female Mallard calling her young. Prenatal exposure ceased just before hatching and later, when tested, the young ducklings made no significantly greater choice of this sound than of the "gock" call normally used by Hess in his imprinting procedure.

Possible explanations for these conflicting results may lie, firstly, in the fact that auditory stimulation was presented in a different fashion in the two experiments. Whereas the stimulus was presented intermittently by Impekoven (1973), Hess (1959) exposed the embryos to the stimulus constantly for 48 hours. Constant exposure could simply lead to habituation (the waning of a response tendency under repeated stimulation). Secondly, there might have been differences in the intensity of the auditory stimulus. Fischer & Gilman (1969) found that there is a functional relationship between the intensity of an auditory stimulus and following and that this relation was a normal one for the species. In Impekoven's study the call was played to the embryos at a level of 72 db which is in the normal range for the Peking. The intensity used in Hess' study is unknown.

To summarize the research findings so far:

1. Parentally naive ducklings display selective responsiveness to conspecific maternal calls and electronic simulations of these calls. (Gottlieb, 1965, 1971, Heaton, 1971, chapter 3 of this report). The responsiveness to these calls was measured in terms of the incidence, latency and duration of following and/or approach responses to the calls.
2. There is conflicting evidence with regard to the effect of prenatal auditory stimulation on posthatching filial responses. In an apparently well controlled experiment Impekoven (1973) found that prenatal exposure to the species specific maternal call resulted in a significant increase in the strength of the approach response to that call after hatching. The attempt by Hess (1959) to demonstrate prenatal auditory imprinting failed. Doubts about his methodology have been expressed.
3. There is further evidence to support the notion that prenatal experience of parental calls influences the later effectiveness of these calls in eliciting filial responses. Guillemot chicks "learn", or acquire recognition of, the individual characteristics of the luring calls of both their parents while still in the egg. (Tschanz, 1965, 1969). A similar study by Beer (1970 a & b) suggests that Laughing Gull chicks also acquire individual recognition of the voices of their parents during their prenatal life.

Experiment 4 in this series was designed to ascertain whether prenatal experience of an artificial call, for which naive Peking X Aylesbury Ducklings show the greatest preference, affects the strength of responsiveness to that call, 20 ± 2 hrs. posthatching.

Experiment 4: The Effect of Prenatal Stimulation with an Optimal Artificial Call on the Postnatal Responses of Peking X Aylesbury Ducklings to that Call.

Method:

The subjects for experiment 4 were 40 Peking X Aylesbury ducklings. Half of these ducklings were incubated and hatched in the control incubator in a sound attenuated room. The other 20 birds were incubated and hatched in the experimental incubator in a separate sound attenuated room. Commencing on the 18th day of incubation the eggs in the experimental incubator were subjected daily to six half hour spells of exposure to the intermittently presented optimal call (12 seconds on time: 6 seconds off-time). The optimal call used in this experiment was the same call for which naive ducklings in Experiment 3 had shown the greatest preference. Prenatal auditory stimulation was maintained until the day of hatching. Further details of incubation, prenatal stimulation and brooding are provided in chapter 2.

Ducklings from the experimental and control groups were tested individually at 20 ± 2 hrs. posthatching for responsiveness to the same optimal call used in prenatal stimulation of the experimental group. Each subject was subjected to a 12 minute following test and a 5 minute approach test. As usual the birds were allowed a 5 minute pretest acclimatization period.

The latency and duration of following and approach responses of experimental and control subjects were evaluated statistically by means of the Mann Whitney U test. The proportions of birds responding in each group was evaluated by the Chi square test.

Results:

The incidence of responses, mean scores and standard deviations of the experimental and control groups are shown in Table 13. As shown in Table 13 the prenatally stimulated experimental group responded more often and displayed the strongest mean responses (shortest latency, longest

TABLE 13

Experiment 4 : Response Measures of Prenatally Stimulated Peking X Aylesbury Ducklings (Experimental Subjects) and Non Stimulated Control Subjects in Following and Approach Tests with the Optimal Call.

Response Measure	Experimental Group (N = 20)	p	Control Group (N = 20)
Following Response			
Incidence (%)	85	ns	75
Mean Latency (in seconds)	180.0	$<.05$	298.8
S.D.	237.7		267.9
Mean Duration (in seconds)	220.1	$<.05$	131.9
S.D.	157.0		106.6
Approach Response			
Incidence (%)	95	ns	85
Mean Latency (in seconds)	35.7	ns	81.9
S.D.	71.0		104.3
Mean Duration (in seconds)	256.9	$<.002$	170.5
S.D.	70.9		100.8

Note: The p-values in the table refers to data in the columns to which they are interposed.

ns = non-significant statistical difference (two tailed p .05)

TABLE 14

Experiment 4: Response Measures of Prenatally Stimulated Peking X Aylesbury Ducklings (Experimental Subjects) and Non Stimulated Control Subjects in Following and Approach Tests with the Optimal Call : Responders Only.

Response Measure	Experimental Group	Control Group
Following Response		
Incidence (%)	85	75
Mean Latency (in seconds)	847	158.4
S.D.	52.8	113.7
Mean Duration (in seconds)	258.9	175.9
S.D.	136.4	84.5
Approach Response		
Incidence (%)	95	85
Mean Latency (in seconds)	21.8	43.4
S.D.	35.2	49.0
Mean Duration (in seconds)	270.5	200.5
S.D.	38.1	75.3

duration) to the optimal call.

The results of the Mann-Whitney U tests indicated that there were significant differences between the two groups with respect to latency of following ($u = 117.5$, n_1 $n_2 = 20$, $p<.05$), duration of following ($u = 125.5$, n_1 $n_2 = 20$ $p<.05$) and approach duration ($u = 70,5$, n_1 $n_2 = 20$, $p<.002$). In the case of approach latency the differences between the two groups did not prove to be reliable ($u = 133, 5$, $n_1 = 20$, $n_2 = 20$, $p>.05$).

With regard to incidence of response there was no significant difference between the experimental and control groups in the proportion of birds that followed ($X^2 = 0.625$, df = 1, $p>.05$) and approached ($X^2 = 1.11$, df = 1, $p>.05$) the model emitting the optimal call.

Discussion

The fact that the proportion of birds in each group to respond to the optimal call in following and approach tests did not differ significantly was not unexpected. Earlier experiments have indicated that the large majority of birds respond to the optimal call even without prenatal experience of the call i.e. they show a natural preference for the call. In fact, a low incidence of response in the control group would have been an indication of something amiss.

Of greater concern is the strength of response of subjects in each group. The results of statistical analyses indicate that in three out of the four main response measures the experimental group showed significantly stronger responses than the control group. It is therefore concluded that prenatal auditory stimulation with an optimal artificial call resulted in enhanced responsiveness to that call at 20 ± hrs. post-hatching. The lack of a statistically significant difference in latency of approach was not regarded as sufficient grounds for negating the finding of positively modified responsiveness in other measures.

The implications of these findings for imprinting theory and research should not be missed. Since imprinting is most frequently discussed, and even defined, in quantitative terms (incidence or strength of following and approach responses) it is essential that workers in this field take into account the factors which affect the strength of responses of birds in imprinting situations. It is proposed that greater cognisance be taken of the natural and acquired preferences which birds bring to the imprinting situation. Too few workers view imprinting from a developmental viewpoint. On the whole the tendency has been to concentrate on the initial exposure to the object of attachment in the postnatal imprinting situation as the event of major importance in the establishment of long term filial bonds. However, the classical notion of imprinting that compares the imprinting process to the impressing of a pattern upon a _tabula rasa_ is clearly inadequate in the light of this and other recent research. Imprinting can no longer be construed as a simple process of "acquisition of recognition" during a "critical" post-hatching period. In the wider sense of the term, "imprinting", particularly in natural situations, is a complex process involving the dynamic interaction of organismic, sensory stimulative and situational factors.

In the present study a start has been made in the attempt to determine just how much of responsiveness of duckling in the initial imprinting situations is the result of natural stimulus preferences and how much can be credited to prenatal stimulative factors. Although it would be unwise to speak, at the present stage, in quantitative terms it is not unreasonable to suggest, tentatively, that the difference in response strength between the experimental and control groups in Experiment 4 may be seen as a measure of the influence of prenatal experience of the call.

To summarise, it has been demonstrated so far that:

1. naïve birds respond selectively to certain calls. That is, they display natural or innate preferences, which to the best of our

knowledge cannot be related to any known stimulative factors.

2. but, it has also been shown that the strength of response to the preferred call is enhanced by prenatal experience of this call.

The results of Experiment 4 thus add support to a probabalistic interpretation of the epigenesis of stimulus preferences in ducklings. That is, this study provides evidence that sensory stimulation plays a regulative role in the development of stimulus preferences in ducklings and that preferential responses are not simply the result of the passive translation of genetic material. It would appear that a species specific genetic complement underlies the existence of preferences for certain classes of stimulus. But it is also evident that the strength of preferential responsiveness is regulated, in part, by auditory stimulation originating from the embryos themselves, their siblings and their parents. The notion that prenatal stimulation with the parental call influences postnatal responsiveness to that call is consistent with naturalistic observations of the dynamic relationship which exists between the parent and the embryo inthe egg. (Impekoven, 1969, Hess, 1972).

The findings of the present study, although being mainly of relevance to the general theoretical issues discussed in the preceding paragraphs, also raise some questions concerning the "critical period" concept. Over the years the "all-or-nothing" conception of the critical period has largely been replaced in the literature by the notion of a "sensitive period", a period during which the strongest imprinting is likely to occur. Nevertheless it is widely accepted that the period when the bird is most receptive occurs some time after hatching. Such an assumption is implicit in Hess' (1973) definition of imprinting as a "...process in which there is an extremely rapid attachment, during a specific critical period, of an innate behaviour pattern to specific objects which thereafter become important elicitors of that behaviour pattern (p.65)."

Since the "behaviour pattern" Hess is referring to is most frequently a locomotor response this definition automatically disallows the possibility that imprinting might occur prenatally. It follows, therefore, that this definition also excludes the possibility that there might exist some time during embryological development a period when birds are particularly receptive to becoming attached to auditory stimuli. Yet the studies of Tschanz (1965, 1968) and Beer (1970 a & b) have shown that birds "acquire recognition" of their parental calls before hatching. Birds with prenatal experience of their parents calls respond positively to these calls but avoid the calls of neighbouring parents. Surely these are examples of prenatal auditory imprinting. And if a sensitive period for imprinting does exist in these birds then it must be some time before hatching.

These conceptual problems will continue to arise so long as imprinting is conceived of as necessarily involving locomotor behaviour responses. (Suggestions for establishing wider and more precise behavioural criteria of imprinting are discussed in Chapter 5). The results of the present study indicate that Peking X Aylesbury ducklings are receptive to an optimal artificial call some time before hatching but they provide no indication of the period when birds were most sensitive. Since prenatal stimulation commenced before the functional development of the auditory system and was continued intermittently until hatching, it is not possible to delineate any sensitive period. Future research, in which prenatal auditory stimulation is presented at specified times only, may throw some more light on this issue.

Experiment 5: The Effect of Prenatal Exposure to an Altered Optimal Call on Postnatal Responses to the Altered and Optimal Calls.

In Experiment 4 it was shown that prenatal exposure to a call with the acoustic characteristics for which naive ducklings show the greatest preference results in strengthening of their responsiveness to that call. One of the aims of the last experiment in this series was to ascertain whether it is similarly possible to enhance following and approach responses to a call with a repetition rate at the upper limits of the attractive rate range through prenatal stimulation with this call. The results of Experiment 2 indicated that a rate of 8/second, although by no means ineffective, was generally less effective than the optimal rate of 4/second, as reflected in response measures.

A number of related questions were now asked:

1. Can this difference in responsiveness be reduced or eliminated through prenatal stimulation with the optimal call altered to a rate of 8/second? In other words, is it possible through sheer exposure to a non-optimal call increase the responsiveness of birds to that call until it equals or surpasses the natural responsiveness of naive birds to the optimal call? That is, can natural preferences be overriden by prenatal experience of a call for which naive birds usually show less preference?

Essentially the same question,but viewed from another angle, is: Does prenatal stimulation only have the effect of strengthening responses to calls to which the birds are already attuned or will it enhance responsiveness to less attractive calls as well? That is, does the existence of natural preferences decrease the probability that birds will become imprinted prenatally on birds of another species through experience of their call?

So far the questions have been concerned with whether it is possible to enhance the responsiveness of birds to non optimal calls through prenatal stimulation. A second group of questions now needs to be asked:

2. Will exposure to a non optimal call result in a weakening of responsiveness to the optimal call? In other words, will experience of an altered call interfere with the natural preference of ducklings.

The object of Experiment 5 was to provide answers to these questions.

Published studies of related problems provide little basis for confident prediction of the outcome of a study designed to answer these questions. Gottlieb (1965), on the one hand, found that natural preferences could not be overriden or interfered with by postnatal experience of a non-preferred call. Ducklings exposed early in postnatal life to the call of another species still showed preference for the conspecific maternal call in a choice test. In Gottlieb's study, however, the hatchlings were exposed to the call of the strange species for only a short period of time posthatching before being tested. The birds in Gottlieb's study did not have experience of the strange call extending as far back in time as the functional development of the auditory system. It was the aim of Experiment 5 to determine whether such extended experience of a call altered from the optimal would override, or interfere with, natural preferences.

In a similar study dealing with a different sensory mode Simner (1971) did succeed in modifying the responsiveness of chicks to a stimulus presented at a non preferred rate. Simner first established that naive chicks preferred a 4/second rate of intermittent visual flicker to a 20/second rate. He then subjected chicks to 24 hours of perinatal exposure to the non preferred rate. His results indicated positively modified approach promoting properties for the 20/second rate.

In a study involving prenatal auditory stimulation Grier, Counter and Shearer (1967) exposed chicken embryos to 1 second beeps of a 200 Hz tone from the 12th to the 18th day of incubation. A second batch received no such stimulation. Within 6 hours of hatching all birds were tested for approach and following responses to sources emitting 200Hz and 2000Hz tones. Grier et al found that the chicks exposed previously to the 200Hz tone chose to respond to it while inexperienced chicks were indifferent in their choice of one or the other. Rajecki (1972), however, was only able to replicate this research when responsiveness was measured in terms of the absence of distress calling. The influence of prenatal experience of the 200Hz call did not manifest itself in the approach response.

In another experiment Rajecki (1972) was unable to achieve prenatal auditory imprinting with a 2000Hz tone. It would thus appear that chickens are only sensitive to prenatal stimulation with stimuli in a certain range, a range into which 2000Hz does not fall.

It is of importance to the present study to note that the acoustic characteristics of the call with which Grier et al achieved success differs widely from the characteristics of the natural call i.e. a 770Hz fundamental frequency presented at a rate of 2,5/second. They thus succeeded in enhancing responsiveness to a non-optimal call (200Hz at a rate of 1/second). The results of Rajecki's (1972) study indicates, however, that, although not optimal, this call does have characteristics in a generally attractive range.

In neither of the studies described above did the researchers compare the responsiveness of prenatally stimulated birds to the non-preferred call with their responsiveness to a preferred call.

In an attempt to answer the questions posed earlier in this introduction the following completely randomized block design (Kirk, 1968) was employed:

	POSTNATAL TESTING WITH EITHER: Optimal call	Altered call
EXPERIMENTAL GROUP Exposed Prenatally to Altered Call	Eopt	Ealt
CONTROL GROUP Incubated in Silence	Copt	Calt

The optimal call used in this experiment for postnatal testing was the same call for which naive ducklings in Experiment 3 had shown the greatest preference (500, 800, 1600Hz, 50msec, 4/sec). The non preferred call used for prenatal stimulation and postnatal testing was the same optimal call but with the repetition rate altered to a non-optimal rate of 8/second. (Hereafter referred to as the "altered call").

One group of birds, the experimental group, was subjected to prenatal stimulation with the altered call and tested with either the optimal call or the altered call. Another group, the control group, received no prenatal auditory stimulation and was tested with either the optimal or altered call.

This experimental design allows the following comparisons to be made:

1. Response strength of Ealt vs Calt.

The results of this comparison will indicate whether prenatal stimulation with an altered call produced enhanced responsiveness to that call after hatching.

2. Response strength of (a) Eopt vs Ealt (b) Copt vs Ealt.

The result of this comparison will indicate whether responsiveness to an altered call can be increased, through prenatal stimulation with that call, to the extent of approaching, equalling or surpassing the natural responsiveness of (a) the stimulated birds to an optimal call (b) naive birds to an optimal call.

3. Response strength of Eopt vs Copt.

The results of this comparison will indicate whether prenatal stimulation with an altered call interferes with the natural responsiveness of ducklings to an optimal call.

Method:

The subjects for Experiment 5 were 60 Peking X Aylesbury ducklings. Half (30) the subjects were incubated in the experimental incubator and from the 18th day of incubation were subjected daily to six half hour spells of exposure to the intermittently presented altered optimal call (500, 800, 1600Hz, 8/sec., 50msec). The procedure of prenatal auditory stimulation was the same as that followed in Experiment 4 and described in chapter 2.

The other 30 birds were incubated in the control incubator in a separate sound attenuated room. Apart from self and sibling vocalizations and the background noise of the airconditioner control,subjects received no prenatal auditory stimulation.

Subjects from each group were randomly divided into a further two groups. Fifteen experimental subjects and 15 control subjects were tested with the optimal call, while 15 subjects from each group were tested with the altered call.

At 20 ± 2 hrs. posthatching each bird was individually subjected to a 12 minute following test and a 5 minute approach test with either the optimal or altered call. In all cases the following test was preceded by a 5 minute pretest period of acclimatization.

Latency and duration scores were transformed by means of a $\sqrt{x + .5}$ transformation (Kirk, 1968) and evaluated statistically by means of a non parametric two way analysis of variance. Hartley's Fmax. test for homogeneity of variance (Winer, 1962) was employed and individual comparisons utilized Tukey's HSD test (Kirk, 1968). The incidence of birds responding in each group was evaluated by means of the Chi square test. The rationale for employing these procedures is discussed in chapter 2.

Results:

The means and standard deviations of test scores of all groups are shown in Table 15. In the upper portion of Table 15 the means and standard deviations of transformed scores of all subjects in each group are given in brackets. As shown in the profiles of means (Figures 18 - 21) responsiveness to the optimal call was clearly stronger (shorter latency, longer duration) than to the altered call irrespective of prenatal rearing conditions. Two way analyses of variance indicated that the latency and duration of following and approach responses of both experimental and control subjects tested with the optimal call were significantly stronger than responses of experimental and control subjects tested with the altered call. (Table 16).

As shown in Figures 18 - 21 the responses of experimental subjects were generally slightly stronger than responses of control subjects except with regard to approach latency in which case the experimental subjects responded more slowly to the altered call than control subjects. That these differences were not significant was indicated by the two way analyses of variance which revealed that there was no significant difference in overall responsiveness between the experimental and control groups. There was no evidence of interaction (Table 16).

The results of important pairwise comparisons shown in Table 17 may be summarized as follows: with regard to latency and duration of following and approach responses

i. Both Eopt and Copt differed significantly with Ealt and Calt.

ii. There was no significant difference between Eopt and Copt in all measures. The same finding held for comparisons between Ealt and Calt.

TABLE 15

Experiment 5 : Response Measures of Peking X Aylesbury Ducklings Exposed Prenatally to the Altered Call (Experimental Subjects) and Non-Stimulated Control Subjects in Following and Approach Tests with the Altered and Optimal Calls

Test Call	N	Following Response					Approach Response				
		Incidence %	Latency,Sec Mean	S.D.	Duration,Sec Mean	S.D.	Incidence %	Latency,Sec. Mean	S.D.	Duration,Sec. Mean	S.D.
Response Measures of All Subjects - Transformed Means and S.D. in ( )											
Experimental Group											
Optimal Call	15	87	204.9 (12.9)	220.3 (6.5)	189.3 (11.6)	200.4 (7.6)	87	71.7 (6.6)	105.2 (5.6)	205.9 (13.3)	107.8 (5.7)
Altered Call	15	67	370.8 (17.9	275.3 (7.5)	46.0 (5.5)	52.8 (4.2)	73	184.9 (12.8)	102.8 (4.8)	73.9 (6.9)	84.3 (5.2)
Control Group											
Optimal Call	15	87	209.3 (13.2)	216.0 (6.2)	169.8 (11.6)	130.5 (6.3)	73	96.1 (7.7)	129.3 (6.3)	172.3 (11.3)	121.1 (6.9)
Altered Call	15	60	433.2 (19.7)	266.3 (6.9)	34.3 (4.5)	42.9 (3.9)	73	174.9 (12.7)	96.1 (4.1)	59.0 (6.4)	62.5 (4.5)
Response Measures of Responders Only											
Experimental Group											
Optimal Call	15	87	125.7	95.0	218.4	199.9	87	36.5	53.7	237.6	73.4
Altered Call	15	67	192.2	127.7	69.0	50.8	73	143.0	86.9	100.8	83.5
Control Group											
Optimal Call	15	87	130.8	65.5	195.9	119.7	73	22.0	26.8	234.9	65.9
Altered Call	15	60	242.0	145.7	57.1	42.0	73	129.4	66.3	80.5	59.7

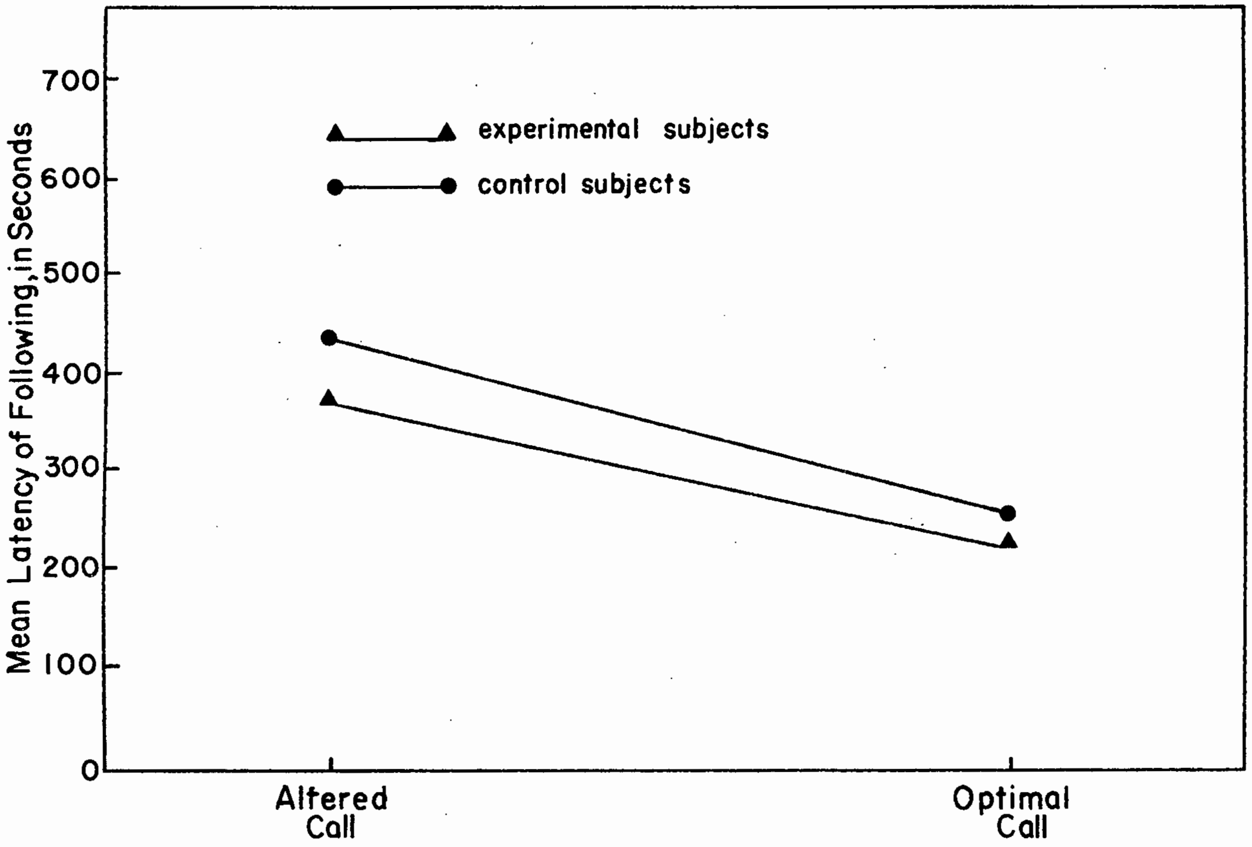


Fig. 18 Profile of mean latency of following of experimental and control subjects tested with optimal and altered calls.

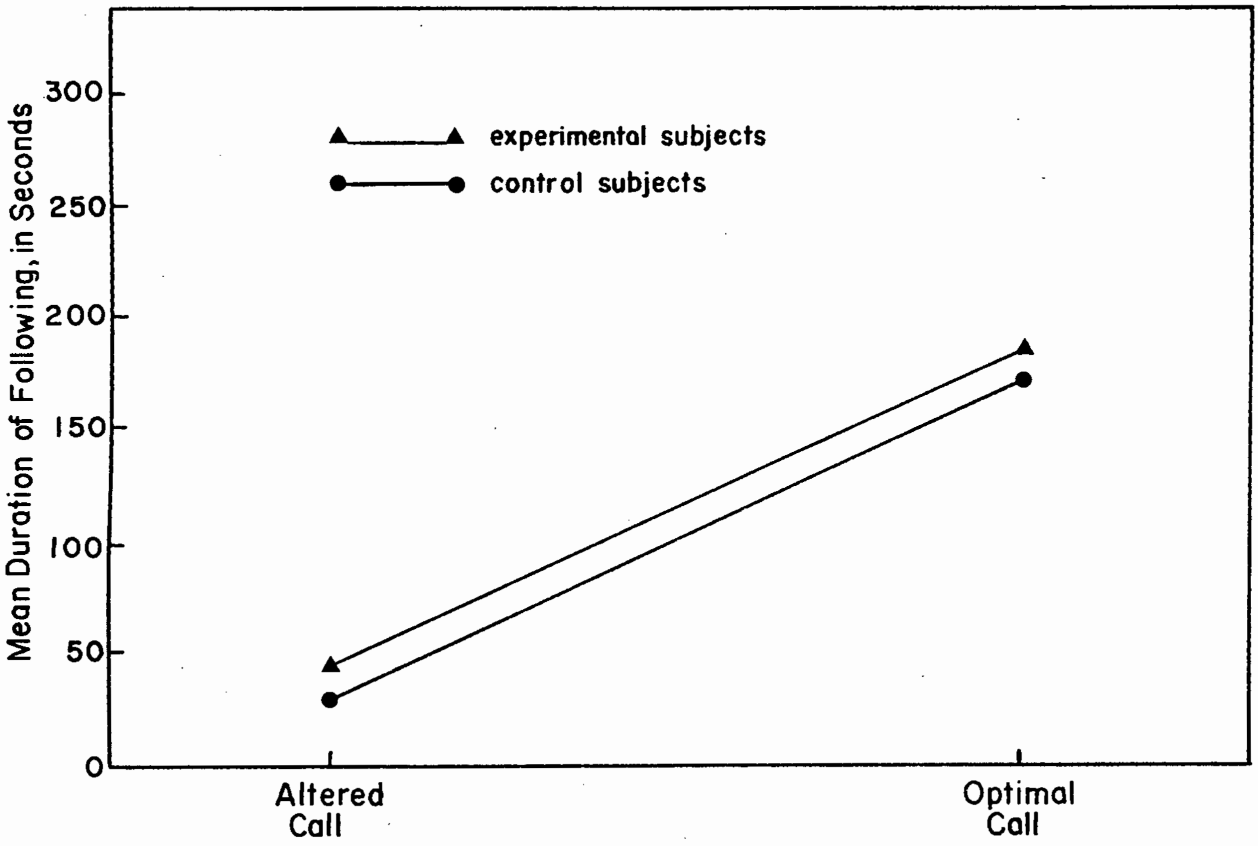


Fig. 19 Profile of mean duration of following of experimental and control subjects tested with optimal and altered calls.

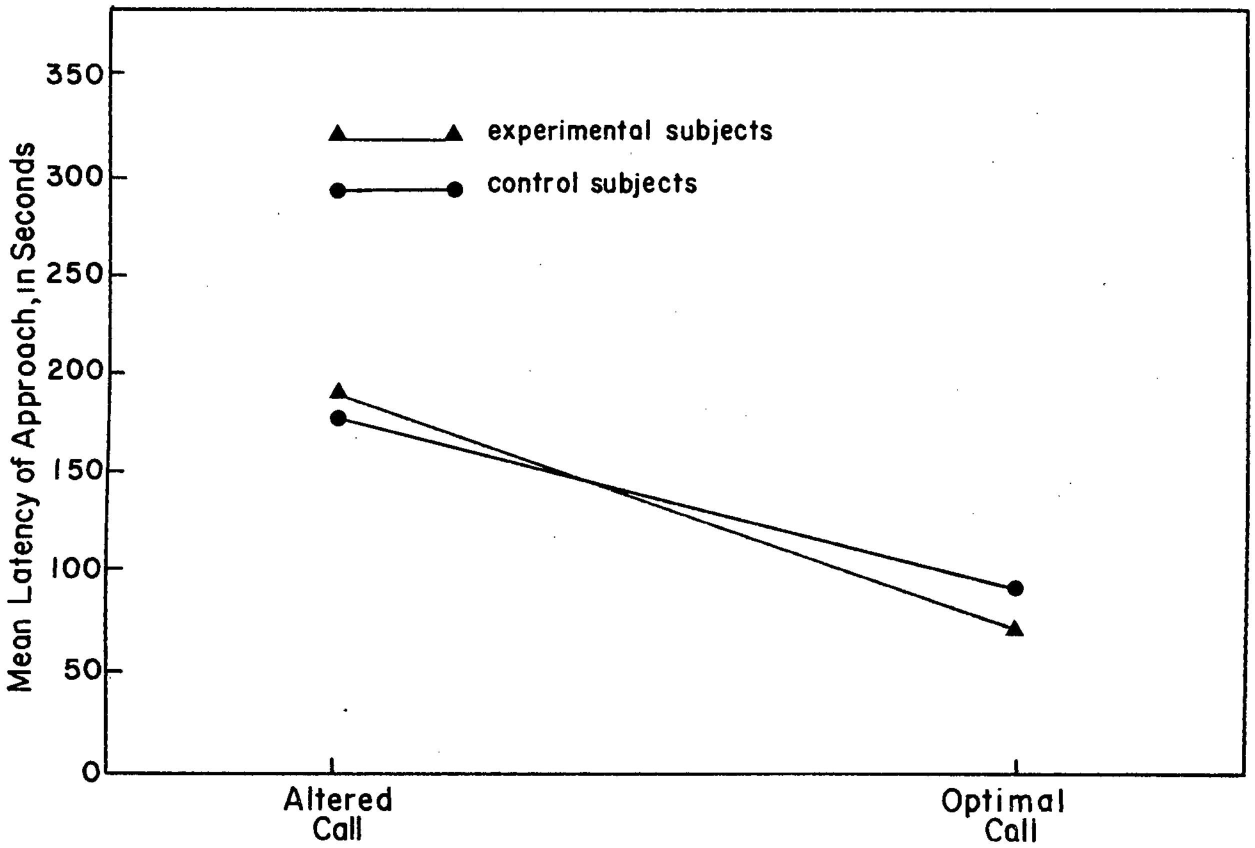


Fig. 20 Profile of mean latency of approach of experimental and control subjects tested with optimal and altered calls.

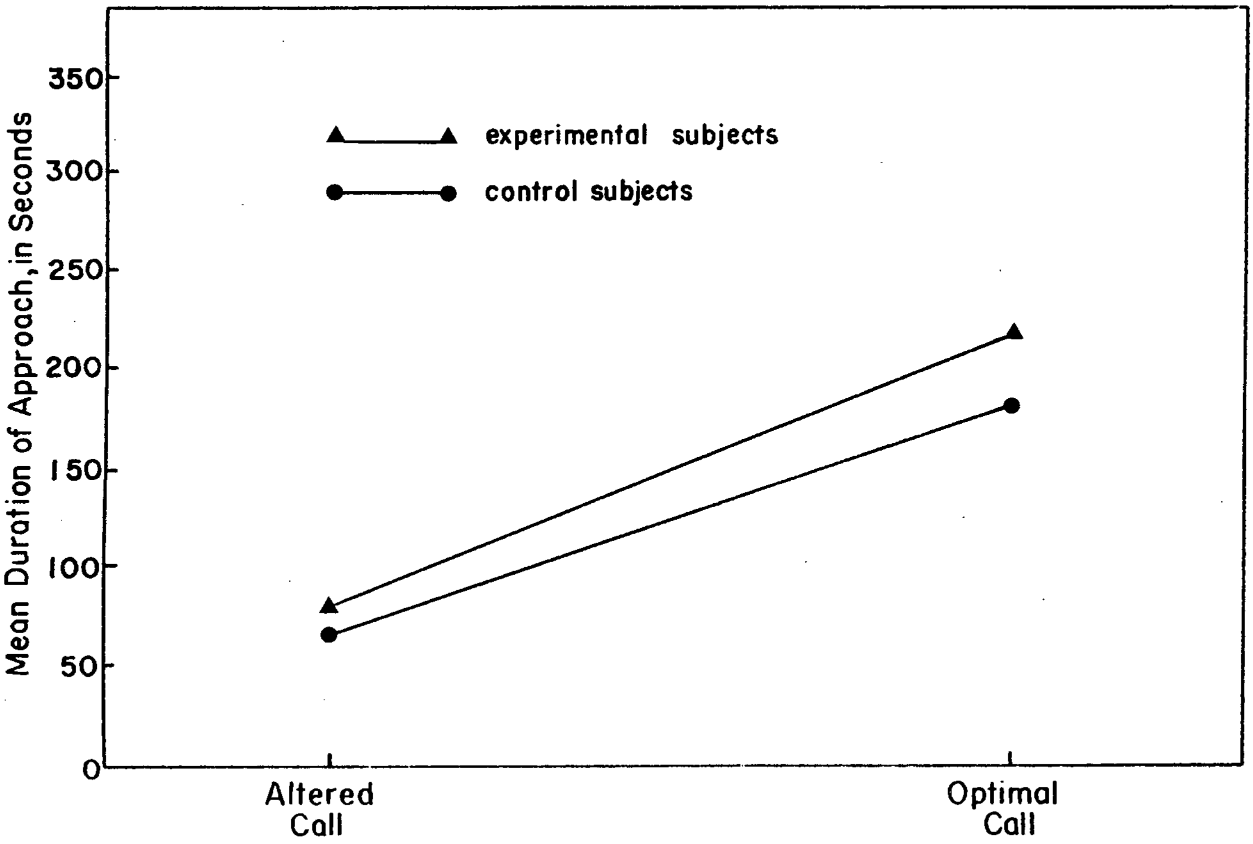


Fig. 21 Profile of mean duration of approach of experimental and control subjects tested with optimal and altered calls.

TABLE 16

Summary Table for Two Way Classification Analyses of Variance on Response Measures of Experimental and Control Groups (Factor A) Tested with an Optimal or Altered Call (Factor B).

Source	df	MS	F	p
Latency of Following				
A (Experimental vs Control Group)	1	17.7	.382	ns
B (Optimal vs Altered Calls)	1	495	10.6	$<.01$
AB (Interaction)	1	8.36	.180	ns
Within	56	46.4		
Duration of Following				
A (Experimental vs Control Group)	1	4.05	.124	ns
B (Optimal vs Altered Calls)	1	655	20.0	$<.01$
AB (Interaction)	1	2.77	.008	ns
Within	56			
Latency of Approach				
A (Experimental vs Control Group)	1	3.79	.134	ns
B (Optimal vs Altered Calls)	1	469	16.9	$<.01$
AB (Interaction)	1	6.38	.230	ns
Within	56	27.6		
Duration of Approach				
A (Experimental vs Control Group)	1	24.4	.767	ns
B (Optimal vs Altered)	1	472	14.8	$<.01$
AB (Interaction)	1	7.25	.227	ns
Within	56	31.8		

Note: ns = non significant statistical difference $(p>.05)$

TABLE 17

Experiment 5: Summary table of Pairwise Comparisons of Following and Approach Measures of Experimental Subjects tested with the Optimal (EO) and Altered calls (EA) and Control Subjects Tested with the Optimal (CO) and Altered Calls (CA) (Tukey's HSD test).

Following Latency

	EO ($\bar{x}$ = 204.9)	EA ($\bar{x}$ = 370.8)	CO ($\bar{x}$ = 209.3)	CA($\bar{x}$ = 433.2)
EO	-			
EA	2.84 p = .05	-		
CO	.194 ns	2.64 ns	-	
CA	3.88 p<.01	1.04 ns	3.69 p<.01	-

Following Duration

	EO ($\bar{x}$ = 189.3)	EA ($\bar{x}$ = 46.0)	CO ($\bar{x}$ = 169.8)	CA($\bar{x}$ = 34.3)
EO	-			
EA	4.18 p<.01	-		
CO	.006 ns	4.12 p<.01	-	
CA	4.83 p<.01	.643 ns	4.77 p<.01	-

Approach Latency

	EO ($\bar{x}$ = 71.7)	EA ($\bar{x}$ = 184.9)	CO ($\bar{x}$ = 96.1)	CA($\bar{x}$ = 174.9)
EO	-			
EA	4.59 p<.01	-		
CO	.851 ns	3.74 p<.05	-	
CA	4.48 p<.01	.110 ns	3.63 p<.05	-

Approach Duration

	EO ($\bar{x}$ = 205.9)	EA ($\bar{x}$ = 73.9	CO ($\bar{x}$ = 172.3)	CA($\bar{x}$ = 59.0)
EO	-			
EA	4.32 p<.01	-		
CO	1.35 ns	2.97 p<.05	-	
CA	4.72 p<.01	.398 ns	3.37 p<.05	-

Notes: 1. Key EO = Experimental group tested with Optimal call.
EA = Experimental group tested with Altered call.
CO = Control group tested with Optimal call.
CA = Control group tested with Altered call.

2. In all cases degrees of freedom = 2/56.

3. ns = non significant statistical difference (p>.05)

The chi square analyses revealed no statistically significant difference between any of the four groups with respect to the incidence of following ($X^2 = 4.53$, df = 3, $p > .05$) and approach responses ($X^2 = 1.12$, df = 3, $p > .05$).

Discussion:

Since both calls used in this experiment were generally attractive the insignificant differences in incidence of response were expected. Of major concern were any alterations in the strength of responding which may have occurred.

The results of this study indicate that there was no significant alteration of latency and duration of approach and following responses to the optimal or altered call as a result of prenatal stimulation with the altered call. Specifically, there was no marked increase in the strength of response of prenatally stimulated experimental subjects to the altered call and no evidence of interference with responses to the optimal call. Both experimental and control subjects showed a strong preference for the optimal call.

As shown in Table 15 and Figures 18 - 21 there was a slight, but generally consistent, decrease in latency scores and increase in duration scores in the groups with prenatal experience of the altered call (i.e. Eopt, Ealt). The change in responsiveness of the Ealt group did not appear to be related to experience of the unique characteristics of the altered call since the change was found in the Eopt group as well. This suggested that a factor or factors common to both calls might be responsible for the slightly stronger responsiveness of prenatally stimulated birds. It is possible that prenatal experience of any sound at the optimal intensity might positively influence postnatal responses to sounds at the same intensity. (Both altered and optimal calls were presented at the same intensity). The mechanism operative here might be analogous to a priming mechanism.

With regard to the questions posed earlier it is now possible to conclude that:

1. Prenatal stimulation with a non-preferred call did not result in a significant increase in the strength of postnatal responsiveness to the non-preferred call.
2. It thus proved impossible to alter ducklings' natural preference for the optimal call.
3. Prenatal stimulation with a non-preferred call did not interfere with the natural responsiveness of the ducklings to the optimal call.

CHAPTER 5

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Conclusions.

The results of the present series of experiments indicate that naive Peking X Aylesbury ducklings react selectively to certain classes of stimuli and that their differential responsiveness takes place without the benefits of any known form of learning. The species specificity of their responsiveness suggests that ducklings inherit a highly attuned response predisposition directed towards specific stimulus complexes. In natural circumstances this predisposition is for the conspecific maternal call. The beneficial value of this ability to respond selectively to certain classes of stimuli is clear. In natural situations precocial ground nesting hatchlings may be prevented from enjoying constant visual contact with the parent because of the terrain. However, by means of calling the hen is able to maintain a high degree of social control over her hatchlings, directing them towards sources of food and away from predators.

This ability does not represent merely the unfolding of a fixed or predetermined organic substrate independent of normally occurring sensory stimulation. The results of Gottlieb's (1971) elegant study indicate that the epigenesis of species specific auditory perception is a probabalistic phenomenon, the threshold, timing and ultimate perfection of such perception being regulated jointly by organismic and sensory stimulative factors originating from the embryo's and sibling vocalizations.

That the strength of postnatal responses is influenced as well by prenatal auditory stimulation from other sources is indicated by the results of experiment 4 in the present study. Duckling exposed prenatally to a preferred artificial call displayed stronger postnatal responses (shorter latency, longer duration) to that call than ducklings incubated in silence. This finding provides further support for a probabalistic interpretation of the epigenesis of differential responding in ducklings.

The results of the final experiment have shown that prenatal stimulation only enhances responsiveness to calls for which ducklings show a natural preference. It proved impossible to alter the preferences of ducklings by extended prenatal stimulation with a non preferred call. Again the biological significance of this evident. The presence of a predisposition for specific classes of calls would seem to greatly reduce the likelihood of the birds' becoming imprinted to species other than their own while still in the egg and after hatching.

Suggestions for future research

Approximation of experimental conditions to the natural situation

In natural situations auditory stimulation emanating from the parent does not occur independently of other parental activities. For example, it has been observed that egg shifting goes together with exposure to light and lowering of temperatures and parental calling either precedes or follows shifting. (Impekoven, 1973). The close temporal correlation of these activities may prove to have an important influence on the later behaviour of the bird. It is possible that there is some sort summation of effectiveness of different sensory modalities.

One way in which such influences might be detected would be to simultaneously vary stimulation in various sensory modalities and observe for differences in postnatal responses. For example, one group of embryos could be exposed to auditory stimulation at the same time the eggs are turned while another group could be stimulated at times when the eggs are still. Similarly exposure to light and cooling could be varied with different combinations of calling and turning patterns. Experimental studies of this kind combined with naturalistic field observations might provide the investigator with information about the most natural way of presenting experimental stimuli.

The importance of approximating the natural conditions in experimental research may have been underestimated. If a researcher uses unnatural types and patterns of stimulation it would not be inappropriate to question statements about the biological significance of resultant behaviour.

The Quantitative Analysis of Vocalization Patterns: Emergence of an Additional Index of Social Attachment.

Apart from following and approach behaviour,that aspect of the behaviour repertoire of ducklings which appeared to be most closely related to social attachment was the vocalization patterns. The impression was gained that those ducklings which showed strong locomotor responses displayed a fairly characteristic pattern of calling which differed markedly from the vocalization pattern of poor or non-responders.

On introduction into the test apparatus most birds would start emitting a stream of intense, high pitched cheep-like sounds. This has been identified as a distress call which is emitted in natural circumstances a variety of aversive situations e.g. reduction of body temperature, during threat from predators, during painful stimulation (Hafez, 1962). Distress calling tended to continue, with short interruptions, for the duration of the 5 minute pretest period in spite of the presence of the silent, stationary model.

It was during the presentation of the auditory stimulus that the characteristic patterns emerged. Whereas the poor responders emitted distress calls almost continuously, interspersed with brief periods of exhausted silence, the strong responders did so only at particular times during testing.

These observations raised the possibility that vocalization patterns might prove to be a sensitive indicant of social attachment. Further observations suggested that it might be even more sensitive than the standard index of imprinting used by most investigators i.e. locomotor responses. In the present study it was noticed that many ducklings in the initial stages of following did so in a laboured and uncoordinated way. Amazing as it is to altricial observers, precocial birds do possess the ability to walk shortly after hatching. However it is possible that their walking abilities are not as perfectly developed as other behaviour patterns. Since birds begin vocalizing well before hatching it seems likely that vocalizing abilities will be at a greater level of perfection, shortly after hatching, than locomotion. If this is indeed the case vocalization might prove to be, not only a sensitive index of imprinting, but also a more sensitive one than locomotor responses. That a relation between imprinting and distress vocalizations exist has been demonstrated by Hoffman (1968). He found that ducklings which had been imprinted on a moving object in the first two days posthatching emitted distress calls when the imprinting object was withdrawn. The distress calling almost invariably terminated when the imprinting object was again presented.

Similar responses were observed in the present study. In this case, however, withdrawal of the auditory stimulus alone was sufficient to evoke distress calling. It was observed that a fairly characteristic pattern of distress and contentment vocalization occurred in relation to the presentation of the auditory stimulus. This pattern is clearly illustrated in the results of running spectrum analyses of duckling vocalizations emitted in relation to the 12 second on-period and the 6 second off period of the auditory stimulus. The running spectrum analyses were performed using the Spectral Dynamics Model S.D. 301 Real Time Analyser, as modified by the Electrical Engineering Department, University of Cape Town (Semmelink, 1974). The spectra were displayed on a storage oscilloscope and photographed using a Polaroid land camera. In Figures 22 and 23, which are reproductions of photographs of the oscilloscope screen, the frequency dimension is represented on the vertical scale and time on the horizontal scale. Although a separate scale for amplitude is not included in the present analyses, the relative intensity of the vocalizations can be guaged from the width of the signals. The rows of repetitive signals seen in the two lower divisions are those of the optimal call which was used as the auditory stimulus. The large gaps in the optimal call signal represent the silent periods of 6 seconds duration. All other signals are those originating from the duckling.

A description of a typical vocalization pattern, with reference to Figures 22 and 23, follows:

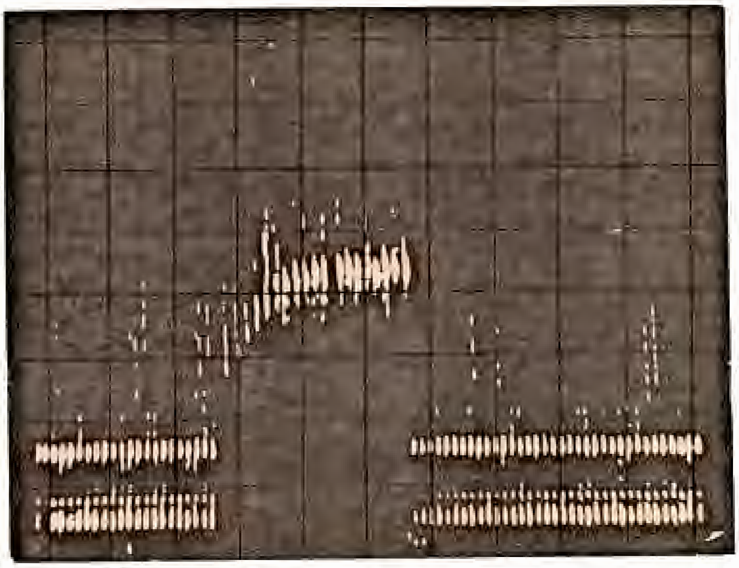


Fig. 22 Running spectrum analysis of the auditory stimulus and duckling vocalizations. Vertical scale: 1 div = 1KHz; Horizontal scale: 1 div. = 2 sec. Time span = 20 sec.

During periods of total silence (e.g. pre-test period) the ducklings would emit high pitched, high intensity distress calls. A half to one second after the start of a 12 second period of auditory stimulus presentation the distress calling stopped abruptly, to be replaced by lower frequency, lower intensity contentment calls. The latter were emitted intermittently for the duration of the presentation of the auditory stimulus. On withdrawal of the auditory stimulus (6 second period of silence) the contentment calls were almost immediately replaced by high frequency, high intensity distress calls. As shown in Figure 22 there was a rapid increase in the frequency and intensity (wider signals) of vocalizations within a few seconds of the start of the silent period. Once a peak was reached it was maintained until shortly after the start of the next 12 seconds of stimulus presentation, to be replaced again by contentment calling.

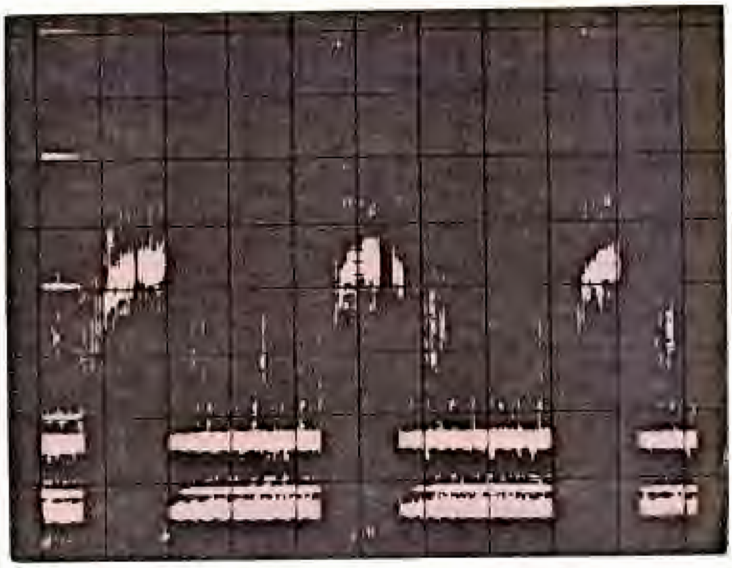


Fig. 23 Running spectrum analysis of the auditory stimulus and duckling vocalizations with time span extended to 50msec. Vertical scale: 1 div = 1KHz, Horizontal scale: 1 div. = 5 sec.

That this pattern was consistent over time is shown in Figure 23. In this spectrum analysis the time span has been extended to 50 seconds to allow the inclusion of three silent periods with the corresponding high frequency, high intensity distress calls elicited by withdrawal of the auditory stimulus. It was observed that these vocalization patterns did not typically emerge with poor or non-responders. Birds which displayed poor locomotor responses tended to continue distress calling irrespective of whether a call was being presented or not.

These observations suggest that characteristic vocalization patterns might be correlated with locomotor responses and other indicants of imprinting. Such a relationship, however, is yet to be established on more objective grounds. Future research findings might support the hypothesis that vocal interaction patterns between the duckling and the parent or surrogate mother is a sensitive and valuable index of social attachment.

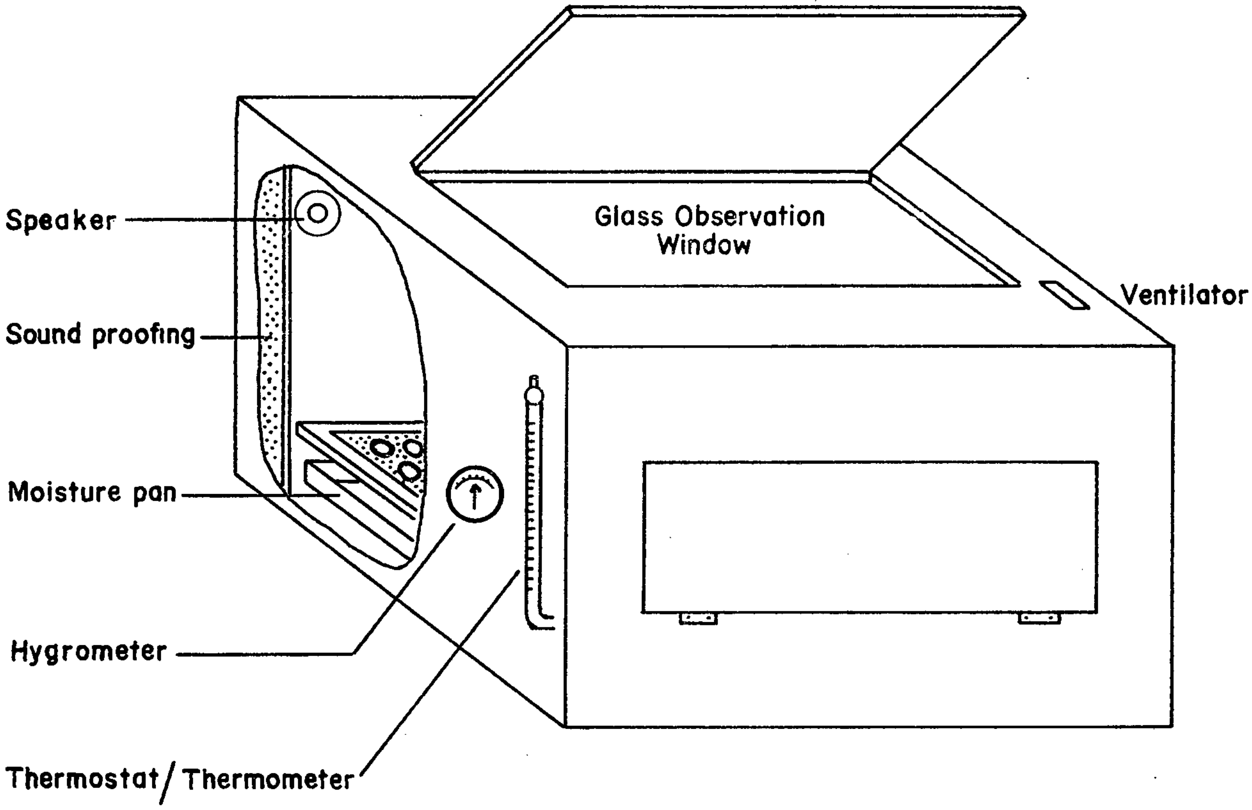
If it is correct that the absence of distress calls is an indication of attachment and that distress is evoked by withdrawal of the imprinting stimulus,then some interesting facts emerge from the present study. It would then appear that those birds imprinted in this study were imprinted solely on the auditory stimulus and not on the object since brief withdrawals of sound evoked distress vocalizations in spite of the fact that the object was not removed i.e. the visual and tactile attributes of the model alone did not prevent distress calling.

Whilst many authors have commented on the vocalizations of birds in imprinting situations few have gone so far as to attempt quantitative analyses. Those workers that have attempted quantification such as Hoffman, Stratton, Newby & Barrett (1970), have concentrated on recording the total time of distress calling and not on vocalization interaction patterns. Observations made during the present study indicate that such interaction patterns warrant attention. It is proposed that future research be directed towards establishing, more objectively, the relationship between the patterns and proportions of distress and contentment vocalizations, locomotor responses and long term effects of early social attachment. Until this is done the validity of using vocalizations as a criterion of long term attachment will remain suspect.

APPENDICES

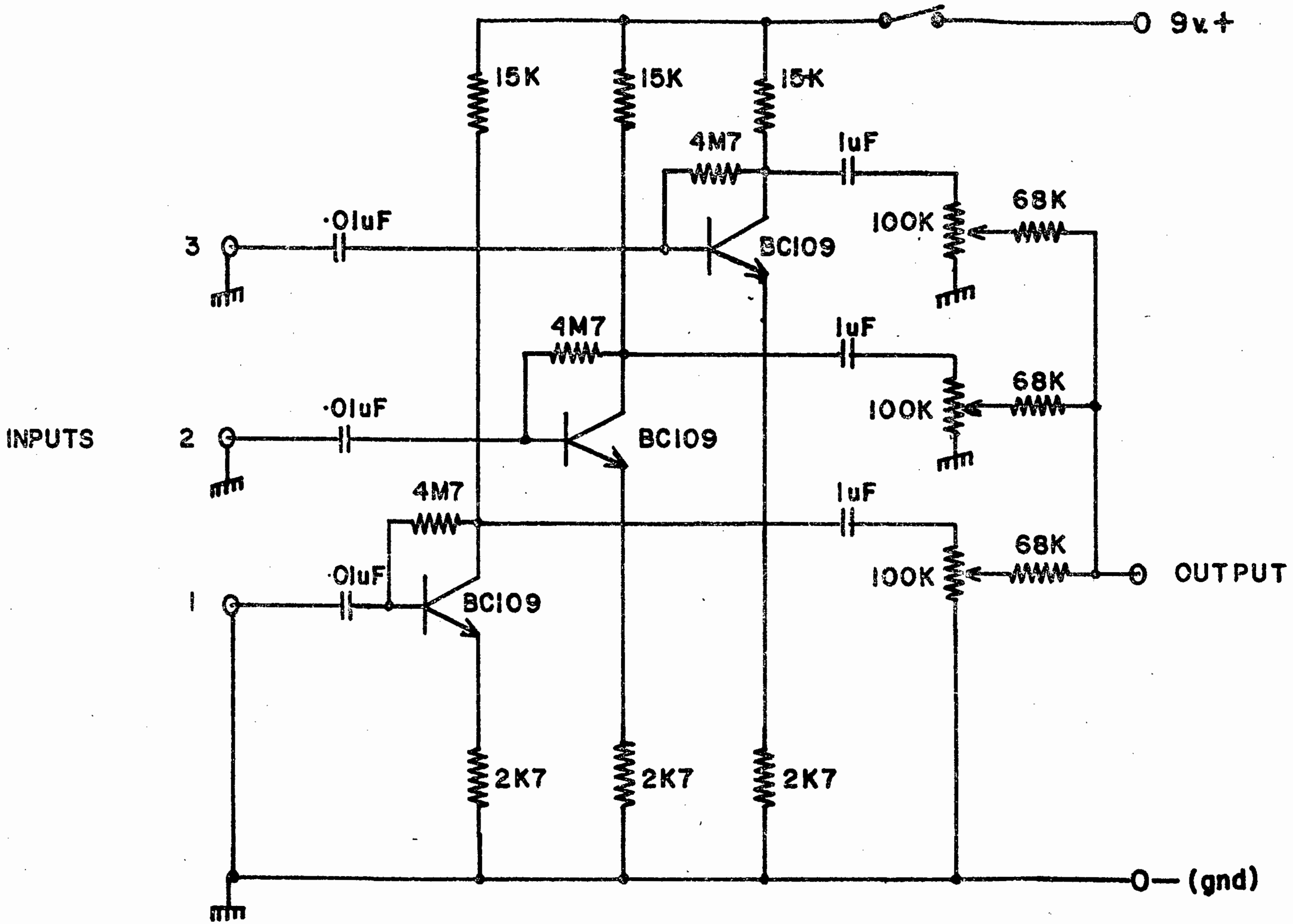
1. Diagram of Experimental Incubator.
2. Tone-mixing Circuit Diagram.
3. Print-out of the Absolute Assembler Tape.
4. Proposed Score Sheet of Behavioural Responses.
5. Response Measures in Following and Approach Tests (Raw data).
6. Notes on Audio-Visual Illustrations.

APPENDIX I



EXPERIMENTAL INCUBATOR

APPENDIX 2



TONE-MIXING CIRCUIT DIAGRAM

APPENDIX 3

Printout of Absolute Tape

```
0001                    ASMB,A,B,L
0002  00100                   ORG  100B
0003  00010             TBG   EQU  10B
0004  00015             OUT   EQU  15B
0005  00100  000000     COUNT BSS  1
0006  00101  000000     T1    BSS  1
0007  00102  000000     T2    BSS  1
0008  00103  000000     P1    BSS  1
0009  00104  102077     START HLT  77B
0010  00105  102501           LIA  1B
0011  00106  070100           STA  COUNT
0012  00107  102001           HLT  01B
0013  00110  102501           LIA  1B
0014  00111  070101           STA  T1
0015  00112  102002           HLT  02B
0016  00113  102501           LIA  1B
0017  00114  070102           STA  T2
0018  00115  102003           HLT  03B
0019  00116  102501           LIA  1B
0020  00117  070103           STA  P1
0021  00120  060202           LDA  ONE
0022  00121  102610           OTA  TBG
0023  00122  002400           CLA
0024  00123  102601           OTA  1B
0025  00124  102055           HLT  55B
0026  00125  002400     LOOP  CLA
0027  00126  070203           STA  TIME
0028  00127  103710           STC  TBG,C
0029  00130  102310     L1    SFS  TBG
0030  00131  024130           JMP  L1
0031  00132  103710           STC  TBG,C
0032  00133  060203           LDA  TIME
0033  00134  002004           INA
0034  00135  070203           STA  TIME
0035  00136  050103           CPA  P1
0036  00137  024141           JMP  *+2
0037  00140  024130           JMP  L1
0038  00141  002400           CLA
0039  00142  070204           STA  KOUNT
0040  00143  006400     GO    CLB
0041  00144  074203           STB  TIME
0042  00145  060202           LDA  ONE
0043  00146  102615           OTA  OUT
0044  00147  102310     L2    SFS  TBG
0045  00150  024147           JMP  L2
0046  00151  103710           STC  TBG,C
0047  00152  060203           LDA  TIME
0048  00153  002004           INA
0049  00154  070203           STA  TIME
0050  00155  050101           CPA  T1
0051  00156  024160           JMP  *+2
0052  00157  024147           JMP  L2
0053  00160  002400           CLA
0054  00161  102615           OTA  OUT
0055  00162  070203           STA  TIME
0056  00163  102310     L3    SFS  TBG
0057  00164  024163           JMP  L3
```

```
0058   00165 103710          STC TBG,C
0059   00166 060203          LDA TIME
0060   00167 002004          INA
0061   00170 070203          STA TIME
0062   00171 050102          CPA T2
0063   00172 024174          JMP *+2
0064   00173 024163          JMP L3
0065   00174 060204          LDA KOUNT
0066   00175 002004          INA
0067   00176 070204          STA KOUNT
0068   00177 050100          CPA COUNT
0069   00200 024125          JMP LOOP
0070   00201 024143          JMP GO
0071   00202 000001   ONE    OCT 1
0072   00203 000000   TIME   BSS 1
0073   00204 000000   KOUNT  BSS 1
0074                         END START
**  NO ERRORS*
```

APPENDIX 4

TEST / PRETEST

SUBJECT =

DATE & TIME OF BIRTH =

TIME OF TESTING =

AGE AT TESTING =

	LATENCY	DURATION
FOLLOWING RESPONSE		
FOLLOWING RESPONSE (R.O)		
APPROACH RESPONSE		

ORIENTATION

✓ = towards
– = away

POSTURE

C = Sitting & Crouching
S = Standing
– = Walking

DEFAECATION

✓ = Yes
– = No

CALLS

P = Pleasure
D = Distress
S = Silence

POSITION CHANGE

S = Stationary
A = Approach
W = Withdraw

CONTACT WITH OBJECT

✓ = Yes
– = No

APPENDIX 5

RESPONSE MEASURES IN FOLLOWING AND APPROACH TESTS (RAW DATA).

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 1 : Response measures to Complex Call 1.						
1	-	-	120	88	63	81
6	-	-	316	106	300	0
11	-	-	720	0	129	37
16	-	-	20	188	3	254
21	-	-	156	175	44	22
26	192	3	126	146	12	182
31	-	-	88	306	11	188
36	-	-	318	106	40	122
41	-	-	720	0	300	0
46	-	-	56	74	44	154
Experiment 1: Response measures to Complex Call 2.						
2	-	-	720	0	300	0
7	-	-	496	14	300	0
12	-	-	320	51	139	36
17	-	-	720	0	258	16
22	73	11	194	88	95	110
27	-	-	278	24	23	123
32	-	-	720	0	300	0
37	-	-	720	0	300	0
42	9	4	159	71	156	76
47	-	-	211	45	131	141

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 1 : Response measures to Complex Call 3.						
3	-	-	422	21	191	43
8	-	-	242	81	83	137
13	-	-	274	16	12	168
18	-	-	720	0	300	0
23	-	-	720	0	202	9
28	-	-	497	18	134	48
33	-	-	720	0	178	21
38	-	-	720	0	300	0
43	-	-	177	20	74	90
48	-	-	720	0	300	0
Experiment 1: Response measures to Complex Call 4.						
4	-	-	209	27	126	28
9	-	-	88	105	17	180
14	-	-	720	0	300	0
19	-	-	24	184	78	93
24	271	4	375	70	149	26
29	-	-	720	0	300	0
34	-	-	720	0	300	0
39	-	-	720	0	300	0
44	-	-	234	58	214	14
49	-	-	476	21	34	173

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 1 : Response measures to Silent Control						
5	-	-	720	0	300	0
10	281	6	720	0	300	0
15	-	-	720	0	300	0
20	-	-	346	11	300	0
25	-	-	720	0	300	0
30	-	-	720	0	300	0
35	-	-	720	0	300	0
40	-	-	416	13	223	7
45	-	-	720	0	300	0
50	-	-	720	0	300	0
Experiment 2 : Response measures to Repetition Rate 1/Sec						
1	147	6	720	0	300	0
6	-	-	324	34	228	33
11	-	-	494	8	300	0
16	-	-	720	0	300	0
21	-	-	720	0	300	0
26	-	-	370	21	37	184
31	-	-	720	0	236	28
36	-	-	192	27	191	46
41	91	47	720	0	300	0
46	-	-	210	33	88	22

	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 2 : Response measures to Repetition Rate 4/Sec						
2	-	-	68	137	31	201
7	46	3	144	59	87	46
12	-	-	44	145	27	273
17	-	-	720	0	26	154
22	-	-	720	0	300	0
27	-	-	183	113	122	178
32	192	7	284	140	55	221
37	8	5	76	131	70	193
42	-	-	184	97	14	237
47	-	-	184	91	53	247
Experiment 2 : Response measures to Repetition Rate 8/Sec						
3	-	-	720	0	300	0
8	-	-	418	6	300	0
13	-	-	272	40	101	171
18	-	-	246	151	46	216
23	-	-	373	47	154	16
28	-	-	720	0	300	0
33	-	-	197	101	141	48
38	-	-	720	0	300	0
43	-	-	201	37	93	107
48	-	-	54	39	99	142

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 2 : Response measures to Repetition Rate 16/Sec						
4	-	-	720	0	300	0
9	-	-	720	0	300	0
14	-	-	720	0	300	0
19	261	3	518	7	211	11
24	-	-	720	0	300	0
29	91	9	720	0	300	0
34	-	-	720	0	300	0
39	-	-	311	15	300	0
44	-	-	720	0	300	0
49	-	-	720	0	173	23
Experiment 2 : Response to Silent Control						
5	-	-	720	0	300	0
10	201	18	416	22	300	0
15	-	-	720	0	300	0
20	-	-	720	0	300	0
25	-	-	720	0	300	0
30	-	-	720	0	300	0
35	-	-	720	0	300	0
40	-	-	720	0	300	0
45	-	-	720	0	300	0
50	-	-	720	0	300	0

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 3 : Response measures to Duration 25msec.						
1	17	7	121	125	30	217
6	-	-	362	77	166	4
11	-	-	221	43	23	244
17	-	-	720	0	300	0
22	-	-	202	96	101	98
27	-	-	356	92	36	175
32	-	-	720	0	12	125
37	-	-	143	231	90	181
42	-	-	720	0	300	0
47	-	-	197	141	182	14
	*S16 died before testing.					
Experiment 3 : Response measures to Duration 50msec.						
2	-	-	76	291	3	262
7	-	-	132	184	100	110
12	184	3	158	60	26	229
18	79	7	720	0	300	0
23	-	-	40	404	66	52
28	-	-	720	0	21	261
23	-	-	62	158	31	171
38	-	-	116	196	3	294
43	-	-	143	121	10	286
48	-	-	243	197	18	279

Experiment 3 : Response measures to Duration 100msec.

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec
3	-	-	720	0	300	0
8	-	-	303	48	149	24
13	-	-	577	57	300	0
19	-	-	466	37	153	12
24	-	-	720	0	300	0
27	-	-	720	0	172	40
34	-	-	246	24	148	49
39	-	-	317	63	107	124
44	-	-	720	0	300	0
49	-	-	191	111	73	133

Experiment 3 : Response measures to Duration 150msec.

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec
4	-	-	720	0	300	0
9	-	-	720	0	300	0
14	-	-	329	13	204	23
20	-	-	423	9	177	48
25	-	-	720	0	300	0
30	-	-	720	0	300	0
35	-	-	720	0	245	12
40	116	6	720	0	300	0
45	-	-	298	18	118	27
50	203	20	720	0	300	0

Experiment 3 : Response measures to Silent Control

S	Pre-Test Approach Responses		Following Response		Approach Response	
	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec
5	-	-	720	0	300	0
10	201	11	720	0	300	0
15	-	-	720	0	300	0
21	-	-	720	0	300	0
26	-	-	493	18	209	13
31	-	-	720	0	300	0
36	-	-	720	0	300	0
41	-	-	720	0	300	0
46	-	-	511	12	300	0
51	-	-	720	0	300	0

S	Pre-Test Approach Responses		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
	Experiment 4 : Experimental Group					
1	-	-	75	389	5	268
2	-	-	118	96	68	232
3	-	-	24	302	11	280
4	-	-	46	278	5	292
5	-	-	720	0	10	290
6	-	-	21	568	2	298
7	-	-	174	240	4	296
8	-	-	94	274	8	292
9	-	-	117	118	28	231
10	101	27	57	216	12	273
11	-	-	33	372	3	297
12	-	-	39	329	4	296
13	-	-	720	0	11	281
14	117	11	99	151	71	200
15	209	7	66	436	5	295
16	-	-	73	191	15	278
17	-	-	54	268	3	288
18	-	-	203	18	141	159
19	-	-	147	156	7	293
20	-	-	720	0	300	0

S	Pre-Test Approach Responses		Following Response		Approach Response	
	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec
	Experiment 4 : Control Group					
1	-	-	162	95	300	0
2	-	-	274	115	96	13
3	-	-	205	184	153	147
4	86	3	720	0	62	224
5	-	-	68	189	6	201
6	-	-	214	181	6	294
7	-	-	91	368	3	288
8	-	-	42	232	18	252
9	-	-	136	116	136	78
10	-	-	110	176	4	260
11	-	-	720	0	74	120
12	263	14	156	148	16	262
13	-	-	720	0	300	0
14	191	2	720	0	43	230
15	-	-	100	273	11	241
16	-	-	206	126	18	166
17	-	-	488	14	84	200
18	-	-	720	0	300	0
19	-	-	76	258	3	218
20	-	-	48	164	4	215

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 5 : Experimental Group - Response to Optimal Call						
E1	-	-	720	0	194	106
E3	-	-	212	176	2	298
E5	-	-	58	372	3	297
E7	-	-	100	22	300	0
E9	-	-	156	118	79	101
E11	182	14	163	76	48	236
E13	-	-	59	179	3	297
E15	-	-	22	533	3	297
E17	-	-	213	158	54	238
E19	-	-	137	287	3	297
E21	54	4	46	197	15	261
E23	-	-	62	668	3	297
E25	-	-	720	0	300	0
E27	-	-	143	22	22	163
E29	-	-	263	31	46	201

S	Pre-Test Approach Responses		Following Response		Approach Response	
	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec	Latency, Sec	Duration, Sec
Experiment 5 : Experimental Group - Response to Altered Call						
E2	-	-	720	0	300	0
E4	-	-	433	34	239	61
E6	-	-	720	, 0	300	0
E8	63	17	91	109	11	257
E10	-	-	720	0	162	138
E12	-	-	720	0	196	14
E14	-	-	99	91	73	98
E16	-	-	233	47	241	21
E18	9	4	720	0	154	71
E20	148	7	327	20	300	0
E22	-	-	324	14	300	0
E24	-	-	96	181	247	31
E26	-	-	67	73	101	143
E28	-	-	104	86	142	42
E30	-	-	188	35	7	233

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 5 : Control Group - Response to Optimal Call						
C1	-	-	34	292	3	297
C3	-	-	78	293	6	294
C5	-	-	720	0	300	0
C7	-	-	184	89	16	87
C9	111	9	102	28	300	0
C11	-	-	73	381	7	293
C13	-	-	222	171	11	207
C15	-	-	186	83	47	194
C17	-	-	161	301	14	274
C19	-	-	247	24	300	0
C21	-	-	720	0	300	0
C23	-	-	98	177	94	184
C25	-	-	88	349	5	295
C27	-	-	152	157	17	211
C29	-	-	75	202	22	248

S	Pre-Test Approach Response		Following Response		Approach Response	
	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec	Latency,Sec	Duration,Sec
Experiment 5 : Control Group - Response to Altered Call						
C2	-	-	720	0	197	103
C4	-	-	720	0	300	0
C6	-	-	264	47	84	31
C8	-	-	142	94	20	226
C10	-	-	720	0	191	41
C12	-	-	102	119	43	93
C14	-	-	534	17	113	64
C16	-	-	343	9	300	0
C18	-	-	153	12	201	95
C20	-	-	256	57	79	63
C22	-	-	720	0	300	0
C24	9	43	67	110	127	125
C26	-	-	317	49	173	12
C28	-	-	720	0	300	0
C30	-	-	720	0	195	32

APPENDIX 6

NOTES ON AUDIO-VISUAL ILLUSTRATIONS.

The following films are available at the Department of Psychology, University of Cape Town.

1. 16mm Colour film:

A 300 ft. (± 12 minutes), 16mm colour film has been produced. In this film neonatal Peking X Aylesbury ducklings are shown performing the characteristic following and approach responses on the circular imprinting apparatus. A short sequence in which a duckling attempts and finally succeeds in mounting and balancing on top of the moving object is included.

The definition of this film is good but, unfortunately, it lacks sound. Consequently the characteristic vocalization patterns which emerged are not illustrated.

2. Black and white video-tape film:

A 30 minute video tape film is available in which all characteristic behaviour patterns are illustrated. In this film the lack of crisp definition obtained in the colour film is compensated for by the good recordings of vocalizations emitted in relation to the presentation of the auditory stimulus.

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