

## MECHANISMS OF AVIAN IMPRINTING: A REVIEW

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### CONTENTS

I. Introduction . . . . .	303
II. Characteristics of filial imprinting . . . . .	304
III. Predispositions . . . . .	307
IV. Sensitive periods . . . . .	310
V. Reversibility . . . . .	311
VI. The learning process of imprinting . . . . .	314
(1) Associative learning interpretations . . . . .	314
(2) Perceptual learning interpretations . . . . .	316
VII. The influence of social interactions on the formation of social preferences . . . . .	318
(1) Interactions between the subject and the parent (-surrogate) . . . . .	318
(2) Interactions between the subject and its siblings . . . . .	319
VIII. Auditory imprinting . . . . .	320
(1) Auditory learning . . . . .	320
(2) Species-specific predispositions . . . . .	323
IX. Sexual imprinting . . . . .	324
(1) General characteristics . . . . .	324
(2) Reversibility and sensitive periods . . . . .	325
(3) Predispositions and social interaction . . . . .	326
X. Hormones and imprinting . . . . .	327
(1) Pituitary-adrenocortical hormones . . . . .	327
(2) Gonadal hormones . . . . .	328
XI. Neural mechanisms of filial imprinting . . . . .	330
(1) Neural mechanisms of the learning process . . . . .	330
(2) Predispositions and individual recognition . . . . .	331
XII. Conclusions and Discussion . . . . .	333
(1) Learning and representations . . . . .	333
(2) Imprinting and the development of behaviour . . . . .	334
(3) General considerations . . . . .	335
XIII. Summary . . . . .	335
XIV. Acknowledgments . . . . .	336
XV. References . . . . .	336

### I. INTRODUCTION

Twenty-five years ago, Bateson (1966) reviewed imprinting in this journal. At about that time, Sluckin (1965; see Sluckin, 1972) published a monograph providing a comprehensive review of research into the development of filial and sexual preferences in birds and mammals (for other reviews see Moltz, 1960; Hess, 1973; Rajecki, 1973; Smith, 1983; for early reviews see Spalding, 1873; Heinroth, 1911; Lorenz, 1935). The evidence on avian imprinting that has accumulated since then is reviewed in the present

paper, illustrating how this research has enhanced the understanding of mechanisms of learning, memory and behavioural development.

Although several studies have shown that imprinting-like phenomena may occur in mammals (e.g. Sluckin, 1968), most of the work on imprinting has used birds. For this reason, this review is limited to avian imprinting. In a paper such as this, a quarter of a century of research cannot be reviewed exhaustively. Therefore, this review is selective and presents evidence that is representative of the major research trends in the study of imprinting. Recent years have witnessed an upsurge of research into the mechanisms of imprinting, not in the least as a result of neurobiological investigations (e.g. Horn, 1985). The neurobiological study of imprinting has concentrated on the neural mechanisms of the learning process involved. This research will be summarized briefly in the present paper; for a comprehensive review of this work, see Horn (1985, 1990).

The emphasis in this review is on the causal analysis of imprinting. Functional considerations of imprinting have been discussed by Immelmann (1972*b*) and Bateson (1979, 1983*a, b*). In the study of imprinting, on the one hand there are attempts to describe and analyse the behaviour as it occurs in a naturalistic context, shaped by natural selection. On the other hand, imprinting is used as a means to study learning and development at the psychological and neurobiological level. The latter approach is not so much concerned with providing an accurate analysis of the naturally occurring behaviour, but uses standardized laboratory methods to study underlying mechanisms. This review is concerned with the latter approach, and deals with the mechanisms involved in learning, memory and development, as studied within the imprinting paradigm.

According to Lorenz (1935), one of the consequences of imprinting is the determination of adult sexual preferences. Subsequent research suggests that filial and sexual imprinting are two different (although perhaps analogous and partially overlapping) processes (Immelmann, 1972*a*; Bateson, 1979; Vidal, 1980; Ten Cate, 1989*b*). Most of the present review is concerned with filial imprinting. Sexual imprinting will be explicitly discussed in Section IX. Although in the natural context auditory stimuli may affect the formation of filial preferences (e.g. Gottlieb, 1971), historically the research has dealt mainly with visual imprinting. As a consequence, the present paper is primarily concerned with the development of preferences for visual stimuli. However, there have been important developments in the field of auditory imprinting which will be discussed in Section VIII.

## II. CHARACTERISTICS OF FILIAL IMPRINTING

The formation of filial preferences has been studied mostly in precocial birds such as mallard ducklings (*Anas platyrhynchos*) and domestic chicks (*Gallus gallus domesticus*). These birds can move about shortly after hatching and will approach and follow a conspicuous object to which they are exposed. In a natural situation this is likely to be the bird's mother or sibling. It has been shown that in the absence of mother and siblings, a wide range of inanimate mother-surrogates also elicit filial behaviour (cf. Bateson, 1966; Sluckin, 1972; Horn, 1985). When the chick or duckling is close to the appropriate object it will attempt to snuggle up to it, frequently emitting soft 'twitters'. When the object is removed the chick becomes restless and emits shrill calls. Initially the young bird approaches any conspicuous object to which it is exposed, but after it

has had some experience with a particular object the bird will remain close to this object and actively avoid novel ones. When given a choice between the familiar stimulus and a novel one the bird preferentially approaches the familiar stimulus. Filial imprinting is defined here as the process through which social behaviour of the young animal becomes limited to a particular object or class of objects. Thus, it refers to the acquisition of a social preference and not just an increase in the following response (cf. Salzen, 1966; Sluckin, 1972). Lorenz (1935) pointed out that imprinting is not a universal phenomenon that applies to all species of birds. For example, he noted that newly hatched chicks of the curlew (*Numenius arquata*) could not be made to follow their human keeper, whilst chicks of the greylag goose (*Anser anser*) could. In Lorenz's terms, the curlew has an innate 'Schema' of the appropriate 'companion' ('Kumpan'), whereas in the greylag goose, the Schema is formed by experience with a particular object.

Lorenz (1935, 1937) and others (cf. Hess, 1959*a*) have suggested that filial imprinting is different from other forms of learning. Firstly, it occurs without any obvious conventional reinforcement. Further, imprinting was thought to be irreversible. Thirdly, imprinting was believed to occur during a 'sensitive period' (or 'critical period'). It has become clear that some of Lorenz's claims cannot be maintained. Evidence concerning all of these claims will be reviewed in this paper. To begin with, evidence on the role of predispositions in imprinting will be discussed. These findings have implications for research into those characteristics of imprinting that Lorenz and others thought made it unique.

To study imprinting in the laboratory, chicks or ducklings may be hatched in darkness, and exposed to a conspicuous object when they are about 24 h old (see McCabe, Horn & Bateson, 1981; Horn, 1985; Bateson, 1991*a*, and Bolhuis & Johnson, 1991*a* for details of experimental procedures). After exposure (training) the animals are returned to a holding incubator and kept in darkness, until their preferences are tested in a sequential or simultaneous choice test. Bateson (1966) concluded that, in general, the more conspicuous an object is to the human eye, the more effective it will be as an imprinting stimulus. Movement of the object increases its attractiveness (e.g. Hoffman, 1978; Eiserer, 1980; Ten Cate, 1989*a*) as does the presentation of an auditory stimulus with a visual stimulus (e.g. Smith & Bird, 1964; Evans, 1972). The effectiveness of stimuli for imprinting varies with their size and colour (see Bateson, 1966; Sluckin, 1972). Fabricius and Boyd (1952/3) reported that young ducklings approached and followed objects larger than a matchbox, but pecked at smaller objects. For chicks it was shown by Schulman, Hale & Graves (1970) that circular objects with a diameter of 10–20 cm were approached more readily than a number of other objects. Several authors have investigated the effectiveness of different colours of imprinting stimuli. Red and blue were found to be more effective than yellow and green in eliciting approach (Schaefer & Hess, 1959; Gray, 1960; Kovach, 1971; Salzen, Lily & McKeown, 1971). Kovach and his collaborators (Kovach, 1980, 1983; Kovach & Wilson, 1981, 1983; Kovach, Yeatman & Wilson, 1981) succeeded in selecting, over a number of generations, for naïve preferences for different colours in quail chicks (*Coturnix coturnix japonica*). So far, it has not been reported that chicks or ducklings learn better, or faster, with naturalistic imprinting stimuli (such as stuffed models of ducks or fowl) than with artificial imprinting stimuli (e.g. Bolhuis, Johnson & Horn, 1985; Horn, 1985; Bolhuis & Trooster, 1988). On the contrary, some authors have

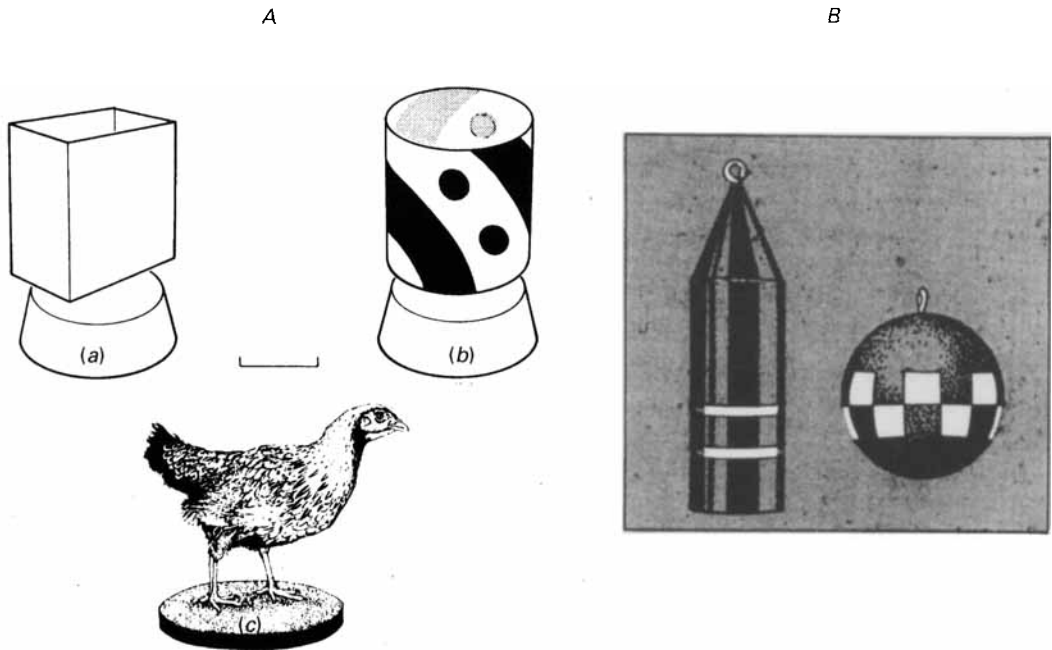


Fig. 1. Examples of objects used in laboratory studies of imprinting. Scale bar in A is 10 cm. The cylinder in B is 13 cm high, diameter 3.7 cm. (Drawing of the stuffed jungle-fowl by Priscilla Barrett. A taken from Horn (1985), *Memory, Imprinting and the Brain*, by permission of the Oxford University Press. B taken from Bolhuis & Bateson, 1990; reprinted with permission.)

reported that chicks (Johnson & Horn, 1987) and ducklings (Johnston & Gottlieb, 1981a) actually require exposure to stuffed models for longer to achieve preference scores that are similar to those for artificial imprinting objects. In Section III, evidence will be reviewed demonstrating a predisposition in chicks to preferentially *approach and follow* certain objects more than others. Fig. 1 shows some of the objects used in laboratory studies of filial imprinting.

A widely used measure of the animal's filial preference is the approach to the familiar object relative to a different, novel object (Sluckin, 1972; Horn, 1985). Thus, variations in absolute approach activity are not considered as an index of the strength of imprinting. Another measure of the birds' level of attachment to the imprinting object is the reduction in distress calling in the presence of the familiar object, compared to the presence of a novel object (e.g. Hoffman, Ratner & Eiserer, 1972; Boakes & Panter, 1985; De Vos & Bolhuis, 1990). Means of measuring the strength of sexual preferences will be discussed in Section IX.

Contrary to what the term suggests, imprinting is not an instantaneous process. The animal needs to be exposed to the stimulus for some time, usually 1–2 h (cf. Bateson, Rose & Horn, 1973). Bateson & Jaeckel (1974) reported a significant but weak correlation between chicks' approach activity during training and the strength of filial preferences. The authors concluded that the relationship was too weak to form the basis of a 'law of effort' as had been suggested previously (Hess, 1959a). Bateson & Seaburne-May (1973) and Bateson & Wainwright (1972) showed that a brief period of

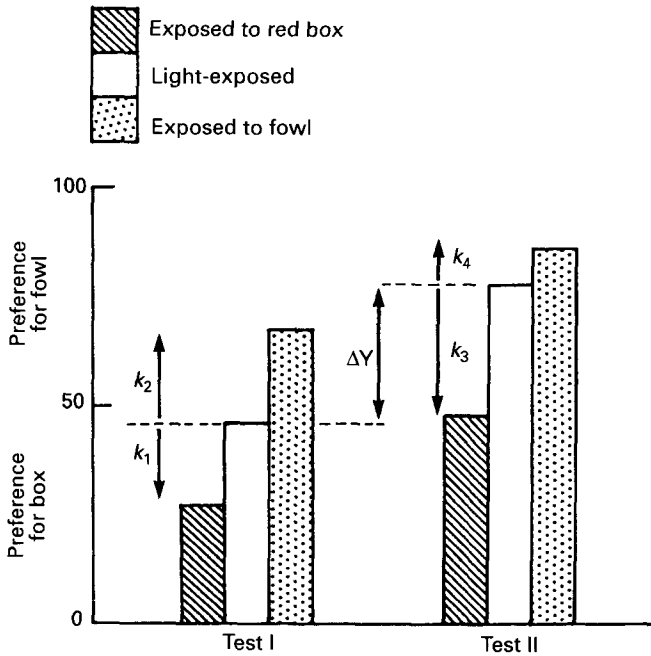


Fig. 2. Mean preference scores, expressed as a preference for the stuffed fowl, of chicks previously trained by exposure to a rotating stuffed fowl, a rotating red box, or exposed to white light. Preference scores are defined as:

$$\frac{\text{activity when attempting to approach the stuffed jungle-fowl}}{\text{total approach activity}} \times 100.$$

Preferences were measured in a simultaneous test either 2 h (Test I) or 24 h (Test II) after the end of training.  $k_1$ - $k_4$  represent the differences between the preferences of the trained chicks and the controls;  $\Delta Y$  represents the difference in preference between the control chicks at Test II and at Test I. See text for further explanation. (After Johnson *et al.* 1985. Reprinted with permission.)

exposure to white light enhanced subsequent following of a conspicuous object and increased the rate of imprinting.

### III. PREDISPOSITIONS

Evidence for the role of predispositions in filial imprinting in chicks has been reviewed by Horn (1985) and by Johnson & Bolhuis (1991). Findings were discussed in Section II, showing that chicks and ducklings have certain naïve biases to preferentially approach stimuli of a certain size and colour. The influence of such naïve biases on imprinting is illustrated by a study by Bateson & Jaeckel (1976; cf. Bateson, 1983*a*). Chicks were trained by exposing them to either a red or a yellow flashing light. Bateson and Jaeckel found that the chicks in both groups showed a significant preference for the training stimulus, but that the preference of the red-trained chicks was significantly greater than that of the yellow-trained chicks. Furthermore, chicks in an untrained control group showed a small but significant preference for the red light over the yellow light. Bateson (1983*a*) concluded that the preferences of the trained chicks were affected both by experience with the training object and by a naïve bias for red over yellow.

Johnson & Bolhuis (1991) distinguished between *general* and *specific* predispositions. The different biases to preferentially approach objects of particular colours, shapes, sizes, etc., are examples of the former, where elementary features of stimuli are involved. Specific predispositions are thought to be qualitatively different from general predispositions, and involve more complex clusters of features. The underlying mechanisms of the two kinds of predispositions are likely to be different (see below; cf. Johnson & Horn, 1988; Bolhuis & Johnson, 1991*b*). Evidence for a species-specific auditory predisposition in ducklings is discussed in Section VIII. A specific visual predisposition in the chick was demonstrated by Johnson, Bolhuis & Horn (1985) and Bolhuis, Johnson & Horn (1985). This predisposition became apparent as a growing preference for a rotating stuffed jungle fowl hen over a simple artificial stimulus (a rotating red box; see Fig. 1). Bolhuis *et al.* (1985) placed dark-reared chicks in running wheels, in darkness, at about 24 h after hatching for two periods of 1 h. Preferences of these dark-reared chicks were tested 2 or 24 h after the end of this treatment, in a simultaneous choice test involving a stuffed jungle fowl and a red box. A significant preference for the stuffed fowl was manifest in the chicks that were tested at 24 h after the end of treatment, when the chicks were approximately 50 h old, but not in chicks that were tested 2 h after the end of treatment. Johnson *et al.* (1985) found that when chicks were trained by exposing them to the red box or the stuffed fowl when they were 24 h old, filial preferences of these chicks at 50 h were not only a result of exposure to the particular conspicuous object, but were also affected by the developing predisposition to approach stimuli such as the fowl. That is, there was a significantly greater preference for the fowl at 24 h after training compared to 2 h after training, irrespective of whether the chicks were trained by exposure to the fowl, or the red box, or whether they were exposed to white light only.

Fig. 2 illustrates the main findings of Johnson *et al.* (1985), with all preferences expressed as a preference for the stuffed fowl. The increase in preference is represented as  $\Delta y$ , and was significant in all three groups. The difference between the mean preference scores of the trained groups and that of the light-reared control group, a result of exposure to these stimuli, is represented in Fig. 2 as  $k_1 - k_4$ ; this difference was stable over time. The preference for the fowl also appeared in dark-reared chicks, provided that they received a period of non-specific stimulation (in this case being placed in running wheels in darkness for two periods of 1 h; Bolhuis *et al.*, 1985; Johnson & Horn, 1988). Interestingly, the preference for the fowl failed to appear when the chicks did not receive this non-specific stimulation and, furthermore, was not apparent 2 h after this treatment, but 24 h later. Thus, if the emergence of the predisposition were due to 'stress' or 'arousal' caused by placement of the chicks in the wheels, the effects of this treatment would be delayed, and not manifest 2 h after such treatment. It was found that exposure to a complex visual pattern accelerated the development of the predisposition (Bolhuis *et al.*, 1985). Bolhuis & Trooster (1988) confirmed the hypothesis of two interacting mechanisms in filial imprinting using a reversibility paradigm (see Section V). Johnson, Davies & Horn (1989) showed that there was a 'sensitive period' within which non-specific experience could induce the development of the predisposition (see Section IV).

In a series of experiments, Johnson & Horn (1988) investigated the characteristics of the stuffed fowl that caused it to be preferred over the red box. They attempted to

'titrate' the visual complexity of the stimulus against its 'fowl-like' characteristics. To this end, the preferences of dark-reared chicks, which had been placed in running wheels for 2 h when they were approximately 24 h old, were tested either 2 or 24 h later. Stimuli used during the tests were an intact stuffed jungle fowl versus one in a series of increasingly degraded versions of a stuffed jungle fowl. The degraded versions ranged from one where different parts of the model (wings, head, rump, legs) were reassembled in an unnatural way, to one in which the pelt of a jungle fowl had been cut into small pieces that were stuck onto a rotating box. It was found that the intact model was preferred at the second test, when the chicks were approximately 52 h old, only when the degraded object possessed no distinguishable jungle fowl features. In addition, Johnson & Horn (1988) demonstrated that chicks did not prefer an intact jungle fowl model over an alternative object that contained only the head and neck of a stuffed fowl. Thus, it seems likely that the head and neck region contains stimuli that are relevant for the predisposition. In subsequent experiments, Johnson & Horn (1988) found that the chicks did not prefer a stuffed jungle fowl hen over a stuffed Gadwall duck (*Anas strepera*) or even a stuffed pole-cat (*Mustela putorius*). Thus, the predisposition is not species- or even class-specific.

Bolhuis, Johnson & Horn (1989*a*) investigated whether the predisposition served as a filter or 'template' (Marler, 1976; Staddon, 1983; Bolhuis & Johnson, 1991*b*), restricting the information that the chick can store in memory, or, alternatively, whether the predisposition acts independently of the effects of learning during development. Dark-reared chicks were allowed to develop the predisposition, manifest as a significant preference for the stuffed fowl over the red box, by placing them in running wheels in darkness for 2 h when they were approximately 24 h old. When the chicks were approximately 50 h old, they were trained by exposing them to the rotating red box. In subsequent preference tests, it was found that these chicks, after the predisposition had developed, were still capable of learning the characteristics of conspicuous objects. On the basis of these results, Bolhuis & Johnson (1991*b*) argued that, although the term 'template' could be used to characterize the behavioural phenomena discussed here, it is inadequate when addressing the problem of underlying mechanisms.

The complex way in which in chicks, the development of the predisposition is dependent on non-specific experience, and the nature of the interaction of the predisposition with learning, supports the distinction between general and specific predispositions, as defined above. That is, there is no evidence to suggest that general predispositions to approach stimuli of a particular colour, size, etc., are dependent upon non-specific experience occurring during a certain period of life. Therefore, Horn (1985) and Bolhuis (1989) have suggested that a bias to approach stimuli of certain colours, etc., reflects a relatively coarse sensory 'filter', that selects the information entering memory, or constrains the ease with which it is stored. In contrast, the specific predisposition to approach objects with a head and neck configuration has been suggested to reflect the influence of a 'special purpose system' (Horn, 1985, p. 194) or 'predisposition system' (Bolhuis, 1989) that is separate both from the sensory filter and the memory system involved in imprinting.

From a functional perspective, Bolhuis *et al.* (1985) suggested that the predisposition may ensure that the young animal directs its attention to a particular class of objects (i.e.

stimuli with a head and neck, cf. Johnson & Horn, 1988) or indeed to conspecifics (Gottlieb, 1971). Learning the visual and auditory characteristics of a particular object may then lead to the recognition of individuals, in filial as well as in sexual imprinting.

#### IV. SENSITIVE PERIODS

The notion of a sensitive period is that "an individual's characteristics can be more strongly influenced by a given event at one stage of development than at other stages" (Bateson, 1979; cf. Bornstein, 1987). Hinde (1962) and Bateson (1966, 1979) proposed the term 'sensitive period' rather than 'critical period', which, in the words of Bateson & Hinde (1987), "implies a sharply defined phase of susceptibility preceded and followed by lack of susceptibility; if the relevant experience is provided before or after the period, no long-term effects are supposedly detectable".

A number of authors have suggested that there is a sensitive period for filial imprinting. For instance, Hess (1959*a*) reported that the percentage of 'positive responses' by ducklings toward a conspicuous object gradually increased after hatching until about 15 h, when there was a decline until, at 30 h after hatching, the percentage of positive responses was almost zero (cf. Hess, 1959*b*, for similar findings in chicks). In contrast to this much-cited account, Smith & Nott (1970) reported that an audio-visual imprinting stimulus could induce following in domestic chicks up to 10 days after hatching, whilst the chicks maintained the following response until at least day 28 after hatching.

As reviewed in Section V, the reversibility of imprinting has been demonstrated in a number of studies (e.g. Salzen & Meyer, 1967; Hoffman *et al.*, 1972; Cherfas & Scott, 1981; Kent, 1987; Bolhuis & Bateson, 1990) indicating that the so-called 'critical period' is not as circumscribed as has been thought previously (Hess, 1959*a*; cf. Bateson, 1966). Gottlieb (1961) reported that the following response in ducklings was a function of developmental time, i.e. time since the start of embryonic development. However, Landsberg (1976) found that preferences of ducklings were related to the time since hatching as well as to developmental time (cf. Kovach, 1970; Bateson, 1983*a*), suggesting that post-hatch experience also affects the beginning and the end of the sensitive period (see also Williams, 1972, for a critique of Gottlieb, 1961). Young chicks and ducklings are not capable of approaching and following a moving object immediately after hatching. Thus, it is plausible that the development of sensory and motor systems is related to the onset of a 'sensitive period'. With regard to the decline of the ability to imprint, Horn (1985) suggested that there is no evidence for a change in the ability to form a representation of imprinting stimuli, but that the sensitive period may relate to the link between the neural representation of the imprinting object and the system controlling approach behaviour. It is part of the nature of the imprinting process that once the young bird has formed an attachment to a particular object, it avoids novel objects. Therefore, the decline in the ability to imprint on novel stimuli is not so much the result of an independent endogenous process, but may be a result of the process of imprinting itself (Sluckin & Salzen, 1961). Indeed, as Hoffman *et al.* (1972) and others have shown, the fear of novel objects can be overcome by forced exposure, and chicks or ducklings can imprint onto those novel objects (see Section V), which refutes the concept of a strict sensitive period for imprinting. The decline of the ability to imprint is thus dependent upon the time it takes to form a preference for a particular object. In filial imprinting this process can be completed within hours.



During the formation of sexual preferences, the animals remain susceptible to the effects of sensory stimulation for a much longer period, and at different times. Thus, the periods during which imprinting is possible (or 'sensitive periods') for filial and sexual imprinting are different (Gallagher, 1977; Bateson, 1979; cf. Section IX(2)).

In a rigorous experiment to investigate sensitive periods, the groups of animals that are tested at different times after hatching should not be exposed to an object before being tested with the particular stimulus. Thus, it could be argued that the birds would not have had an opportunity to imprint before the time of testing. However, it has been shown (Bateson, 1964*a*) that chicks can learn about certain aspects of their rearing environment and later preferentially approach and follow stimuli that resemble this environment. Thus, it is difficult to deny the animal all sensory input on which it might imprint, before testing its filial responses, making the investigation of sensitive periods difficult. However, Moltz & Stettner (1961) showed that the period of responsiveness to a conspicuous object could be extended by rearing ducklings in diffuse, non-patterned light.

Recent evidence suggests sensitive periods of a different kind, involved in the development of filial preferences. Gottlieb (1965*a, b*) found that a predisposition to prefer species-specific calls influences the formation of preferences in ducklings (cf. Section VIII(2)) and that the induction and maintenance of this predisposition was dependent on specific auditory experience during embryogenesis. Gottlieb (1985) found that this auditory stimulation of the embryo had to occur within a certain period of time before hatching in order to have an effect on the development of the species-specific preference.

Evidence for a sensitive period in the development of a predisposition in chicks (see Section III) was reported by Johnson *et al.* (1989). For the predisposition to develop, the chicks needed to receive a certain amount of non-specific experience (in this case the treatment used was placement in running wheels in darkness for two periods of 1 h) approximately between 20 and 40 h after hatching. Treatment of the chicks in this way before or after this period failed to induce the development of the predisposition (cf. Bolhuis *et al.*, 1989*a*; Johnson, Bolhuis & Horn, 1991). Johnson *et al.* (1989) varied the times of treatment and of preference-testing, demonstrating that time of testing was not the determining factor. Nevertheless, it should be stressed that their results show a 'sensitive period' in the descriptive sense. It is possible that, analogous to what was found in imprinting, the length of what appears to be a sensitive period can be altered by longer, or different, exposure conditions. Furthermore, non-specific experience at a later date might induce the emergence of the predisposition (see also Bateson, 1979, and Bateson & Hinde, 1987, for discussions of the criteria for a sensitive period).

#### V. REVERSIBILITY

As Jaynes (1956) has pointed out, Lorenz's (1935) claim regarding the irreversibility of imprinting can be interpreted in two ways. On the one hand, it could mean that once the chick has formed an attachment with a particular object, it will never direct its social behaviour towards a different, novel object. A weaker form of the claim is that, although the animal may show social behaviour towards novel objects, it will not forget what it has learned about the object to which it was exposed originally.

The strong form of the claim of irreversibility has been refuted, both for filial imprinting (e.g. Jaynes, 1956; Salzen & Meyer, 1967, 1968; Hoffman *et al.*, 1972;

Einsiedel, 1975; Cherfas & Scott, 1981; Kent, 1987; Bolhuis & Trooster, 1988; Bolhuis & Bateson, 1990) and for sexual imprinting (Immelmann, 1972*a*; Kruijt & Meeuwissen, 1991). For instance, Salzen & Meyer (1967, 1968) reared chicks with a coloured ball that was suspended in their home cage for 3 days. When given a simultaneous preference test, the animals preferred the familiar stimulus to a novel stimulus of a different colour. When the familiar stimulus was then removed and replaced with the alternative coloured ball for a further 3 days, the chicks had reversed their preference to a preference for the novel stimulus. These findings were replicated by Cherfas & Scott (1981) and Bolhuis & Bateson (1990; see Fig. 3).

Boakes & Panter (1985) suggested that imprinting is irreversible when a live hen is used as the first stimulus. The authors exposed chicks to a stimulus on the first 2 days after hatching. The stimulus was a live hen for half of the chicks, and a moving toy windmill for the other half. In both cases, after the exposure period, the stimuli could suppress distress-calling in a test. 'Secondary imprinting' was tested subsequently by exposing the chicks during 3 days to a novel stimulus, a moving cup. The authors found that secondary imprinting occurred in the chicks that had been exposed previously to the windmill, but not in the group of chicks that had been exposed to the live hen.

In a study by Bolhuis & Trooster (1988) a rotating red box as well as a rotating stuffed jungle-fowl hen (see Section III and Fig. 1A) were used, stimuli that were matched for their attractiveness. Day-old chicks were exposed to one of the two stimuli and their preferences were tested in a simultaneous choice test. The next day they were exposed to the alternative stimulus, and then subjected to a second preference test. It was found that, even when, in the first test, the preference score of the chicks trained on the box was higher than that of fowl-trained chicks, the preference of the former was significantly altered by exposure to the fowl, whilst the preference score of the fowl-trained chicks remained stable. Bolhuis & Trooster (1988) explained their results by reference to the model of interacting mechanisms, discussed in Section III. When artificial objects (or indeed two naturalistic objects: see below) are used as imprinting stimuli, filial preferences are reversible. However, when one of the stimuli used is relevant for the predisposition (as in the case of a live hen or a stuffed fowl), the two mechanisms are engaged, leading to a relatively stable preference when such a stimulus is the first object to which the animal is exposed.

This interpretation predicts that filial preferences are reversible when two naturalistic stimuli are used. This hypothesis was confirmed in a study by Kent (1987) in which chicks were exposed to live hens. After 3 days of exposure the chicks preferred the familiar hen to a novel one in a simultaneous choice test. When the chicks were subsequently exposed to another hen for 3 days and tested again, they preferred the second hen to which they had been exposed (see also Shapiro & Thurston, 1978). Kent (1987) found that the chick's preferences were not very stable: 4 h of separation from the familiar hen were sufficient for the chicks to lose their preference for it. Hindman (1981) exposed chicks to either another chick or a guinea-pig for 3 weeks. Subsequent exposure to the alternative stimulus significantly affected, but did not reverse, preferences. The rather long period of exposure may have led to a relatively resistant preference for the original stimulus (cf. Bateson, 1987).

Recent evidence supports a weak version of the claim of irreversibility, i.e. that information about the first stimulus is not forgotten. Specifically, it was found that,

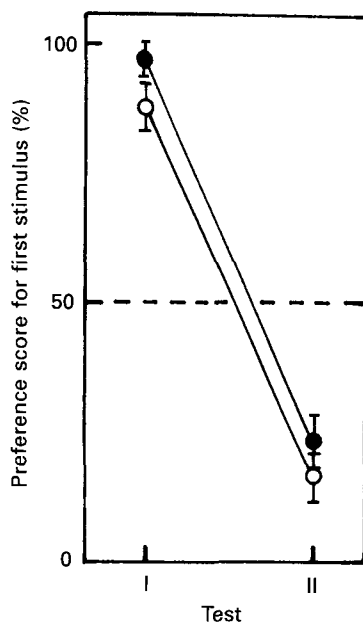


Fig. 3. Mean preference score ( $\pm$ s.e.m.) for the first imprinting object in simultaneous preference tests in chicks. The animals were exposed to a blue cylinder (●) or to a yellow cylinder (○) until Test I, then to the alternative stimulus until Test II. (Adapted from Bolhuis & Bateson, 1990; with permission.)

although filial preferences are reversible, under certain circumstances there may be a primacy effect, expressed as a 'resurfacing' of the original preference. Cherfas & Scott (1981) attempted to replicate the original experiments of Salzen & Meyer (1968). In contrast to the latter authors, Cherfas & Scott (1981) found that the reversal of filial preferences was not permanent after the chicks has been isolated for 3 days at the end of the experiment. Bateson (1981, 1987, 1990) suggested a simple 'competitive exclusion' model to explain these findings. He distinguished between a large capacity recognition system and a limited capacity executive system that is responsible for the animal's behavioural output. During exposure to an imprinting stimulus, links are made between the recognition system and the executive system, with a limited access to the latter. Once part of the executive system is 'captured' by links from the recognition system, that part cannot be captured by inputs from another store in the recognition system. Connections between the two systems can wane with disuse, but can be re-established if used again. The model predicts that when the animal is exposed to an attractive stimulus for a certain length of time, it will be difficult to change its preference by exposing it to a novel stimulus. Furthermore, under certain circumstances the original preference may 'resurface' (see Bateson, 1987, for further discussion).

Bolhuis & Bateson (1990) attempted to test some of the predictions of the competitive exclusion model. As in the experiments of Salzen & Meyer (1968) and Cherfas & Scott (1981), chicks were exposed to conspicuous objects for periods of three days. Usually, when exposure to object A was followed by exposure to object B, there was a reversal of preference, similar to earlier findings by Salzen & Meyer (1967, 1968). When the chicks were subsequently exposed to the first and second object simultaneously for 3

days, there was a change in preference towards the original object, but the eventual preference did not differ significantly from the random choice level. The two objects used in these experiments differed only in colour. However, when two stimuli were used that differed in colour, shape and pattern, 3 days of exposure to one object, followed by 3 days of exposure to the other object and 3 days to both objects simultaneously, led to a significant resurfacing of a preference for the first object.

In summary, filial preferences are reversible, but that does not mean that information about the first object is forgotten. Under certain conditions this may become manifest as a return to a preference for the first object to which the animal was exposed. Filial preference for the first stimulus may be difficult to reverse when it has head and neck features and the second stimulus has not. This stability of preference is due to the combined influence of a memory of the imprinting object and a predisposition to approach stimuli with a head and neck.

## VI. THE LEARNING PROCESS OF IMPRINTING

### (1) *Associative learning interpretations*

A characteristic of filial imprinting is that it proceeds without conventional reinforcement such as food or warmth. In the animal's natural environment, such reinforcement may be provided by the parent and siblings, and this reinforcement may influence the formation of social bonds. Indeed, in the case of sexual imprinting, the amount of social interaction with the different (foster-)parents has been shown to affect the strength of sexual preferences (Ten Cate, 1984; see Section IX).

Bolhuis, De Vos & Kruijt (1990) reviewed some of the evidence for an associative learning account of imprinting, explicitly formulating the requirements for such an interpretation. The most important assumption is that, since filial imprinting proceeds in the absence of a conventional reinforcer, the imprinting object itself must provide the unconditioned stimulus (UCS; cf. Horn, 1985, p. 118). However, the nature of this UCS is not apparent. Hoffman and his collaborators have formulated a classical conditioning theory of imprinting (Hoffman *et al.*, 1972; Hoffman & Ratner, 1973 *a, b*; Hoffman *et al.*, 1974; Hoffman, 1978; Hoffman & Segal, 1983; Hoffman, 1987), in which movement is thought to act as the UCS (cf. James, 1956). During exposure, the bird will associate initially neutral aspects of the object (e.g. colour and shape) with the UCS (movement). Thus, the bird acquires a conditioned response to aspects of the conspicuous object other than movement (the conditioned stimuli) through a process of classical conditioning. This interpretation of imprinting was supported by results of Hoffman & Ratner (1973 *a*), who found that young ducklings initially emitted distress calls in the presence of a stationary object, but not when the object was moving. After the birds had been exposed to the moving object, the ducklings ceased to emit distress calls in the presence of the stationary object. A second process that is important for Hoffman *et al.*'s interpretation of imprinting, in addition to classical conditioning, is an increase in fear for novel objects that is thought to occur independently of experience with an imprinting object (Hoffman *et al.*, 1972). This increase in fear would make it increasingly difficult for the young animal to become attached to novel objects.

Bolhuis *et al.* (1990) showed that, if it is assumed that movement of an imprinting object is the UCS, certain predictions from animal learning theory, such as latent

inhibition (Eiserer, 1978; Zolman, 1982; Shettleworth, 1983) and extinction (Eiserer, Hoffman & Klein, 1975; Hoffman, 1978) are not confirmed by the data available. Furthermore, several studies have shown that movement of the imprinting object is not necessary for imprinting to occur (Gray, 1960; Sluckin & Salzen, 1961; Bateson, 1964*a*; Salzen, 1969; Eiserer, 1980; Ten Cate, 1986*a*; De Vos & Bolhuis, 1990). It is conceivable that exposure to a conspicuous object (CS) automatically leads to a 'motivationally significant event' (UCS). Experiments in which presentation of a conspicuous object is used as a UCS in an operant (e.g. Bateson & Reese, 1968) or in a Pavlovian (Evans, 1972) learning task show that presentation of an imprinting object can be reinforcing. Assuming then that a UCS occurs at presentation of an imprinting object, certain predictions can be made, for instance as regards blocking (Kamin, 1969) and overshadowing (Pavlov, 1927) in an imprinting situation (cf. Rescorla & Wagner, 1972; Dickinson, 1980; Mackintosh, 1983). However, if movement or some other dissociable element of the stimulus does not provide a UCS (or is not the only UCS), it is impossible to expose an animal to the CS without also simultaneously exposing it to the UCS. Thus, phenomena like latent inhibition and extinction, which are a result of procedures in which CS and UCS occur independently, cannot be measured in imprinting.

De Vos & Bolhuis (1990) investigated whether blocking (Kamin, 1969) occurs in filial imprinting. The authors exposed chicks to pairs of cylinders for a period of 6 days, either two red cylinders (group RR) or two yellow cylinders (YY). The chicks were subsequently exposed to a yellow and a blue cylinder (YB) for 7 days, during which preferences were measured regularly. It was found that the formation of an attachment to the novel blue cylinder was impaired in the YY group compared to the RR group, consistent with the suggestion that blocking occurs in an imprinting situation. However, further research is needed to test alternative interpretations (see Bolhuis *et al.*, 1990, for further discussion). The possible occurrence of overshadowing in filial imprinting was investigated by Van Kampen & De Vos (in preparation). When jungle-fowl chicks were simultaneously exposed to two objects that differed in colour and in shape, it was found that approximately half of the chicks came to prefer one of the two stimuli ('A') whilst chicks in the other half strongly preferred the other object ('B'). Thus learning about a particular stimulus was not overshadowed by learning about another, possibly more salient stimulus. Rather, the chicks tended to become attached to one or other of the two objects in a seemingly random fashion. Van Kampen & De Vos (in preparation) suggested an attentional explanation for their findings, in which the young chick becomes attached to the first object that captures its attention.

In a different experiment, Van Kampen & De Vos (1991) investigated the interaction between learning about the shape of an imprinting object and learning about its colour. Chicks were exposed to either a red object of a particular shape, or a yellow object of the same shape. During testing the birds were exposed to an object with the familiar shape and one with a different shape. It is known that in chicks, red objects are more attractive imprinting stimuli than yellow objects (e.g. Kovach, 1971; De Vos & Bolhuis, 1990; cf. Section III). Rather than learning about the shape of the object being overshadowed by learning about colour, the authors found that chicks exposed to the red object learned more about its shape than chicks exposed to the yellow object. Thus, learning about shape appeared to be 'potentiated' in the case of the stimulus with the

more attractive colour. As Van Kampen & De Vos (1991) note, it is possible that chicks attend more to a more attractive stimulus and consequently learn more about other aspects of it.

Suboski (1990) proposed a 'releaser-induced recognition learning' model to account for seemingly unreinforced learning, such as imprinting. This account assumes that, in certain types of learning, the UCS is a releaser rather than a conventional reinforcer. In the course of learning, previously neutral stimuli acquire the ability to 'release' certain behaviour due to their association with releasers that can induce the behaviour from the outset (cf. Lorenz, 1937). Two important elements of the model are that learning proceeds without conventional reinforcement and is not restricted to a 'predictive' temporal relationship between the events that are associated (cf. Rescorla, 1968; Dickinson, 1980). Releasers can be seen as a special form of reinforcers, rendering Suboski's model not dissimilar to Pavlovian interpretations. Furthermore, as yet there is insufficient evidence to discount the principle of temporal predictability as being crucial for Pavlovian conditioning to proceed (e.g. Mackintosh, 1983). As noted above, in imprinting, the CS and the UCS are always presented together.

#### (2) *Perceptual learning interpretations*

Imprinting has been classified as a form of 'perceptual learning' (Sluckin & Salzen, 1961) or 'exposure learning' (Sluckin, 1972), stressing the absence of obvious reinforcement. According to Sluckin (1972), the young animal learns the characteristics of a conspicuous object solely as a result of exposure to it. The animal will respond filially to this object and come to avoid novel objects, a process that Jaynes (1958) has called 'emergent discrimination'. Salzen (1962) suggested that imprinting involves the formation of a 'neuronal model of the object stimulus pattern'. Subsequent stimulus input is compared to this model. When it matches the internal representation, the animal will approach and follow the object, whilst a mismatch results in avoidance of it.

These perceptual learning accounts of imprinting are descriptive. However, a number of studies have provided some insight into the nature of the representation formed during imprinting, by studying the effects of imprinting on subsequent discrimination learning involving the imprinting stimulus. Bateson (1964*b*) and Kovach, Fabricius & Fält (1966) found that chicks imprinted on a stimulus subsequently learned a food-rewarded discrimination between it and a novel stimulus better than chicks for which both stimuli were novel. Furthermore, Kovach *et al.* (1966) found that the beneficial effects of familiarity with the imprinting stimulus were only exhibited by chicks that had approached the stimulus during the original imprinting session. Chicks that did not approach the stimulus, but presumably received the same amount of exposure to it, behaved like non-imprinted control chicks in the discrimination task. A study by Chantrey (1972) confirmed the main findings of Kovach *et al.* (1966) and showed that discrimination learning was enhanced even when approach to the object that had been used as imprinting stimulus was not rewarded. All these results suggest that during discrimination learning the animals can benefit from the representation of the imprinting stimulus that was formed during initial exposure.

Chantrey (1972) and Bateson & Chantrey (1972) demonstrated that discrimination

learning was *impaired* when chicks had previously been exposed to both stimuli. The authors interpreted this retardation of learning as a result of the two stimuli being 'classified together' or combined into a single representation (Bateson, 1990) by the animal. During discrimination learning the two stimulus arrays need to be 'declassified' (Chantrey, 1972) in order to be associated with different responses. This suggestion was supported by a study by Chantrey (1974) with a similar design to Chantrey (1972), but in which the time between presentation of the two objects during initial exposure was varied. Chantrey found that discrimination learning was impaired if the objects had been presented 30 s or less apart, whilst chicks in which onset of exposure to the two stimuli had been more than 5 min apart learned the discrimination task faster than controls. Stewart *et al.* (1977) could only replicate Chantrey's results when the experimental conditions were exactly the same. Despite this caveat, Chantrey's (1974) findings suggest that the closer stimuli were presented together in time, the greater the chance that they were integrated into a single representation.

Bateson (1979, 1990) suggested that, since the plumage of siblings changes with age, young birds need to 'update' the representation of their siblings. This hypothesis was supported by results from a study by Ryan & Lea (1989). These authors exposed domestic chicks to an artificial stimulus made up of a string of four table-tennis balls, for a total of 21 days. For half of the chicks the balls were white, for the other half they were brown. In one subgroup of chicks (the experimental group) one ball in the string was replaced by a ball of the opposite colour every 4 days. Thus, by day 17 all four balls had been replaced by balls of the other colour. Chicks in other subgroups were either exposed to one of the two colours for the full 21 days, or they were exposed to four balls of one colour for 17 days, after which the whole string was replaced with a string of balls of the other colour. Preference testing occurred on day 21, involving exposure to a string of brown balls and a string of white balls simultaneously, in a *y*-maze. Ryan & Lea (1989) found that chicks that had been exposed to a string of balls of one colour for 21 days strongly preferred that colour in the test. The chicks for which the whole stimulus was changed at day 17 spent more time with the second stimulus than the chicks in the 21-day group, but on average still preferred the first stimulus. Chicks in the experimental group did not show a significant preference for either of the two stimuli, although there was still a bias towards a preference for the first stimulus. Ryan & Lea (1989) suggested that the most likely explanation for their results is that chicks in the experimental group gradually increased the representation of the imprinting stimulus to accommodate for all the different versions of it, rendering all versions equally attractive. They called this process 'category enlargement', and pointed at the similarity with the findings of Chantrey and Bateson discussed above. Further experiments are needed to investigate this hypothesis. For instance, the chicks in the experimental group are exposed to the novel colour at an earlier age than the chicks in the control groups. Also, the chicks in the experimental group received more exposure to both colours than the chicks in the other groups. It would have been useful to have a group where the colour of the whole stimulus was changed at day 10, to have chicks with the same amount of experience to the two colours but a sudden, as opposed to a gradual, change of colour.

The nature of the representation formed during sexual imprinting was investigated by Ten Cate (1986*b, c*; see also Hollis, Ten Cate & Bateson, 1991). Bateson's (1981,

1987) competitive exclusion model (see Section V) proposed that representations of different objects are separate and that they compete for access to an executive system.

#### VII. THE INFLUENCE OF SOCIAL INTERACTIONS ON THE FORMATION OF SOCIAL PREFERENCES

##### (1) *Interactions between the subject and the parent (-surrogate)*

In laboratory investigations of filial imprinting, the opportunity for the experimental animals to interact with the imprinting object is minimized. However, in a number of studies birds were exposed to the stimulus in an instrumental learning task (Bateson & Reese, 1968, 1969; Gaioni *et al.*, 1978; Johnson *et al.*, 1985; Johnson & Horn, 1986; Ten Cate, 1986*a*; Bolhuis & Johnson, 1988). Chicks and ducklings readily learn to perform such an operant task, with exposure to the imprinting object as the reinforcer. Bateson & Reese (1968) showed that chicks learned to step on one of two pedals in an operant chamber in order to be exposed to a conspicuous moving object, to which they had not been exposed previously. Impekoven (1973) reported prenatal instrumental learning with maternal calls as the reinforcer and head and foot movements as the operant in duck embryos. Bolhuis & Johnson (1988) demonstrated that operant control over the presentation of an imprinting object did not enhance chicks' subsequent filial preference, compared to animals in a yoked control group (cf. Ten Cate, 1986*a*). Rather, it was found that the variable exposure to the imprinting object that occurred as a result of the operant performance of the chicks improved imprinting, compared to chicks that were exposed to the object according to a fixed interval presentation schedule (Bolhuis & Johnson, 1988).

Ten Cate (1989*a*) investigated the effects of interaction with a live hen on the development of filial preferences in Japanese quail. Quail chicks that were exposed to a live hen had a greater preference for this stimulus than chicks that were exposed to a moving stuffed model. Furthermore, in the group of chicks that were exposed to the live hen there was a significant positive correlation between the strength of preference for the hen and the behaviour of this hen during initial exposure. For instance, the more pecking and chick-directed behaviour the hen displayed, the stronger the resulting attachment of the chick to the hen. As similar correlations were found between the hen-directed behaviour of the chick and its subsequent attachment to the hen, the possibility that the behaviour of the hen was affected by that of the chick cannot be excluded. However, qualitative observations of the animals' behaviour indicated that the interactions between hen and chick were primarily an influence of hen behaviour on chick behaviour.

Jackson & Bateson (1974) presented evidence suggesting that the young animal actively seeks exposure to novel stimuli during imprinting. Day-old chicks were exposed to either a red or to a yellow flashing light for 15, 30 or 60 min. Shortly afterwards, the chicks were placed individually in an operant chamber (cf. Bateson & Reese, 1968) where they could press a pedal to change the colour of the light to which they were exposed. The chicks pressed the pedal to be exposed to the novel colour significantly more than chance in the 15 min pre-exposure group, but not in the 60 min pre-exposure group, whilst the 30 min group was in between these values. Thus, the results suggested that the young chick interacts with the imprinting stimulus in order to be exposed to different aspects of it, thereby forming a more complex representation



of the stimulus. These findings are consistent with those of Bateson & Jaekel (1976), who reported that chicks may show a weak preference for a novel stimulus after a short period of training. Jackson & Bateson (1974) provided a functional argument for the behaviour of the chicks in their study, suggesting that it is advantageous for the chick to be able to recognize the parent from different angles.

(2) *Interactions between the subject and its siblings*

The role of siblings in the formation of filial preferences in ducklings was studied by Gottlieb and his collaborators (Johnston & Gottlieb, 1981*b*, 1985*a, b*; Lickliter & Gottlieb, 1985, 1986*a, b*, 1987, 1988; Dyer, Lickliter & Gottlieb, 1989; Dyer & Gottlieb, 1990; see also Johnston & Gottlieb, 1981*a*). In these experiments dark-reared mallard ducklings were exposed to a stuffed mallard model for 30 min when they were about 24 h old. Preferences were tested at 48 h and/or at 72 h after hatching, in a simultaneous test involving the familiar mallard model and a novel stuffed model of a different species of wildfowl.

These experiments showed that exposure to siblings can enhance or impair learning about stuffed mallard models, depending on the time at which this exposure occurred. For instance, Johnston & Gottlieb (1985*a*) found that social rearing of ducklings after training with the mallard model led to a significant preference for the mallard model over a novel model at 72 h, whilst such a preference was not acquired in ducklings that remained isolated until testing. In contrast, exposure to siblings before (Lickliter & Gottlieb, 1987; Dyer *et al.* 1989; cf. Guiton, 1959) or during training exposure to the mallard model interfered with imprinting on the model (Lickliter & Gottlieb, 1986*b*). Results by Lickliter & Gottlieb (1985) suggest that it is not mere exposure to siblings, but social interaction with more than one sibling, that improves imprinting on a model.

Lickliter & Gottlieb (1987) found that ducklings did not show a significant preference for the familiar mallard model over a novel model at 48 h when social rearing occurred for a period of 1 h after training. Thus, according to Lickliter & Gottlieb (1987) the relevant features of the mallard model "become consolidated only after more than 1 hr into the posttraining social rearing". The authors called this process 'retroactive excitation'. Lickliter & Gottlieb (1988) found that ducklings showed a significant preference for the familiar mallard model only when they were reared with conspecific siblings, not when reared in a group of domestic chicks, or Muscovy ducklings (*Cairina moschata*).

When considered together, these results suggest that, in ducklings, the development of filial preferences involves a complex interplay between experience with the maternal model, exposure to siblings and social interactions with these siblings. It is likely that ducklings imprint on their siblings as well as on the mother. When they are exposed to the mother (model) first, they are likely to acquire a preference for it. This preference is strengthened by subsequent exposure to conspecific siblings, but not by exposure to young of other species. Direct social interaction is necessary for 'retroactive excitation' by exposure to siblings to occur (Johnston & Gottlieb, 1985*b*), but mere exposure is sufficient to acquire a preference for siblings over the mallard model (Dyer *et al.*, 1989; but see also Zajonc, Wilson & Rajecki, 1975).

The extent to which these results can be generalized is limited by methodological considerations such as the unbalanced design in these studies (only a mallard model was

used during training). Furthermore, 30 min training exposure was used in all these experiments, which may have been too brief to obtain significant preferences (cf. Bateson *et al.*, 1973, and Johnson & Horn, 1987). Lickliter & Gottlieb (1986*b*) criticized conventional laboratory studies of imprinting, as they usually do not consider the effects of social interaction with siblings on filial imprinting. Considering the constraints on the interpretation of the results mentioned above, the authors' critique needs to be put in perspective. Furthermore, Gottlieb and his collaborators often used only some elements of the natural situation, combined with relatively 'unnatural' laboratory designs. In all of the studies cited, a stuffed model was presented, rather than a live hen. In a more naturalistic situation, where there is the opportunity for social interaction with the mother (cf. Ten Cate, 1989, and Section IX) and the siblings, the role of siblings might be less important than found in the laboratory (Dyer *et al.*, 1989). The results of the studies by Gottlieb *et al.* show that ducklings can learn the characteristics of siblings as well as those of the hen, but not *how* they learn them. The effects of relatively non-specific experience, through a process of 'retroactive excitation' (Lickliter & Gottlieb, 1987) are relevant to the mechanisms of learning and retention and need to be investigated further.

Zajonc *et al.* (1975) investigated the development of individual recognition in day-old domestic chicks. The chicks were housed in pairs for a period of 1, 4 or 16 h. Half of the pairs had the opportunity for physical contact during exposure, whilst the pairs in the other half were separated by a wire-mesh screen, such that they could see, but not peck at each other. The main variable studied was the rate of pecking of familiar and unfamiliar chicks in testing sessions involving four different chicks. The chicks in the wire-mesh group pecked equally at familiar and unfamiliar birds. In contrast, the chicks in the group without the wire-mesh partition pecked significantly more at novel birds than at familiar birds after 16 h of exposure. Thus, the opportunity for direct physical interaction was necessary to achieve individual recognition.

#### VIII. AUDITORY IMPRINTING

##### (1) *Auditory learning*

Auditory stimulation plays an important role in filial behaviour in ducklings and chicks (e.g. Gottlieb, 1963, 1971, 1988; Smith & Bird, 1963, 1964; Grier, Counter & Shearer, 1967; Kent, 1987; Dyer & Gottlieb, 1990). A visual model that also emits sounds is followed more than a silent visual model (Gottlieb, 1963; Smith & Bird, 1963, 1964; Boyd & Fabricius, 1965; Porter & Stettner, 1968). A number of authors have provided evidence that domestic chicks can discriminate different artificial sounds (e.g. Fischer, 1972; Cowan, 1974*a*). These results concern the *following* response, and not imprinting in the sense of the formation of a filial *preference*. Sluckin (1972) noted that "The dominant influence of hearing upon the approach behaviour of chicks does not of itself suggest anything about possible imprinting to sounds" (p. 124).

Evans (1982) and Bolhuis & Van Kampen (in preparation) have provided critical reviews of the evidence for auditory imprinting in precocial birds. Klopfer (1959) did not find auditory imprinting in a number of ground-nesting species. This led to the hypothesis (Klopfer & Gottlieb, 1962) that in ground-nesting species, visual stimulation was important in the formation of filial preferences, whilst auditory stimulation was

thought to affect attention. Thus, the question arises as to whether auditory stimuli merely act to direct the young bird's attention towards a visual stimulus, the characteristics of which are learned.

Fisher (1966) performed an experiment with domestic chicks to distinguish between an attentional and a 'model recognition' role for auditory stimuli. Day-old chicks were exposed to a combination of a visual and an auditory stimulus. Twelve hours later they were tested with the familiar or a novel visual model, paired with the familiar or a novel sound. During testing, chicks followed the familiar and the novel visual object equally. In contrast, the model emitting the training sound was followed significantly more than the model emitting the novel sound, which in turn was followed more than a silent model. Unfortunately, the experiment was not balanced, since only one of two auditory stimuli (a combination of sounds, including clucks of a broody hen) was used during training. The alternative stimulus (chick 'contentment' twitters) was familiar to the experimental chicks, and may have been less attractive than the sound used during training. Several studies of auditory imprinting have included an unbalanced design, thus rendering the results inconclusive (e.g. Grier *et al.*, 1967; Porter & Stettner, 1968; Bailey & Ralph, 1975; see Bolhuis & van Kampen (in preparation) for review).

Cowan (1974*a*) performed an experiment with a balanced design. Day-old chicks were exposed to a pure tone in combination with a visual stimulus for a total of 40 min. Within 3 min of the end of training the chicks' preferences were tested by exposing them sequentially to the familiar sound and novel sounds. The chicks followed the familiar sound more than the novel sounds. It is not clear whether the chicks' auditory preferences were stable, given the rather short retention interval used. Furthermore, Cowan found that the chicks showed significantly *more* distress calling with the familiar stimulus than with novel stimuli (see also Cowan, 1973; Graves, 1973; Evans & Cosens, 1977, for similar results). Usually, imprinting on a particular visual stimulus leads to a reduction in distress calling (e.g. Hoffman, 1978; De Vos & Bolhuis, 1990). Distress calls play a role in auditory interaction with the parent, but usually parental clucking leads to a reduction in distress calling by the young (e.g. Evans, 1975). Thus, although the procedure used by Cowan (1974*a*) led to significant discrimination between different artificial sounds, it is not clear whether this discrimination constitutes auditory imprinting, in the sense of forming an *attachment* to the stimulus whose characteristics were learned.

A common feature in studies of auditory imprinting is that a combination of a visual and an auditory stimulus is used during training (e.g. Fisher, 1966; Porter & Stettner, 1968; Evans & Mattson, 1972). The importance of such compound training was demonstrated by Cowan (1974*b*), who exposed 1- or 2-day-old chicks to either a parental call paired with a visual stimulus (a moving pendulum) or to a parental call alone. Approach to the familiar call and a novel parental call was measured in a sequential test, 5 min after the end of training. It was found that only chicks trained by exposure to a combination of the visual and the auditory stimulus preferred the familiar call to the novel call during testing. Cowan (1974*b*) concluded that the visual stimulus served as a 'reinforcer' in auditory discrimination learning, but that there was no auditory imprinting (i.e. learning by exposure) as such. A number of studies have confirmed the role of visual stimuli as reinforcers for learning about auditory stimuli (e.g. Evans, 1972; Evans & Mattson, 1972; Wallhäusser & Scheich, 1987).

Evidence for prenatal auditory imprinting was provided by Grier *et al.* (1967). These authors showed that in a preference test, domestic chicks preferred the artificial sound that they had been exposed to before hatching. Unfortunately, these authors only used one tone (200 Hz) as a training stimulus, in which case the chicks' preferences may have been affected by a naïve bias for this tone over the novel tone (see Collias & Joos, 1953; Fischer, 1972, for evidence for such a bias and Bolhuis & Van Kampen, in preparation, for a critical review). A further complication in the experiment of Grier *et al.*, as in other studies of prenatal auditory learning (e.g. Wallhäusser & Scheich, 1987), is that the embryos were exposed to the tone for a long period of time (6 days) at a high intensity (85 dB). It is not known whether such high-intensity stimulation may bias the responsiveness of neurons in the auditory projection areas of the brain, much like restricted visual experience has been shown to bias the orientation selectivity of neurons in the visual cortex of the kitten (Hirsch & Spinelli, 1970).

Gottlieb (1988) reported that mallard ducklings can learn individual mallard maternal calls after a total of only 12 min of exposure on the first day after hatching. Both embryonic and post-hatch exposure to the calls was studied. Gottlieb (1988) found that after 48 h of prenatal exposure to a call (1 burst/3.5 min; 40 min/h), ducklings preferred this call to a different, novel call in a simultaneous test. However, the ducklings did not show a significant preference when tested the following day. Similar experiments were performed in domestic chicks by Fält (1981) and Kent (1987). The latter found that the chicks' preferences for the familiar call had disappeared after 4 h of separation from the hen. In both these studies the chicks were exposed to the clucks in a 'natural' situation, i.e. with a hen and siblings present during training exposure. Furthermore, there was no retention interval between the end of initial exposure and the simultaneous test. Kent (1987) found that the preferences were stronger when live hens were presented during testing, suggesting that vocal interactions between the hen and chick may be important.

Recently, Van Kampen & Bolhuis (1991) conducted an investigation of auditory imprinting, with training and testing conditions such as have been used in studies of visual imprinting (e.g. Horn, 1985). In a series of experiments, dark-reared day-old chicks were exposed to either pure tones or maternal clucks for periods ranging from 1.5 to 3.5 h. The animals were exposed to the auditory stimuli in training cabinets with either diffuse overhead light or with an additional rotating red box (see Fig. 1A) between the chick and the auditory speaker emitting the training sound. Two hours after the end of training exposure, sequential tests were performed without the red box present. The tests showed no evidence for the formation of a significant preference for the familiar sound in the chicks that were exposed to a pure tone without the red box. However, the addition of the red box during training led to a significant increase in a preference for the training stimulus. When chicks were trained with a maternal cluck for a total of 3.5 h, without the red box, they showed a small but significant preference for the training sound (see Fig. 4). Box-exposure during auditory training again led to significantly greater preferences in the subsequent tests. These results confirm that learning about auditory stimuli is relatively weak, under conditions that normally lead to strong preferences for visual imprinting objects (e.g. Horn, 1985). Training with both a visual and an auditory stimulus significantly improves learning about the auditory stimulus. Further research is needed to determine whether this effect is due

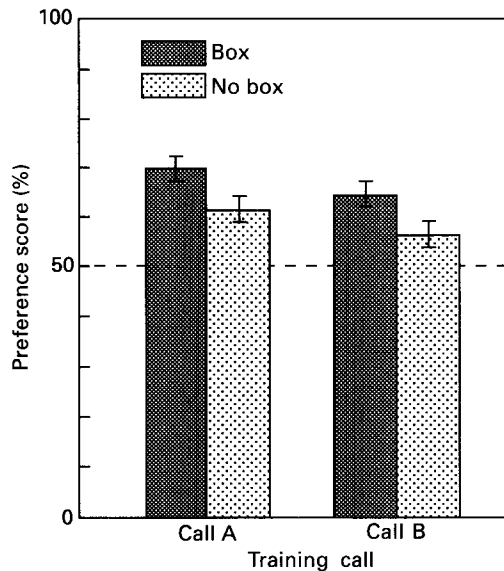


Fig. 4. Mean preference scores ( $\pm$ S.E.M.) of chicks exposed for a total of 3.5 h to one of two different maternal calls. Half of the chicks were exposed to a rotating red box (see Fig. 1a) during exposure to the training call. (Adapted from results by Van Kampen & Bolhuis, 1991.)

to an increase in 'arousal', improved attention, reinforced learning or some other factor.

#### (2) *Species-specific predispositions*

Auditory preferences in naïve chicks and ducklings have been investigated by a number of authors (Gottlieb, 1965a; Snapp, 1969; Impekoven, 1973; Heaton, Miller & Goodwin, 1978). Gottlieb (1965a) found that both naïve mallard ducklings and chicks preferred the species-specific parental call to that of other species. When mallard ducklings were exposed briefly to a model emitting a wood duck (*Aix sponsa*) parental call, they later preferred that call to that of a chicken when given a simultaneous choice test. However, the ducklings preferred a mallard call to a wood-duck call. Prolonged exposure to a model emitting a wood-duck call reduced the preference for the mallard call, but only to the no-preference level. Thus, the ducklings could learn about the wood-duck call, but their behaviour was also strongly affected by a tendency to approach the parental call of their own species, although they had not heard this before.

In a subsequent study, Gottlieb (1965b) recorded responses of the embryo to different parental calls. It was found that communally incubated mallard embryos, 12–24 h before hatching, showed an increased oral response (bill clapping) to the mallard parental call, but not to calls of the wood-duck, the chicken or to sibling calls. When the embryos were incubated in isolation, they were not able to make this auditory discrimination before hatching, but did prefer the mallard parental call in a preference test conducted a day after hatching. Thus, the incomplete auditory deprivation (the animal could still hear its own vocalizations) induced a time-lag in the development of

species-specific preferences. Subsequent experiments, in which embryos were isolated as well as temporarily devocalized, showed that the preference for the species-specific parental call developed in advance of auditory experience (Gottlieb, 1979). However, when the embryos were deprived of hearing their own or sibling vocalizations, the preference became less specific (Gottlieb, 1978). It was found that exposure to the embryonic 'contact-contentment call' (4 notes per second) was necessary for the species-specific preference to be maintained after hatching. Exposure to different rates of the embryonic call was not sufficient for the maintenance of the post-hatch preference (Gottlieb, 1980). Furthermore, Gottlieb (1985) found that exposure of the embryo to the contact-contentment call needed to occur within a certain 'sensitive' period in order for the predisposition to be expressed. Thus, the work of Gottlieb shows that the appearance and maintenance of a species-specific auditory predisposition is dependent in a complex way upon the influence of specific auditory experience (see also Section XII(2)).

#### IX. SEXUAL IMPRINTING

##### (1) *General characteristics*

In contrast to the extensive research into filial imprinting, for a long time the study of the formation of sexual preferences has been relatively limited and anecdotal (for reviews see Immelmann, 1972*b*; Bateson, 1978*a*). However, more recently the investigation of sexual imprinting has been conducted in a systematic fashion (cf. Kruijt, 1985; Ten Cate, 1989*b*).

Apart from the different ways in which the behaviour is expressed, an obvious difference between filial and sexual imprinting is in the time-course involved. Sexual preferences are expressed later than filial preferences, usually a considerable period of time after exposure to the imprinting stimulus. The period of exposure to this stimulus is also longer in sexual imprinting than in filial imprinting, and sexual preferences are influenced by experience after filial imprinting is completed. Results by Bateson (1978*b*, 1980, 1982) suggest that the eventual preferences may be for an individual that is different from the ones that the animal was reared with (cf. Ten Cate & Bateson, 1989; Bolhuis *et al.*, 1989*b*). An important factor that differentiates the two processes is that, in sexual imprinting, external reinforcement may affect the formation of preferences (see below). Thus, different mechanisms may underlie the two processes, or, as Kruijt (1985) has put it, "the causal factors of filial and sexual imprinting only partially overlap".

The relationship between filial and sexual imprinting was investigated directly in a number of studies. Bambridge (1962) and Andrew (1964) gave young chicks injections of testosterone and investigated androgen-induced sexual behaviour towards a filial imprinting object. Andrew (1964) showed that elements of the aggressive and sexual behaviour of older chicks (30–45 days) towards an imprinting object developed from behaviours shown by these chicks when they were a day old. The chicks received daily injections of testosterone, starting on day 3 after hatching. Bambridge (1962) imprinted day-old chicks to one of two artificial objects and gave the chicks daily testosterone injections from day 5 onwards. It was found that the chicks' sexual behaviour, measured on days 19 and 20, was directed almost exclusively at the training model. Since the sexual behaviour of the chicks in these two studies was induced artificially,

it is not clear whether sexual behaviour in normally developing animals is also preferentially directed towards an imprinting object that the chicks have been exposed to shortly after hatching. Vidal (1980) performed an experiment to investigate this problem. Male domestic chicks were exposed to an artificial object for 15 days from day 1 to day 15 (group I), or from day 16 to day 30 (group II) or from day 31 to day 45 (group III) after hatching. The chicks were then isolated and their sexual preferences tested when they were 5 months old, in simultaneous choice tests with the training object and a novel object. Vidal found that in the chicks in the groups with a strong filial preference for the training object (groups I and II) there was no significant preference for either object in the sexual preference test, although the cockerels showed sexual behaviour towards the stimuli. In contrast, the males in group III, that did not show a significant filial preference for the training object, had a strong sexual preference for the training object when tested at 5 months. The author concluded that the formation of a sexual preference is not a direct result of filial imprinting.

In sexual imprinting experiments, birds are usually reared up to a certain age with parents of their own species, or foster-parents of a different species. When the animals are sexually mature, their sexual preferences are tested. Measures of sexual preference used are proximity to the test stimuli (e.g. Bateson, 1978*b*; Bolhuis *et al.*, 1989*b*), copulation preferences (Bateson, 1978*b*; Gallagher, 1976) or preferential courtship singing (e.g. Immelmann, 1972*a*; Ten Cate, 1985*b*). Formation of a sexual preference is expressed as preferential responding to a member of the opposite sex of the rearing species. Bateson (1978*b*, 1980) found that in Japanese quail (*Coturnix coturnix japonica*) a preference for certain individuals also developed. Specifically, it was found that male and female Japanese quail preferred an individual that was different, but not too different, from the ones with which it had been reared. Bateson (1982) showed that group-reared quail, when presented with a number of individuals of different relatedness, preferred a first cousin to either siblings (whether familiar or novel) or less related or unrelated novel individuals (cf. Bateson, 1980, 1983*b*; Ten Cate & Bateson, 1988). Furthermore, quail reared with their siblings and paired with their first cousins lay fertile eggs before those paired with siblings or distant relations (Bateson, 1988). Bolhuis *et al.* (1989*b*) reared female domestic chicks in small groups with a male. When the animals were approximately 3 months old, the males were removed from the rearing pens and after 5 days simultaneous preference tests were conducted involving the familiar male, an unfamiliar male from the rearing strain and an unfamiliar male from a novel strain. It was found that the females spent significantly more time with the novel male of the rearing strain than with either of the other two males. Bateson (1983*b*) has provided a functional interpretation of these phenomena in terms of 'optimal outbreeding'. That is, the deleterious consequences of both extreme inbreeding and outbreeding are avoided through such a mechanism (see also Ten Cate & Bateson, 1988, for a discussion of these issues).

## (2) *Reversibility and sensitive periods*

Gallagher (1977) found that when male quail were exposed to an albino female from days 6–15 after hatching, a considerably greater proportion of the males showed a significant preference for an albino female over a normal female, compared to males that received the same period of exposure when they were either younger or older.

The stability of sexual preferences in the zebra finch (*Taeniopygia guttata castanotis*) was investigated by Kruijt & Meeuwissen (1991). The authors reared male zebra-finch young with Bengalese-finch (*Lonchura striata*) foster parents for 40 days, after which the young were isolated. In the control males this rearing procedure led to a strong preference to direct courtship singing to Bengalese-finch females when tested at 100 days of age. However, when the males were not tested but given the opportunity of breeding experience with a zebra-finch female for 3 months, there was a clear shift in sexual preference towards a preference for a zebra-finch female. Thus, these birds' sexual preferences were reversed. However, Kruijt & Meeuwissen also showed that cross-fostered zebra-finch males that were given a series of preference tests between 100 and 120 days, before they received breeding experience with the zebra-finch female, also showed a shift in preference towards a zebra-finch female, but, when tested after the breeding experience, maintained a preference for the foster-parent species. Thus, it appears that courtship experience can serve to consolidate previously established preferences. Similar results have been found by Immelmann, Lassek, Pröve & Bischof (1991).

### (3) *Predispositions and social interaction*

Kruijt (1985) has discussed research on sexual imprinting in mallards (*Anas platyrhynchos*) and zebra-finches. Several researchers in this field have suggested that sexual imprinting is affected by a 'predetermined bias' or predisposition to preferentially respond to stimulus characteristics of conspecifics. For instance, Schutz (1965) reported that mallard males tended to mate with a female of the foster-species with which they were reared. However, a minority of males reared in this way still preferred to mate with conspecific females. Moreover, females preferred to mate with a conspecific male, even when reared with another species. Schutz (1965) interpreted these data as evidence for "innate" responding to conspecific characteristics. However, as Kruijt (1985) points out, the females in Schutz' study were released onto a large pond where they were likely to be exposed to directed courtship of males that had been reared with their own species. Thus, differential exposure to mallard courtship could have biased the results. In order to test this hypothesis, Bossema & Kruijt (1982) reared male mallards of a wild and a white strain with either their own strain (straight-reared) or with the other strain (cross-reared). Females of both strains were all straight-reared. The authors found that females mated with the males that directed their activity towards them, irrespective of the colour of the male's plumage. Further experiments confirmed this finding, even when males and females were separated by wire (Kruijt, Bossema & Lammers, 1982). When the situation was arranged such that the different males were equally active towards the female, the latter tended to choose males of their rearing strain. Kruijt *et al.* (1982) concluded that choice of female mallards is based on the intensity of male courtship activity directed towards them, and on a visual resemblance of the male to members of the rearing strain (cf. Klint, 1978; Weidmann, 1990). The suggestion of a species-specific response bias was not confirmed. An apparent own-species bias in zebra-finch females could be accounted for in a similar way (Ten Cate & Mug, 1984; Ten Cate, 1985*a*).

A conspecific bias in sexual imprinting has also been suggested for zebra-finch males (e.g. Immelmann, 1972*a, b*). The work of Ten Cate and his collaborators (e.g. Ten



Cate, 1984; Ten Cate, Los & Schilperoord, 1984) has demonstrated that the formation of sexual preferences in zebra-finches is rather more complex than this account suggests. In one study (Ten Cate, 1982), zebra-finch young were cross-fostered with a mixed pair of parents, a zebra-finch and a Bengalese-finch. Ten Cate made detailed observations of the behaviour of the young and the foster-parents during the first 55 days of the young birds' life. In preference tests, Ten Cate replicated the findings of Immelmann (1972 *a*), showing that the zebra-finch males preferred to court females of their own species when adults. However, analysis of the behaviour of the parents revealed that the zebra-finch parents spent significantly more time with the zebra finch young in a number of social behaviours, compared to the Bengalese finch foster parents. Thus, the conspecific bias in the sexual preference tests might well have been affected by the differential social interactions with the conspecific parent during rearing. This suggestion was confirmed in a subsequent study (Ten Cate, 1984), in which young zebra-finch males were reared with mixed pairs of a zebra-finch and a Bengalese-finch parent, and the amount of social interaction of the zebra finch parent with the young was manipulated. Decreasing the number of social interactions between the zebra-finch parent and the young, e.g. by placing the parent behind wire mesh or exposing the young to a stuffed zebra-finch, led to a corresponding shift in sexual preference toward a preference for a Bengalese-finch female. In Immelmann's experiments, the young were usually reared in sibling groups. Kruijt, Ten Cate & Meeuwissen (1983) investigated the role of siblings in the development of sexual preferences. Zebra-finch males that were reared with Bengalese-finch parents and no or one zebra-finch sibling later showed an exclusive preference for a Bengalese-finch female. When the males were reared with Bengalese-finch parents and 2-4 zebra-finch siblings, a large proportion of them showed at least 5% courtship singing for a zebra-finch female, with some males preferring a zebra-finch female to Bengalese-finch female (see also Klint, 1978).

Thus, in all these cases it was shown that the eventual sexual preference was likely to be affected by the differential social interactions that the young bird experienced during development. It is not necessary to suggest a role for species-specific predispositions to explain the behaviour.

#### X. HORMONES AND IMPRINTING

##### (1) *Pituitary-adrenocortical hormones*

Several authors have investigated the relationship between pituitary-adrenocortical hormones and imprinting (Landsberg & Weiss, 1976; Weiss, Kohler & Landsberg, 1977; Martin, 1978, 1981). Landsberg & Weiss (1976) reported findings suggesting that subcutaneous injections of adrenocorticotrophic hormone (ACTH) impaired imprinting in ducklings. However, it is not clear from their report how preferences were measured. The ducklings received a 5 min simultaneous test, during which the novel model was either mobile or stationary and both models were either silent or emitted sounds. The measure of preference was derived from the approach to the familiar model during all these different conditions. Landsberg & Weiss (1976) reported an increase in plasma corticosterone levels only after injection of ACTH combined with training with an imprinting model. It is possible that the ducklings' behaviour during the test was influenced by an inhibition of approach caused by elevated corticosterone

levels (see Martin, 1981). Furthermore, Landsberg & Weiss do not report the following activity of the ducklings during the training exposure, leaving open the possibility that behaviour during testing was affected by an effect of the drug on training approach. Weiss *et al.* (1977) reported an increase of corticosterone levels with age, but found that this increase was mainly attributable to the imprinting experience itself, with only 8% of the variance in corticosterone level being determined by the age of the ducklings.

Suggestions that the effects of corticosterone on imprinting behaviour are relatively non-specific were confirmed by Martin (1978, 1981). This author allowed day-old ducklings to follow a moving object for 17 min. Twenty minutes later the birds were decapitated and bloodsamples were taken. There was a significant negative correlation between time spent following and plasma corticosterone concentration (Martin, 1978). Martin (1981) investigated the effects of administration of ACTH segments, corticosterone, and the corticosterone blocker metapyrone on ducklings' approach to an imprinting stimulus during training and testing. Pretraining injection of ACTH segments did not affect training approach nor the ducklings' preferences in a choice test. Injection of corticosterone inhibited training approach and affected retention, the latter effect probably being a consequence of the former. Metapyrone did not affect training approach but impaired retention. The effects of this drug were likely to be non-specific, since they could not be reversed by injections of corticosterone, nor could the effects be mimicked by administration of corticosterone antibodies. Martin (1981), in reviewing the work suggested that "The more parsimonious conclusion is that ACTH-like peptides and corticosterone act not on the learning process of imprinting, but on the approach and avoidance machinery associated with the learning tasks. It is not necessary to postulate an effect on memory or learning to explain available data in birds" (p. 105).

## (2) *Gonadal hormones*

James (1962) and Balthazart & de Rycker (1979) found that testosterone injections reduced the following-response in chicks, but these authors did not investigate the effect of this hormone on preferences. Andrew, Clifton & Gibbs (1981) reported effects of testosterone on memory formation and attention in chicks (cf. Clifton, Andrew & Gibbs, 1982; Rogers, 1974). These processes are involved in imprinting. Thus, Bolhuis, McCabe & Horn (1986) investigated the relationship between androgens and imprinting. They found that injection of testosterone-*enanthate* (a long-acting testosterone ester) shortly after hatching significantly increased preference scores of chicks that were trained by exposing them to a rotating stuffed jungle-fowl, but not when trained with a rotating red box (cf. Section III). Furthermore, the strength of preference of vehicle-injected control chicks was significantly positively correlated with plasma androgen levels in fowl-trained chicks, but not in box-trained chicks. Bolhuis *et al.* (1986) suggested that testosterone does not influence the learning process of imprinting *per se*, but may affect the developing predisposition for stimuli such as the stuffed fowl (see Section III, cf. Bolhuis *et al.*, 1985). It was suggested that placing the chicks in the running wheels might induce a surge in the levels of testosterone. There is evidence from studies with rats that handling and a number of other procedures stimulated the secretion of a number of pituitary hormones, including luteinizing hormone, LH (Kruhlich, Hefco & Read, 1974). An increase in levels of LH would

probably lead to a rise in plasma testosterone. A similar chain of events might be occurring when chicks are handled and placed in running wheels. Testosterone, or one of its metabolites, may have an effect on the brain and influence the development of the predisposition in a process which Horn (1985, p. 194) has called "functional validation" (cf. Jacobson, 1970).

Pröve (1983, 1985) studied the relationship between the development of plasma steroid levels and sexual imprinting in zebra-finches. Pröve & Immelmann (1982) gave zebra-finch males injections of cyproterone-acetate. The authors found that this anti-androgen reduced the amount of courtship song in the males, but Pröve & Immelmann did not investigate the effects of these drugs on imprinting *per se*, as evaluated in preference tests. In another study, Pröve (1983) reported age-related changes in plasma testosterone levels, the time-course of which showed certain similarities with the time course of a sensitive period for sexual imprinting. More recently, Pröve (1985, 1990) has begun to investigate the causal relationship between steroid hormones and the learning process of sexual imprinting. Zebra-finch males received subcutaneous silastic implants with testosterone,  $5\alpha$ -dihydrotestosterone, oestradiol, or vehicle (Pröve, 1985), or with one of a number of anti-androgens and anti-estrogens (Pröve, 1990) shortly after hatching. The males were cross-fostered with Bengalese-finch parents until day 35, when the implants were removed and the birds were isolated until sexual-preference testing at 100 days after hatching. Pröve (1990) found that the mean preference score for a female of the foster species was significantly greater in males treated with testosterone or  $5\alpha$ -dihydrotestosterone and significantly smaller in males treated with oestradiol, compared to control animals. The effects of the anti-androgens and anti-estrogens were not clear. The effects of the hormones were relatively small and there was considerable variation between individuals. From Pröve's preliminary reports it is not clear how these hormones affected preferences. For instance, it is possible that the behavioural interactions between the young and the parents, or the physical appearance of the young, changed as a result of hormone treatment. This suggestion is supported by a further experiment by Pröve (1990), in which males treated with testosterone and cross-fostered, as before, were not isolated between day 35 and testing, but reared with a zebra-finch female. This courtship experience led to a significant shift in preference toward a preference for a zebra-finch female in preference tests at 160 and 250 days after hatching (cf. Kruijt & Meeuwissen, 1991, and Section IX(2)). However, males that received implants of the anti-androgen cyproterone-acetate during the period of exposure to the zebra-finch female did not show such a shift in preference, and at 250 days strongly preferred the Bengalese-finch female in the preference tests. As noted above, cyproterone-acetate suppresses sexual behaviour in males (Pröve & Immelmann, 1982). Thus, the effects of the anti-androgen on preference may have been mediated by a change in the males' behaviour. Likewise, the effects on sexual preference of the different hormones in the earlier experiments (Pröve, 1985, 1990) may have been a result of a change in behaviour in the treated males towards the parents.

Hutchison & Hutchison (1983) reared male quail chicks with brown females. Sexual preferences were measured in a simultaneous-choice test with a white and a brown female (cf. Bateson, 1980). There was a significant positive correlation between levels of plasma androgen (combined testosterone and  $5\alpha$ -dihydrotestosterone) and preference

for the familiar morph. The authors present preferences as the difference between time spent near the familiar brown morph minus time spent near the novel white morph. This leaves open the possibility that the significant correlation was a reflexion of the relationship between the birds' activity and plasma androgen levels. This issue is particularly relevant in the light of a study by Hutchison & Bateson (1982), who investigated the effects of castration and testosterone replacement on sexual imprinting in male Japanese quail. When castrated males were not given testosterone replacement before sexual preference testing they did not show sexual behaviour at all. However, when castrated males did receive hormone replacement before testing they showed a sexual preference for the strain that they were reared with, as did the unoperated controls. The authors concluded that in Japanese quail, gonadal hormones are not required during the period of exposure to the imprinting stimulus to ensure the formation of a subsequent sexual preference for that stimulus. However, as Hutchison & Bateson (1982) note, castration may leave the production of testosterone by the adrenals unaffected (cf. Tanabe, Nakamura, Fujioka & Doi, 1979). Levels of testosterone of adrenal origin may be sufficient to affect the formation of sexual preferences.

#### XI. NEURAL MECHANISMS OF FILIAL IMPRINTING

##### (1) *Neural mechanisms of the learning process*

Horn (1985) has provided an extensive review of research into the neural mechanisms of filial imprinting in chicks (see also Horn, 1986, 1990, 1991 *a, b*). In a series of experiments it was found that filial imprinting was accompanied by an increased incorporation of radioactive uracil into ribonucleic acid (RNA) in the roof of the forebrain (Bateson, Horn & Rose, 1972). In a subsequent series of experiments it was established that these biochemical changes are likely to be linked to the learning process itself and are not side-effects of the training procedure (Bateson *et al.*, 1973; Horn, Rose & Bateson, 1973; Bateson, Horn & Rose, 1975). In an autoradiographic study, Horn, McCabe & Bateson (1979) found that imprinting led to a significant increase in incorporation of tritiated uracil into RNA in the intermediate and medial part of the hyperstriatum ventrale, or IMHV (Horn, 1981). Kohsaka, Takamatsu, Aoki and Tsukada (1979) reported a similar localization of biochemical changes during imprinting using the 2-deoxyglucose technique.

Following the discovery of these localized changes as a result of imprinting, bilateral electrolytic lesions were placed in IMHV before training. Chicks with such lesions did not acquire a significant preference for the training stimulus (McCabe *et al.*, 1981). Further, bilateral lesions to IMHV placed shortly after training severely impaired retention of a preference for the familiar stimulus, whilst lesions to the visual Wulst or to the lateral part of the cerebral hemispheres did not have such an effect (McCabe, Cipolla-Neto, Horn & Bateson, 1982). These and other results (McCabe, Horn & Bateson, 1979; Johnson & Horn, 1986, 1987) suggested that IMHV is critically involved in imprinting and may be the site of information storage.

Electrophysiological investigations showed that the spontaneous activity of units in IMHV was affected by imprinting (Brown & Horn, 1979; Payne & Horn, 1982, 1984; Bradford & McCabe, 1991). Recent experiments demonstrated that the evoked responses of units in left IMHV are affected by training and are dependent upon the

object with which the chicks were trained (McLennan & Horn, 1991). Imprinting was found to lead to changes in certain aspects of synaptic morphology in IMHV. Specifically, there was a significant increase in the length of the postsynaptic density (Bradley, Horn & Bateson, 1981; Horn, Bradley & McCabe, 1985). This increase was limited to synapses on dendritic spines; there was no such increase in shaft synapses. Furthermore, the increase only occurred in synapses in the left IMHV, not in the right, and was correlated with approach activity during training (Horn *et al.*, 1985). Training approach is correlated with preference score (Bateson & Jaekel, 1974). The hemispheric asymmetry in the involvement of IMHV in imprinting was corroborated by a series of studies involving sequential lesions to left and right IMHV (Cipolla-Neto, Horn & McCabe, 1982; Horn, McCabe & Cipolla-Neto, 1983; Davey, McCabe & Horn, 1987). A model was proposed for the role of the IMHV at both sides of the brain in memory storage during imprinting (Cipolla-Neto *et al.*, 1982; Horn, 1985). The left IMHV is thought to be a long-term memory store, whilst the right IMHV functions as a buffer store for information that is subsequently transferred to a store outside IMHV, called S' (see also McCabe, 1991).

The postsynaptic density is a site of high receptor density, so that an increase in size of this area might be accompanied by an increase in the number of receptors for the neurotransmitter. In the mammalian brain, some axospinous synapses are excitatory (e.g. Errington, Lynch & Bliss, 1987). Thus, McCabe & Horn (1988) investigated binding of the excitatory amino acid L-glutamate to membranes from IMHV after imprinting. It was found that imprinting led to a 59% increase in N-methyl-D-aspartate (NMDA)-displaceable binding of L-[<sup>3</sup>H]glutamic acid in the left IMHV, but not in the right IMHV (McCabe & Horn, 1988). Furthermore, it was found that in left IMHV, NMDA-sensitive glutamate binding was positively correlated with preference scores for the training stimulus, suggesting that the changes are indeed related to the learning process (see Fig. 5). Recent evidence (McCabe & Horn, 1991) shows that a significant increase in NMDA-sensitive glutamate binding in left IMHV does not occur until 8 h after the end of training.

It has been suggested that NMDA-receptor-related neural plasticity might play an important role in information storage in the brain (e.g. Horn & McCabe, 1987; Morris, 1989). This proposal gained prominence after it was discovered that NMDA receptors are crucial for the initiation of an artificially induced form of synaptic plasticity called 'long-term potentiation' (Bliss & Lømo, 1973; Collingridge & Bliss, 1987; see Horn, 1990, and Morris, 1989, for reviews). The synaptic changes found as a result of filial imprinting could increase the effectiveness of neurotransmission and form the neural basis of memory (Horn, 1985).

### (2) *Predispositions and individual recognition*

Several studies have shown that bilateral lesions to IMHV impair the formation of filial preferences as a result of exposure to a conspicuous object (see Horn & McCabe, 1984). Johnson and Horn (1986) showed, however, that such lesions did not affect the development of the predisposition. Thus, the neural systems that are involved in the predisposition must be outside IMHV (see also Davies, Horn & McCabe, 1985; Bolhuis *et al.*, 1986).

Bolhuis *et al.* (1985) suggested that the predisposition ensures that the young chick

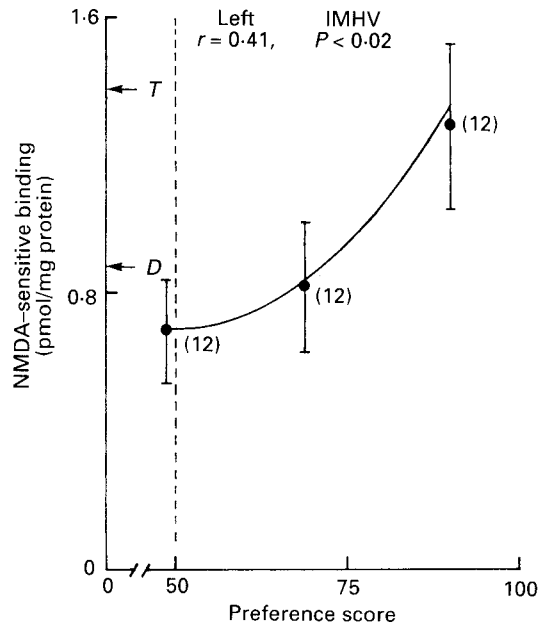


Fig. 5. Relationship between *N*-methyl-D-aspartate-sensitive binding in the left IMHV and preference score (means  $\pm$  s.e.m.). The preference score is a measure of the strength of imprinting. Preference scores of 100% or 0% indicate that during the preference test the chick directed all its activity to the imprinting or the novel object, respectively. The 'no preference' level of 50% is indicated by the vertical broken line. Each point represents the mean of 12 values. The curve is a polynomial, fitted to all 36 points by least-squares regression. (From McCabe & Horn, 1988. Reprinted with permission.)

attends to stimuli that resemble conspecifics. Learning processes would then be involved in the recognition of individuals. Thus, IMHV might be involved in learning the characteristics of individual conspecifics (Horn & McCabe, 1984). Johnson & Horn (1987) tested this hypothesis. Day-old chicks received bilateral lesions to IMHV, or to the visual Wulst, or were sham-operated, before being exposed to one of two stuffed jungle-fowl hens. Two hours after training, preferences were measured in a simultaneous choice test. It was found that chicks in the sham-operated group, and those in the Wulst-lesioned group showed a significant preference for the training model, whilst the IMHV-lesioned chicks did not show a significant preference. Similarly, Bolhuis *et al.* (1989*b*) found that lesions to IMHV, placed shortly after hatching, impaired the recognition of individual conspecifics in 3-month-old chickens (cf. Section IX).

The role of IMHV in other types of learning was studied by Johnson & Horn (1986), who found that although bilateral lesions to IMHV severely impaired filial imprinting, they did not affect learning of an operant task in which presentation of the imprinting object was the reinforcer (see Section VI). Previously, McCabe *et al.* (1982) found that chicks with bilateral lesions to IMHV were not impaired in performing a simultaneous visual discrimination task with a blast of warm air as the reinforcer. Davies, Taylor & Johnson (1988) reported that bilateral IMHV lesions impaired one-trial passive avoidance learning (Lee-Teng & Sherman, 1966). Johnson & Horn (1986) and Davies

*et al.* (1988) suggested that lesions to IMHV cause an impairment in recognition memory. Recognition is an important feature of both imprinting and passive avoidance learning. Horn (1985, pp. 115–118) and Horn & Johnson (1989) have stressed the parallels between the findings in the chick and dichotomies in memory impairments that have been reported after medial temporal or thalamic damage in humans (cf. Squire, 1987). In human amnesia, dissociations have been made between ‘episodic’ or ‘declarative’ memory on the one hand and ‘procedural’ memory, or memory for skills on the other. The former kind of memory is impaired in temporal-lobe amnesia while the latter is not. Similar dissociations have been proposed for primates (cf. Squire, 1987) after lesions to the hippocampus.

## XII. CONCLUSIONS AND DISCUSSION

### (1) *Learning and representations*

The study of the development of social preferences is moving away from traditional and increasingly less useful concepts such as sensitive periods and irreversibility, whilst focussing on underlying neural and psychological mechanisms. The emphasis is on the analysis of these different mechanisms, and their relationship to phenomena in other forms of learning (e.g. Horn, 1985, 1991*a*; Ten Cate, 1989*b*; Bolhuis *et al.*, 1990; Bateson, 1991*b*; Hollis *et al.*, 1991). The difference between an associative and a perceptual learning interpretation of imprinting, as discussed in Section VI, may not be substantial. Apart from the question of whether or not there is a UCS for imprinting, both interpretations need to explain the mechanism of the formation of a representation of the imprinting stimulus. The evidence suggests that the mechanisms involved in the formation of a representation of the imprinting stimulus may be similar to those involved in other forms of recognition memory (cf. Horn & Johnson, 1989; Bateson, 1990; Hollis *et al.*, 1991).

Some contemporary approaches to associative learning assume that the conditioned stimulus is not unitary, but consists of many elements (e.g. Pearce, 1987; McLaren, Kaye & Mackintosh, 1989). Associations may be formed between the different elements of the CS, and between the CS and the context. In the course of conditioning, different elements of the stimulus may enter into an association with the UCS. These ideas were incorporated into a connectionist model of stimulus representation to explain the differential effects of CS pre-exposure in perceptual learning and in latent inhibition (McLaren *et al.*, 1989). Similarly, during filial imprinting it is likely that a representation of the stimulus is formed gradually, with learning about some elements of the imprinting stimulus affecting learning about other elements (e.g. Van Kampen & De Vos, 1991, for shape and colour; Hoffman & Ratner, 1973*a*, for movement and other stimulus elements; see also Chantrey, 1974). For a connectionist model of the formation of representations in imprinting, the distinction between a conditioning and a perceptual learning interpretation is not essential. Even so, it remains unclear whether the learning process may involve the formation of an association between the representation of the stimulus and the representation of reinforcing aspects of the stimulus (see Section VI(1) and Bolhuis *et al.*, 1990 for further discussion).

(2) *Imprinting and the development of behaviour*

Imprinting is often regarded as paradigmatic for the study of behavioural development, for example with regard to concepts such as sensitive periods, irreversibility and the 'nature versus nurture' controversy (e.g. Lorenz, 1935; Bateson, 1983*a*, 1990; Hogan, 1988). The evidence reviewed in the present paper supports the view that attempts to dissociate causal mechanisms of ontogeny into 'innate' and experiential factors are misleading (see also Kruijt, 1964; Bateson, 1990; Kruijt & Ten Cate, 1988; Bolhuis & Johnson, 1991*b*). For example, the term 'predisposition' is used to indicate that the preference for stimuli with a head and neck emerged without experience with the relevant stimulus (Section III). However, the evidence showed that the emergence of this preference is dependent upon non-specific experience in a complex manner.

Gottlieb (1976, 1980) distinguished a number of ways in which experience might affect the likelihood of a certain behaviour occurring, namely induction, facilitation and maintenance. Bateson (1983*a*) suggested a fourth way, i.e. where a certain event predisposes another event to induce a certain behaviour to occur subsequently. All of the possibilities suggested by Gottlieb's classification have been shown to occur in imprinting. For instance, Gottlieb (1980) showed that specific embryonic experience was needed to maintain a species-specific auditory preference in ducklings (see Section VIII, 2). The effect of exposure to light on following of an imprinting object (Bateson & Seburne-May, 1973) is an example of facilitation of the development of behaviour. The effect of non-specific experience on the development of a predisposition, as described in Section III, is an instance of induction (Gottlieb, 1980) or 'initiation' (Bateson, 1983*a*) of preference behaviour.

Kruijt (1964) was among the first to apply ethological concepts concerning the causation of behaviour (e.g. Tinbergen, 1951) to the study of ontogeny, especially the development of aggressive and courtship behaviour in the jungle-fowl (*Gallus gallus spadiceus*). Central to Kruijt's approach is the suggestion that behaviour is often a result of conflict between different motivational systems or 'behavioural tendencies'. For instance, the form and occurrence of courtship displays can be interpreted as the result of an interaction between the simultaneously activated tendencies to escape, to attack, and to behave sexually. Kruijt suggested that, initially, the motor components of behaviour may function independently in the young animal. In the course of development, possibly after particular experience, these motor components become integrated into more complex behaviour systems such as hunger or sex (see Kruijt, 1964, for a detailed discussion of these issues).

Hogan (1988) adapted some of Kruijt's ideas and proposed that behaviour is a result of the influence of various kinds of perceptual, motor and central mechanisms. In Hogan's words, "the study of development is primarily the study of changes in these components themselves and in the connections among them" (p. 63). Hogan interprets imprinting as the development of perceptual mechanisms that become linked to motor mechanisms for filial or sexual behaviour. Analogous to Lorenz's (1935) concept of 'Schemata' (see Section II), Hogan suggests that these perceptual mechanisms serve a species-recognition function. Furthermore, in some species (such as the curlew) the perceptual mechanism has developed 'prefunctionally', whilst in species such as the



greylag goose 'functional' experience is necessary for its development. Hogan proposes that different kinds of perceptual mechanism may be organized in an hierarchical way. They include mechanisms involved in the processing of simple features such as colour and pattern, e.g. what Horn (1985) and Bolhuis (1989) have called a filter in filial imprinting. Higher up in the hierarchy of perceptual mechanisms are what Hogan calls 'object recognition mechanisms', such as of 'grainlike' or 'wormlike' objects in the hunger behaviour system. What was described in Section III as a specific predisposition for stimuli with a head and neck can be interpreted as an object recognition mechanism.

### (3) *General considerations*

Lorenz (1935) described imprinting as the establishment of "a sort of consciousness of species in the young bird" (Lorenz, 1937, p. 265). Many authors have followed Lorenz in maintaining that imprinting leads to recognition of, and a preference for the rearing species (e.g. Gottlieb, 1971; Ten Cate, 1984; Hogan, 1988). As Bateson (1966) has argued, however, imprinting may be concerned with learning the characteristics of *individuals*. Examples of experience-dependent individual recognition are provided for both sexual (Bateson, 1982; Bolhuis *et al.*, 1989*b*) and filial imprinting (Johnson & Horn, 1987; Kent, 1987; Gottlieb, 1988; see also Zajonc *et al.*, 1975). In sexual imprinting, adult birds tend to prefer a member of the rearing strain or rearing species to that of another strain or species (see Section IX). This may be a result of what is learned about certain individuals. That is, when an animal prefers an individual that is different, but not too different, from an individual that it was reared with (Bateson, 1978*b*, 1982; cf. Section IX), such an individual is likely to be of the rearing species. In other words, what is termed 'species recognition' may be a result of the recognition of individuals.

Filial imprinting has proved to be a fruitful paradigm to study neural mechanisms of learning and memory, partly because the learning process and the chicks' visual experience before and after learning can be brought under experimental control (Horn, 1985). The localization of a discrete region of the brain that is involved in memory storage and the correlation of a number of aspects of synaptic plasticity with filial preference have made filial imprinting one of the most important paradigms in this field. Furthermore, it has been demonstrated that neural and physiological intervention may yield important insights into the organization of behavioural mechanisms (e.g. Horn, 1991*a, b*; Johnson & Bolhuis, 1991). The evidence reviewed in the present paper shows that the laboratory study of imprinting has increased greatly our understanding of the neural and psychological mechanisms of learning, memory and development.

### XIII. SUMMARY

Filial imprinting is the process through which early social preferences become restricted to a particular object or class of objects. Evidence is presented showing that filial preferences are formed not only as a result of learning through exposure to an object, but also under the influence of visual and auditory predispositions. The development of these predispositions is dependent upon certain non-specific experience.

There is little evidence for an endogenously affected sensitive period for imprinting. It is more likely that the end of sensitivity is a result of the imprinting process itself.

Similarly, it is now firmly established that filial and sexual preferences are reversible. Evidence suggests, however, that the first stimulus to which the young animal is exposed may exert a greater influence on filial preferences than subsequent stimuli.

The learning process of imprinting is often regarded as being different from conventional associative learning. However, the imprinting object itself can function as a reinforcer. Recent studies have attempted to test predictions from an interpretation of filial imprinting as a form of associative learning. The first results suggest that 'blocking' may occur in imprinting, whilst there is no evidence for 'overshadowing'.

Social interactions with siblings and parent(-surrogates) have been shown to affect the formation of filial and sexual preferences. The influence of these interactions is particularly prominent in sexual imprinting, making earlier claims about naive species-specific biases unlikely.

Although auditory stimuli play an important role in the formation of social attachments, there is little evidence for auditory imprinting *per se*. Auditory preferences formed as a result of mere (pre- or postnatal) exposure are relatively weak and short-lasting. Exposure to visual stimuli during auditory training significantly improves auditory learning, possibly through a process of reinforcement.

It is becoming increasingly clear that filial and sexual imprinting are two different (although perhaps analogous) processes. Different mechanisms are likely to underlie the two processes, although there is evidence to suggest that the same brain region is involved in recognition of familiar stimuli in both filial and sexual imprinting.

There is little evidence for a direct role of hormones in the learning process of imprinting. Androgen metabolism may be a factor constraining the development of a predisposition in the chick. Research into the neural mechanism of filial imprinting in the chick has revealed that a restricted part of the forebrain (IMHV) is likely to be a site of memory storage. Changes in synapse morphology and in the number of NMDA receptors have been found, limited to this region, and correlated with the strength of preference.

#### XIV. ACKNOWLEDGMENTS

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