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*Phil. Trans. R. Soc. Lond. B* 1990 **329**, 125-131  
doi: 10.1098/rstb.1990.0157

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# Is imprinting such a special case?

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## SUMMARY

As the result of relatively brief exposure to a particular type of object early in life, many birds and mammals will form strong and exclusive attachments to that object. This is known as 'filial imprinting'. Early experience can also have long-lasting effects on sexual preferences, but the conditions are different from those in which the first attachments are formed. Some of the characteristics of imprinting are undoubtedly because of the naive animal searching for and responding selectively to particular stimuli. But that is not all. At least two types of plastic change seem to be involved: establishing an internal representation of the familiar object and pre-emptive capturing by that representation of the systems controlling filial behaviour and, much later in development, sexual behaviour. The second plastic change is likely to generate the phenomenon of a sensitive period and gives the formation of social attachments some of its other peculiar properties. The first change is likely to be the process used in most forms of recognition. Distinguishing between the sub-processes that underlie an overall change in behaviour serves to make some overdue links between different areas of knowledge about learning which have hitherto been poorly connected.

## 1. AN UNFORGETTABLE PHENOMENON

Imprinting is undoubtedly startling. Goslings treating an eminent ethologist as though he were their mother always causes a stir. The learning process occurs early in the lives of many birds and mammals and, in some cases at least, can have profound and lasting effects on the sexual preferences of adults. The image conjured up by the term is vivid and simple. At a certain stage the wax of the young animal's brain is soft and it receives the imprint of the first conspicuous thing which the animal encounters.

The German term *Prägung* (translated as 'imprinting') was first used by Heinroth (1911), although Spalding (1873) had used a very similar metaphor, namely 'stamping in'. Konrad Lorenz (1935), who did so much to make the phenomenon famous, liked the image because it suggests, as he believed to be the case, an instantaneous, irreversible process. It also led to strong claims that imprinting is quite different from associative learning (Hess 1973). As more evidence became available, the claims were disputed and the term was held to be misleading (Bateson 1966; Sluckin 1972). Nevertheless, Lorenz (1981) continued to treat the process as special and 'imprinting' has been retained in the literature by advocates and critics alike.

Astonishing retention of sexual preferences is found in the face of considerable sexual experience with other objects (Immelmann 1972). However, changes in preference may take place under at least two conditions. As birds learn the characteristics of siblings at an early age and the plumage of siblings changes with age, it seems likely that they update the representation of the sibling (Bateson 1979). Indeed, Ryan & Lea (1989)

have found that when small changes were made to an artificial object as chicks age, the chicks were more likely to prefer the object seen most recently. Secondly, numerous anecdotes suggest that under conditions of great stress, plasticity may be renewed (Bateson 1983). Even without this evidence, the stability of the preference is no longer treated as a reason for regarding the learning process as special (Immelmann 1984). The special flavour of the phenomenon comes from the particular biological job that the learning process has to perform and the context in which it occurs.

The biological function of imprinting is probably to enable the animal to recognize close kin. Filial imprinting enables a young animal to distinguish between its parent and other members of its own species and sexual imprinting enables an animal to mate with an individual that is neither too closely nor too distantly related (Bateson 1979). Filial imprinting occurs just before the stage in the life cycle when, for its own safety, the young animal needs to discriminate between its parents and other members of its own species that might attack it. In precocious species this occurs shortly after hatching or birth. The animal is predisposed to set the learning process in motion.

Despite the changes in thought, the striking character of both the phenomenon and the commonly used image had two opposed but equally unfortunate effects. On the one hand, inferences about the nature of underlying mechanisms were uncritically accepted and used to explain many other processes, such as the development of social attachments in humans. On the other hand, the evidence was tainted by popularization and over-critically rejected by many of those whose primary interest was the experimental analysis of learning. It was therefore regarded as a peculiar case

and excluded from any broad statement about learning in general. Even so, one consequence of forming a social attachment is recognition by the animal of the object to which it had been previously exposed. Recognition is a feature that surely must be shared with a large number of other learning processes. As scientific attention has become focused on the character of neural representations of the external world, forming a social attachment has presented itself increasingly as an extremely attractive instance of a general phenomenon.

## 2. WHAT IS IN THE PROCESS?

Imprinting with a novel and conspicuous object usually occurs most readily at a particular stage of development (see reviews in Bateson (1966, 1979); Hess (1973); Sluckin (1972)). Many factors have relatively short-term effects on responsiveness and much research has been devoted to sorting them out. For example, Polt & Hess (1966) found that domestic chicks given two hours of social experience with siblings beforehand followed a moving object more strongly than isolated birds (see also Lickliter & Gottlieb (1985, 1988)). Stimulation in other modalities, when presented concurrently with visual stimuli, can have a powerful motivating effect. Gottlieb (1971) found that, in domestic chicks and mallard ducklings, the sounds most effective in eliciting pursuit of a moving visual stimulus are conspecific maternal calls. Furthermore, young birds learn the characteristics of auditory stimuli played to them shortly after hatching (Gottlieb 1988). In the process of forming a social attachment under natural conditions auditory signals are very important. None the less, studies of imprinting provide unambiguous evidence for the formation of visual stimulus representations. The visual image is not only retained for a long period of time in the case of sexual imprinting, but also the details held in memory are remarkably specific, enabling the subsequent identification of individuals (see, for example, Bateson (1982); Johnson & Horn (1987)). Objects with the right features probably have a positive effect on motivational state since birds approach more readily as they are exposed to a conspicuous object for the first time (Horn *et al.* 1973; Bateson & Jaeckel 1974). Also, ten Cate (1989) has found that in Japanese quail, the posture of a live adult female has a powerful motivating effect on the response to her by the chicks. The range of objects that motivate, and which can elicit social behaviour is obviously restricted by the animal's experience. Thus when the young bird becomes familiar with one object the likelihood of it withdrawing from dissimilar conspicuous objects increases. The so-called sensitive period seems to be brought to an end by the formation of a social attachment (Bateson & Hinde 1987).

The importance of developmental stage, motivational state and the active role of the animal in the process are not difficult to incorporate into a coherent theoretical scheme (see Bateson 1990). As a bird reaches a particular stage in development, the system that controls searching is activated. The searching may

bring the animal into contact with an object that has features to which it is predisposed to respond strongly. The object's features drive the executive system controlling approach. Simultaneously, searching is inhibited. At an early stage in the process the recognition system is addressed, but nothing has yet been stored there. When the bird is more experienced, a familiar object matches its representation in the recognition system, which by now exclusively controls approach movements. Finally, when a bird encounters a strange object, its features fail to match the representation of the familiar object and so the bird withdraws. In the presence of a familiar object, of course, withdrawal is inhibited.

In the present context of focusing on learning and memory, the way of thinking about imprinting outlined above helps to separate factors that are likely to influence motivational state or are peculiarities of the context in which this particular form of recognition learning takes place. The crucial part that deals with the storage of visual information is shown in more detail in figure 1 and involves three stages: analysis, recognition and execution. These are ideas that Gabriel Horn and I have developed over the years (Bateson 1981, 1987, 1990; Horn 1985).

As far as visual stimulus analysis is concerned, domestic chicks and domestic ducklings have relatively unstructured social preferences at hatching. At one time, movement was regarded as essential in 'releasing' the following response and hence in initiating the imprinting process. However, the effectiveness of the many visual stimuli used in the imprinting situation depends on such properties as their size and shape, as well as on the angle they subtend and the intensity and wavelength of light they reflect. Moreover, the rates at which these variables change are also important, hence the undoubted effectiveness of movement and flicker.

The bird clearly responds to a pattern of stimulation, and characterization of the most effective stimulus must be cast in terms of clusters of features. Attention has been increasingly focused on stimulus features found in the natural world (see, for example, Johnston & Gottlieb (1981)). Strong evidence suggests that the features of the jungle fowl, the ancestral form of the domestic fowl, are particularly attractive to chicks (Horn & McCabe 1984). In this case, the preference for naturalistic stimuli had been missed because, under laboratory conditions, the necessary feature detectors seem to take longer to develop than do the ones driven by the flashing lights and movement (Horn 1985; Bolhuis *et al.* 1985, 1989; Johnson *et al.* 1985). At first it seemed as though chicks might have a predisposition to respond to the head and neck of jungle fowl. However, the head and neck of a duck or even a small mammal turned out to be just as effective (Johnson & Horn 1988).

Only some of the feature detectors are shown in figure 1 addressing the recognition system. This flagrantly connectionist proposal for establishing a representation of the imprinting object is essentially that of Hebb (1948). Each of the feature detectors is connected to each of a population of neurons in the recognition system and, at least in a subset of those

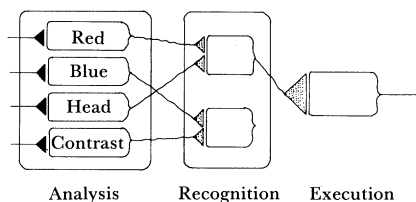


Figure 1. A scheme of the stages from input to output involved in filial responses to a mother hen or a substitute imprinting object. Only some of the feature detectors thought to exist in the analysing system are shown. Plasticity resulting from imprinting occurs both where the feature detectors connect with the recognition system and where the output from a given representation connects to the executive system controlling filial behaviour. Another representation of an object to which the bird is tame is also shown. This does not have access to the executive system because all available connections have been captured by the first.

neurons, the particular connections that had been active during imprinting are strengthened. The strengthened connections between the analysis and recognition systems subsequently constitute the representation of the imprinting object.

The final step in the proposed process is establishing a link between the representation of the imprinting object and the executive system controlling social behaviour. The first preferences to be formed are likely to be the ones that last, within certain constraints such as the age of the animal at its first exposure and the length of that exposure (Immelmann & Suomi 1981; Cherfas & Scott 1981; Bolhuis & Bateson 1990). When a bird is well imprinted, it can be exposed to another object. At first the bird withdraws showing every sign of great alarm. Gradually, this alarm habituates and the bird becomes tame. However, tame birds do not necessarily express any social behaviour towards the object that is by now very familiar. They evidently recognize it but that is all. These results led Horn and myself to the speculation that two forms of plasticity might be involved, one concerned with recognition of previously experienced inputs and another concerned with connecting up the mechanism involved in recognition of familiar inputs to the execution of filial or, later in life, sexual behaviour (Bateson 1981).

Suppose that gaining access involves growth of neural connections and that the area available for connections has finite size. When growth has proceeded beyond the half-way point and cannot be reversed easily, the input experienced first will be better able to control the behaviour than other forms of input. It is a form of competitive exclusion. If the first object is highly attractive to the bird, then access is captured much more quickly than if it is not. Boakes & Panter (1985) obtained evidence that imprinting with a second object is indeed much more difficult if the first object was a live hen than if it was a toy wind-mill (see also Bolhuis & Trooster (1988)).

In the case of sexual imprinting, the final hook-up between the representation of the imprinting object stored in early life and the executive system controlling sexual behaviour probably does not occur until much

later than original storage of the representation (Hutchison & Bateson 1982). Prolonged exposure to one individual, with which the young bird becomes familiar, followed by exposure to a second can still lead to a sexual preference for the second (Schutz 1965; Vidal 1980). Delay in hooking-up to the executive system for sexual imprinting makes good biological sense. It allows the bird's sexual preferences to be affected by the appearance of siblings when they are adult-like, as well as by the appearance of their parents.

Two types of plasticity have been proposed here, but that is not all. In his paper, Horn provides evidence that the two anatomically separate representations of the imprinting object may occur in parallel. Furthermore, we have good reason to think that with appropriate training techniques, a representation of an imprinting object can control other responses such as running up an alley to obtain food (Bateson 1973).

To summarize, the view of imprinting presented here, the recognition mechanisms have large capacities for storing representations of different objects. Once change has occurred here, further changes are made more difficult by escape from all novel objects. However, when escape from a particular object has waned, its characteristics can also be represented in the recognition system as a result of further exposure. By contrast the possibilities for accepting new connections into the executive system are limited. The capacity for plastic change here is believed to be severely restricted. Once this capacity is used up, the animal may become tame to a novel object, but will not respond to it socially.

### 3. UNIQUENESS REVISITED

As attention has focussed on neural representations of external objects, the recognition aspect of forming a social attachment has started to look more and more like a paradigm case (see Green 1982). Associations of a kind seem to be formed but the experimental operations by which a social attachment is influenced and shown to differ in significant ways from classical conditioning and from discrimination learning in an instrumental situation. The procedure involves a period of exposure to a particular object and a subsequent test in which the behaviour of the bird to that same object and to a dissimilar one are measured. Generally, if the birds direct stronger social responses towards the first object than towards the second, or follow the first more than the second, they are said to have been imprinted with the first one.

A recurring line of thought has been to use the methodology of animal learning experiments to look behind the distinctive procedure used in imprinting experiments (Zolman 1982; Hoffman 1987). Animal learning theory is, after all, well established and has led to the formation of a great body of techniques and empirical literature. Although it is not necessary to pair the training stimulus with any other event, a particular feature might act as an unconditioned stimulus, with the other characteristics around that feature being learned by association. James (1959)



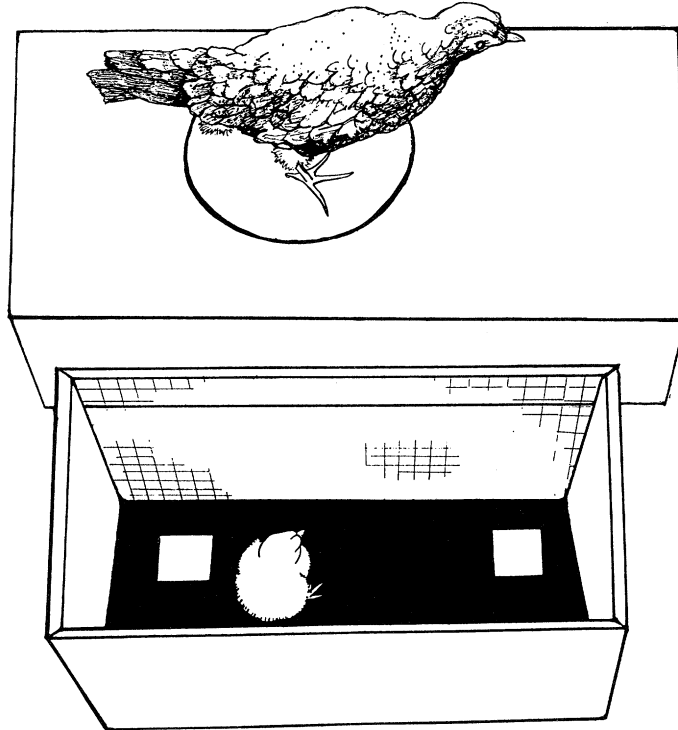


Figure 2. When one of the pedals is pressed the stuffed jungle fowl rocks until the chick approaches and leaves the pedal. Newly hatched chicks will learn rapidly to return to the correct pedal. As they become more experienced with one view of the fowl, they will learn to press a pedal that turns the fowl through 90° (Bateson (1976), drawn by Priscilla Barrett).

showed that chicks could be induced to approach a flashing light in preference to one that was not flashing. When a stationary object was placed alongside a flashing light, chicks subsequently approached the stationary object in the absence of the light (Abercrombie & James 1961). Similarly, a conspicuous object can be used to reinforce a newly hatched chick's activity of pressing a pedal (Bateson & Reese 1969). Apparatus that uses a rocking jungle fowl is shown in figure 2.

Continuing in the same vein of combining methodologies, Kroodsmma *et al.* (1984) suggested that if recognition learning consists of establishing links between the initially effective features of an imprinting object and the subtle details, then it should be possible to do the equivalent of a backward conditioning experiment, varying the order in which moving and static objects are presented. More recently, Bolhuis *et al.* (1990) have discussed the use of blocking and overshadowing experiments. De Vos & Bolhuis (1990) obtained analogous results to blocking in classical conditioning in the imprinting situation. The issue, however, is whether blocking experiments or others like them, tell us anything about whether or not the recognition learning involved in social attachments is associative in the classical sense. Such experiments tell us something about the general character of information processing, but not plausibly about the way in which links between stimuli are formed.

The evidence might be taken to suggest that, behind the superficial differences in procedure, lie fundamental similarities between associative learning and imprinting. However, some evidence points against

such a view. Horn (1990) considers the neural system specifically involved in storage of the representation of the imprinting object. When this system was lesioned, and the lesioned birds were put into the pedal-pressing apparatus of Bateson & Reese (1969), the birds learned to press so as to present themselves with a conspicuous object but they did not learn to recognize it (Johnson & Horn 1986). This evidence suggests dissociation of the operant conditioning from the recognition part of forming social attachments. Where does it leave the associations that may be formed in recognition learning?

#### 4. DIFFERENT TYPES OF ASSOCIATION

'Associative learning' is in danger of being stretched to cover too many different ideas. Its original usage was for associations between separately occurring neutral and significant external events. Are these really the same as associations between jointly occurring features of an external event? Again, are they the same as an association between an internal representation and one controlling behaviour? When an animal learns to use one event to predict the arrival of another, that is not the same as when it forms a new representation of something in the outside world. Neither are the same as when, with a certain condition fulfilled, an already established representation begins to influence a motor system, such as that involved in sexual behaviour. They are not the same because the links postulated to explain what happens are serving very different jobs.

When characterizing classical conditioning, Dickin-

son (1980) used a functional definition. The learning process serves to uncover the causal structure of the environment. My point is that the job of learning to predict and control the environment is not the same as that of learning to categorize it. At the cellular level similar if not identical mechanisms may be used to achieve these different jobs, but at the behavioural level we should expect different design rules. Detecting causal structure may require classification, but establishing a classification does not obviously involve association of cause with effect. If forming a new category requires its own rules, and that seems likely, then generalizing 'associative learning' from its conventional usage to cover these rules is only going to get in the way of understanding what those rules might be.

In uncovering causality, detecting order is crucial. If the supposed cause follows an event, then it is not a cause. By contrast, when establishing a category temporal contiguity may be important, but the order in which the features occur is not. I shall show this with what I regard as an important contribution from the study of imprinting in the 1970s. Consider the problem facing the bird that has to gather information about the front, side and back views of its mother. All these views are physically distinct and they may also take on different appearances when viewed at different distances. Information from two separate arrays of features may be combined into a single representation when the two arrays occur in the same context or within a short time of each other (Bateson 1973; Bateson & Chantrey 1972). Chantrey (1974) varied the time between the onset of presentation of one imprinting object and the onset of presentation of another and subsequently required domestic chicks to discriminate between the two familiar objects (see figure 3). If the objects were presented five or more minutes apart, the birds learnt to discriminate between the two objects more quickly than those in the control group, which had not been exposed to these two objects. However, when the two objects were presented 30 s or less apart, the imprinted birds took longer than the control group to learn the discrimination. The effect is sometimes elusive and Stewart *et al.* (1977) were only able to obtain it when they replicated Chantrey's experimental conditions exactly. Perhaps the fragility is less surprising than if the birds had had a simple categorization rule, which meant that arrays of features that occurred within a short time of each other were always combined into a single representation. Circumstances must surely arise when stimuli occurring in rapid succession are processed separately. Nevertheless my point is that, when they are treated as part of the same event, the order of presentation does not matter in the least.

In brief, those of us who work at the behavioural level should not imply that all the different jobs that learning can perform have the same rules because we can employ the word 'association' for all of them. I think we serve our physiological colleagues best if we use our behavioural knowledge of the whole animal to tease out the different sub-systems that are likely to exist in the brain and that are put together in different ways for different sorts of jobs.

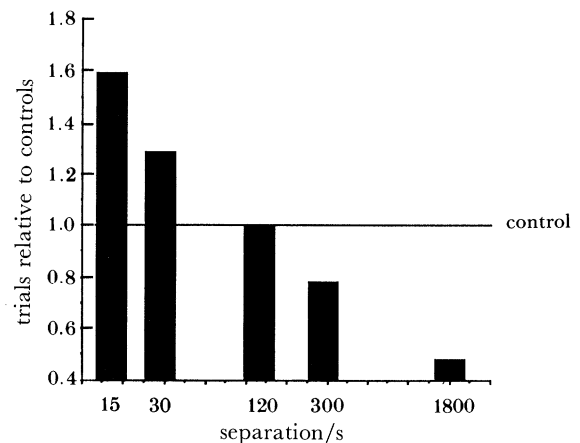


Figure 3. The mean number of trials to reach criterion in a food rewarded discrimination between two cylinders of different colours taken by domestic chicks that were previously imprinted with both objects. The scores are expressed as ratios relative to control groups that had not previously been exposed to the two cylinders used in the visual discrimination. The imprinting conditions of the experimental groups differed in the time that elapsed between the onset of successive presentations with first one object and then the other object. These absolute values of the inter-onset times are given, but they are expressed on a logarithmic scale (redrawn from Chantrey 1974).

## 6. SEPARATING THE SUB-PROCESSES

Part of my aim has been to consider what we might infer about the nature of underlying mechanisms from what is known about the formation of social attachments at the behavioural level. I have suggested that

- (i) the peculiarities of the phenomenon are due to the special context in which it occurs;
- (ii) at least two types of plasticity are involved which may not necessarily coincide in time;
- (iii) 'association' is used for different functions and (possibly) different mechanisms, and
- (iv) the rules for establishing a representation of a familiar object are likely to be general.

Perhaps the most important conclusion from the behavioural work is the need to think of a given phenomenon in terms of a series of sub-processes. I have dwelt on the analysis of the features of the stimuli which will start off the formation of the social attachment, the establishment of a representation of that combination of features and the linking of such a representation to the system controlling social behaviour. The common denominator with a great many other learning processes is creating a representation of the object to which the animal has been exposed (Suboski 1989).

If the explanations seem coherent, the inferences about the sub-processes will be examined from the standpoint of what is known about the nervous system. The behavioural theories make assumptions about the nervous system and these must be checked against reality. As the neural reality becomes more complete, the enquiry has to return to the behavioural level. If the assumptions turn out to be false, as many will, the models will have to be rethought and, in all likelihood,

new behavioural experiments will have to be done. The return flow of ideas from lower to higher levels of analysis seems a much more attractive picture of collaboration between disciplines than the one of relentless reductionism in which the behavioural people hand a problem to the neural people who, having done their work hand it on to the molecular people.

In conclusion, the reality of what happens in the formation of social attachments in birds lies somewhere between the views of the enthusiasts and those of the sceptics. Many of the implications stemming from the original concept are simply wrong. Nevertheless, the phenomenon provides a particularly striking case of the representations that presumably form during exploration, latent learning and, indeed, virtually every transaction that a complicated animal has with its environment. For this reason alone, it warrants the close scrutiny of those who are interested in the sub-processes involved in learning and memory.

Many of the ideas in this paper have arisen in discussion with Gabriel Horn with whom I have collaborated for more than 20 years, and with Karen Hollis and Carel ten Cate. I am grateful to Johan Bolhuis for his comments on the manuscript.

#### REFERENCES

- Abercrombie, B. & James, H. 1961 The stability of the domestic chick's response to visual flicker. *Anim. Behav.* **9**, 205–212.
- Bateson, P. P. G. 1966 The characteristics and context of imprinting. *Biol. Rev.* **41**, 177–220.
- Bateson, P. P. G. 1973 Internal influences on early learning in birds. In *Constraints on learning: limitations and predispositions* (ed. R. A. Hinde & J. Stevenson Hinde), pp. 101–116. London: Academic Press.
- Bateson, P. 1979 How do sensitive periods arise and what are they for? *Anim. Behav.* **27**, 470–486.
- Bateson, P. 1981 Control of sensitivity to the environment during development. In *Behavioural development* (ed. K. Immelmann, G. W. Barlow, L. Petrinovich & M. Main), pp. 432–453. Cambridge University Press.
- Bateson, P. 1982 Preferences for cousins in Japanese quail. *Nature, Lond.* **295**, 236–237.
- Bateson, P. 1983 The interpretation of sensitive periods. In *The behavior of human infants* (ed. A. Oliverio & M. Zappella), pp. 57–70. New York: Plenum Press.
- Bateson, P. 1987 Imprinting as a process of competitive exclusion. In *Imprinting and cortical plasticity* (ed. J. P. Rauschecker & P. Marler), pp. 151–168. New York: John Wiley.
- Bateson, P. 1990 Making sense of behavioural development in the chick. In *Neural and behavioural plasticity: the use of the domestic chick as a model* (ed. R. J. Andrew). Oxford University Press. (In the press.)
- Bateson, P. P. G. & Chantrey, D. F. 1972 Discrimination learning: retardation in monkeys and chicks previously exposed to both stimuli. *Nature, Lond.* **237**, 173–174.
- Bateson, P. & Hinde, R. A. 1987 Developmental changes in sensitivity to experience. In *Sensitive periods in development* (ed. M. H. Bornstein), pp. 19–34. New Jersey: Lawrence Erlbaum Associates.
- Bateson, P. P. G. & Jaekel, J. B. 1974 Imprinting: correlations between activities of chicks during training and testing. *Anim. Behav.* **22**, 899–906.
- Bateson, P. P. G. & Reese, E. P. 1969 The reinforcing properties of conspicuous stimuli in the imprinting situation. *Anim. Behav.* **17**, 692–699.
- Boakes, R. & Panter, D. 1985 Secondary imprinting in the domestic chick blocked by previous exposure to a live hen. *Anim. Behav.* **33**, 353–365.
- Bolhuis, J. J. & Bateson, P. 1990 The importance of being first: a primacy effect in filial imprinting. *Anim. Behav.* (In the press.)
- Bolhuis, J. J. & Trooster, W. J. 1988 Reversibility revisited: stimulus-dependent stability of filial preference in the chick. *Anim. Behav.* **36**, 668–674.
- Bolhuis, J. J., De Vos, G. J. & Kruijt, J. P. 1990 Filial imprinting and associative learning. *Q. Jl exp. Psychol. B* (In the press.)
- Bolhuis, J. J., Johnson, M. H. & Horn, G. 1985 Effects of early experience on the development of filial preferences in the domestic chick. *Devl Psychol.* **18**, 299–308.
- Bolhuis, J. J., Johnson, M. H. & Horn, G. 1989 Interacting mechanisms during the formation of filial preferences: the development of a predisposition does not constrain learning. *J. exp. Psychol.: Anim. Behav. Proc.* **15**, 376–382.
- Chantrey, D. F. 1972 Enhancement and retardation of discrimination learning in chicks after exposure to the discriminanda. *J. comp. Physiol. Psychol.* **81**, 256–261.
- Chantrey, D. F. 1974 Stimulus preexposure and discrimination learning by domestic chicks: effect of varying interstimulus time. *J. comp. Physiol. Psychol.* **87**, 517–525.
- Cherfas, J. J. & Scott, A. M. 1981 Impermanent reversal of filial imprinting. *Anim. Behav.* **29**, 301.
- De Vos, G. J. & Bolhuis, J. J. 1990 An investigation into blocking of filial imprinting in the chick during exposure to a compound stimulus. *Q. Jl exp. Psychol. B*. (In the press.)
- Dickinson, A. 1980 *Contemporary animal learning theory*. Cambridge University Press.
- Gottlieb, G. 1971 *Development of species identification in birds*. University of Chicago Press.
- Gottlieb, G. 1988 Development of species identification in ducklings: XV individual auditory recognition. *Devl Psychobiol.* **21**, 509–522.
- Green, P. R. 1982 Problems in animal perception and learning and their implications for models of imprinting. In *Perspectives in ethology: ontogeny* (ed. P. P. G. Bateson & P. H. Klopfer), vol. 5, pp. 243–273. New York: Plenum Press.
- Hebb, D. O. 1949 *Organization of behavior*. New York: John Wiley.
- Heinroth, O. 1911 Beiträge zur Biologie, namentlich Ethologie und Psychologie, der Anatiden. *Verh. 5 int. Orn Kongr.* 589–702.
- Hess, E. H. 1973 *Imprinting*. New York: Van Nostrand Reinhold.
- Hoffman, H. S. 1987 Imprinting and the critical period for social attachments: some laboratory investigations. In *Sensitive periods in development* (ed. M. H. Bornstein), pp. 99–121. New Jersey: Lawrence Erlbaum Associates.
- Horn, G. 1985 *Memory, imprinting, and the brain*. Oxford: Clarendon Press.
- Horn, G. & McCabe, B. J. 1984 Predispositions and preferences: effects on imprinting of lesions to the chick brain. *Anim. Behav.* **32**, 288–292.
- Horn, G., Rose, S. P. R. & Bateson, P. P. G. 1973 Experience and plasticity in the central nervous system. *Science, Wash.* **181**, 506–514.
- Hutchison, R. E. & Bateson, P. 1982 Sexual imprinting in male Japanese quail: the effects of castration at hatching. *Devl Psychobiology* **15**, 471–477.
- Immelmann, K. 1972 Sexual and other long-term aspects of imprinting in birds and other species. *Adv. Stud. Behav.* **4**, 147–174.



- Immelmann, K. 1984 The natural history of bird learning. In *The biology of learning* (ed. P. Marler & H. S. Terrace), pp. 271–288. Berlin: Springer-Verlag.
- Immelmann, K. & Suomi, S. J. 1981 Sensitive phases in development. In *Behavioral development* (ed. K. Immelmann, G. W. Barlow, L. Petrinovich & M. Main), pp. 395–431. Cambridge University Press.
- James, H. 1959 Flicker: an unconditioned stimulus for imprinting. *Can. J. Psychol.* **13**, 59–67.
- Johnson, M. H. & Horn, G. 1986 Dissociation between recognition memory and associative learning by a restricted lesion to the chick forebrain. *Neuropsychologia* **24**, 329–340.
- Johnson, M. H. & Horn, G. 1986 Dissociation between recognition memory and associative learning by a restricted lesion to the chick forebrain. *Neuropsychologia* **24**, 329–340.
- Johnson, M. H. & Horn, G. 1987 The role of a restricted region of the chick forebrain in the recognition of individual conspecifics. *Behav. Brain Res.* **23**, 269–275.
- Johnson, M. H. & Horn, G. 1988 Development of filial preferences in dark-reared chicks. *Anim. Behav.* **36**, 675–683.
- Johnson, M. H., Bolhuis, J. & Horn, G. 1985 Interaction between acquired preferences and developing predispositions in an imprinting situation. *Anim. Behav.* **33**, 1000–1006.
- Johnston, T. D. & Gottlieb, G. 1981 Development of visual species identification in ducklings: what is the role of imprinting? *Anim. Behav.* **29**, 1082–1099.
- Kroodsma, D. E. & *et al.* 1984 Biology of learning in non-mammalian vertebrates. In *The biology of learning* (ed. P. Marler & H. S. Terrace), pp. 399–418. Berlin: Springer-Verlag.
- Lickliter, R. & Gottlieb, G. 1985 Social interaction with siblings is necessary for the visual imprinting of species-specific maternal preference in ducklings. *J. comp. Psychol.* **99**, 371–379.
- Lickliter, R. & Gottlieb, G. 1988 Social specificity: interaction with own species is necessary to foster species-specific maternal preference in ducklings. *Devl Psychobiol.* **21**, 311–321.
- Lorenz, K. 1935 Der Kumpan in der Umwelt des Vogels. *J. Orn.* **83**, 137–213, 289–413.
- Lorenz, K. Z. 1981 *The foundations of ethology*. New York: Springer-Verlag.
- Polt, J. M. & Hess, E. H. 1966 Effects of social experience on the following response in chicks. *J. comp. Physiol. Psychol.* **61**, 268–270.
- Ryan, C. M. E. & Lea, S. E. G. 1989 Pattern recognition, updating, and filial imprinting in the domestic chicken (*Gallus gallus*). In *Models of behavior: behavioral approaches to pattern recognition and concept formation* (ed. M. L. Commons, R. J. Herrnstein, S. Kosslyn & D. Mumford), vol. 8, pp. 89–110. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Schutz, F. 1965 Sexuelle Prägung bei Anatiden. *Z. Tierpsychol.* **22**, 50–103.
- Sluckin, W. 1972 *Imprinting and early learning*, 2nd edn. London: Methuen.
- Spalding, D. A. 1873 Instinct with original observations on young animals. *Macmillan's Magazine* **27**, 282–293.
- Stewart, D. J., Capretta, P. J., Cooper, A. J. & Littlefield, V. M. 1977 Learning in domestic chicks after exposure to both discriminanda. *J. comp. Physiol.* **91**, 1095–1109.
- Suboski, M. D. 1989 Recognition learning in birds. In *Perspectives in ethology: whither ethology?* (ed. P. P. G. Bateson & P. H. Klopfer), vol. 8, pp. 137–171. New York: Plenum Press.
- ten Cate, C. 1989 Stimulus movement, hen behaviour and filial imprinting in Japanese Quail (*Coturnix coturnix japonica*). *Ethology* **82**, 287–306.
- Vidal, J.-M. 1980 The relations between filial and sexual imprinting in the domestic chick: effects of age and social experience. *Anim. Behav.* **28**, 880–891.
- Zolman, J. F. 1982 Ontogeny of Learning. In *Perspectives in ethology: ontogeny* (ed. P. P. G. Bateson & P. H. Klopfer), vol. 5, pp. 275–323. New York: Plenum Press.