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# A Model of Imprinting Evolved from Neurophysiological Concepts

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*With 8 figures*

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## Abstract

The imprinting process is described by a model evolved from physiological data. For the case of sexual imprinting in zebra finches a second sensitive phase, occurring at sexual maturity, is considered. The first sensitive phase is not restricted exclusively to the imprinting of sexual objects.

Properties of the model allow for the explanation of apparent reversibility of imprinting. The same physiological mechanisms involved in the organization of simple neuronal connections are assumed to operate in the highly complex networks associated with imprinting phenomena.

## 1. Introduction

The phenomenon of imprinting has long been a major focus of ethological research and over the past few decades a wealth of literature on the topic has accumulated (for review see Bateson 1966; Klinghammer 1967; Immelmann 1972a; Hess 1973; Hoffman and Ratner 1973). Only recently however has attention been addressed to the possible physiological mechanisms underlying the imprinting process (Bateson 1979b). The excellent studies conducted in Bateson's laboratory have provided us with important data on the physiological changes that take place along with the imprinting process and Bateson has discussed the implication of these data for the theoretical aspects of the imprinting phenomenon (Bateson 1974, 1976; Bateson, Rose and Horn 1973; Bateson, Horn and Rose 1975; Bateson, Horn and McCabe 1978a and b; McCabe, Horn and Bateson 1978).

Unfortunately, despite the abundance of data on imprinting, few heuristic models of the phenomenon have been suggested. Hoffman and Ratner (1973) have described the imprinting process in relation to classical conditioning. Another model, developed from results of research on filial imprinting and presented by Bateson (1978), interprets the effects of imprinting stimuli exposure time. Using the same basic model, Bateson (1979b) introduces a

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few more conditions which allow for the interpretation of IMMELMANN's recent results on sexual imprinting of zebra finches (IMMELMANN in prep.).

The model which is presented here has much in common with that of BATESON. In contrast, however, it is evolved strictly from results of neurophysiological investigations and is applied to the phenomenon of sexual imprinting. It is based on a concept put forward by HEBB (1949) concerning the neuronal changes which occur during learning processes, and it shows in a formal manner the connection between neuronal processes and the imprinting phenomenon.

For the sake of simplicity, many aspects of the imprinting phenomenon are not dealt with in the model and a number of classical studies have not been cited. A comprehensive review of the literature and data on imprinting that have bearing on this model is not intended. Furthermore, mathematical formulations, although not complicated, have been omitted. In this manner we hope to emphasize the more important aim of the model, that is, to demonstrate the similarities between ethological and neurophysiological results of "imprinting" research.

## 2. Origin of the Model: Hebb's Theory on Learning Process and its Effect at the Neuronal Level

HEBB (1949) postulated that changes in synaptic connections occur as a result of learning. Fig. 1 illustrates according to HEBB how simple nervous connections are altered when learning takes place. Two cells x and y are 'first order cells' which receive information and in turn relay the information to a higher order cell. Prior to learning, both x and y connections are functional and the higher order cell responds indiscriminantly. Through the learning process, the appropriate pathway is selected, so that information is relayed from only one of the two cells. The pathway between the appropriate first order cell and the second order cell is strengthened, the other pathway(s) remain unused, and the higher order cell responds only to the selected lower cell after the learning process. Experimental evidence exists to support the notion that changes in synaptical connection, as described by HEBB, do occur as a result of use or disuse (BLISS and LØMO 1970, 1973; LYNCH et al. 1976). Furthermore, HEBB demonstrates that his model for changes which occur in simple neural connections during learning can easily be applied to the functioning of complex neuronal structures, an application of importance if we are to relate HEBB's model to the complex imprinting process.

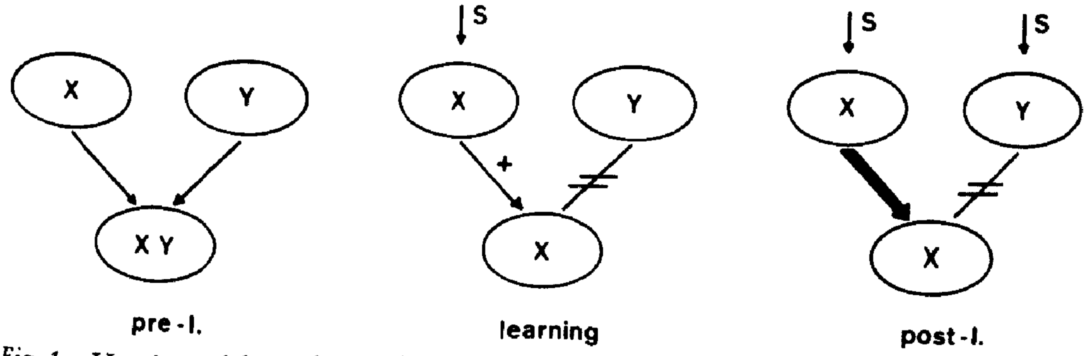

*Fig. 1:* HEBB's model. Left: pre-learning situation: the connections from cells x and y are established and functioning. Center: learning: only x will be given a stimulus (S), the higher order centre receives input only from x, this connection will be made stronger, the other will be avoided. Right: post-learning: the high order cell responds only to stimulation from x

## 3. Application of Hebb's Model to a Well-known Neurophysiological Phenomenon, and the Introduction of the Sensitive Phase Concept

HUBEL and WIESEL (1963) in their discussion of the plasticity of the visual cortex, present the following interesting observation. Certain cells in the visual cortex of the cat receive input from both eyes, while others receive input from only one eye. If the eyelids of one eye are sutured during early development and then later re-opened, the ratio of cells capable of receiving input from both eyes to cells capable of receiving input from only one is changed. Prior to suturing, nearly all cells receive input from both eyes, but after restricting visual input to one eye during early development these cells function on the input of only one eye. This study provides further evidence that neuronal connections can be influenced through use and disuse of pathways (Fig. 2).

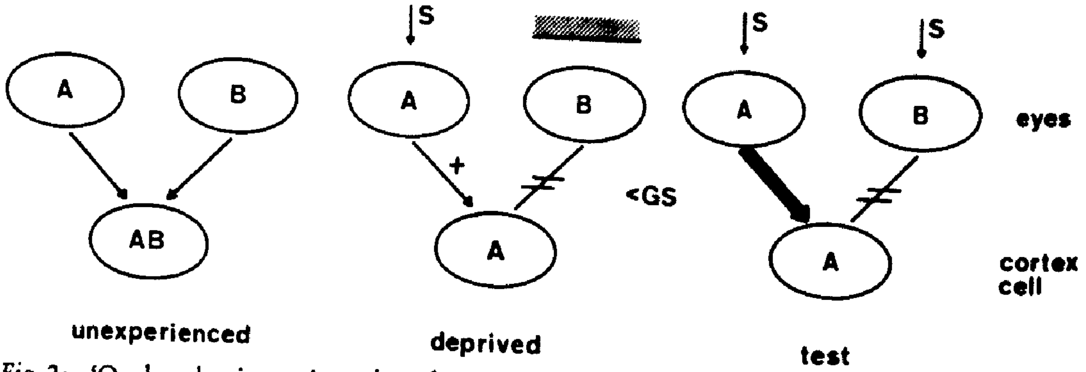

*Fig. 2:* 'Ocular dominance' results of HUBEL and WIESEL. Left: The cortex cell gets input from both eyes. Center: eye B is sutured, the cortex cell receives information only from eye A (simplified). Right: test-situation: eye B is re-opened, the cortex-cell responds only to eye A. GS = gating system. (expl. see text)

Further studies of HUBEL and WIESEL (1970) demonstrate that this modification in neuronal connections can only occur during a specific period of development. Thus, there appears to be a 'sensitive phase' during which environmental stimuli can affect neuronal pathways. BLAKEMORE's (rev. 1974) work on orientation selectivity of cortex cells provides additional evidence for the existence of such a sensitive phase.

SINGER (1979) summarizes the conditions necessary for the existence of a system which operates with sensitive phases. Factors essential in such a system include a stimulus capable of exciting a particular pathway, a genetically controlled 'readiness' on the part of the neurons to react to this stimulus through a change in connectivity, and various endogenous factors which have been summarized as 'motivation' by SINGER. BATESON (1979a) illustrates the operation of these factors with an instructive analogy: A developmental train travels to its destination from a point called 'conception'. As it begins its journey, all of the windows are closed, and along the way the windows of various compartments (one of which might be the filial imprinting compartment) open up, either temporarily or permanently, allowing the passengers to receive information from outside.

## 4. Relationship of the Neurophysiological Concepts to the Results of Sexual Imprinting Studies

A rather large step must be made between the neurophysiological and the behavioral understanding of the imprinting phenomenon. First, we recall the hypothesis of Hebb (1949), that populations of neurons will organize themselves in a manner similar to that of simple neural networks. Let us consider various neuronal populations in the brain which accept and process stimuli from the outside environment. Information is distributed from some lower center to a higher center, capable of receiving input from a number of other lower centers (Fig. 3). The information which is allowed to pass from a lower to a higher center is determined by a system such as the 'gating-system' of Singer, which for the purposes of this model, we shall term the Sensitive Phase Control (SPC). This SPC consists of the same principal components as does Singer's GS, that is, an external stimulus, a genetic control, and motivation. Motivation can only be assessed through the observation of an animal's behavior and operationally we may say that motivation is demonstrated only through the interaction of one animal with another. This implies that the reaction, or more precisely, the reaction ability, of an animal is part of the SPC (see dotted line in Figs.). This is a view suggested as well by Hoffman and Ratner (1973), in their 'reinforcement model of imprinting'. Becker-Carus et al. (1972) define the term 'motivation' in a very similar way.

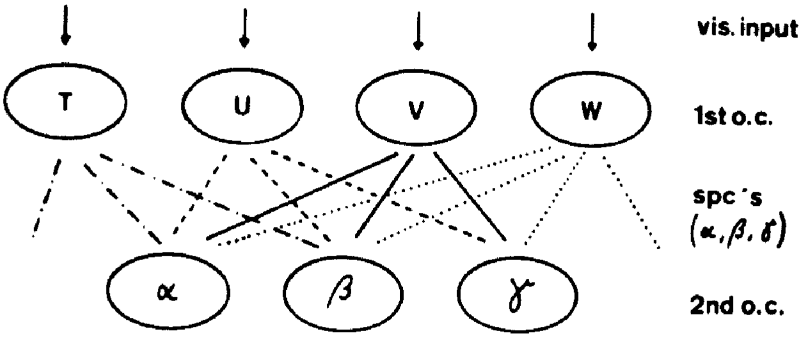

*Fig. 3:* Convergent and divergent pathways. The first order centers project to different 2nd order centers, second order centers receive input from many first order centers. SPC = Sensitive Phase Control (expl. see text): different SPC's are involved in the organization of different pathways and centers

An example will help to illustrate what is intended with the presentation above: During their early development, or more specifically, during the time in which imprinting will occur, young zebra finches receive various types of visual stimuli, the most important of which may fall into the following cate-

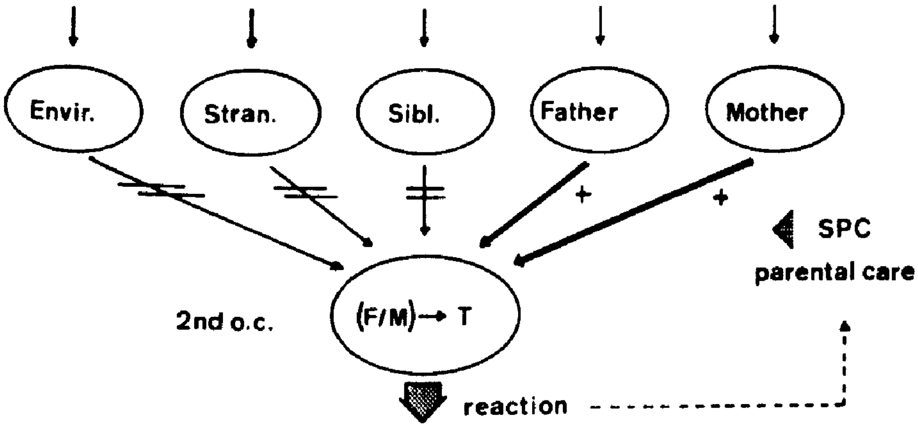

*Fig. 4:* First sensitive phase in zebra finches. Different centers are organized by input signals (e. g. father, mother). By the action of the SPC only two pathways will be strengthened, the others are suppressed. Envir. = environment, Stran = strangers, Sibl. = siblings, (F/M) = father/mother, T = *Taeniopygia* (zebra finch)

gories: strange birds, siblings, parents, and physical structures in the environment (Fig. 4). Stimuli in each of these categories are processed in different '1st order' or 'lower' centers. Simultaneously, the SPC controls the release of information to the higher order (2nd order) centers.

An example of such control is the processing of information about the appropriate object for the feeding response of nestling. During the sensitive phase, young zebra finches are ordinarily fed only by their parents. Thus, the higher order center receives information only from the 'parent' 1st order center, and input from other potential feeders (other 1st order centers) does not take place (Fig. 4). The process of information transfer occurs as follows: Before the SPC allows the nervous system to change its connections as a reaction to outside stimuli (in this example, 'feeders'), the young zebra finch responds to all stimuli in the same way; that is, the second order center receives information from all 1st order centers. During the sensitive phase, the SPC selects the appropriate information, restricting transfer so that information from only one 1st order center is processed. In this case, it is clear that the selection of the appropriate 1st order center is influenced by use and disuse.

The above system of control can be extended to the case of sexual imprinting: In the zebra finch the same 1st order center may also be responsible for the transport of information about the appropriate object for sexual response. During the sensitive phase for sexual imprinting, the appropriate 1st order center is selected. Recent studies conducted by IMMELMANN (in prep.) demonstrate that more than one sensitive phase may be involved in the final selection of the appropriate 1st object. In the following section, we describe these studies and show how the notion of a second sensitive phase fits easily into the model.

## 5. The Second Sensitive Phase in the Sexual Imprinting Process

In investigating the sensitive phase for sexual imprinting in zebra finches, IMMELMANN (in prep.) carried out the following cross-fostering study. Two groups of zebra finches were raised by Bengalese finch foster parents. They were then isolated between the 40th and 100th day of age, and on day 100, one of the groups was given a double-choice test. When presented with both Bengalese and zebra finches, the male zebra finches preferred to court their foster species. Following the double-choice test, this group and the untested group of birds were paired with conspecifics. In most cases, the pairs eventually produced and reared clutches. After breeding experience with conspecifics, both groups of birds were given a series of double-choice tests. Interestingly the two groups performed differently from one another in this series of tests. The birds that had not been given a double choice test prior to their breeding with conspecifics demonstrated a preference for zebra finches over Bengalese finches. However, the birds that had been given the first double choice test, displayed a preference for zebra finches only in the beginning of the series of tests. After the first test, preference was exhibited for Bengalese finches. The important differences between the two groups of birds is that the groups given the first double-choice test was exposed to Bengalese finches in a sexual context before having had breeding experience with conspecifics.

Several conclusions from this study are of importance with respect to our model: first, the object of sexual response does not appear to be completely imprinted by the end of what has been traditionally thought of as the sensitive phase for sexual imprinting (in the case of zebra finches, approximately between days 8 and 30 post-hatch). Secondly, since the group of finches which demonstrated consistent preference for zebra finches in the second double choice test had not been exposed to conspecifics during the sensitive period, their preference suggests an underlying, genetically pre-organized species-specific recognition.

We can now show how the above study fits into our model (Fig. 5).

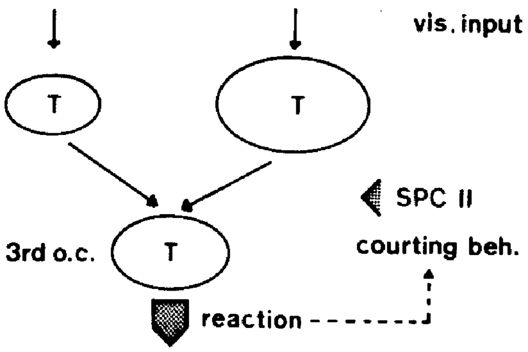

*Fig. 5:* Second sensitive phase. Upper left: genetically pre-organized center; upper right: center organized by experience. 3rd o.c. = third order center, T = *Taeniopygia* (zebra finch). Expl. see text

During the early development of the zebra finch, a 'picture' of the parent is organized and processed by the second order center. ('Picture' in this sense implies a set of relevant features of the stimulus, which may not necessarily be visual, but could consist of acoustic or other elements). At the same time, another second order center exists which reacts to a genetically pre-organized species-specific 'picture'. The influence of this center is less than that of the center which processes the learned picture, and thus is drawn smaller in the Fig. The pre-organized 'inborn' center functions as a second input source and the information from both centers converges on a higher (third) order center. We postulate here the existence of a second sensitive phase and thus a second SPC controlling the passage of information between second and third order centers. Once again the selection process exercised by the SPC is influenced by the use or disuse of the pathway.

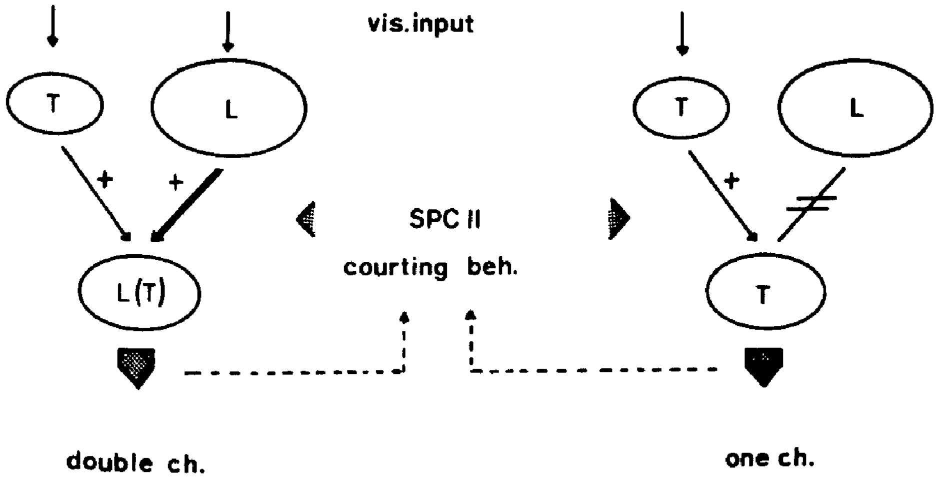

*Fig. 6:* Experiment by IMMELMANN: differences between the result of rearing zebra finches with foster parents, given a subsequent double choice test (left) and not given a test (right). L = *Lonchura* (Bengalese finch), T = *Taeniopygia* (zebra finch). Further expl. see Fig. 5 and text

It follows that under ordinary circumstances a zebra finch sees only its conspecifics during the second sensitive phase. Thus the identical information will pass through the 'learned' and the 'inborn' centers, both pathways will be 'stabilized' and the bird will be imprinted on zebra finches. At the same time that a 'picture' develops in the third order center, it is modified by the inborn center to more closely match the species specific picture. This mechanism helps to prevent too great a variation from the phenotype of the zebra finch, a variation which could occur in a system that operates only through learning.

The process is altered when zebra finches are raised by foster parents. The learned center, which will be modified by experience, reacts only to the stimulus 'Bengalese Finch', while the inborn center responds to the stimulus 'Zebra Finch' (Fig. 6). If the zebra finch is given a double-choice test before the second SPC has restricted flow of information from particular second order centers, both the learned and inborn pathways will be used. However, if the influence of the 'learned' system is much greater, this system will supercede the inborn system, and the reaction of the bird will be directed to the foster parent (Fig. 6, left side). Nonetheless, the inborn system is still functional and thus, the zebra finch can and will eventually court conspecifics, when no other species are available. For the case of zebra finches imprinted on conspecifics, courting of other species should not occur since no contrasting 'learned' pathway is in operation. These predictions are born out by the experiments of IMMELMANN (1972b).

When a zebra finch is raised by foster parents, has not been given a double-choice test during the second sensitive phase, and is subsequently kept with its own species, the only pathway in operation is the genetically pre-organized one, and the zebra finch is imprinted on its own species (IMMELMANN, in prep.; Fig. 6, right side).

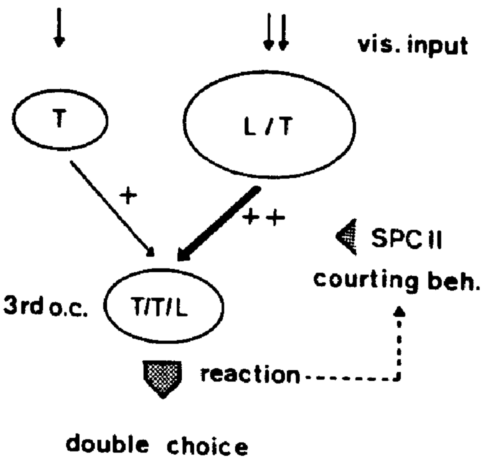

*Fig. 7:* Cross-fostering with a mixed pair. Expl. see Figs. 5, 6 and text

Now we see how the model can be applied to yet another experimental set-up. If zebra finches are raised by a mixed pair (one Bengalese finch and one zebra finch), they are imprinted on their own species (IMMELMANN 1972b). Fig. 7 illustrates the imprinting process: The 'learned' center is organized to react to both species equally. However, when the information which passes through this center is summed with the information provided by the genetically pre-organized one, we see that there is greater input about zebra finches than there is about Bengalese finches. The system now selects the object with the strongest pathway as the object for reaction, and the birds will react as imprinted on their own species. An as yet untested hypothesis is that, given the appropriate conditions, zebra finches raised by mixed pairs can be made to court Bengalese finches.

## 6. Application of the Model to Filial Imprinting

In the case of filial imprinting, there is no reason to expect that a second sensitive phase exists, since there is no time lag between the imprinting process and the process of reaction to the imprinting object. However, within the context of our model, two steps in the process of filial imprinting can be said to occur: The first SPC operates on the object of the filial response and selects the appropriate object. The second SPC then operates on the genetically pre-organized picture and selects for the final object of reaction (Fig. 8). Information important to the selection process of the first SPC might be the interchanging of contact calls between mother and young (Hess 1973). In these interactions, the young receive the greatest input from the mother, but receive input as well from siblings. When organization of the center is finished, the bird should demonstrate filial response with proportionately greater preference for the mother, but response to siblings as well. This behavior is seen among duck species (Schutz 1965). The selection process of the second SPC allows for input from the genetically pre-organized pathway, and thus the preference for the mother is strengthened. Especially in discussing filial imprinting it is important to compare the model with that of Bateson (1978) and to assess the data thus far collected; for the reasons mentioned above however this will not be handled here.

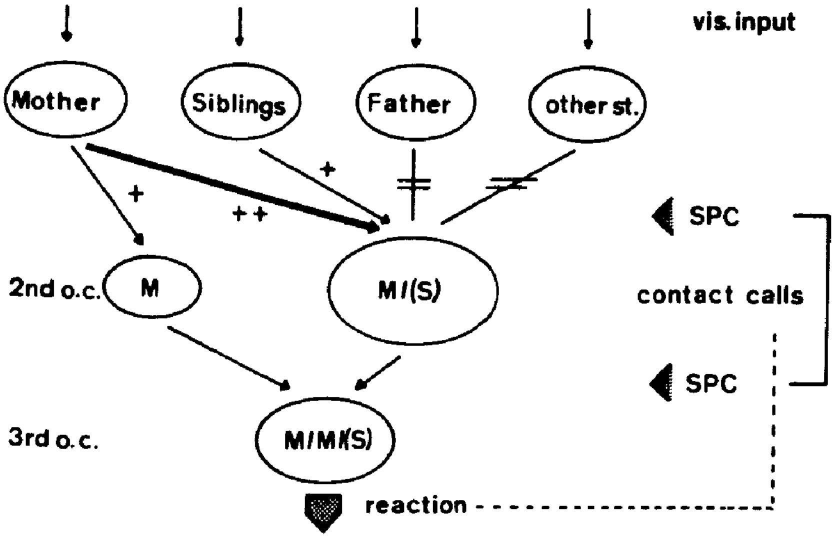

*Fig. 8:* Filial imprinting in ducklings. Expl. see Figs. 5, 6 and text.
Other st. = other stimuli, M = mother, S = siblings

## 7. Discussion

The model which we have presented here seeks to interpret some of the data currently available on the imprinting phenomenon. For certain aspects of the model, in particular for the concept of the second SPC, it must be pointed out that there is little experimental backing. The notion of a second sensitive phase is based only on the studies by Immelmann described here. Nonetheless, speculation seems appropriate. By suggesting the existence of a second SPC, we hope to stimulate research in this area. It is likely that until now, because it was not suspected to occur, the effects as well as the evidence of this second phase have been masked by the design of experiments.

It was the intention of the author to present here only the simple framework of the imprinting model, thus avoiding a series of conditions and exceptions which serve to confuse the reader and complicate the system unnecessarily. In the following discussion, however, several conditions shall be dealt with, in order to demonstrate the broad scope of the model.

### 7.1 Dependence on the Effectiveness of the Input and the Motivational State of the Bird; Changes in the Selectivity of the System

Our model requires that both the importance and the effectiveness of the input signal be dependent on the motivation of the bird. Experimental evidence on motivation and learning support this idea. TODT et al. (1979) observe that hand-reared nightingales will learn songs from a tape-recorder more readily when their caretaker is in view, i.e. when their attention is greater. HESS (1973) presents a similar idea with his Law of Effort: Young precocial birds are more strongly imprinted on an imprinting object when they have exerted effort in order to follow it.

The particular neural pathway that is put into use by the SPC as a result of the interaction between first and second order centers will, in the case of imprinting, become a highly specific pathway, operating only with the input of the appropriate signals from the imprinting object. (This does not imply, as we have seen, that in all circumstances the bird will respond only to its object of imprinting.) HESS (1973) describes the process of increasing selectivity toward stimuli which occurs during filial imprinting: At first, young chickens follow all moving stimuli, but gradually they direct their response only to the appropriate object that is, the stimulus selected by the SPC. Young foals demonstrate the same increase of selectivity, following all moving objects indiscriminantly at first, and then narrowing their response to the mother. The case of imprinting in young foals fits easily into our model: the used pathway is that which carries information about the mother, since during feeding the foal interacts primarily with the mother (KLINGEL and KLINGEL 1966).

Increases in the selectivity of responsiveness are found in systems other than imprinting. TINBERGEN and KUENEN (1939) have demonstrated that the begging responses of young blackbirds become more selective as the birds develop. Increases in the selectivity exhibited by young zebra finches have not yet been documented and in the case of sexual imprinting would be difficult to show because of the time lag between imprinting and sexual behavior (SOSSINKA 1975).

It is important to point out here that once the SPC in our model selects a particular pathway, the responses of the bird are not exclusively stimulus-leading-to-reaction events, that is, responses can be variable. For example, courting can occur as vacuum behavior, mediated by internal stimuli rather than external visual input. Furthermore, variability in responsiveness can be an intended part of the system, particularly when the picture in the third center is not especially sharp.

### 7.2 Temporal Course of the Sensitive Phase

In contrast to the model of BATESON (1978) which concerns itself with the duration and sequencing of events that take place within the imprinting process, our model has ignored the time element. Clearly there is a compatibility between the two models and one can show here how a time element is easily introduced into our system.

Earlier an example was given of two stimuli simultaneously providing input to first order centers, in which young zebra finches were raised by a mixed pair. If the two differing 'parent' stimuli are presented sequentially rather than simultaneously, the results as measured by a double-choice test will depend on the duration, and the particular developmental stage in which the stimuli were first presented (IMMELMANN 1972b). Ultimately the important factor in the outcome will be the quantity of the stimulus, determined by either its quality or the length of its exposure.

Once the sensitive phase is ended, the centers are no longer modifiable and the imprinting process is thus an irreversible one. Nonetheless, when more than one pathway between first and second order centers has been established, (Figs. 7a, 8), the process may appear reversible. That is, under appropriate conditions more than one external stimulus may provide the proper input to elicit a response. This is an important attribute of the model: Ordinarily, when a third order center receives input from more than one second order center, the system allows for response to the stimulus which provides input along the strongest pathway. In the absence of this stimulus however, the system will allow for response to the stimulus associated with the weaker pathway. As IMMELMANN (in prep.) points out, this switching of responsiveness from one pathway to another is not an instantaneous process: Zebra finches imprinted on Bengalese finches, but allowed to nest for a time with conspecifics, show initial preference for zebra finches. Gradually, over the course of a series of double-choice tests, the preference is shifted toward Bengalese finches.

BATESON (1979b) suggests that this choice of one pathway takes place at the interface between sensory and motor systems: The motor system for the sexual response will be coupled to different sensory pathways and the influence of the pathways can change.

The timing of the second sensitive phase will greatly influence the outcome of various exposure conditions. Under conditions in which zebra finches are exposed during early development first to one species and then to another, several results are possible. If exposure to both species occurs prior to the onset of the second sensitive phase (in the case of sexual imprinting, we should expect the onset to occur with sexual maturation), the results of a double-choice will be dependent on the ratio of time spent with the first to time spent with the second species. However, if exposure to the second species overlaps with the onset of the second sensitive phase, preference should be demonstrated for the second species. It is of great interest, with regard to this model, to define the onset and duration of this second sensitive phase.

HEBB (1949) distinguishes between two types of learning processes, one in which a long-term storage of new information takes place as a result of some underlying physiological process, the other in which associations are rapidly made as a result of the utilization of pre-existing pathways. The first type of learning process might be the type of process which occurs during the first sensitive phase, the second process during the second phase. Thus, we might postulate that the consolidation process which occurs within the second sensitive phase would be short in duration. This, of course, needs to be verified with experimental evidence.

### 7.3 The Influence of Sex on Imprinting Ability

Various views are held concerning sexual differences in imprinting ability (e.g. SCHUTZ 1965, 1975; KLINT 1975; WALTER 1973). SCHUTZ (1965) suggests that female ducks recognize male conspecifics through a genetic mechanism. Such a mechanism seems plausible when the high inter-specific variability in plumage coloration of male ducks is considered. As this inter-specific variability is low among females, we would expect that the preference displayed by ♂♂ is established through imprinting.

Contrary to SCHUTZ's idea, SONNEMANN and SJÖLANDER (1977) have demonstrated that, in female zebra finches, sexual preferences are in fact imprinted. They point out that one reason such imprinted preferences may be hard to detect is that the ♀'s role in pair formation is a passive one and the preference is less likely to exert itself strongly.

We suggest that our model operates in the same manner for both sexes (Fig. 7). The difference in process should only be seen with regard to the response of the bird. Thus, the particular motor output coupled with a stimulus will be different for ♂♂ and ♀♀.

### 7.4 Is it Possible yet to Relate this Model to the Neural Processes Involved in Imprinting?

We are not, at this stage, ready to provide a detailed clarification of the relationship between the neurophysiological and the behavioral processes involved in imprinting, although on the basis of experimental evidence speculation is possible. It is clear that similarities in the sequencing of events occur in neuronal sensitive phases (e.g. HUBEL and WIESEL 1970; BLAKEMORE 1974) and in filial (HESS 1973) and sexual imprinting (IMMELMANN, in prep.). WOLFF et al. (pers. comm.) observe degeneration of nerve terminals in the visual centers of the zebra finch with the onset of the sensitive phase. This may be a necessary condition for the construction of new connections, and evidence of restriction of the inputs of higher order centers to only one or a few lower order centers.

The lesioning investigations of SALZEN et al. (1975, 1978) and BATESON et al. (1978) in distinct parts of the brain show different results. SALZEN et al. affected the filial imprinting process with lateral lesions and BATESON et al. with frontal lesions. BISCHOF and PRÖVE (in prep.) found no influence on sexual imprinting with either lateral or frontal lesioning.

BATESON et al. (1973, 1975; BATESON, HORN and MCCABE 1978) demonstrated that in different parts of the forebrain of chicks an extremely high uracil uptake, which indicates a high protein turnover, occurs at the time of the sensitive phase.

Other investigations (MCCABE et al. 1979; JONES and HORN 1978 a, b) have demonstrated that evoked potentials in some forebrain areas are altered by visual experience during the sensitive phase for filial imprinting.

Despite these results, it is impossible at present to locate any specific 'imprinting center' in the brain, and thus to correlate brain structures with parts of the model is neither possible nor intended. It is possible that imprinting information is not stored in distinct centers, but widespread throughout the brain; in this case it may be a good idea to look for changes at the narrow path between sensory input and motor output and to try to clarify the information exchange process there. Unfortunately, little is as yet known about the location of this specific processing.

## Summary

The imprinting process is explained through a model evolved from physiological data. The most important points the model attempts to bring out are the following:

1. In addition to what has been regarded traditionally as the sensitive phase, there exists a second sensitive phase, which in the case of sexual imprinting occurs at sexual maturity. In this second phase the selection of the object for sexual reaction is based on previously established 'pictures' which are either genetically pre-organized or learned.
2. Second order centers are not restricted in their function to handling the process of sexual imprinting and the first sensitive phase may likewise not be restricted in function. Thus during the first sensitive phase imprinting of other types of information about the environment may take place.
3. The apparent 'reversibility' of imprinting seen in some recent works of IMMELMANN (in prep.), can be explained as an effect of two different properties of the system.
4. It is assumed in this model that the same mechanisms described by HEBB (1949) for simple changes in neural pathways which take place as a result of learning are operating in the much more highly complex cases of filial and sexual imprinting.

## Zusammenfassung

Es wird versucht, Prägungsvorgänge durch ein aus der Neurophysiologie stammendes Modell formal zu erklären. Die wichtigsten Gesichtspunkte, die sich aus der Formulierung ergeben, sind folgende:

1. Es wird eine zweite sensible Phase gefordert, die aus der schon in einem vorhergehenden Schritt gespeicherten Information speziell die Objekte für die sexuelle Reaktion auswählt.
2. In der ersten sensiblen Phase wird daher nicht unbedingt nur das Objekt für sexuelle Reaktion geprägt; die hier erworbene Information ist auch in anderen Funktionskreisen verfügbar.
3. ‚Reversibilität' von Prägung wird durch zwei Eigenschaften des Systems erzeugt: Es können auch mehrere Kanäle zu einem Zentrum organisiert werden; aus diesen Kanälen wählt das System bei Einwirken aller zugehörigen Außenreize den während der Wirkung der Sensitive Phase Control (SPC) am besten etablierten Kanal aus. Eine echte Umorganisation ist aber nach Beendigung der SPC nicht mehr möglich.
4. Es wird angenommen, daß von der Bildung einer einfachen Konvergenzschaltung bis zur Organisation komplexer Konvergenzen und Divergenzen, wie sie bei der Prägung vorliegen müssen, ähnliche Mechanismen beteiligt sind.

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