

INFLUENCE OF DEVELOPMENTAL FACTORS ON IMPRINTING

Hans-Joachim Bischof

Lehrstuhl Verhaltensphysiologie
Fakultät Biologie, Universität Bielefeld
Postf. 8640, 4800 Bielefeld 1, F.R.G.

INTRODUCTION

Since Konrad Lorenz (1935) published his famous "Kumpan" paper, where he defined imprinting as a special learning process, a wealth of literature on the topic has accumulated (for reviews see Bateson 1966, Klinghammer 1967, Immelmann 1972, Hess 1973, Hoffman and Ratner 1973, Immelmann and Suomi (1981)). As a consequence, the definition of "imprinting" has been changed, as not all of the criteria originally proposed by Lorenz could be applied to all those "imprinting - like" phenomena that needed to be included in a useful definition of this learning paradigm.

Thus Immelmann and Suomi (1981) defined imprinting as "an early learning process with very stable results". The two criteria, namely that learning occurs only during a sensitive period early in development of an animal and that the information acquired in the course of this sensitive period is very stably stored, are special features of imprinting and cannot be found to the same degree in other learning paradigms (Immelmann and Suomi 1981).

Whereas the existence of a sensitive period for the acquisition of external influences is generally accepted by students of imprinting and the discussion at present concentrates more on the question of determining the limits of this sensitive period and the influence of experimental conditions on its onset and duration, there is no such general agreement concerning the stability of storage. From filial imprinting, some authors argued that at the end of the sensitive period a bird has become familiar with the object to which it has been exposed. This familiarity with one object leads to an "unwillingness" to learn new features subsequently (Bateson 1979). If this unwillingness can be erased by appropriate experimental conditions, the bird can learn new features and become attached to a new object. However, in filial as well in sexual imprinting, it was recently demonstrated that this new preference is erased if the bird is exposed after some time to a double choice test between the first and the second object: in this case it prefers the first object again (Cherfas and Scott 1981, Immelmann 1979). This is not an effect of primacy and recency of stimuli, as Bateson (1983) points out, but demonstrates that there must be some sort of internal protection of the information previously stored. The latter is what is meant by the notion of permanent or irreversible storage.

In the development of the visual cortex, which shares many features with imprinting (Bischof 1983), such permanent storage may be explained by the fact that the storage of information takes place during a period of development of cortical tissue. As LeVay and Stryker (1979) demonstrated, the development of the physiological characteristics of the adult visual cortex coincides with morphological segregation of geniculocortical projections into columns. They speculated that the last step following this segregation is the myelination of the acquired wiring. This subsequently protects the visual cortex connectivity from alterations by outside stimulation. The same view was expressed by Wolff (1981).

In this paper, I want to discuss the question whether such developmental processes may be involved in imprinting also. I will present some recent behavioural data on the participation of the development of the zebra finch visual pathway in the onset of the sensitive period for sexual imprinting. Furthermore, I present a speculative model which shows a reciprocal dependency between the occurrence of a sensitive period and the stability of storage. This model is illustrated by a simple computer simulation. Finally, I discuss the relevance of the data concerning the development of the visual system of the zebra finch for the speculations mentioned above.

SEXUAL IMPRINTING IN ZEBRA FINCHES

Sexual imprinting is an early learning process by which the young zebra finch learns the features of the object to which he courts as an adult. Careful studies of sexual imprinting in zebra finches were provided by Immelmann (1972, 1975, 1979, Immelmann and Suomi 1981). He demonstrated that the sensitive period for the acquisition of the features of the imprinting object was longer and occurred later than that obtained by Hess (1973) for filial imprinting (Fig. 1). The peak of sensitivity for sexual imprinting is at about 13 to 15 days posthatching. This sensitivity is reduced considerably before the zebra finch reaches sexual maturity, and thus long before the bird has any courting experience. However, in one series of experiments Immelmann demonstrated that sensitivity does not reach zero, but descends asymptotically. Sometimes, imprinting can take place as late as 70 days of age (Immelmann and Suomi 1981).

Storage of information acquired in the course of the sensitive period is indeed very stable in the zebra finch. Immelmann caged adult zebra finches, which had been imprinted to a foster species, together with conspecifics for a long time. These birds eventually courted to conspecific females and even reared clutches. When, after this experience with conspecifics, the finches were tested in a double choice test with a conspecific and a female of the foster species, the birds preferred the foster species again. Thus, information stored during the sensitive period had not been forgotten in the

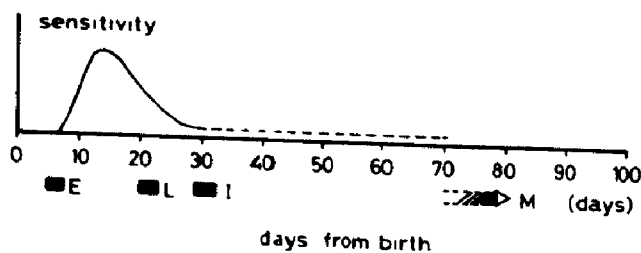


Fig.1: Idealized sensitivity diagram for sexual imprinting in zebra finches. Data from Immelmann and Suomi (1981). E = Eye opening, L = Leaving of the nest, I = Independence. Further explanations see text.

meantime. Obviously, it was masked for the time the birds lived with conspecifics and came to the surface again in a situation of choice.

THE ONSET OF THE SENSITIVE PERIOD FOR SEXUAL IMPRINTING

Immelmann (1972) investigated the phase of sensitivity to the imprinting stimulus by separating young birds at different times from their parents and transferring them to a foster species, the Bengalese finch. Using this procedure, it was found that 13 days of age was the earliest age of transfer, in which a stable preference for the first object could be demonstrated when the birds were adult. As the birds need some time of visual experience before that time to learn the features of the imprinting object, susceptibility to external stimulation should start earlier than this age. Immelmann proposed that the sensitive period may start between day 5 from hatching, when the eyes begin to open, and day 10, when the eyes are fully open. Bischof and Lassek (in press) looked at the development of the gaping reactions of young birds to determine the age at which they can use visual stimuli as triggers for gaping. Whereas the birds react to acoustic and tactile stimuli from the first day of life, gaping to visual stimuli does not occur before 10 days of age (fig.2). Thus, imprinting to visual stimuli, which seem to be the most important for the elicitation of courtship (Bischof, unpubl. results), cannot start earlier than 10 days. At day 15, the gaping reaction towards stuffed dummies is replaced by a reaction of fear; however, gaping towards the parents remains until the young birds reach independence at about 30 days of age. Thus, at 15 days they are able to discriminate between a dummy and their parents. Some of the birds, as revealed by Immelmann's studies (1972), are already stably imprinted at this time. However, most of the birds are imprinted at later age. Thus, storage of new information is still possible beyond 15 days of age, but under normal conditions the development of fear prevents the bird from attending to and learning such new information (Bischof and Lassek in press).

We have found (Herrmann and Bischof in prep.) that there are some correlations between the development of the visual system of the zebra finch and the behavioural data mentioned above. As can be seen from fig.3, the myelination of the thalamic nucleus of the tectofugal pathway, the nucleus rotundus, does not start before 5 days of age. Accordingly, the myelination of the telencephalic station of this pathway, the Ectostriatum, does not start before day 10. We suggest that the stabilization of the wiring of the nuclei, which may be indicated by the myelination of the axons (Wolff 1981), starts in nucleus rotundus when the eyes open, and in the Ectostriatum at the time when the birds can react to visual stimuli. Whether this is only an arbitrary coincidence in time or there are functional relationships,

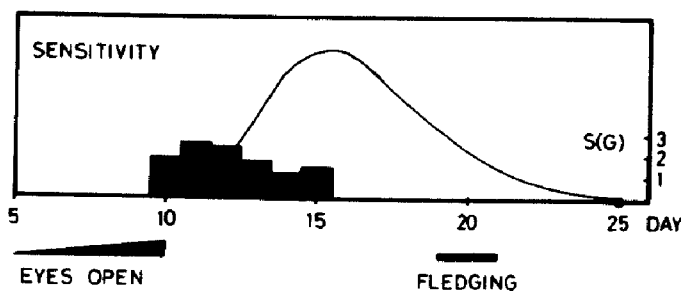


Fig.2: Gaping responses of young zebra finches and sensitivity curve for sexual imprinting. S (G) = Gaping score, hatched bars: Gaping responses.

cannot be decided from these experiments. To investigate this, we just perform anatomical and behavioural experiments with visually deprived animals. However, one conclusion of the results presented above is that the beginning of the sensitive period is most likely determined by the developmental state of the visual nuclei, and that the learning of the features of the parents coincides in time with the development of the visual pathway.

THE TIME COURSE OF THE SENSITIVE PERIOD FOR SEXUAL IMPRINTING:
EFFECTS OF IRREVERSIBLE STORAGE

As shown in the preceding section, developmental aspects surely play a role for the onset of the sensitive period. It demonstrates that under normal conditions the development of fear prevents the animal from acquiring new information from the environment.

However, this fear reaction has to be overcome by the birds in the case of the cross fostering experiments made by Immelmann, as they depend on feeding and thus have to gape to the new parents after transfer even if they are older than 15 days of age. As the sensitivity to environmental stimulation goes down despite of the elimination or at least diminution of the fear components (Fig.1), there must be another internal mechanism which protects the acquired data. This internal mechanism, however, cannot be fixed to an appointed time of development, as the course of decline can be essentially altered by experimental manipulations (Bateson 1978).

One possibility of how such flexibility may be achieved is that the storage process itself has some influence on the termination of sensitivity. For example, the increasing amount of stored information may lead to a decrease of the proportion of information which can be stored subsequently. This is easily demonstrated by a simple computer model which simulates the filling of limited stores by a random process (Fig.4). In the model, information from the outside flows in a chain through three concatenated stores, but with certain constraints. These stores would represent several levels of processing in the brain from the periphery to more central stations. The random procedure chooses one of the elements of the first store and puts the information in, if the element is still empty. Otherwise this information is lost. Thus, the probability of storage depends on the filling of the store: the more information is already stored, the lower is the probability for new storage.

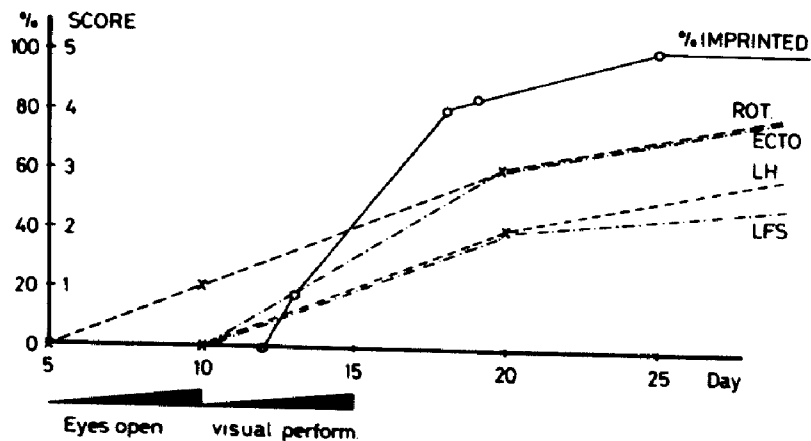


Fig.3: Myelination of different brain areas. Left ordinate scale: % of birds imprinted at that time (Data from Immelmann and Suomi 1981). Right ordinate scale: Myelination score. Rot = n. rotundus, E = Ectostriatum, LH = Lamina hyperstriatica, LFS = Lamina frontalis superior.

The probability of transfer of information from one store to the next is constrained by the filling of the preceding store. The more that one is filled, the higher is the probability of transfer to the next one. The procedures are the same for store two and three, respectively (Fig.5).

In the computer simulation, the above process is replicated 275 times. Then the computer plots the percentage of stored bits for each store; this is done for 230 time bins (Fig.5). As the percentage of storage within each time bin can be interpreted as an indicator of the "sensitivity" of the storage medium for information arriving from the outside, the diagrams can be directly compared with the sensitivity curves obtained in imprinting experiments (Fig.1). The shape of the resulting curves for the second and the third store are very similar to those obtained in experiments of sexual imprinting. In each case "sensitivity" to new information rises quickly. Then, after reaching a peak, the curve declines to zero as a consequence of the amount of the information already stored. From more peripheral to more central stores, the peak of the curve shifts to the right and the shape is more and more flattened.

From the similarity of the sensitivity diagram obtained in the imprinting experiment and the curves obtained from the computer simulation, one can speculate that a storage process may be involved in imprinting which has the two characteristics mentioned above of limited space and permanent storage. The length of the sensitive period can be easily altered in the model by varying the speed of information input or can be prolonged by assuming that only part of the incoming information can get access to the storage medium.

The question now is whether physiological correlates of such a storage process can be found. If one takes the development of the visual cortex of the cat as a model for what may happen in the zebra finch brain in the course of imprinting (Bischof 1983), one can argue that a given brain area may be capable for permanent plastic changes as long as this area can be morphologically altered.

In the zebra finch, Teuchert et al. (1982) observed degeneration of axon terminals in different brain nuclei of the visual pathway. Degeneration occurred in a sequence from peripheral to central stations. As these authors argue, this degeneration may be a prerequisite for subsequent rewiring of connections under the influence of external stimulation as it occurs in imprinting. This process of rewiring is finished when a certain balance of inhibitory and excitatory inputs to a given neuron is reached. Afterwards, by myelination of the involved areas, the newly installed connections are stabilized and consequently cannot be altered by external influences later (Wolff 1981).

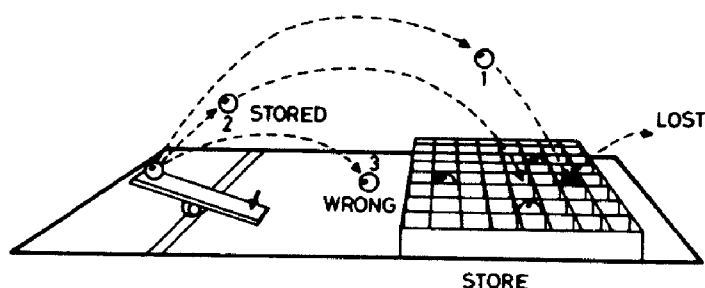


Fig.4: Randomly filling of a store. Explanations see text.

If myelination follows the rules we applied to the computer model, the amount of myelination per time should follow a similar time course to that we obtained in the simulation. To examine this, we differentiated the myelination curves obtained in the experiments already mentioned above (Herrmann and Bischof in prep.) to estimate the speed of myelination for different brain areas at different times. Fig.6 shows that these diagrams are similar to those of the computer simulation and those obtained in sexual imprinting.

However, the other feature we obtained from the simulation, the delay of development from peripheral to more central stations of a given pathway, is not easily detectable in the course of myelination of the different nuclei. This does not affect the parallels mentioned above, as the time shift in the model can be made smaller by altering the coupling conditions between the stores in a sense that more throughput of information is allowed from the very beginning of the simulation.

It is not possible from our data to speculate which of the brain areas is involved in imprinting. All telencephalic areas we examine have their

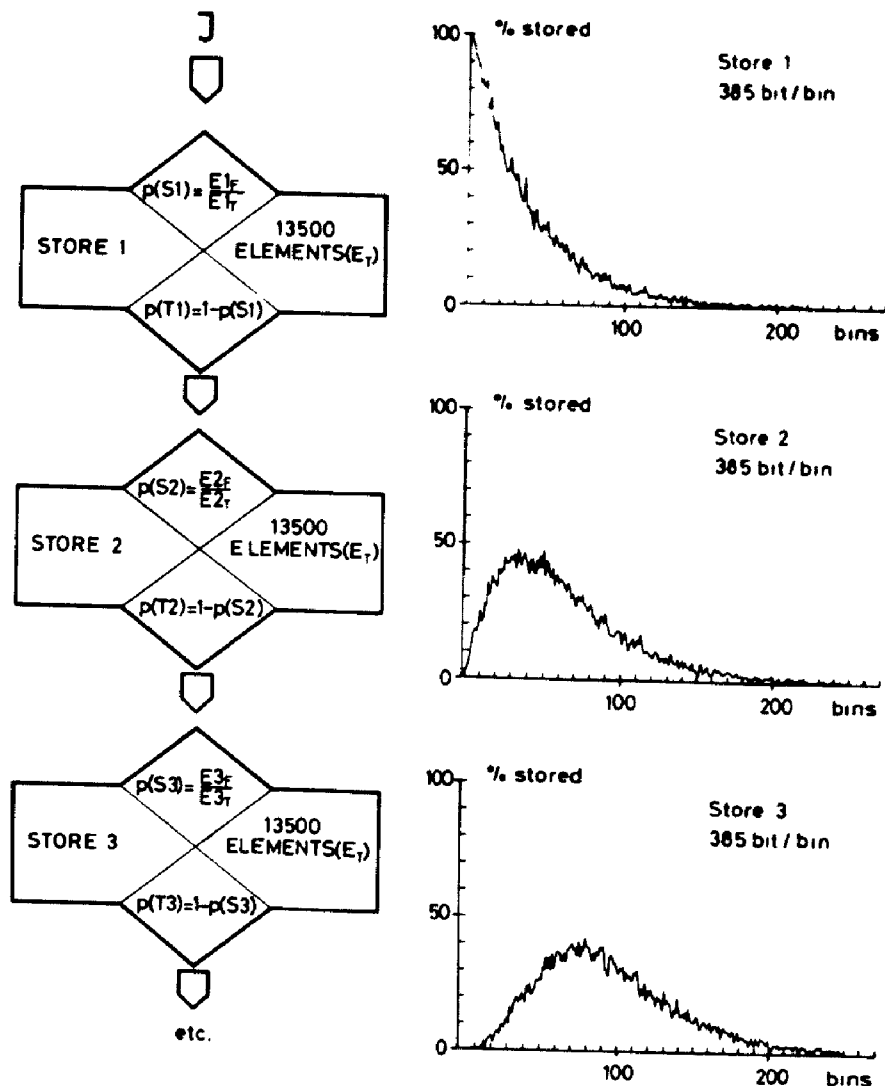


Fig.5: Left: Mathematical formulation of the computer model. Right: Sensitivity diagrams of the different stores. E_i^f = Elements full, E_i^t = Elements total, $p(S_i)$ = probab. of storage, $p(T_i)$ = probab. of transfer.

fasted rate of development at the time when imprinting occurs. There are two exceptions to this rule, the nucleus robustus archistriatalis (RA, not shown in the Fig.6), and the hyperstriatum ventrale pars caudale (HVC), two nuclei involved in control of song in songbirds (Nottebohm 1980). Interestingly, the development of HVC coincides in time with the development of song in the zebra finch (Böhner, pers. comm.). As song learning is in many aspects similar to imprinting, this may be an additional indication that stable learning as demonstrated by imprinting and song learning may be coupled to developmental processes.

Again, one has to stress that it is not possible to prove a direct link between the sensitive period for imprinting and the development of the different brain nuclei from our data; for direct evidence one has to perform deprivation experiments in which the sensitive period for sexual imprinting and, if the above mentioned considerations are correct, the development of different brain areas are shifted forwards.

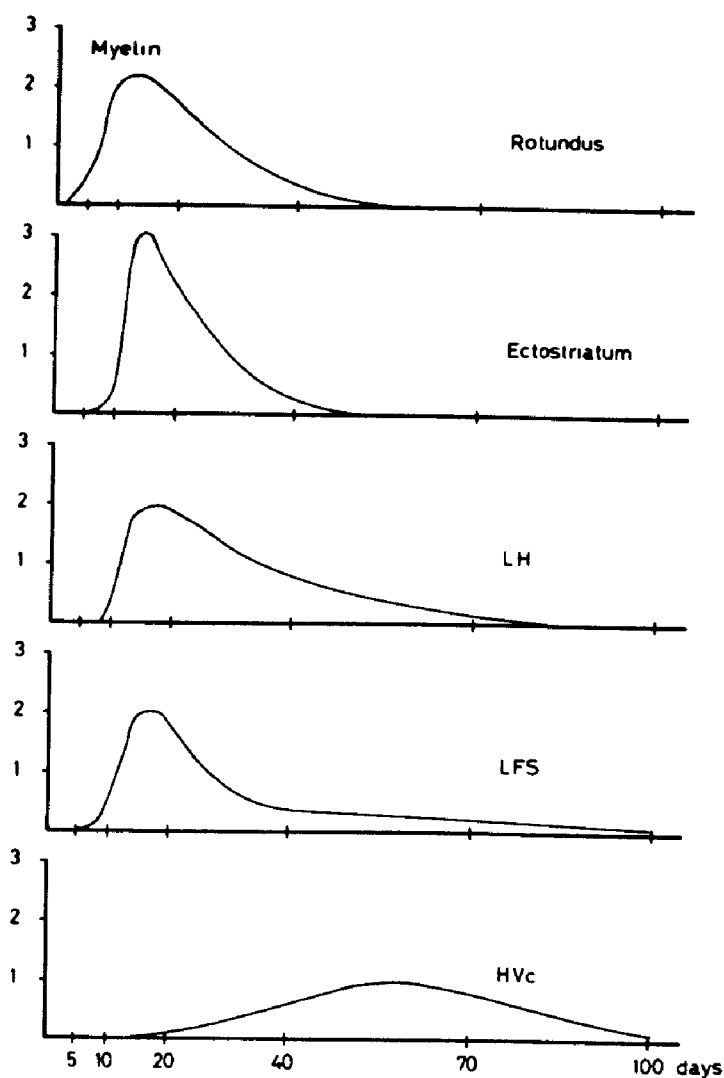


Fig.6: Rate of myelination in different brain areas. Ordinate scale is arbitrary. HVC = Hyperstriatum ventrale pars caudale. For other abbreviations see Fig.3.

CONCLUSIONS

I would like to stress here that the arguments presented above are an attempt to show certain time-dependent parallels which represent another way of thinking about the physiological processes involved in imprinting. The main argument is that imprinting is not different from other learning paradigms in terms of the features which are to be learned and the process of acquisition of the data (Immelmann 1975), but that the stability of storage, which is an important feature of imprinting, is due to the developmental state of the brain areas involved. As long as the neuronal tissue is still developing, it seems to be more vulnerable to external stimulation. This may lead to morphological changes of the neuronal connectivity in the young animal (for example, elimination or construction of new synapses), which may be more stable than the submicroscopic or biochemical changes observed in adult animals. Myelination might be a process which stabilizes the newly acquired connections and prevents them from further alterations; however, this stability could also be reached by a balance of excitatory and inhibitory inputs to a given neuron, as was proposed by Wolff (1981).

If a comparable stability of storage is required in older animals, as for example in song learning, the related neuronal area is held for a longer time in a state of early development, as demonstrated by the delayed myelination of RA and HVC. Nottebohm and Goldman (1983) have found that even new neurons appear in HVC, evidence which is consistent with the present.

If we accept the assumptions presented above, the occurrence of a sensitive period may be explained simply by the fact that the remaining "plastic" tissue is reduced as a consequence of a stabilization process, which in turn depends on external stimulation. As shown in the model, it may be that a certain small amount of neuronal tissue remains alterable for a long time and may also be accessible for further imprinting processes, but not as easily as in the young animals. Bateson (1983) argues that imprinting-like processes can readily occur in adult organisms under certain conditions such as stress; this view would fit in the speculations above if one presumes that under stress conditions the input of external information is so massive that part of it gets access to the remaining brain tissue that can be altered.

Admittedly, the view presented above is simplistic and obviously cannot be a complete description of what occurs in imprinting phenomena. The assumptions may represent some basic process which is complicated by many other conditions. However, the physiological basis of features such as, for example the influence of motivation and arousal on the learning process, or the way the bird selects between the different stimuli occurring in the environment, is still poorly understood. Some speculations concerning their influence on imprinting are discussed by Bischof (1983).

REFERENCES

- Bateson, P.P.G., 1966, The characteristics and context of imprinting. Biol. Rev., 41: 177
- Bateson, P.P.G., 1978, Early experience and sexual preference, in: "Biological Determinants of Sexual Behaviour", J.B. Hutchinson, ed., John Wiley, London.
- Bateson, P.P.G., 1981, The control of sensitivity to the environment during development, in: "Behavioural Development. The Bielefeld Interdisciplinary Project", K. Immelmann, G.W. Barlow, L. Petrinovich, M. Main, eds., Cambridge Univ. Press, Cambridge, Mass.

- Bateson, P.P.G., 1983, The interpretation of sensitive periods, in: "The Behavior of Human Infants", A. Oliverio, M. Zapella, eds., Plenum, New York.
- Bischof, H.-J., 1983, Imprinting and cortical plasticity: a comparative review, Neurosci. Biobehav. Rev., 7: 213
- Bischof, H.-J., and Lassek, R., 1985, The gaping reaction and the development of fear in young zebra finches (*Taeniopygia guttata castanotis*), Z. Tierpsychologie: in press
- Hess, E., 1973, "Imprinting", Van Nostrand Reinhold, New York.
- Immelmann, K., 1972, The influence of early experience upon the development of social behaviour in estrildide finches, Proc. XV. Int. Orn. Congr. 1972: 317
- Immelmann, K., 1975, Ecological significance of imprinting and early learning, Ann. Rev. Ecol. System., 6: 15
- Immelmann, K., 1979, Genetical constraints on early learning: a perspective from sexual imprinting in birds, in: "Theoretical Advances in Behaviour Genetics", J.R. Royce, L.P. Mos, eds., Sijthoff and Noordhoff, Germantown, Maryland.
- Immelmann, K., and Suomi, S., 1981, Sensitive phases in development, in: "Behavioural Development. The Bielefeld Interdisciplinary Project", K. Immelmann, G.W. Barlow, L. Petrinovich, M. Main, eds., Cambridge Univ. Press, Cambridge, Mass.
- Klinghammer, E., 1967, Factors influencing choice of mate in altricial birds, in: "Early Behavior. Comparative and Developmental Approaches", H.E. Stevenson, E.H. Hess, H.J. Rheingold, eds., John Wiley, New York.
- Le Vay, S., and Stryker, M.P., 1979, The development of ocular dominance columns in the cat, in: "Society for Neuroscience Symposia IV. Aspects of Developmental Neurobiology", J.A. Ferrendelli, eds., Soc. Neuroscience, Bethesda.
- Lorenz, K., 1935, Der Kumpan in der Umwelt des Vogels, J. Orn., 83: 132 and 289
- Nottebohm, F., 1980, Brain pathways for vocal learning in birds: a review of the first ten years, Progress in Psychobiol. and Physiol. Psychol., 9: 85
- Nottebohm, F., and Goldman, S.A., 1983, Connectivity and kinetics of neurons born in adulthood, Soc. of Neuroscience Conf. Abstr., 40.2.
- Teuchert, G., Wolff, J.R., and Immelmann, K., 1982, Physiologische Degeneration in der Ontogenese des ZNS von Vögeln: eine Einflußnahme auf die sensible Phase für Prägung?, Verh. Dtsch. Zool. Ges. 1982, 259.
- Wolff, J.R., 1981, Some morphogenetic aspects of the development of the central nervous system, in: "Behavioural Development: The Bielefeld Interdisciplinary Project", K. Immelmann, G.W. Barlow, L. Petrinovich, M. Main, eds., Cambridge Univ. Press, Cambridge, Mass.