

Imprinting and Cortical Plasticity: A Comparative Review

HANS-JOACHIM BISCHOF¹

*Universität Bielefeld, Lehrstuhl für Verhaltensphysiologie
Fak. Biologie, Postfach 8640, 4800 Bielefeld 1, West Germany*

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BISCHOF, H.-J. *Imprinting and cortical plasticity: A comparative review.* NEUROSCI BIOBEHAV REV 7(2) 213–225, 1983.—Results of research on imprinting and developmental neurobiology of the visual cortex are compared to evaluate the evidence for or against a frequently hypothesized linkage of the two phenomena. The comparison reveals striking similarities. In both paradigms a sensitive period exists. Once this sensitive period is over, the storage of early influences from the environment remains stable throughout life. Storage of “natural” stimuli is facilitated by a certain preorganisation of the receiving brain areas. It is stated that the two phenomena are not directly linked, but are two expressions of a developmental process, which may be common for the organisation of the connectivity of single cells as well as for complex neuronal networks as they are likely to be involved in imprinting. This process is basically self-organizing, but can be influenced by superimposed controls. Differences of the stability of storage of external influences might be explained by the difference in the overall amount of morphological alterations, which is large in the young and small in the adult animal. This holds for both the modifiability in the visual cortex and imprinting.

Imprinting Visual cortex Plasticity Early learning

THE development of an organism is guided by an interaction of genetically determined and epigenetic factors. In early embryogenesis factors such as cell–cell interactions, chemical gradients or mechanical guidance of growing nervous tissue play an important role (reviews [1, 66, 127]). Later, at a point of development not yet defined and perhaps different for distinct structures, external stimulation is involved in the instruction of nervous connections [96]. For example, restriction of the visual stimuli to one eye alters the connectivity of the visual cortex in cats [126]. Even changes in the orientation of visual stimuli can alter such connectivity, not only in cats but other animals as well [12,57].

Like the connectivity of nervous tissue, the behaviour of the adult animal is strongly influenced by early experience. One of the best known cases of early learning is the so-called “imprinting” process [80], by which, in its original definition, a young bird learns the target object for a distinct behaviour pattern, which is believed to be mainly inherited. In the course of filial imprinting, for example, a young chick or duck learns about the object it has to follow when leaving the nest (reviews [4, 5, 50]). Zebra finches in the course of sexual imprinting learn the features of an object which release courting behaviour in fully grown birds [62].

The influences of external stimuli on the development of neuronal structures of the visual cortex and of imprinting have some common characteristics: sensitivity for those stimuli is high only during a restricted period of development (sensitive period) and can rarely be demonstrated in adults, and the changes of structures or stored information remain remarkably stable throughout life of the animals.

Considering these similarities, one can assume that there might be some linkage between the neurophysiological processes and the behavioural processes mentioned above [8,56]. Some authors, however, state that the paradigms might not be comparable [56].

While imprinted animals can detect stimuli other than the imprinted one (and react to these stimuli with avoidance reactions in the case of filial imprinting), the neurons of area 17 of the visual cortex appear insensitive or “blind” to such not imprinted stimuli after the end of the sensitive period.

This difference might not be a real one: recent experiments [34] demonstrated that this physiological “blindness” is true for a single neuron, but not for the whole animal subjected to a restricted environment.

Another argument against the comparability of the phenomena is the fact that the plasticity of the visual cortex might be coupled with the existence of binocular vision. Plasticity of this kind, for example, cannot be demonstrated in rabbits, a species with only a very small binocular field (e.g. [24,46]).

In birds, the plasticity of visual neurons has been demonstrated yet only in the barn owl, which has a large binocular visual field [94]. The results obtained in this study by recording from neurons of the visual wulst (hyperstriatum asseccorium) of normal and monocularly deprived animals resemble very closely those found in studies of the visual cortex of cats. The bird species observed for imprinting unfortunately lack a prominent binocular field. However, this does not mean that no neuronal plasticity occurs in those birds with small binocular fields. A reasonable amount of

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plasticity has been demonstrated by histological procedures in chicks in brain centers involved in imprinting [18], in song control areas of canaries (for review see [89]) and in different visual areas of the zebra finch (Wolff *et al.*, in preparation). In these examples it is not as easy as in the visual cortex paradigm to evaluate the functional consequences of environmental influences. Thus, it is likely that plasticity is a common feature of the developing brain, but it may be that it can be demonstrated easier in binocular neurons than in other cell types.

Imprinting phenomena, in turn, might be common among species other than ducks, chicks and zebra finches; they can be demonstrated too in a variety of other animals, including mammals and even man (review [65]), but most of the research is done on the birds, as here the phenomenon is obvious.

In this study I will try to compare two paradigms of physiological and behavioural research, plasticity of neurons of the visual cortex and imprinting, to find some indications for or against a linkage of the two phenomena. Surely one cannot define cortical plasticity as the physiological phenomenon underlying imprinting [103], but it might be possible that both cases are expressions of a common principle of influence of external stimuli on the organisation of certain brain areas.

PARADIGMS

Imprinting

The term "imprinting" was first used by Lorenz [80]. As did other researchers before (e.g. [27,49]), he observed that young geese, bred in an incubator, follow the first object they can see after hatching. This object need not be a conspecific; it can even be the man taking the bird out of the incubator. This preference for the first moving object proved to be stable for the entire period during which the following behaviour persists (filial imprinting). From other observations Lorenz concluded that the choice of the sexual partner in birds is also influenced by early experience (sexual imprinting).

The conclusions Lorenz drew from his observations were the basis for a wealth of subsequent research designs which tried to confirm or disprove part of the arguments or even the whole theory. A review of all these studies is not intended here, as there are some excellent overviews available [4, 50, 53, 63, 65, 72].

The experiments mentioned above revealed that Lorenz was essentially right in his view of imprinting. However, a series of "imprinting-like" features have been discovered during the last few years, which fulfilled one or the other, but not all, of the criteria of Lorenz. The next paragraph will deal with Lorenz' definitions of imprinting and some of the arguments of other authors against and in favour of those criteria.

(1) Learning occurs only in a restricted period during the development of the animal, the so-called sensitive period (sensitive phase, critical period).

In a series of experiments with chicks Hess (review [50]) demonstrated that in filial imprinting acquisition of the object is restricted to a short period within 13 and 16 hours after hatching, while the following reaction persists for at least some weeks.

Very careful quantitative studies of sexual imprinting were made by Immelmann [62,63] with zebra finches (*Taeniopygia guttata castanotis*). He found a sensitive period for acquisition of the object features which was longer

in duration and occurred later than that obtained by Hess for filial imprinting. The peak of sensitivity was at about 12 days post-hatching, and sensitivity to external stimuli ends long before the zebra finch reaches sexual maturity, and therefore long before he can get any courting experience.

Recent reports demonstrate that sensitive periods in both filial and sexual imprinting are not as short and sharply defined as believed before; a low degree of sensitivity can persist for a long time after occurrence of the peak of the sensitive period (see *Time Course* under Comparison of Paradigms).

(2) Imprinting is irreversible, the features learned in the course of the sensitive period cannot be forgotten.

This statement has often been challenged in subsequent reports, some results seemed to demonstrate that preferences could be reversed later (e.g. [107]). However, it was recently demonstrated that preferences acquired in ontogenesis are really stable throughout life. If the imprinted object is not available, the birds eventually can acquire a new preference for another one, if they are caged together with this object for a long time. However, this preference is not stable, but disappears if the imprinted stimulus is offered as a choice object in a double choice experiment against the new object. This holds for sexual imprinting [64] as well as for filial imprinting [23]. The disagreement concerning irreversibility of imprinting is evidently based on the differences of interpretation of the term [63]; it does not mean that the bird is restricted in his reaction to the one object acquired during the sensitive period, but it prefers this object in the case of choice (see *Irreversibility* under Comparison of Paradigms).

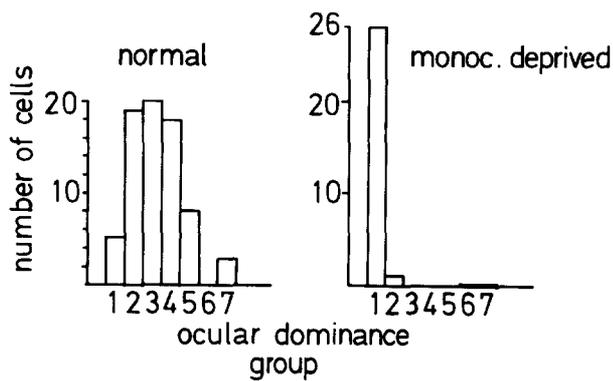
(3) In imprinting, only species specific characters are learned, not individual ones.

This conclusion was drawn by Lorenz from the fact that the animals do not choose exclusively their parent as sexual partner, but as a rule court all opposite-sexed birds of their species. Schutz [108] stated that for filial imprinting this statement cannot be true, as ducks in a natural situation follow their mother and not each duck crossing their way. Bateson [6] argued that generalisation can occur even if the bird in the imprinting situation learns the characteristics of an individual. He developed the "optimal discrepancy" theory, which is based on individual recognition of the imprinting object. According to this theory, the bird should choose a sexual partner which is only slightly different from the parent's image (but see [118]).

(4) Imprinting occurs at a time when the appropriate behaviour is not developed.

Therefore Lorenz states that imprinting differs from other learning paradigms by a lack of reinforcement. This suggestion was challenged by many authors; especially in filial imprinting there is no time lag between imprinting and the behavioural response, and probably conditioning is involved in the acquisition process [50,53]. For sexual imprinting this fourth statement seems to be almost correct. As Immelmann (review [63]) demonstrated, the sensitive period for sexual imprinting ends before the bird is sexually mature and can get any sexual experience. However, as he points out, some sort of reinforcement cannot be excluded even in this case.

This short overview cannot cover the whole area of imprinting research of the last 45 years; however, it demonstrates the degree of current acceptance of the criteria evolved by Lorenz. The first two criteria have been proved to be correct, whereas the latter two are not as unquestioned and cannot be applied to all imprinting paradigms. Therefore, at best, they should be stated as facultative, not essen-



from: BLAKEMORE and VAN SLUYTERS (1974)

FIG. 1. Ocular dominance distribution in area 17 of normally raised and monocularly deprived cats. For details see text.

tial, conditions. From the first two statements a new definition of imprinting was designed by Immelmann [64], which considers the view [65] that many of the so-called "imprinting-like" phenomena should better be grouped under the label of imprinting. Thus, imprinting is defined simply as "an early learning process with very stable results."

Another statement by Lorenz concerning imprinting, but not mentioned in the previous four tenets, must be added here, as it was the source of many controversial opinions: he stated that the preferences of the birds, although mostly influenced by external factors, may be under the control of genetically determined factors. This was rejected by many authors. Some evidence, however, is available for the demonstration of such an influence (see *Canalization* under *Comparison of Paradigms*).

Plasticity of the Visual Cortex

As in the preceding section, a comprehensive review of recurrent literature is not intended. An excellent overview has been written by Blakemore [12].

Most neurons in area 17 of the visual cortex of an adult cat can be driven by visual stimulation of the left as well as the right eye, thus being defined as binocular. Hubel and Wiesel [57] developed a classification scheme for binocularity (Fig. 1a). Class 7 is built by neurons driven exclusively by the ipsilateral eye, class 1 of those excited by the contralateral eye only. Neurons equally driven by either eye fall within class 4, the 4 other classes consist of cells with asymmetrical input. In the normal adult cat more than 80% of the neurons of area 17 are binocular.

If one eye of the kitten is briefly sutured closed in its early postnatal life, the ocular dominance distribution, which can be measured in the adult cat, proves to be altered drastically: There is an obvious lack of binocular cells in the visual cortex of such animals and most of the neurons can solely be driven by the nondeprived eye (Fig. 1b). Further experiments [60] revealed that these changes in the ocular dominance distribution follow only if monocular deprivation occurs for a distinct time during development of the kitten (see *Time Course* under *Comparison of Paradigms*).

Similar deprivation in an adult cat does not alter the ocular dominance distribution, even if the suturing is maintained for several months or more. Such alteration in ocular domi-

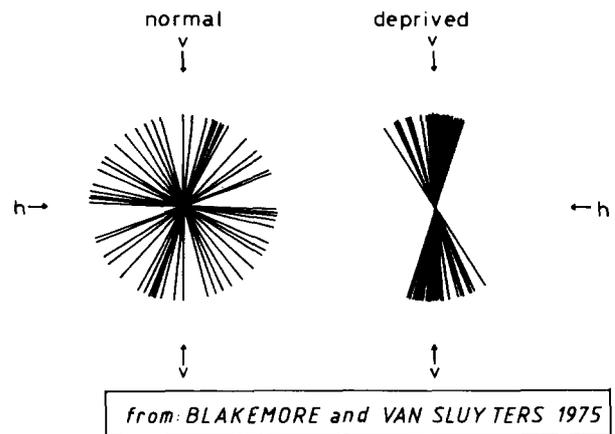


FIG. 2. Distribution of orientation selectivity of cortical neurons of area 17 in normal and monocularly deprived cats. For details see text.

nance is proved to be persistent throughout life after the sensitive period is over (see *Irreversibility* under *Comparison of Paradigms*).

In other laboratories [13, 51, 52], it was demonstrated that shifting of neuronal preference could also be observed in another feature domain cortical cells, i.e., their selectivity for distinct stimulus orientations. Under normal circumstances the proportion of visual cortical neurons which have different orientation selectivity distributes evenly around the clock (Fig. 2a).

If one rears the kittens with goggles, which restrict the visible features to black and white stripes with one orientation [51, 52, 101, 111], or in an environment with stimuli of one single orientation, most cortical cells of such animals when recorded in adulthood respond preferentially to the visual target which has the experienced orientation (Fig. 2b). Again this alteration of orientation preference has a sensitive period during the early development of the kitten [12]. When the sensitive period is ended, no alteration of the acquired pattern is possible.

As in imprinting, a genetically determined influence on the organisation of wiring of the visual cortex can be demonstrated: The adult pattern is obviously already present in the newborn cat, although not as rigid and clear-cut as in the adult (see *Canalization* under *Comparison of Paradigms*).

COMPARISON OF PARADIGMS

The preceding section reveals that there are at least 3 common features of imprinting and plasticity of the visual cortex:

(a) In both paradigms alterations by external stimuli can only be accomplished during a sensitive period in the early development of the animal.

(b) "Imprinted" information seems to be stable against further influences of the environment when the sensitive period is ended.

(c) In both paradigms acquisition of external stimuli seems to be canalized by genetical instructions.

With careful comparison some other similarities can be detected, as shall be demonstrated below.

Time Course of Sensitive Periods

The time course of the sensitive period for sexual imprinting has been determined yet only for a few species. The most careful research has been done on zebra finches (*Taeniopygia guttata castanotis*). The sensitive period for these birds has been examined by Immelmann [62,63].

The zebra finch is an altricial bird; at the time of hatching it is relatively poorly developed and the eyes are closed. Eye opening occurs at 5 to 7 days of age, fledging at 20 days. The birds become independent at about 30 days, the first signs of courting behaviour can be observed at 70 days. At this time the testosterone level of the birds rises strongly and fully developed sperms are to be found within the testicular tissue [97].

The sensitive period, as demonstrated by Immelmann, begins during days 5–7 (presumably at eye opening). The sensitivity for imprinting stimuli rises strongly until day 13 and then slowly decreases until day 40. Recent results of Immenmann [64] demonstrate that sensitivity does not decrease to zero at this time; minimal effects of external stimulation can be detected as long as day 70 (Fig. 3a).

Like zebra finches, cats are born underdeveloped with closed eyes. The eyes open at about 15 days. Sexual maturity is reached at 7 months. The sensitive period for the influence of external stimulation on the organization of the visual cortex was evaluated by several authors under different experimental conditions [15, 16, 58, 59, 60, 126] (review [12]). These data demonstrate that the sensitive period starts with eye opening as in the zebra finch, sensitivity rises until day 40, then slopes downwards until day 100. As in the preceding paradigm, slight influences of external stimuli can be detected some time later [25].

The time course for sensitivity seems to be very different for both examples, until one considers the different developmental speed of the two species. In the zebra finch development is much faster than in the cat. Sexual maturity in this species is reached at about day 70, whereas in the cat maturing is as late as 7 months. Superimposing the birth dates as well as the time at which the animals reach sexual maturity to standardize developmental rates reveals that the ascent, peak and decline of the two sensitivity curves match very closely, as do the values for eye opening (Fig. 3a,b).

Correcting the data obtained by Gallagher [36] for the sensitive period of the Japanese quail by the same procedure used above, these data again match those of the two preceding examples. However, in this case the ascent of the curve is different; since the quail is a nidifugous bird which has open eyes at birth, the sensitive period starts a little bit earlier (Fig. 3c).

The sensitive period in the zebra finch was investigated by cross-fostering experiments [62–64]. The birds were first raised for a limited time by their parents and then transferred to other parents of a different species, the Bengalese finch (*Lonchura striata*) which served as foster parents until the birds reached the age of independence. Subsequently, the young zebra finches were visually isolated from other birds and tested for their preference in a double choice test with zebra and Bengalese finches at about day 100 after hatching. An example of the reversal of sexual preferences is demonstrated in Fig. 4 (left). In these experiments the time of rearing by the biological parents was varied between 6 and 25 days. Subsequently the young birds were transferred to the foster species for 16 to 84 days.

If transferred between days 6 and 13, it turned out that all

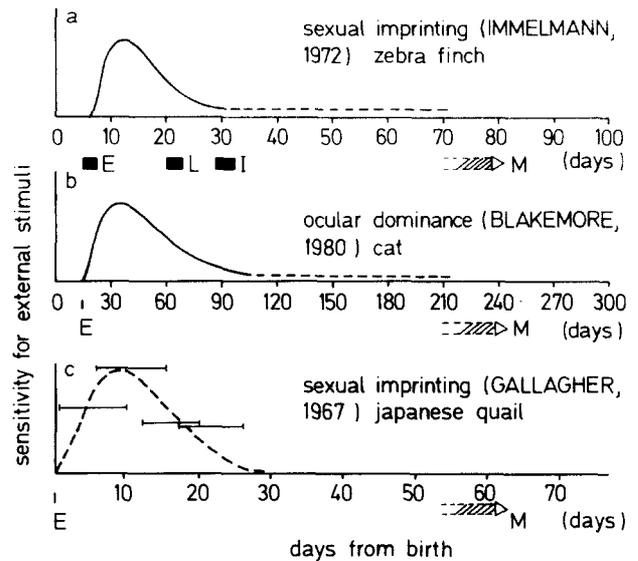


FIG. 3. Time course of the efficiency of external stimulation in 3 different paradigms. Ordinate scale is arbitrary. E=Eye opening, L=Leaving of the nest, I=Independence, M=sexual Maturity.

birds were imprinted to their foster parent species. Transfer between days 13 and 18 resulted both in pure preferences for either foster or own species and mixed preferences, although still with a bias towards one or the other species (bL and bT). If transferred after day 18, all birds were imprinted on their own species.

This sort of experiment can be compared with those concerning the plasticity of the visual cortex which start with the suturing of one eye of the kitten before opening, reopening of this eye and the closure of the other some time later [15]. Distribution of neurons within ocular dominance classes is then evaluated in the adult cat.

In animals reverse sutured at week 5, almost all neurons appeared to be driven solely by the eye which was sutured first (Fig. 4, upper right). With reverse suture at week 6, neurons driven by either eye could be demonstrated, at week 10 almost all cells were driven by the secondarily deprived eye (data from [15]). The similarity between the time course of reversibility obtained for the sexual imprinting and that for ocular dominance under the reverse suture paradigm is obvious. The developmental time, corrected as mentioned before, is the same for each left-right pair of diagrams of Fig. 4.

Although there may exist other examples of the above mentioned similarity of sensitive periods, e.g., in human development [2,54], surely this is not common to all examples of neuronal plasticity and imprinting. Directional selectivity of visual cortical neurons, for example, can be influenced in a period slightly earlier than that for ocular dominance and orientation earlier than that for ocular dominance and orientation selectivity [28]; however, the shape of the sensitivity curve is essentially the same. Sensitive periods for filial imprinting seem to be much shorter than those for sexual imprinting, although some experiments (e.g. [19]) have revealed that they might not be as short as previously believed. Again, the shape of the sensitivity curve seems to be essentially the same in filial imprinting and the paradigms

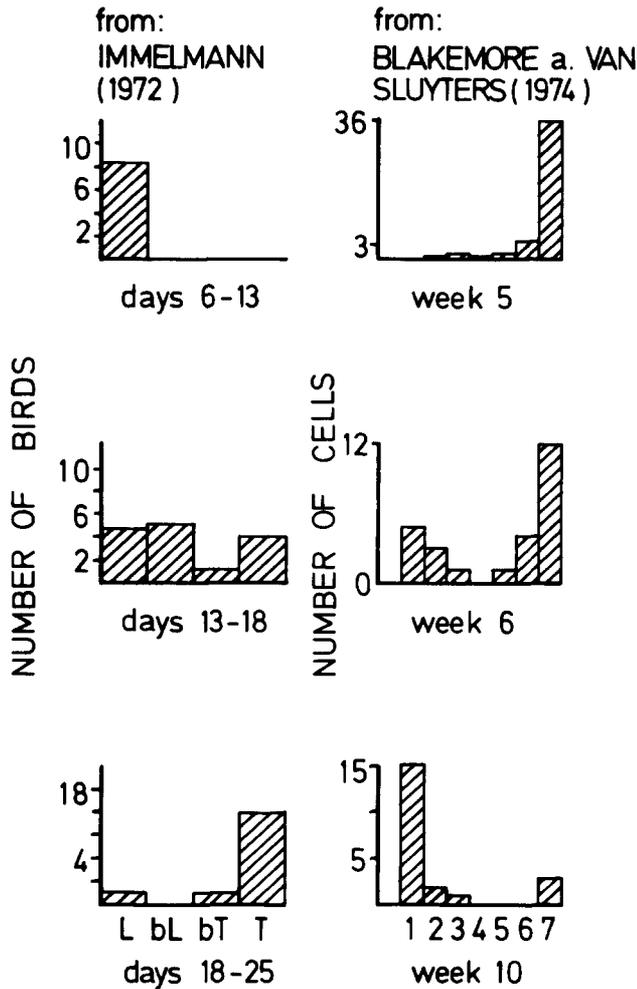


FIG. 4. Results of transfer experiments on sexual imprinting in birds and on plasticity of the visual cortex in cats. Left: Transfer of the birds from their parents to a foster species at the time indicated below the x-axis. Each bar represents the number of birds with a preference in a double choice test between zebra and Bengalese finches. L=Lonchura (Bengalese finch, the foster species); T=Taeniopygia (zebra finch); bL=bias towards Lonchura; bT=bias towards Taeniopygia. Right: Reverse suturing experiments. Cats were deprived soon after birth by suturing one eye. Reopening and reverse suturing occurred at the time indicated below the x-axis. Each bar represents the number of neurons falling in the ocular dominance class indicated below the bar.

exemplified in Fig. 3, especially when the sensitivity is plotted against the developmental age of the animal (Fig. 5, data from [38,41]).

Irreversibility

Lorenz assumed that information acquired at the imprinting process is stored irreversibly throughout life. Hubel and Wiesel drew the same conclusion from their experiments on cortical plasticity. Both opinions did not remain unchallenged.

A difficulty in the evaluation of irreversibility is the fact that sensitivity to external stimuli does not end abruptly, but

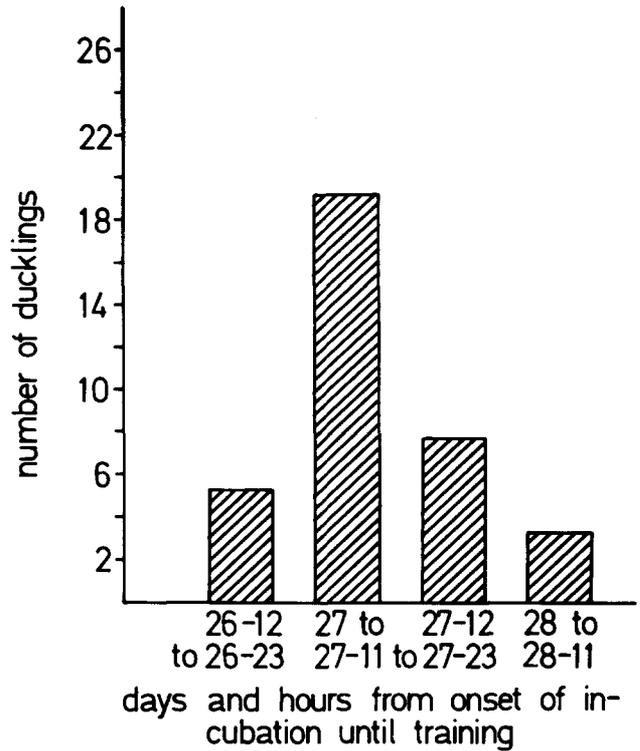


FIG. 5. Success of an imprinting session of the time span of development indicated below the bars. Ordinate: Number of ducklings following adequately in a test some days later. Data from Gottlieb [38].

asymptotically declines to zero. Immelmann [64] demonstrated that imprinting preferences can be reversed sometimes as late as day 70, if the zebra finches are exposed long enough to the second species after transfer.

The critical period for the plasticity of neurons of the visual cortex is also not definitively limited. Influences of monocular deprivation [15,25] or rearing with patterns of one orientation [119] can be minimized by long periods of normal vision. Rotation of one eye [117] results in changes of ocular dominance distributions even in cats 3 months of age.

Changes in the responses of cortical neurons or behavior can be obtained even in adult animals. These changes, however, do not seem to be stable, in contrast to those acquired in the course of the sensitive period. Recent experiments have revealed that the imprinted information might be in fact irreversible. Immelmann [64] pointed out that zebra finches reared by Bengalese finches, and therefore imprinted on that species, can eventually court and breed with conspecifics, if they are kept exclusively with birds of their own species. However, in a double choice test between the two species, these birds, after some time, preferred the imprinted species again. Thus, it seems most likely that preferences acquired by imprinting can be masked sometimes, but cannot be eliminated from memory.

Similar results can be obtained in filial imprinting. Long after the end of the sensitive period the birds can develop a preference for stimuli other than the imprinted one. Cherfas and Scott [23], however, demonstrated that this new preference again is not permanent, but will be replaced by that for the imprinted stimulus in a double choice test.

In mammals, the influence of early experience on adult behaviour can be demonstrated too, but it disappears in later life. Thus, it can be hardly detected in adult animals under normal conditions. However, these influences are not really lost, but can come to the surface again in extraordinary situations such as stress (Ågren and Myers, from [65]).

In monocularly deprived cats with enucleation of the experienced eye at a time when the sensitive period is over, the proportion of cells driven by the deprived eye appears to increase from 0 to 30% [77]. Blakemore and Hillman [14], however, concluded from other experiments that this effect might not be due to a real increase in the proportion of neurons driven by the deprived eye, but due to better registration of these cells as a result of lack of inhibition from the previously dominating eye. That means that even by the enucleation of one eye there is no real alteration of the neuronal connectivity acquired in the sensitive period. Thus, in both paradigms information acquired in the course of the sensitive period seems to be stored irreversibly; under certain circumstances this previously acquired information can be masked but not eliminated by other effects.

Canalization of the Acquisition of External Stimuli by Genetic Influences

It is widely accepted among ethologists that the behavioural reaction towards a target object to which the bird has been imprinted (e.g., the following reaction in filial imprinting or courting in sexual imprinting) is constant and not readily alterable by experience. In contrast, the choice of target object seems to be almost free of limitations. Some experiments, however, demonstrate that the ability to learn distinct features may be narrowed and canalized by genetical instructions. For filial imprinting there seems to be no apparent restriction for stimulus parameters, but some features, such as a moving stimulus of circular shape, a distinct dimension, and colour, are learned better than others [9, 31, 37]. Zebra finches raised by mixed pairs (one zebra—one Bengalese finch) prefer their own species in double choice experiments. Thus, in this case, features of conspecific animals are learned better than those of heterospecific ones [63].

A series of experiments reveal that neurons of the visual cortex of newborn kittens have response properties similar to those in the adult animal. Although cell responses are very weak and difficult to analyze, and only a small percentage (about 25%) responds to visual stimuli [3, 16, 20, 35, 59, 61, 92, 93], neurons of each ocular dominance class and orientation preference can be detected, revealing an adult-like distribution of feature detecting neurons. Columnar organization of the visual cortex can as well be demonstrated in the newborn monkey [99]. This organization apparent at birth is strengthened and stabilized by normal visual experience, and can be altered in the course of the sensitive period by variation of the visual input.

One can conclude then that both the cortical substrate and the structures storing the imprinting information consist, to a certain extent, of a perhaps genetically determined predisposition which facilitates acquisition of the "normally" occurring input features.

Nothing can be said yet about the relative importance of genetical and environmental factors. Moreover, we cannot be sure that the conditions we meet in experiments directly after birth are really unaffected by external influences. Young ducks, for example, can learn features of the voice of

their mother before hatching [38, 39, 40, 76]. Organization of the geniculate nucleus of monkeys can be affected by enucleation of one eye before birth [100]. Therefore some sort of influence from the eyes might be important for proper organization of visual centers even before birth. Likewise, development of ocular dominance columns, which are incomplete at birth in kittens and are sensitive to visual experience [110], seem to be established to a higher degree in monkeys [99]. In this species, however, ocular dominance columns can already be changed prenatally by enucleation of one eye [100]. Blakemore [12] describes the recent point of view with a nice analogy: "Perhaps, the visual cortex of the kitten behaves in some sense like the empiricist's tabula rasa, but genetic instruction has, at the very least, put together the wax tablet and ruled the lines on which experience writes its message, and, at the most, may have done everything except dotting the i's and crossing the t's."

Hebb's Postulate on Learning as a Description of Plasticity Phenomena and the Influence of Selective Attention, Motivation, and Arousal

One of the basic problems concerning the evaluation of learning processes is the question of how the animal selects between numerous incoming information those which are so important that they must be learned. It may be that simply those features are learned, which occur very frequently and are of good contrast to the background. Those parameters surely play a role in imprinting situations [4]. However, evaluation of stimuli should be influenced by other factors too, such as attention towards the stimulus, arousal, and motivation of the animal (e.g. [42,85]).

As "arousal" and "motivation" are very poorly defined and a lot of different factors are collected under these terms [10], it is very difficult to evaluate the exact degree of participation of these factors in a given paradigm. Similarly, one cannot define exactly what the reasons are for increases or decreases of arousal levels and motivation. Genetically determined preferences might play a role (see *Canalization* under *Comparison of Paradigms*). On the other hand, the arousing value of certain stimuli might be increased by conditioning [53]. Imprintability on visual features occurs more readily in the presence of acoustic stimuli [32, 33, 95]. Learning success may also be influenced by certain other factors which arouse the animal. For example, nightingales [123] learn a larger amount of acoustic features from a tape if their caretaker is in view. Similarly, the success rate of imprinting is higher if young chicks are aroused by light electric shocks [74] or by application of stimulative drugs [75].

Some of the connections between arousal, choice of the appropriate external stimulus, and imprinting can be described by a concept developed by Hebb [48] for classical conditioning [11]. Rauschecker and Singer [102] demonstrated that processes underlying plastic changes within cortical structures can also be described by Hebb's concept.

Hebb postulates that in the course of learning, connections between two neurons are newly established or strengthened only if their cell bodies, dendrites or axons are very close, or possess already weak synaptic contact, and if they are excited simultaneously very often. Thus, from all stimuli reaching the visual cortex from the retina, those which are equally successful in simultaneously exciting pre- and postsynaptic neurons, are most effective in making connections. This effect can be attained in two different ways:

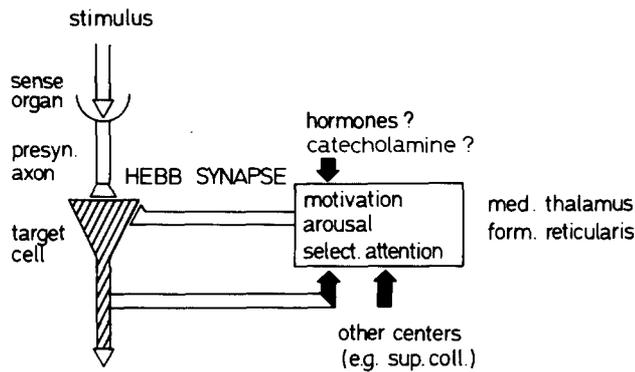


FIG. 6. Hebbian synapse simplified from the conclusions of Singer. Plasticity occurs with coincidence of pre- and postsynaptic activity of the system. Postsynaptic sensitivity is dependent on predetermined preferences for certain presynaptic activity and on additional factors such as selective attention, arousal and motivation. These factors may be mediated from brain centers like the formatio reticularis and/or the medial thalamus by direct neuronal connections, or may be influenced by changes in hormonal concentrations.

either the various presynaptic terminals ending on one postsynaptic neuron are differentially successful in driving that postsynaptic neuron, or the responsiveness of the postsynaptic cell may be differentially facilitated. This may be done, for example, by other brain systems which can be triggered either by the stimulus or by a change of excitability independent from the stimulus occurrence (Fig. 6). Other connections, which are not as good in exciting the postsynaptic target, fail to be strengthened and may be eliminated after some time.

These rules lead to competitive interactions between convergent afferents, whereby those pathways become consolidated, at the expense of others, which possess the highest probability of being active together with the postsynaptic target cell [101, 102, 113, 114]. Hubel and Wiesel [57] proposed such a competition process during formation of ocular dominance distribution within area 17. They stated that there might occur a selection of adequately working synaptic junctions from a larger number of primarily established connections. With asymmetrical stimulation of only one eye the postsynaptic target cells seem to lose the connections from the other eye.

Differences in presynaptic activity alone seem not to be sufficient for plastic changes. Singer and co-workers [101, 102, 113, 114, 116] demonstrated that excitation of the postsynaptic target cell and the occurrence of plasticity is dependent on the adequacy of the incoming information: Unstructured stimuli, as applied by covering the open eye in a monocular deprivation experiment with a translucent contact lens, fail in altering ocular dominance distribution in young kittens.

Another prerequisite for plastic changes seems to be the adequacy of stimuli in a more global context. Singer, Treter and Yinon [117] demonstrated that by a mismatch of visuo-motor coordination, as can be accomplished by surgical rotation of the normal eye within the eyesocket, no changes of binocularity was observed in monocularly deprived cats. Other essential conditions seem to be selective attention of the animal towards the stimulus [21], and the overall arousal

level [113]. If the brain centers which are believed to be involved in the functions mentioned above (e.g., the formatio reticularis or the medial thalamus) are destroyed by a lesion, again no plasticity can be observed [113,114]. The same lack of plasticity can be observed in paralyzed preparations. Livingstone and Hubel [79] demonstrated that neurons during states of higher arousal of the animal (awake versus REM sleep) respond to equal stimuli with stronger and longer lasting spike sequences and a simultaneous reduction of spontaneous activity. This result may support the theory of Singer [112,114], which states that with the coincidence of all parameters mentioned above, some sort of resonance of the neuronal circuit will be produced, which, by changing the neuronal activity of the postsynaptic neuron from phasic to phasic-tonic properties, gives the "now print" signal for increasing the probability of synaptic transmission for the connections active at the same time.

SOME EXPERIMENTS CONCERNING THE MORPHOLOGICAL AND BIOCHEMICAL CORRELATES OF IMPRINTING AND CORTICAL PLASTICITY

This section again shall not give an overview of the current literature. Only some of the direct evidence for the phenomena described above shall be mentioned. In particular, the large body of literature on the pharmacological aspects of memory shall not be dealt with. A review of this research area is provided by Rosenzweig and Bennett [105]

The biochemical and morphological correlates of neuronal plasticity and imprinting are not well known. Most theories [22, 29, 48] are based on the hypothesis that plasticity is coupled with changes in synaptic transmission. These changes, however, can be accomplished by different mechanisms [17, 43, 78, 82, 122]. It may be possible that within a given neuronal network one part of the synaptic junctions are facilitated by learning, others suppressed without changing of the morphological pattern. The existence of so-called "silent" synapses [124] and some evidence that cortical neurons, monocularly driven under normal conditions, can be excited binocularly in other test situations (Kato *et al.*, 1977 from [81]) support this possibility.

Similarly it may be possible that the number of synaptic connections or their effectiveness can be changed by morphological alterations, e.g., enlargement or reduction of the synaptic contact zone, or outgrowth and elimination of axonal processes and dendritic spines. Both instructive and selective processes have been demonstrated in different experiments.

Cortical Plasticity

The number of dendritic spines changes rapidly within the sensitive period in the kitten [26]: After a rise until week 8, the number of spines decreases slowly until the sensitive period is over. Rats reared in the dark from birth have a smaller amount of spines at the apical dendrites of pyramidal cortical cells [106]. Enriched environment during ontogenesis enlarges the number of cortical spines [44,109]. Hubel and Wiesel [57] state that in the course of the sensitive period only the most effective synapses remain stable, whereas the others are eliminated. Rauschecker and Singer [102] conclude from their experiments that there must be additional instructive processes (enhancement of synaptic conduction), as otherwise there should be a larger amount of visually unresponsive neurons in deprived preparations.

Unknown as well are the factors involved in the regula-

tion of the sensitivity of nervous structures to external stimulation. The cortex might be a self-optimizing system, which is vulnerable to external stimulation during development but remains unaffected once the optimal structure has been established. However, changes should be possible after reaching stability, if the cortical tissue is destroyed by lesion and therefore the optimal wiring is disturbed.

The stable end position might be reached if all postsynaptic sites of a given neuron are occupied by functionally valid presynaptic endings, and an equilibrium between excitatory and inhibitory influences is adjusted [127]. The number of postsynaptic offerings should be genetically determined in this case [47].

Another possibility may be the control of sensitivity by other, superimposed centers [113,114]. Kasamatsu and Pettigrew [67,68] assume that such control can be mediated by biogenic amines; they demonstrated that plasticity within the visual cortex of the kitten is blocked by the depletion of norepinephrine. Kasamatsu *et al.* [69,70] elevated sensitivity to external stimulation after the end of the usual sensitive period by application of norepinephrine. Other experiments revealed that neurons of the monoamine system, which seem to remain alterable throughout life [90] show a large amount of growth in areas which were destroyed by lesion before [87,121].

Apparently the above mentioned morphological effects are restricted mainly to the early development of an animal. Rosenzweig *et al.* [104] reported that the size of the visual cortex is enlarged in the adult rat as a consequence of rearing in an enriched environment. Greenough [45] stated that these effects are mainly results of glial growth but not of the development of new neuronal structures. On the other hand, training of rats in a Hebb-Williams maze is followed by an enlargement of the numbers of dendritic spines. These changes, however, are very small and not comparable with the drastic effects occurring in ontogeny [45]. Loss of spines in adult rats as caused by deprivation is compensated within several weeks after reopening of the eyes [91]; the effects do not seem to be stable (see *Irreversibility* under Comparison of Paradigms).

One can conclude that significant morphological effects of deprivation are observed only in young animals; in adult animals such effects are drastically reduced. Surely the large learning capacity of the adult animal cannot be explained by these minimal effects. Thus, most theories imply that learning in the adult is mainly an effect of biochemical or submicroscopic changes of synaptic transmission (review [105]).

Imprinting

Experiments on the physiological correlates of imprinting have been mainly carried out by Bateson, Horn and co-workers (review [55]). They demonstrated that in chicks the destruction of a distinct part of telencephalon, the so-called IMHV (intermedial part of hyperstriatum ventrale) prevents imprinting or retention of the imprinting experience [86]. Directly after the imprinting experiment they could demonstrate a large protein turnover, as revealed by the incorporation of radioactive uracil, within this area [55]. Glucose consumption in IMHV is heightened too, as Kohsaka *et al.* [73] demonstrated with 14-C-deoxyglucose autoradiography. During imprinting apparently the synaptic appositions are enlarged in IMHV [18]: At the beginning of the imprinting experiment synaptic contacts of the left hemisphere are smaller than those on the right; this difference is eliminated

in the course of the experiment. The absolute number of contacts, however, seems to remain stable.

In addition to the instructive processes mentioned above, evidence for selective ones was obtained by Wolff, Teuchert and Immelmann (in preparation). They demonstrated that terminal degeneration occurs within the visual system of the zebra finch at stages of development which resemble the time course of the sensitive period for sexual imprinting (see *Time Course* under Comparison of Paradigms).

As in the visual cortex paradigm, in imprinting the factors influencing the sensitivity of an organism to external stimulation are not well determined. Optimizing processes surely play a role [7]. Influences of superimposed centers mediated by hormonal systems have been considered as well (e.g. [83,125]). These authors assume that the end of the sensitive period of filial imprinting is defined by a rise of corticosterone levels (ACTH). Martin *et al.* [84], however, state that ACTH might not directly influence sensitivity, but instead inhibits the following reaction. The work of Nottebohm and co-workers (review [89]) adds further evidence. Their results concerning the plasticity of song control areas in different song birds reveal that this plasticity cannot be elicited throughout the life of the birds, but might be dependent on gating by some superimposed systems. The influence of those systems on the song control areas might be mediated by hormones [98].

IMPRINTING AND CORTICAL PLASTICITY: DIFFERENT EXPRESSIONS OF A COMMON DEVELOPMENTAL PROCESS?

Apparently the similarity of imprinting and cortical plasticity is not only superficial. Both are restricted to early ontogenesis (see [2] and *Time Course* under Comparison of Paradigms). The time course of the sensitive periods has a similar shape: after eye opening sensitivity rises quickly, reaches a peak and declines slowly (Fig. 3, [5]). The developmental age and the rate of development seem to be crucial for this time course. If significant events of development are superimposed on a time scale, all examples mentioned above show remarkable similarity.

Information storage revealed in both paradigms seems to be almost irreversible: influence which reaches the system after the sensitive period is over is only superimposed over the previously stored information. The former does not alter the latter (see *Irreversibility* under Comparison of Paradigms). Moreover, in both phenomena some sort of genetically determined pre-wiring plays a role. This pre-wired neuronal network will be precisely adapted to the environmental needs of the animal by the influence of external stimulation.

The influences on the kinds of information to be stored seem to be equal in the physiological and the behavioural paradigm too: besides the above mentioned genetical influences factors like selective attention, motivation and arousal may play a role.

The following discussion will assert that both phenomena in fact have a common basis and therefore hypotheses and results from one paradigm can be transferred to the other.

Specification of Neuronal and Behavioural Reactions

Considering the similarity between the two paradigms, one can assume that brain centers involved in the storage of imprinting information should be of a similar organisation as the visual cortex. There need not be columnar systems of the same shape as found within cortical areas, but the neurons

should be clustered in subsystems with distinct tasks. Plasticity should mainly occur within intrinsic connections of these subsystems [88].

At birth only a limited number of neurons reveal clear stimulus preferences; the majority reacts very weakly to a wide range of stimulation. The number of synaptic contacts, free spines and free postsynaptic offerings is larger than in the adult. Following the development of sense organs capable of relaying information from external stimulation to the neuronal area involved in imprinting, connections are stabilized under the control of a Hebbian mechanism according to the suggestion of Singer (see *Hebb's Postulate* under Comparison of Paradigms).

By this control mechanism neuronal connections are stabilized and extended by the construction and consolidation of synaptic contacts in the course of a competition process. Neurons of the neuronal network underlying this competition process get more sharply tuned and respond not only more selectively, but in a stronger and more clear-cut manner.

Hess [50] describes the process of increasing selectivity towards stimuli which occurs during filial imprinting: at first, young chickens follow all moving stimuli, but gradually they direct their response only to one object. Young foals demonstrate the same increase in selectivity, following all moving stimuli at first indiscriminantly, and then narrowing their response to their mother [71]. An increase in the selectivity exhibited by young zebra finches has not yet been documented and in the case of sexual imprinting it would be difficult to show such increase because of the time lag between imprinting and sexual behaviour.

The Temporal Course of the Sensitive Period

As more and more neurons become specified and unalterable in the course of development, the probability becomes smaller and smaller for a given stimulus to meet a neuronal connection which has remained alterable. Subsequently, the rate of differentiation will decline slowly, and the efficiency of external stimulation therefore should slope asymptotically towards zero, but not reach it. In this case, some neuronal connections should remain variable very long, possibly throughout life. Therefore morphological plasticity should be possible in the adult animal, although only to a small degree and under exceptional conditions (see below).

If there are neurons of different complexity within one neuronal subsystem, those excitable by simpler stimuli should lose their potential for plasticity first, as simple stimuli should be more likely to occur than complex ones, and therefore the neuronal connections excitable by these simple stimuli should more often become resonant.

With the assumption that there might be some sort of hierarchical organisation from simple to more complex neurons, as Hubel and Wiesel [57] propose for the visual cortex, stabilization of complex neurons should be delayed further, as they can only get adequate, i.e., resonance eliciting, stimulation after the simple neurons are differentiated properly.

If this hierarchy is not only established within a given area, but continues for the different brain centers along a specific sensory pathway, the differentiation of these nuclei should proceed from more peripheral to more central stations. This is consistent with a result obtained by Wolff, Teuchert and Immelmann (in preparation) in the visual system of the zebra finch. They demonstrated that degeneration

of axon terminals occurs in different brain centers along the tectofugal pathway of the visual system. Earliest degeneration occurred in the most peripheral optic tectum, some time later degeneration was found in the next station of that pathway, n. rotundus, and at the termination of this visual projection, the ectostriatum. The time at which degeneration could be demonstrated in the ectostriatum is very close to that of the peak of the sensitive period for sexual imprinting.

Alterations of brain tissue by external stimulation should therefore start with the attainment of functional sense organs. This can be supported by ethological data: in ducklings acoustical features are to be learned before hatching [38–40], the sensitive period is then continued for some time after birth. Sensitivity for external stimulation in sexual and filial imprinting, which is mainly based on visual features, starts with eye opening (Fig. 3, [5]).

The differences of the peak positions and duration of sensitive periods for different imprinting paradigms should then be mediated by two different influences, namely the difference of complexity of the involved neuronal tissue and the distance as measured by the number of synapses between sense organ and the involved brain area.

Filial imprinting should then be possible using simpler features than sexual imprinting, and/or the center involved in filial imprinting should be situated more peripherally than that for sexual imprinting. "Motor"-imprinting (song learning) should occur later in development than "sensory" imprinting, as motor centers are believed to be situated behind sensory centers in the course of sensory processing. All these findings can be supported by behavioural evidence, as demonstrated in the preceding chapters.

Surely these mechanisms cannot be solely responsible for the apparent complexity of imprinting. The process of self-termination described above might be imposed upon by the influences of more global mechanisms, as proposed by Singer (see *Hebb's Postulate* under Comparison of Paradigms and Some Experiments . . .). In these sections evidence for such systems is demonstrated. Assuming that these systems can switch on or off plasticity of distinct brain areas or can influence the brain as a whole, the whole system becomes so complex that one can hardly make significant predictions about the participation of the different systems which are responsible for regulation of sensitive periods. However, the similar time course for all plasticity and imprinting paradigms may indicate that the influence of higher order centers cannot fully suppress the basic features of this self-organizing process.

Learning in Adult Animals

The amount of plasticity demonstrated by histological methods in the adult brain seems to be very small. Evidently adult learning cannot be explained solely by morphological changes, as its capacity is about as large as in the young animal.

Information is processed in the young and in the adult animal by the same pathways. There is no evidence that the acquisition process might be essentially different in these two age groups. Hebb's theory was developed for classical conditioning, and its applicability to cortical plasticity was demonstrated by Rauschecker and Singer [101], and to imprinting by Bischof [11]. Thus, as Rauschecker and Singer state, the mechanisms underlying the different learning paradigms may be similar. Learning occurs then in all cases by the above mentioned (see *Hebb's Postulate* under Com-

parison of Paradigms) resonance effects within neuronal subsystems. By this resonance the pathways, which are mainly involved in transduction and processing of incoming stimuli, can be altered.

The difference between young and adult learning may depend on the vulnerability of brain tissue to these resonance events. In young animals the brain responds to resonance with morphological alterations. In the time course of development this sort of plasticity is reduced more and more to solely biochemical and submicroscopical alterations of nervous tissue. The morphological changes observed in young animals seem to be more stable than the purely submicroscopical changes in the adult. Therefore, information acquired in early stages may be irreversibly stored.

From this point of view, imprinting is not a separate learning paradigm, but an effect of age-dependent alterations on brain responsiveness to external influences. The more that morphological changes can be observed as effect of a learning event, the more stable should be the storage of information. Thus, in each example of learning, information storage should be more stable in younger animals.

This statement, however, does not touch upon learning ability as such. The acquisition process itself should not be diminished in any essential way by aging. On the contrary, the occurrence of resonance states might be more frequent in older animals, as there are many more already determined structures, which in turn should facilitate selection of stimuli leading to resonance. As mentioned above, only the permanency of storage should be lower in older animals.

However, imprinting-like processes may be observed in adults too. There are two possibilities: If the brain connections are altered by lesions, rewiring might be accomplished by the same rules as the ontogenetic organisation of nervous connections. As a result of the lesion, the inhibition-excitation balance of the brain area should be disturbed, and it might be possible that morphological plasticity could occur until the equilibrium is restored. It must be mentioned that this possibility of morphological recovery is different among species: in lower animals the degree of adult morphological plasticity seems to be greater than in higher animals [66].

On the other hand, there seems to be a small amount of neuronal tissue which remains susceptible to morphological changes throughout life. We cannot decide whether these neurons are evenly distributed all over the brain, or concentrated in higher order centers. The experiments of Nottebohm [89] support the second view: He demonstrated a large amount of plastic changes even in adult birds in song control centers only, but not in any other brain area.

Whenever the remaining morphologically alterable tissue comes into resonance by some stimulation, new connections will be established in the adult animal as well as in the young. However, all those connections easily accessible by resonance eliciting stimulation are already established in older animals. Therefore, for changes of connectivity the resonance state must be higher in older than in younger animals in order to reveal comparable amounts of plasticity. This may be most easily accomplished by superimposed gating systems, controlling the level of motivation and arousal. Thus, in extraordinary situations with high arousal levels or motivation, imprinting-like stability of information storage should also be observed in older animals. One such example may be the permanent storage of information in stress or fear situations which might occur, for example, in traffic accidents.

It may be important to point out here that the division of

plastic changes into morphological and submicroscopic events is somewhat artificial and was done only for the sake of simplicity. There should not be a real separation between these two events. Biochemical changes can precede morphological ones. Both types of changes should coexist in a given brain area over a wide range of time. However, as stated above, the probability of morphological changes declines for each system during development. Whether those morphologically established connections are responsive to further biochemical changes is not yet clear.

SUMMARY

The results of two different fields of research, imprinting in birds and developmental neurobiology of the visual cortex in higher mammals, are compared to evaluate the evidence for or against a frequently hypothesized linkage of the two phenomena. The comparison reveals several common features.

In both paradigms, the sensitivity to external stimulation is only high in a restricted "sensitive period" in the early development of the animal. The shape of the sensitivity curve is also similar in both paradigms. In some examples, even the position of maximum sensitivity to the environment on the development time scale is equal, if one corrects the data for the different developmental rates of each species. Imprinted information and alterations of the response properties of cortical neurons seem to remain stable throughout life after the sensitive period is over. However, under certain circumstances, imprinting-like learning may be possible in older animals too. In both paradigms a certain amount of genetically determined predispositions must be considered which facilitates acquisition of the "naturally" occurring input features. This genetically determined pre-wiring of brain tissue is strengthened and stabilized by normal visual experience and can be altered by variation of the visual input to adapt the animal's brain exactly to the needs of the environment. The effectiveness of external stimulation seems to be dependent on motivational and arousal factors. A concept of learning developed by Hebb for classical conditioning can be adapted to the cortical plasticity paradigm as well as to imprinting. Although there is striking similarity between the two phenomena, one cannot state that there is a direct linkage between them. Then the conclusions which can be drawn from the current comparison are: Plasticity of the visual cortex and imprinting are basically self-terminating processes which are under additional control of superimposed brain centers which are responsible mainly for the efficiency of the incoming stimuli. The stability of connections built during the sensitive period may be explained by the fact that these changes are morphological; connections are eliminated and others are stabilized or to a certain degree even newly tied. Once the sensitive period is over these morphological changes occur rarely. Then changes are mostly dependent on alterations of the efficiency of synaptic contacts by biochemical influences. These assumptions are mainly drawn from the work on visual cortex plasticity, but may be generalized to many other parts of the brain [120].

Since there is striking similarity between cortical plasticity and imprinting, it is suggested that in both cases the stability of imprinted information may be secured by morphological changes in underlying brain structures. This may be the main difference between imprinting and adult learning which in turn may be mainly accomplished by submicroscopic alterations of synaptic connections. Under extraordi-

nary conditions like stress, however, the gating systems may increase the efficiency of incoming stimuli to such a degree that the small amount of morphologically alterable synapses remaining in the adult brain can be affected and morphological changes can take place.

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