Chapter 6

ENVIRONMENTAL INFLUENCES ON EARLY DEVELOPMENT: A COMPARISON OF IMPRINTING AND CORTICAL PLASTICITY

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I. ABSTRACT

A comparison of results in imprinting research and studies of the developmental neurobiology of the visual cortex reveals striking similarities. In both areas information from the environment can only be stored during a sensitive period. The position of this sensitive period seems to be dependent to a certain degree on the developmental stage of the animal. The shape of the sensitivity curve is similar in all cases. Beyond the end of the sensitive period, new information can be superimposed on but cannot alter information acquired in early development. Storage of "normal" stimuli is facilitated by a certain preorganization of the receiving brain areas.

The phenomena may be two expressions of a common developmental process for the organization of the connectivity of single neurons as well as for complex neuronal networks, as are likely to be involved in imprinting. This process is basically self-terminating, but can be influenced by superimposed controls.

Differences of the stability of storage in imprinting in young and in learning in adults may be explained by the difference in the overall amount

of morphological alterations involved, which is large in the young and small in the adult animal.

II. INTRODUCTION

At the turn of the century embryologists developed a number of new hypotheses concerning the development of organisms. For example, the controversy between the so-called "preformists" and "vitalists" was resolved by the hypothesis that development is accomplished by an interplay of both genetically determined and epigenetic factors [for a review see Oppenheim (1982)]. A model of this interaction that was accepted by many biologists is the co-called "epigenetic landscape" of Waddington (1957): the developing part of an organism is compared with a ball that rolls down a landscape with hills and valleys with many bifurcations; the developmental process is canalized in the sense that the ball rolls mainly along the valleys, but influences from the outside decide which valley is to be chosen at a bifurcation, and can eventually drive the ball over the top of a hill into another valley, or the structure into another direction of development.

A related idea was that epigenetic influences are not equally effective over the whole period of development; cells or the whole organism are often specifically sensitive to environmental influences only during "sensitive" or "critical" periods (e.g., Spemann, 1938).

These hypotheses in embryology were adopted by other biological disciplines. For example, the concepts of sensitive periods and of the influence of external stimulation on the organization of the adult organism were found to be valuable for the description of findings in neurophysiology, ethology, and psychology.

In neurophysiology, the best known example of an application of the above theories concerns the influence of the environment on the development of the visual cortex of the cat, which was first described by Wiesel and Hubel (1965). They demonstrated that the development of the feature-detecting neurons of area 17 of the visual cortex is influenced by the structure of the incoming stimuli, and that this influence is strongest during a restricted period in the life of the young kitten. Later in life, a change in conditions does not further alter the connectivity of cortical neurons. A wealth of research has confirmed these findings and has expanded our knowledge about many details of this phenomenon [for review see Blakemore (1978)].

The question of how genetic components and environmental influences are involved in the organization of the visual cortex has not yet been answered definitively (Lippe, 1976). However, most researchers agree that both internal and external influences participate in the developmental process, and the controversies are mostly about the nature of the interaction of the two factors and the developmental mechanism (e.g., Changeux and Mikoshiba, 1978).

Whereas in neurophysiology the discussion of the above phenomena is not partiularly heated at present, discussions in ethology and psychology are as yet not fully emancipated from the controversies that arose at the beginning of the century between the two disciplines over whether behavior is innate or acquired or over whether sensitive or critical periods exist (Oppenheim, 1982). However, most scientists working on animal development agree that the statement given above for neurophysiological events is also true for behavioral development; namely, that the characteristics of the adult are influenced by a combination of genetic and environmental factors (Bateson, 1980), and phenomena like sensitive periods exist in behavioral development (Immelmann and Suomi, 1981; Leiderman, 1981).

Probably the best known example of early external influences of the environment on the organization of behavior is the so-called "imprinting" process (Lorenz, 1935), by which a young bird restricts its social preference to a particular animal or object. In the course of filial imprinting, for example, a young chick or duck learns about the object it has followed when leaving the nest (Bateson, 1966, 1978; Hess, 1973). Young zebra finches in the course of sexual imprinting learn the features of an object that subsequently releases courtship behavior in fully grown birds (Immelmann, 1969).

The similarity of the phenomena in the different disciplines suggests the hypothesis that similar mechanisms may work on different levels of development, in the formation of the embryo as well as in the formation of neuronal connectivity and of behavior. However, it is not easy to decide whether these similarities, which have been noted by many different authors (e.g., Bateson, 1981; Horn et al., 1973, 1979), are only accidental or causal (Rose, 1981). Several arguments have been expressed against the comparability of the paradigms, based on a more careful comparison of the details of the phenomena.

Horn et al. (1973, 1979) argued that imprinted chicks can detect stimuli other than the imprinted one (and react to these stimuli with avoidance reactions in the case of filial imprinting), while the neurons of area 17 of the visual cortex of the cat appear to be insensitive or "blind" to novel stimuli after the end of the sensitive period. However, recent experiments

have revealed that this "physiological blindness" is true for the single cortical neuron, but not for the whole animal subjected to a restricted environment during development (Freeman and Marg, 1975). Admittedly, this result is controversial: minimal effects of restricted rearing on visual acuity were demonstrated by Blasdel *et al.* (1977) and Kratz and Lehmkuhle (1983), whereas Wark and Peck (1982) did not find any effect on visual acuity, but the ability of the cats to discriminate between different angles of stimulation was better in the experienced orientation range. Thus, it may well be that neurons involved in an imprinting process could be as clear-cut in their response characteristics as the visual cortex neurons of the cat.

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 and thus cannot be a universal phenomenon (Gordon *et al.*, 1979). Plasticity of this kind, for example, cannot be demonstrated in rabbits, a species with only a very small binocular field (e.g., K. L. Chow and Spear, 1974; Grobstein and Chow, 1975).

However, in rats, also a species with only very limited binocular overlap, influences of early experience on the development of the response characteristics of the visual cortex can be demonstrated. These effects are not as clear-cut as those obtained in the visual cortex of cats, and thus may have been overlooked by researchers studying other visual systems with only minimal overlap of both eyes (London and Greenough, 1982).

In cats, there is evidence that plastic changes under the influence of external stimulation also occurs in the organization of cortical maps of somatosensory information (Spinelli *et al.*, 1980): in kittens trained to lift one of their forelegs in response to a visual stimulus or receive a mild shock on the forearm the cortical locus for the trained forearm was much larger than that for the untrained one. This occurs only in early development of the animals; no effect can be demonstrated in kittens older than 11 weeks.

In birds, the plasticity of visual neurons has been demonstrated as yet only in the barn owl, which has a large binocular visual field (Pettigrew and Konishi, 1976). The results obtained in this study by recording from neurons of the visual wulst (hyperstriatum accessorium) of normal and monocularly deprived animals resemble very closely those found in studies of the visual cortex of the cat.

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 plasticity has been demonstrated by histological procedures in

chicks in brain centers involved in imprinting (Bradley *et al.*, 1981), in song control areas in the zebra finch and in the canary (Nottebohm, 1980), and in different visual areas of the zebra finch (Teuchert *et al.*, 1982). In these examples of plasticity it is not as easy as in the visual cortex paradigm to evaluate the functional consequences of environmental influences. Thus, it is likely that plastic changes influenced by environmental stimulation are a common feature of the developing brain, but it may be that it is more easily demonstrated in binocular neurons than in other types of cells.

In this study, I will try to compare two paradigms of physiological and behavioral research, the plasticity of neurons of the visual cortex and imprinting, to find indications for or against a linkage of the two phenomena. It is unlikely that cortical plasticity, as currently studied, is the same as the physiological phenomenon underlying imprinting (Rose, 1981), but it might be possible that both phenomena involve common principles.

III. INTRODUCTION TO PARADIGMS

This section is intended as an introduction for the nonspecialist to the paradigms compared in the following sections; it may be skipped by those who are familiar with these paradigms.

A. Characteristics of Imprinting

The term "imprinting" was first used by Lorenz (1935). As did some earlier researchers (e.g., Craig, 1908; Heinroth, 1910), he observed that young geese bred in an incubator followed the first object they see after hatching. This object need not be a conspecific; it can even be the individual 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 behavior persisted (filial imprinting).

The conclusions Lorenz drew from his observations were the basis for a wealth of subsequent research designs attempting to confirm or disprove part of the arguments or even the whole theory. A review of all these studies is not intended here; excellent surveys are available (Bateson, 1966; Hess, 1973; Hoffman and Ratner, 1973; Immelmann, 1972; Immelmann and Suomi, 1981; Klinghammer, 1967).

The experiments cited 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 that fulfilled one or the other, but not all, of the criteria of Lorenz. Lorenz' definitions of imprinting and some of the arguments of other authors against and in favor of those criteria are as follows:

1. Learning occurs most readily at a particular stage in development of the animal, the so-called sensitive period (sensitive phase, critical period).

Sensitive periods have been very carefully studied in two different cases. Data for filial imprinting, are provided by among others, Hess [see Hess (1973) for a review] and for sexual imprinting by Immelmann (1969, 1972). As will be demonstrated in later sections, recent reports demonstrate that sensitive periods are not as short and sharply defined as previously believed. Sometimes there is even evidence for two different sensitive periods in the life of one animal (Vidal, 1980).

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, and some results seemed to demonstrate that preferences could be reversed later (e.g., Salzen and Meyer, 1968). However, recently it has been demonstrated that the preferences acquired in ontogeny are stable, at least for sexual imprinting, throughout life (Immelmann, 1979). The disagreement concerning irreversibility of imprinting is evidently based on differences of interpretation of the terms (Immelmann, 1972): it does not mean that the animal is restricted in its reaction to the one object acquired during the sensitive period, but that it prefers this object in a choice situation (see Section IVB).

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

This conclusion was drawn by Lorenz from the fact that animals do not choose exclusively their parents as sexual partners, but as a rule court all opposite-sexed birds of their species. Results from different authors (Schutz, 1965; Bateson, 1979a, 1982b) show that it is more plausible to propose an individual learning process, which by generalization leads to species recognition.

4. Imprinting occurs at a time where the appropriate behavior is not developed.

Therefore, Lorenz stated that imprinting differs from other learning paradigms by a lack of reinforcement. This statement has been challenged by many authors; especially in filial imprinting there is no time lag between

imprinting and the behavioral response, and conditioning probably is involved in the acquisition process (Hess, 1973; Hoffman and Ratner, 1973). For sexual imprinting, this fourth statement seems to be generally correct. As Immelmann (1972) has demonstrated, the sensitive period for sexual imprinting in zebra finches ends before the birds are sexually mature and can get any sexual experience. However, as he points out, some sort of reinforcement cannot be excluded even in this case.

Thus, of the four criteria defined by Lorenz for imprinting, the first two have been proved to be applicable to all imprinting phenomena described to date, whereas the latter two are not as unquestioned and cannot be applied to all imprinting phenomena. From the first two statements a new definition of imprinting was designed by Immelmann (Immelmann, 1979), which considers the view (Immelmann and Suomi, 1981) that many so-called "imprinting-like" phenomena, such as social attachment in monkeys (Sackett et al., 1965) or in humans (Bowlby, 1969), should be included in a definition of imprinting. Thus, imprinting is defined as "an early learning process with very stable results" (Immelmann and Suomi, 1981).

Another statement by Lorenz concerning imprinting, but not mentioned in the previous four tenets, must be added here, since it was the source of many controversies: he stated that the preferences of the birds, although essentially influenced by external factors, also may be under the control of genetically determined factors. This was rejected by many authors, mostly as a result of the different views evolved by behaviorists and psychologists on the one side and ethologists on the other. Most researchers in the field (Waddington, 1957; Bateson, 1982a) would now agree with the belief that both inheritance and experience are involved in imprinting (see Section IVC).

B. Plasticity of the Visual Cortex of the Cat

As in the preceding section, a comprehensive review of recent literature is not intended. An excellent overview is given by Blakemore (1978).

The best known example of plasticity of cortical neurons involves the visual cortex of the cat, first demonstrated by Hubel and Wiesel (1962). Very similar results were obtained in the monkey (Hubel et al., 1977) and in the owl (Pettigrew and Konishi, 1976). For clarity, only the cat experiments will be mentioned in this section.

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, and are
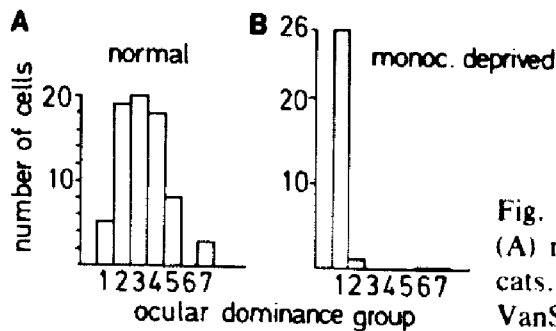
Fig. 1. Ocular dominance distribution in area 17 of (A) normally raised and (B) monocularly deprived cats. For details see text. [From Blakemore and VanSluyters (1974).]

thus defined as binocular. Hubel and Wiesel (1962) developed a classification scheme for binocularity (Fig. 1A). Class seven is made up of neurons driven exclusively by the ipsilateral eye; class one consists of neurons excited only by the contralateral eye. Neurons equally driven by either eye fall within class four; the other four classes consist of neurons with asymmetric 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 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 only be driven by the nondeprived eye (Fig. 1B). Further experiments (Hubel and Wiesel, 1970) 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 Section IVA). Similar deprivation in an adult cat does not alter the ocular dominance distribution, even if the suturing is maintained for several months or more. The alteration of ocular dominance by early deprivation is found to be persistent throughout life after the sensitive period is over (see Section IVB).

In other laboratories (Blakemore and Cooper, 1970; Hirsch and Spinelli, 1970), it was demonstrated that shifting of neuronal preference could also be observed in another feature domain of cortical neurons, their selectivity for distinct stimulus orientations. Under normal circumstances the proportion of visual cortical neurons that have different orientational selectivity is distributed evenly around a circle (Fig. 2A).

If one rears kittens with goggles that restricted the visible features to stimuli of a single orientation (Hirsch and Spinelli, 1970, 1971; Rauschecker and Singer, 1979; Singer, 1976) or in an environment with black and white stripes of a single orientation (Blakemore and Cooper, 1970), most cortical neurons of such animals when recorded in adulthood respond preferentially to the visual target that has the experienced orientation (Fig. 2B). Again this alteration of orientational preference has a sensitive period during the early development of the kitten (Blakemore,
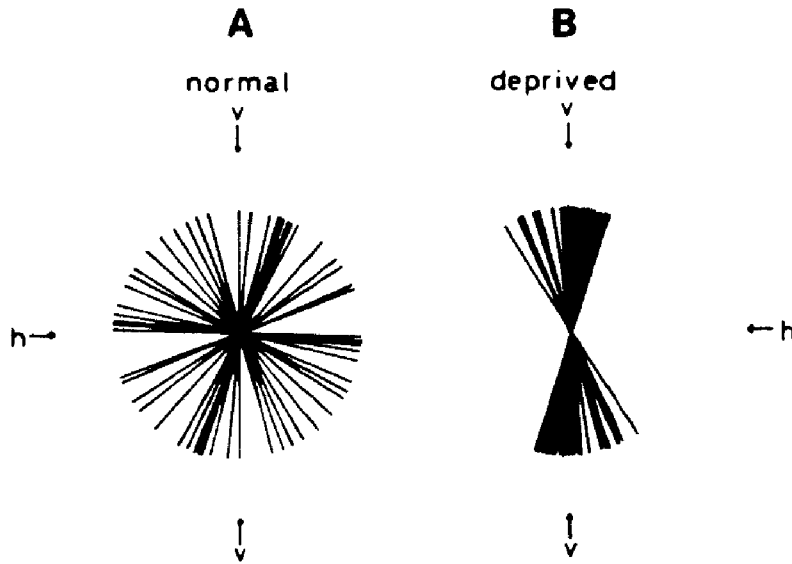
Fig. 2.   Distribution of orientational selectivity of cortical neurons of area 17 in (A) normal and (B) monocularly deprived cats. For details see text. [From Blakemore and VanSluyters (1975).]

1978). When the sensitive period is over, no alteration of the acquired pattern is possible.

As stated above, the influence of the environment on the organization of the cortex during sensitive periods was also demonstrated for other feature domains, e.g., directional selectivity of neurons of area 17 (Daw and Wyatt, 1976) and ocular dominance distribution in area 19 (Leventhal and Hirsch, 1983), and in other animals [e.g., in primates by Hubel et al. (1977) and even in man (Hillesheim, 1967; Hohmann and Creutzfeld, 1975)]. Thus, the plasticity of the cortex and the influence on the environment during sensitive periods on the organization of the brain seem to be common phenomena.

As in imprinting, a genetic influence on the organization of the wiring of the visual cortex can be demonstrated: the adult pattern is obviously already present in the newborn cat, although it is not as rigid and clear-cut as in the adult (see Section IVC). However, it is not yet clear what proportion of neuronal specificy is already there at birth, and how much of this specificity may be determined not by genetic influences, but by those of the environment affecting development before birth (see Section IVC).

IV.   COMPARISON OF THE TWO PARADIGMS

The preceding short overviews reveal that there are at least three common features of imprinting and plasticity of the visual cortex:

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

2. Beyond the end of the sensitive period new information can be superimposed on but cannot erase the information acquired earlier in life.

3. In both paradigms acquisition of external stimuli seems to be influenced by genetic instructions.

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

A. The Time Course of Sensitive Periods

The time course for sexual imprinting has been determined for only a few species. The most careful research has been done on zebra finches (*Taeniopygia guttata castanotis*). The sensitive period for sexual imprinting of these birds has been examined by Immelmann (1969, 1972).

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 5–7 days of age, fledging at 20 days. The birds become independent from their parents at about 30 days; the first signs of courting behavior 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 (Pröve, 1983a).

The sensitive period, as demonstrated by Immelmann, begins at day 5–7 (presumably at eye opening). The sensitivity for imprinting stimuli rises strongly until day 13–15 and then slowly decreases until day 40. Recent results of Immelmann (1979) demonstrate that sensitivity does not decrease to zero at this time; minimal effects of external stimulation can be detected as late as day 70 (Fig. 3B).

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 has been evaluated by several authors under different experimental conditions (Blakemore and VanSluyters, 1974, 1975; Hubel and Wiesel, 1963, 1965, 1970; Wiesel and Hubel, 1965; for a review see Blakemore, 1978). The data demonstrate that the sensitive period starts with eye opening as in the zebra finch; sensitivity rises until day 40, then slopes downward until day 100. As in the case of imprinting, slight influences of external stimulation can be detected some time later (K. F. Chow and Steward, 1972).
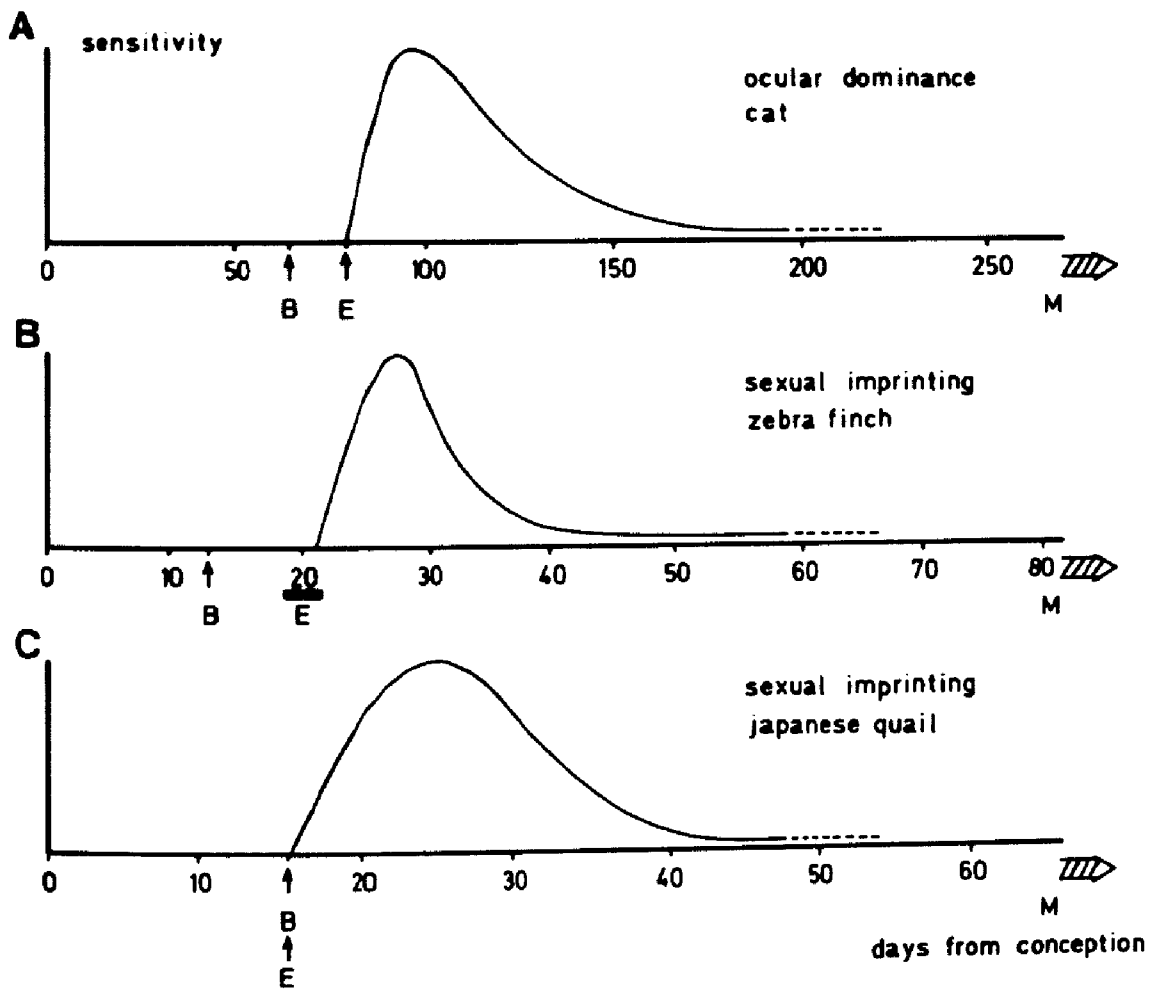
Fig. 3. Time course of the efficiency of external stimulation in three different phenomena. Ordinate scale is arbitrary. B, Birth; E, eye opening. [(A) From Blakemore (1980), (B) from Immelmann (1981), and (C) from Gallagher (1967).]

The time course of sensitivity seems to be very different for both examples, until one considers the different developmental rates 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 day of conception [the time of birth does not seem to be an important event during development of an animal (Prestige, 1970)] as well as the time at which the animals reach sexual maturity in order to standardize developmental rates, reveals that the ascent, peak, and decline of the two sensitivity curves match closely (Figs. 3A and 3B).

Correcting the data obtained by Gallagher (1977) for the sensitive period for sexual imprinting of the Japanese quail by the same procedure used above, one finds that these data again match those of the two preceding examples. However, in this case the ascent of the curve is different;
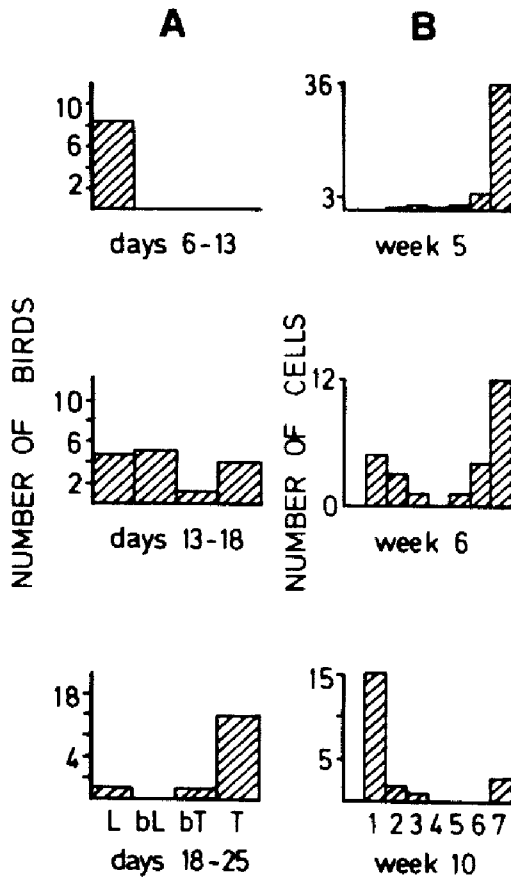
Fig. 4. Results of transfer experiments on (A) sexual imprinting in birds and (B) plasticity of the visual cortex in cats. (A) Transfer of the birds from their parents to a foster species at the time indicated below the X axis. Each bar represents the number of birds with a preference in a double choice test between zebra and Bengalese finches. L. Lonchura (Bengalese finch, the foster species); T,Taeniopygia (zebra finch); bL, bias toward Lonchura; bT, bias toward Taeniopygia. [From Immelmann (1972).] (B) 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 into the ocular dominance class indicated below the bar. [From Blakemore and VanSluyters (1974).]

since the quail is a nidifugous bird, which has its eyes open at birth, the sensitive period can start earlier (Fig. 3C).

The sensitive period in the zebra finch was investigated by cross-fostering experiments (Immelmann, 1969, 1972, 1979). The birds were first raised for a limited period of 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 finch females at about day 100 after hatching. An example of the reversal of sexual preferences is demonstrated in Fig. 4A. In these experiments the time of rearing by the biological parents was varied beetween 6 and 25 days posthatch. Subsequently, the young birds were transferred to the foster species for 16–84 days.

If transferred between days 6 and 13, it turned out that all birds were imprinted to their foster parent species. Transfer between days 13 and 18 resulted in both pure preferences for either foster or own species, and mixed preferences, although still with a bias toward one or the other species (bL or bT). If transferred after day 18, nearly all the 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, then some time later reopening of this eye and closure of the other (Blakemore and VanSluyters, 1974). The distribution of neurons within the 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 that was sutured first (Fig. 4B, upper). With reverse suture at week 6, neurons driven by either eye could be demonstrated, while after reverse suture at week 10, almost all cells were driven by the secondarily deprived eye [data from Blakemore and VanSluyters (1974)]. The similarity between the time course of reversibility obtained for sexual imprinting and that for ocular dominance under the reverse suture experiment is obvious. The developmental time, corrected as mentioned before, is the same for each left–right pair of diagrams of Fig. 4.

The comparison made above demonstrates a striking similarity of the three examples of sensitive periods. However, one has to be aware that in this comparison some simplifications have been made, which should not be overlooked and might make the picture more complicated if considered. First, I have estimated the speed of development to be constant from conception to sexual maturity. This is not really the case. It is more probable that development is fast at the beginning and slows down until the animal is adult. However, with the assumption that the overall time course of the speed of development is essentially the same for all animals, this does not alter the features of the above comparison.

The same time course of sensitive periods can be obtained in other experiments. For example, the sensitive period for establishment of binocularity of area 17 neurons is the same if one uses surgically induced strabismus instead of monocular eye closure (Levitt and VanSluyters 1982). Amblyopia in humans can only be treated successfully during a comparable sensitive period early in life (Banks et al., 1975; Hillesheim, 1967; Hohmann and Creutzfeld, 1975).

However, there are results indicating sensitive periods of other duration, even when estimated in units of developmental time. Directional selectivity of visual cortical neurons, for example, can be influenced in a period slightly earlier than that for ocular dominance and orientation selectivity (Daw and Wyattt, 1976). 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., Brown, 1974) have revealed that they might be not as short as previously believed. Again, the shape of the sensitivity curve
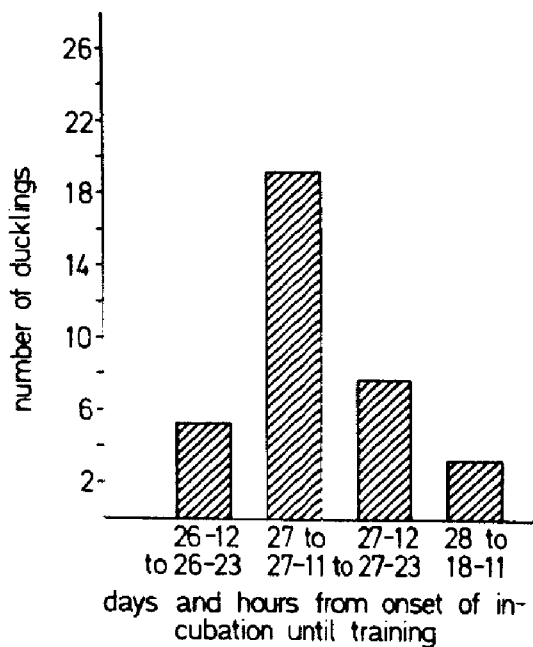
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Fig. 5. Success of an imprinting session as a function of the time span of development indicated below the bars. Ordinate: Number of ducklings following adequately in a test some days later. [Data from Gottlieb (1961).]

seems to be essentially the same in filial imprinting and the situations exemplified in Fig. 3, especially when the sensitivity is plotted against the developmental age of the animal [Fig. 5, data from Gottlieb (1961), Gottlieb and Klopfer (1962)].

Another argument to be careful with is the estimation of "the" sensitive period: the design of an experiment has a large influence on the time course of the sensitive period one determines. Interestingly, the influence of different experimental designs again is comparable in the two classes of phenomena. Rearing young chicks in isolation with diffuse light results in an extension of the sensitive period for filial imprinting (Moltz and Stettner, 1961). Simularly, rearing cats in the dark results in a prolongation of the sensitive period for cortical plasticity (Cynader, 1983).

The "naturalness" of the stimulus has another effect that is presumably similar in the two cases. As Gottlieb (1982) discovered, a consolidation period of about 24 hr was needed for an acoustic stimulus to be really imprinted for birds stimulated before birth with tone bursts of only one frequency. However, if he provided a series of different frequencies as a stimulus before hatching, this consolidation period was not found. Similarly, in cortical plasticity a consolidation period has been demonstrated by several authors in monocularly deprived kittens (Pettigrew and Garey, 1974; Ramachandran and Ary, 1982). In normal cats, however, it could not be found (Freeman and Olson, 1979). Thus, as Gottlieb as well as Freeman and Olson state, it may be that the appearance of a consolidation period is somewhat dependent on the quality of the stimulus in terms of its "naturalness."

Thus, two main conclusions can be drawn from this section. First, it seems as if the position of the peak of the sensitive period may be determined by a certain stage of development of an animal. This connection between developmental age and imprinting was particularly emphasized by Gottlieb (1961) and Gottlieb and Klopfer (1962). Second, the shape of the sensitivity curve is essentially the same for all phenomena, whereas the absolute time course may be different. The following sections will demonstrate that a certain stage of development is a prerequisite for permanent storage of information, but the actual speed and time course of the acquisition of external information are influenced by many other factors, for example, by the "naturalness" of a stimulus or the motivational state of the animal—its readiness to learn a certain feature (Bateson, 1981, 1982a). Thus, the design of an experiment, e.g., the choice of the imprinting stimulus, should have a large influence on what is determined as "the sensitive period."

B. Irreversible Storage of Information

Lorenz assumed that the information acquired at the imprinting process is stored irreversibly throughout life. Hubel and Wiesel drew the same conclusion from their experiments on cortical plasticity. Neither opinion has been unchallenged.

A difficulty in the evaluation of irreversibility is the fact that sensitivity to external stimuli does not end abruptly, but declines asymptotically to zero. Immelmann (1979) demonstrated that imprinting preferences can be altered 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 definitely limited. Influences of monocular deprivation (Blakemore and VanSluyters, 1974; K. F. Chow and Steward, 1972) or of rearing with patterns of one orientation (Spinelli et al., 1972) can be minimized by long periods of normal vision. Rotation of one eye (Singer et al., 1979) results in changes of ocular dominance distributions even in cats 3 months of age.

A certain amount of recovery can even be demonstrated in cats monocularly deprived for 120 days (Cynader et al., 1980). Similarly, binocular deprivation after a period of 2 weeks of monocular deprivation at the peak of the sensitive period can erase the effect of the early experience (Rauschecker and Singer, 1982). However, this study reveals that even with long periods of binocular deprivation of about 1 year the effects of the first experience cannot be completely erased: the distribution of neurons

within the ocularity diagram (see Fig. 1) resembles neither that of normal cats nor that of monocularly deprived animals. Instead of revealing a peak in class 3 as in the normal animal or in class 1 or 7 as in the deprived animal, the neurons are more or less evenly distributed over the dominance classes. Moreover, binocular deprivation in these experiments started clearly within the sensitive period. Thus, this experiment reveals that the visual cortex is sensitive for external stimulation beyond the peak of the sensitive period; however, this is not really an argument for plasticity in animals of an age beyond the time of the sensitive period.

Changes in the responses of cortical neurons or behavior can even be obtained 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 in fact be irreversible. Immelmann (1969) 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, as mentioned above, 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 sometimes can be masked, but cannot be eliminated from memory.

Similar results can be obtained in filial imprinting. Long after the end of the sensitive period the birds will develop a preference for stimuli other than the imprinted one. Cherfas and Scott (1981), 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 behavior also can be demonstrated, but it disappears later in life. Thus it hardly can be detected in adult animals under normal conditions. However, these influences are not really lost, but can come to the surface under extraordinary conditions, such as stress, as Agren and Meyerson (1979) demonstrated by isolation experiments affecting agonistic behavior in Mongolian gerbils (*Meriones unguiculatus*).

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% (Kratz *et al.*, 1976). Similarly, contrast sensitivity of an eye that was lower than normal as an effect of deprivation in early development was increased by enucleation of the normal eye (Kratz and Lehmkuhle, 1983). Blakemore and Hillman (1977), however, concluded from other experiments that this effect might be due not to a real increase in the proportion of neurons driven by the deprived eye, but to better registration of these cells as a

result of lack of inhibition from the previously dominating eye. This means that even by the enucleation of one eye there is no real alteration of neuronal connectivity acquired in the sensitive period.

Singer *et al.* (1982a,b) in adult cats rotated one eye and suture-closed the other for 1 year, then reopened the normal eye and closed the rotated one. They found that the adult cats developed a complete neglect of the visual modality subsequent to a period of severely disturbed visuomotor behavior, together with alterations of the cell characteristics in the visual cortex. Only 47% of the neurons could be driven visually; there was no obvious ocular dominance shift, but there was a substantial loss of binocular neurons. After reopening of the normal eye, behavior, cortical reactivity, and binocularity recovered almost completely.

Apparently the connectivity of the visual cortex could be altered even in the adult cat, but in contrast to those obtained in early development, these alterations were not stable.

Singer *et al.* (1982a,b), on the basis of these experiments, state that the difference between developmental and adult plasticity may not be dependent on the plastic potency of the synapses, but on a mechanism that in the young irreversibly inactivates functionally weakened synapses.

Thus, in both classes of phenomena, in adult animals some sort of plasticity of behavior or of synaptic connections can be observed; however, in contrast to the storage of information in younger animals, these alterations are not stable, but can be reorganized to the initial state. Thus, new information can eventually mask the old, but cannot erase the alterations obtained in the course of the sensitive period. This early information does seem to be stored irreversibly. As will be discussed in Section VIC, there may be one possibility for inducing stable plastic changes even in adults: if the animal is highly aroused and/or the catecholamine level of the involved brain areas is higher than normal, plasticity might be reinstated to a certain degree (Bateson, 1980; Kasamatsu and Pettigrew, 1976, 1979).

In this discussion a series of examples of adult plasticity have been omitted: many experiments demonstrate that after lesions of cortical tissue some sort of repair mechanism may at least partly reinstate the functions of the brain area erased by the lesion. However, these repair mechanisms do not represent what normally happens in the adult brain. Moreover, as Singer (1982) states, these repair mechanisms seem to be more or less perfect reinstitutions of mechanisms normally working in the developing organism. As mentioned elsewhere, Wolff (1981) provides the interesting idea that limited destructions of nervous tissue by normally occurring neuronal death may be preprogrammed in the subadult animal's

brain, and that it is by this mechanism that the capability is reinstated for plastic changes to occur according to environmental influences.

C. Canalization of the Acquisition of External Stimuli by Genetic Influences

It is widely accepted among ethologists that the behavioral reaction toward a target object to which a 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 a 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 [in the sense of Waddington (1957)] by genetic 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 color, are learned better than others (Bateson and Reese, 1969; Fantz, 1957; Goodwin and Hess, 1969). Zebra finches raised by mixed pairs (one zebra finch, one Bengalese finch) prefer their own species in double choice experiments. Thus in this case features of conspecific animals may be learned better than those of heterospecific ones (Immelmann, 1972; but see TenCate, 1983).

Another example of constraints on the acquisition of external stimuli is provided by the process of song learning in birds. As Marler and Peters (1977, 1981) pointed out, songs of alien species are rejected as models for their own song by swamp sparrows. These birds learn selectively from a tape of mixed species-specific and alien songs those that are of their own species. Other examples of this kind are provided by Güttinger (1979).

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%) respond to visual stimulation (Barlow, 1975; Blakemore and VanSluyters, 1975; Buisseret and Imbert, 1976, Fregnac and Imbert, 1978; Hubel and Wiesel, 1963; Imbert and Buisseret, 1975; Pettigrew, 1974, 1978; Sherk and Stryker, 1976), neurons of each ocular dominance class and orientation preference can be detected, revealing an adultlike distribution of feature-detecting neurons. Columnar organization of the visual cortex can also be demonstrated in the newborn monkey (Racic, 1977). 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 that both the cortical substrate and the structures storing the imprinting information have a certain genetically influenced predisposition that facilitates acquisition of the "normally" occurring input features and canalizes the development of the neuronal connections in a given brain area.

Nothing can be said yet about the role of genetic and environmental factors. Moreover, we cannot be sure that the conditions we find 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 (Gottlieb, 1961, 1980, 1981; Kovach, 1979). Even exposure of the egg to different light conditions affects the response to imprinting stimuli after hatching in chicks (Bateson and Wainwright, 1972; Metcalfe, 1976). Organization of the geniculate nucleus of monkeys can be affected by enucleation of one eye before birth (Racic, 1981). Therefore, some sort of influence from the eyes may be important for proper organization of visual centers even before birth. Similarly, ocular dominance columns, which are incomplete at birth in kittens and are sensitive to visual experience (Hubel and Wiesel, 1970), seem to be established to a higher degree in monkeys (Racic, 1977). In this species, however, ocular dominance columns can already be changed prenatally by enucleation of one eye (Racic, 1981).

Blakemore (1978) describes the recent point of view with a nice analogy:

> Perhaps, the visual cortex of the kitten behaves in some sense like the empiricists' 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.

This statement may also be easily adapted to describe the work on imprinting.

D. 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 among numerous incoming pieces of information the set of data that is so important that it must be learned. It may be that simply those features are learned that occur very frequently and are of good contrast to the background. Those parameters

surely play a role in imprinting situations (Bateson, 1966). However, evaluation of stimuli should also be influenced by other factors, such as attention toward the stimulus, arousal, and motivation of the animal (e.g., Gray, 1961; Martin, 1975; Martin and Schutz, 1974).

Since "arousal" and motivation" are very poorly defined and many different factors are collected under these terms (Becker-Carus *et al.*, 1972), it is very difficult to evaluate the exact degree of participation of these factors in a given phenomenon. Similarly, one cannot define exactly the reasons for increases or decreases of arousal levels and motivation. Genetically influenced preferences may play a role (see Section IVC). On the other hand, the arousing value of certain stimuli might be increased by conditioning (Hoffman and Ratner, 1973). Imprintability on visual features occurs more readily in the presence of acoustic stimuli (Fisher 1966, 1970; Pitz and Ross, 1961). Learning success may also be influenced by other factors that arouse the animal. For example, hand-raised nightingales (Todt *et al.*, 1979) learn more 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 (Kovach and Hess, 1963) or by application of stimulative drugs (Kovach, 1964).

Some of the connections between arousal, choice of the appropriate external stimulus, and imprinting can be described by a concept developed by Hebb (1949) for classical conditioning (Bischof, 1979). Rauschecker and Singer (1981) 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 together, or already possess weak synaptic contact, and if they are excited simultaneously very often. Thus, of all stimuli reaching the visual cortex from the retina, those that 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: Either the various presynaptic terminals ending on one postsynaptic neuron are differentially effective in driving this postsynaptic neuron, or the responsiveness of the postsynaptic cell may be differentially facilitated. This may be done, for example, by other brain systems that can be triggered either by the stimulus or by a change of excitability independent of the occurrence of the stimulus (Fig. 6). Other connections, which are not as good in exciting the postsynaptic target or do not discharge at the appropriate time, fail to be strengthened and may be eliminated after some time.

These rules lead to competitive interactions between convergent afferents, whereby those pathways that possess the highest probability of

stimulus

sense
organ

presyn.
axon

HEBB SYNAPSE

hormones ?
catecholamine ?

motivation
arousal
select. attention

med. thalamus
form. reticularis
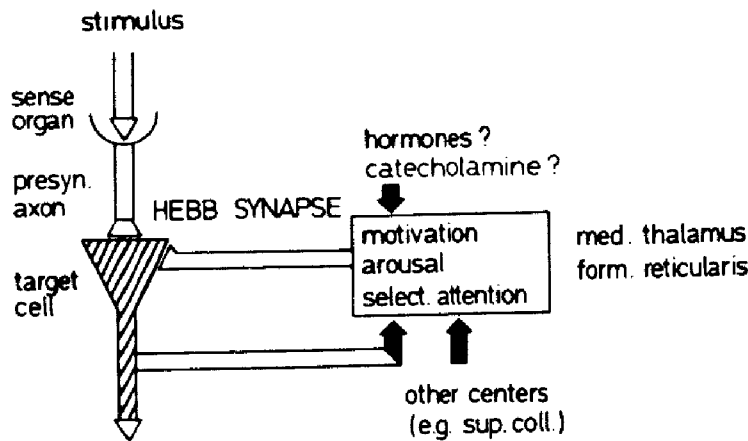
target
cell

other centers
(e.g. sup. coll.)

Fig. 6. Hebbian synapse simplified from the conclusions of Singer. Plasticity occurs with coincidence of pre- and postsynaptic activity of the system. Postsynaptic activity 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 such as the formatio reticularis and/or the medial thalamus by direct neuronal connections, or may be influenced by changes in hormonal concentrations.

being active together with the postsynaptic target cell become consolidated at the expense of others (Rauschecker and Singer, 1979, 1981; Singer, 1979a,b). Hubel and Wiesel (1962) proposed such a competition process during formation of ocular dominance distribution within area 17. They stated that there might occur a selection of primarily established connections. With asymmetric stimulation of only one eye the postsynaptic target cells seem to lose the connections from the other eye.

Differences in presynaptic activity alone do not seem to be sufficient for plastic changes. Singer and co-workers (Rauschecker and Singer, 1979, 1981; Singer, 1979a,b) demonstrated that excitation of the postsynaptic target cell and as well the occurrence of plasticity are 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 to alter ocular dominance distribution in young kittens.

Another prerequisite for plastic changes seems to be the adequacy of stimuli in a more global context. Singer et al. (1979, 1982a,b) demonstrated that with a mismatch of visuomotor coordination, as can be accomplished by surgical rotation of the normal eye within the eye socket, no change of binocularity is observed in monocularly deprived cats. Other conditions affecting the acquisition process seem to be selective attention of the animal toward the stimulus (Burke and Griffin, 1977) and the overall arousal level (Singer, 1979a). If the brain centers that 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 (Singer, 1979a,b). The same lack of plasticity can be observed in paralyzed preparations (Buisseret et al., 1978; Freeman and Bonds, 1979). Livingstone and Hubel (1981) demonstrated that neurons during states of higher arousal of the animal (awake vs. 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 (1979a,b), who states that, given all the factors mentioned above, some sort of resonance of the neuronal circuit will be produced, which, by changing the neuronal activity of the postsynaptic neuron from transient to sustained discharge properties, gives the "now print" signal for increasing the probability of synaptic transmission for the connections that are active at the same time.

Interestingly, Schlag and Schlag-Rey (1983) recently found neurons of the medial thalamic area, that may be involved in the attention mechanism described above. These neurons are activated when a saccade has occurred and the eye stabilizes on a new point of fixation.

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

Rather than give an overview of the current literature in this section, only some direct evidence for the above phenomena will be mentioned. In particular, the large body of literature on the pharmacological aspects of memory will not be dealt with. A review of this research area is provided by Rosenzweig and Bennet (1976).

The biochemical and morphological correlates of neuronal plasticity and imprinting are not well known. Most theories (Cajal, 1955; DeFeudis and DeFeudis, 1977; Hebb, 1949) are based on the hypothesis that plasticity is coupled with changes in synaptic transmission. These changes, however, can be accomplished by different mechanisms (Bliss and Lomo, 1973; Greengard and Kebabian, 1974; Libet et al., 1975; Lynch et al., 1976; Stent, 1973). It may be possible that within a given neuronal network some of the synaptic junctions are facilitated by learning while others are suppressed, without changing the morphological pattern. The existence of so-called "silent" synapses (Wall, 1977) and some evidence that cortical neurons monocularly driven under normal conditions can be excited binocularly in other test situations [Kato et al., cited in Lund (1978)] 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.

Another feature of the developing brain is the occurrence of neuronal death in different stages of development. A large proportion of this neuronal death seems to occur in embryological stages of development (Cowan and Clarke, 1976; Jacobson, 1971). However, this also could be demonstrated in older animals. In the zebra finch, degeneration of axon terminals presumably correlated with neuronal death was observed in different brain centers during early development. However, as the time course of these degenerative processes does not exactly match that of the sensitive period, the authors presume that this degeneration is a prerequisite for subsequent plasticity during imprinting, but not the process itself (Teuchert et al., 1982).

This view that neuronal death might at best preorganize the brain areas for the influence of the imprinting procedure will not be dealt with in the following discussion. However, the possibility of a participation of neuronal death in imprinting and plasticity of the visual cortex cannot yet be excluded.

A. Cortical Plasticity

The morphological events corresponding to the development of the visual cortex of the cat have been examined by many research groups. In adult cats and monkeys, neurons responding preferentially to stimulation of one or the other eye are grouped together in columns that extend vertically through all cortical layers (Hubel and Wiesel, 1965, 1968). The anatomical basis for the development of these columns is the segregation of the terminals of the geniculocortical afferents from the two eyes within layer four of the visual cortex (Le Vay et al., 1978). This segregation is almost completed at 6 weeks from birth in the cat; the overall time course of the segregation resembles that of the sensitive period obtained in neurophysiological experiments.

In the newborn kitten, arborizations of the geniculocortical axons are extended over an area that covers a relative amount that is greater than is found for one column in the adult animal. In the course of development, these arborizations are broken into clumps and gaps of the appropriate dimensions of one ocular dominance column. Thus, as Le Vay and Stryker (1979) mentioned, the columns are generated by a sorting process, which

separates the primary overlapping terminations of the ipsi- and contra-lateral eyes by a reduction of dendrites in one area and establishment of new ones in others. Thus, instructive and selective processes can be involved in the formation of the ocular dominance columns. As demonstrated by Cragg (1975), selective processes, as claimed by Hubel and Wiesel (1962), are predominant in this developmental process. The number of dendritic spines changes rapidly within the sensitive period in the kitten (Cragg, 1975; Spinelli et al., 1980): after a rise until week 8, the number of spines decreases slowly until the sensitive period is ended.

Rauschecker and Singer (1981) conclude from their experiments that there must be additional instructive processes (enhancement of synaptic conduction), since otherwise there should be a larger amount of visually unresponsive neurons in deprived preparations. This idea was demonstrated by direct evidence obtained by Rauschecker (1982). Results from other animals demonstrate that the number of dendrites or dendritic spines is often dependent on visual experience. Rats reared in the dark from birth have a smaller number of apical dendrites of pyramidal cortical neurons (Ruiz-Marcos and Valverde, 1969). Rearing rats in an enriched environment during ontogeny increases the number of cortical spines compared with isolated animals (Greenough, 1976). These experiments again demonstrate the participation of instructive processes in the developmental process.

Apparently the above-mentioned morphological effects are restricted mainly to the early development of the animal. Rosenzweig et al. (1972) reported that the size of the visual cortex is enlarged in the adult rat as a consequence of rearing in an enriched environment. Greenough (1978) 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 increase of the number of dendritic spines. These changes, however, are very small compared with the drastic effects occurring during ontogeny (Greenough, 1978). Loss of spines in adult rats as caused by deprivation is compensated within several weeks after reopening of the eyes (Parnavelas et al., 1973); the effects do not seem to be stable (see Section IVB).

The mechanism that induces the plastic changes of dendrites or synapses is unknown. The cortex might be a self-organizing system that 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 a lesion and therfore the optimal wiring is disturbed (Wolff, 1981).

The stable end position may 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 (Wolff, 1981). The number of postsynaptic offerings should be genetically determined in this case (Hamori, 1980).

The actual event that gives the "now print" signal according to the theory of Singer is not yet determined. Some evidence exists extracellular calcium concentrations may play a role. For example, by reticular stimulation, cortical neurons are drastically depolarized, with an associated potassium efflux and a calcium influx. It may be that the plastic changes have a potential-dependent threshold and occur only when the activation of the postsynaptic element goes beyond this threshold (Singer, 1982). These events in turn may be controlled by influences from other, superimposed brain areas (Section IIID; Singer, 1979a,b). Kasamatsu and Pettigrew (1976, 1979) 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 brain norepineprhine. Kasamatsu et al. (1979, 1981) elevated sensitivity to external stimulation after the end of the usual sensitive period by application of norepinephrine. They also could demonstrate that the signal-to-noise ratio in the visual cortex becomes larger if one applies norepinephrine during recording of cortical neurons (Kasamatsu and Heggelund, 1982). This seems to be the same effect Livingstone and Hubel (1981) described in differently aroused preparations and is consistent with the theory of Singer (see above). Other experiments revealed that neurons of the monoamine system, which seems to be alterable throughout life (Nygren et al., 1971), show a large amount of growth in brain regions that had been previously destroyed by lesions (Moore et al., 1971; Stenevi et al., 1973).

B. Imprinting

Experiments on the physiological correlates of imprinting have been mainly carried out by Bateson, Horn, and co-workers [for a review see Horn (1981)]. They demonstrated that in chicks the destruction of a part of the telencephalon, the intermedial part of hyperstriatum ventrale (imhv), prevents imprinting or retention of the imprinting experience (McCabe et al., 1979). Directly after the imprinting experiment they could demonstrate a large protein turnover, as revealed by the incorporation of radioactive uracil, within this area (Horn, 1981). Glucose consumption is also heightened, as Kohsaka et al. (1979) demonstrated with [^{14}C]-deoxyglucose autoradiography. During imprinting, the synaptic appositions

are apparently enlarged in left imhv (Bradley *et al.*, 1981): 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.

H.-J. Bischof and K. Herrmann (in preparation) compared the development of different neuronal areas of the zebra finch brain with behavioral data concerning sexual imprinting and song learning. They demonstrated that the peaks of the sensitive periods for sexual imprinting and song learning are coincident with the periods of fastest development of the primary sensory areas of the telencephalon, ectostriatum (visual), and field L (acoustic). Similarly, the period where plastic song is uttered by the birds is coincident with that of fastest development of song control nuclei hvc (hyperstriatum ventrale pars caudale) and ra (n. robustus archistriatalis). In the ferret, Apfelback and Rehn (1983) demonstrated similar correlations between food imprinting and the development of the olfactory bulb. Thus, these experiments add evidence to the hypothesis that imprinting is coupled to processes of development.

In addition to the instructive processes mentioned above, evidence for selective ones was obtained by Teuchert *et al.* (1982). They demonstrated that terminal degeneration occurs within the visual system of the zebra finch at stages of development that resemble the time course of the sensitive period for sexual imprinting. However, as mentioned above, it is not clear yet whether this phenomenon is really involved in the imprinting process or if it may be a prerequisite to the initiation of plastic changes in the brain area involved (see Section IVA).

Rausch and Scheich (1982), in the mynah bird (*Gracula religiosa*), compared dendritic spine density and shape in 10-week-old and 1-year-old speech-trained animals. The comparison revealed a reduction of spine density and an enhancement of spine length. They interpret their findings in terms of the mynah's decreasing ability with age to imitate new sounds and the stabilization of the acquired repertoire.

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 (Bateson 1979b). Influences of superimposed centers mediated by hormonal systems have been considered as well (e.g., Martin, 1975; Weiss *et al.*, 1977). The latter authors assume that the end of the sensitive period of filial imprinting is defined by a rise in the corticosterone levels (ACTH). Martin and Delanerolle (1979), however, state that ACTH might not directly influence sensitivity, but instead inhibit the following reaction.

The work of Nottebohm and co-workers [reviewed by Nottebohm (1980)] adds further evidence. Their results concerning the plasticity of song control areas reveal that this plasticity cannot be elicited throughout life of the birds, but may be dependent on gating by some superimposed systems. Kroodsma and Pickert (1980) were able to support this view by the finding that sensitive periods in the marsh wren are dependent on the light cycle: the sensitive period for song learning is shifted toward the next spring if the birds are born late in autumn and cannot learn from adult males, who have already stopped singing at this time. The influence of these superimposed systems might be mediated by androgens (Pröve, 1983a). However, Hutchinson and Bateson (1982) found that in Japanese quails castration of the young male birds had no effect on sexual imprinting. In contrast, Pröve (1983b) demonstrated that in zebra finches imprinting success was influenced by steroid hormones at the time of the sensitive period.

VI. IMPRINTING AND CORTICAL PLASTICITY: TWO EXPRESSIONS OF A COMMON DEVELOPMENTAL PROCESS?

It would seem that imprinting and cortical plasticity have many features in common. Both are restricted to early ontogeny (see Sections III and IVA). The time course of the sensitive periods has a similar shape: after eye opening, sensitivity arises quickly, reaches a peak, and declines slowly (Figs. 3 and 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 the above examples show remarkable similarity.

Information storage in both phenomena seems to be almost irreversible: information that reaches the system beyond the sensitive period is only superimposed on the previously stored information, but does not alter it (see Section IVB). Moreover, in both phenomena some sort of genetically influenced prewiring plays a role. This prewired 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 informatin to be stored also seem to be the same in the physiological and the behavioral cases: besides the above-mentioned genetic influences, factors like selective attention, motivation, and arousal 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.

A. Specification of Neural and Behavioral Reactions

Considering the similarity between the two paradigms, one can assume that the brain centers involved in the storage of imprinting information should have a similar organization to the visual cortex. There is no need for 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 (Mountcastle, 1979).

At birth only a limited number of neurons reveal clear stimulus preferences; the majority react 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 area involved in imprinting, connections are stabilized under the control of a Hebbian mechanism according to the suggestion of Singer (see Section IVD). 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.

In the case of the visual cortex, this increase in selectivity is easily demonstrated by the comparison of cortical neurons in young and in adult kittens. Whereas in young animals most of the neurons respond to stimulation weakly and unselectively, most of the cortical neurons of adults are strong in their responses and very sharply tuned to one orientation or direction (Imbert and Buisseret, 1975).

Hess (1973) describes the process of increasing selectivity toward stimuli that occurs during filial imprinting: At first, young chickens follow many 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 (Klingel and Klingel, 1966). 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 behavior. However, recent results (H.-J. Bischof and R. Lassek, submitted) dem-

onstrate that the gaping reaction of the nestlings toward their parents becomes more and more selective from day 1 to day 15 posthatch. From this time testing with dummies results in a fear response of the young. Day 15 is likewise the day of the peak of the sensitivity curve for sexual imprinting in the zebra finch. This result may be interesting, too, with regard to comparability of sexual and filial imprinting, where some authors speculate that the acquistition of new information is hindered beyond the sensitive period by the development of fear toward new objects.

B. The Temporal Course of Sensitive Periods

At the beginning of sensitivity the brain area that is to be altered by external stimulation should be "empty" in the sense that, besides a certain preorganization that serves to canalize the incoming stimuli, all neuronal connections are relatively unspecified and are alterable by incoming information. Therefore, the probability that an incoming stimulus finds an alterable connection and is stored is near 100%. Whenever information is stored and neurons are tuned to this information, the probability for new incoming stimuli to be stored becomes lower and lower, because fewer modifiable synapses remain. Thus, in the course of the sensitive period, the average time necessary to store a given portion of information becomes longer. This assumption leads to a sensitivity curve of essentially the same shape as that obtained experimentally in imprinting or in the development of the visual cortex: the efficiency of external stimulation slopes down asymptotically to zero, but does not reach it. Accordingly, some neuronal connections should remain available for a long time, possibly throughout life. Therefore, morphological plasticity and imprinting may be possible in the adult animal, although only to a small degree and under exceptional conditions (see Section VIC).

By translating these considerations into a computer simulation one can demonstrate that the resulting "sensitivity curves" are of the same shape as those obtained in the cases of imprinting and cortical plasticity.

For this purpose, a program was written that simulated the filling of three concatenated stores of 2700 elements each (limited by the computer space). Information (the number "one") flew in a chain through all three stores, but with certain constraints (Fig. 7). A random procedure chose one of the elements of the first store and put the bit of information in if the element was at zero before. Otherwise, this information was lost. Thus, the probability of storage depended on the filling of the store: the more information that was already stored, the lower was the probability for a new storage process.
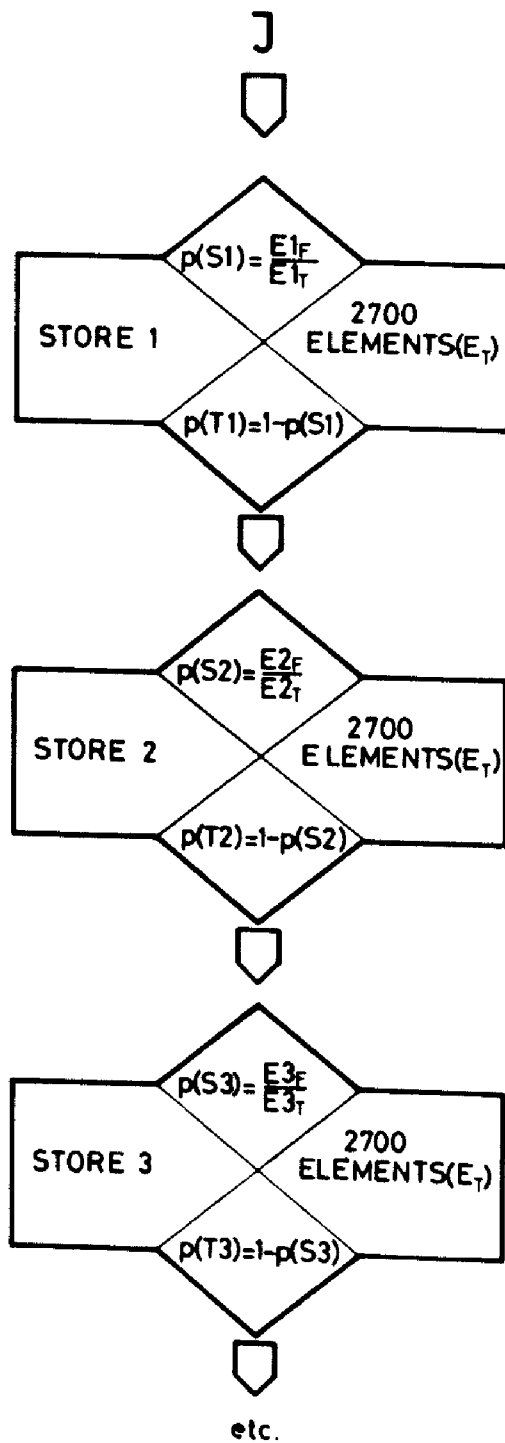
Fig. 7. Flow of information in a computer simulation of the storage process. Here $p(\text{SI})$ is the probability of storage in store 1, El_F is the number of filled elements of store 1, and El_T is the total number of elements of store 1; $p(\text{TI})$ is the probability of transfer from store 1 to store 2. The same formalism is used for the abbreviations for stores two and three, respectively.

The probability of transfer of information from one store to the next was constrained by the filling of the preceding store. The more this was filled, the higher was the probability of transfer to the next one, thus simulating the idea that transmission of information is better in fully organized brain areas. The procedures were the same for stores two and three, respectively.

When the above process had been replicated 75 times, the computer plotted the percentage of stored bits for each store (Fig. 8A); this was done 230 times. Since the computer did not allow for larger stores, the results from five trials were averaged (Fig. 8B), thus roughly simulating a storage capacity of 13,500 elements/store and 385 bits/bin. As one can see from Fig. 8, this averaging procedure did not essentially alter the shape of the resulting curves.

Since the percentage of storage within each bin can be taken as an indicator of the "sensitivity" of the storage medium for information arriving from the outside, the curves can be directly compared with the sensitivity curves obtained in imprinting experiments. The graph of the first store is not similar to the curves demonstrated in imprinting experiments. This store may represent peripheral structures that have to be fully developed under the influence of external stimulation before information can have access to neuronal areas involved in imprinting.

The sensitivity curves of the second and the third stores, representing more central parts of the neuronal tissue, are of the same shape as one obtains in the examples of imprinting and cortical plasticity. Going from "peripheral" to "central" stores, the curves become flatter and the peak occurs later.

According to the model, alterations of brain tissue by external stimulation should therefore start with the attainment of functional sense organs, which is dependent on the developmental state of the animal (Gottlieb, 1961; Gottlieb and Klopfer, 1962). This can be supported by ethological data: in ducklings acoustic features are learned before hatching (Gottlieb, 1961, 1980, 1981), and the sensitive period is then continued for some time after birth. Sensitivity for external stimulation in filial and sexual imprinting, which is based mainly on visual features, starts with eye opening (Figs 3 and 5), although light stimulation before birth has an influence on the preorganization of visual areas and even behavior, as can be demonstrated by exposure of eggs to light of different colors and measurements of color preferences of the newly hatched chicks (Metcalfe, 1976). Bateson and Wainwright (1972) demonstrated that prior exposure to light affects filial imprinting. Within a neuronal system, differentiation of nuclei should start in peripheral stations and then proceed to more central parts. This is consistent with a result obtained by Teuchert *et al.* (1982) 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 of the zebra finch. Earliest degeneration occurred in the most peripheral optic tectum, and some time later degeneration was found in the next station of the pathway, the nu-
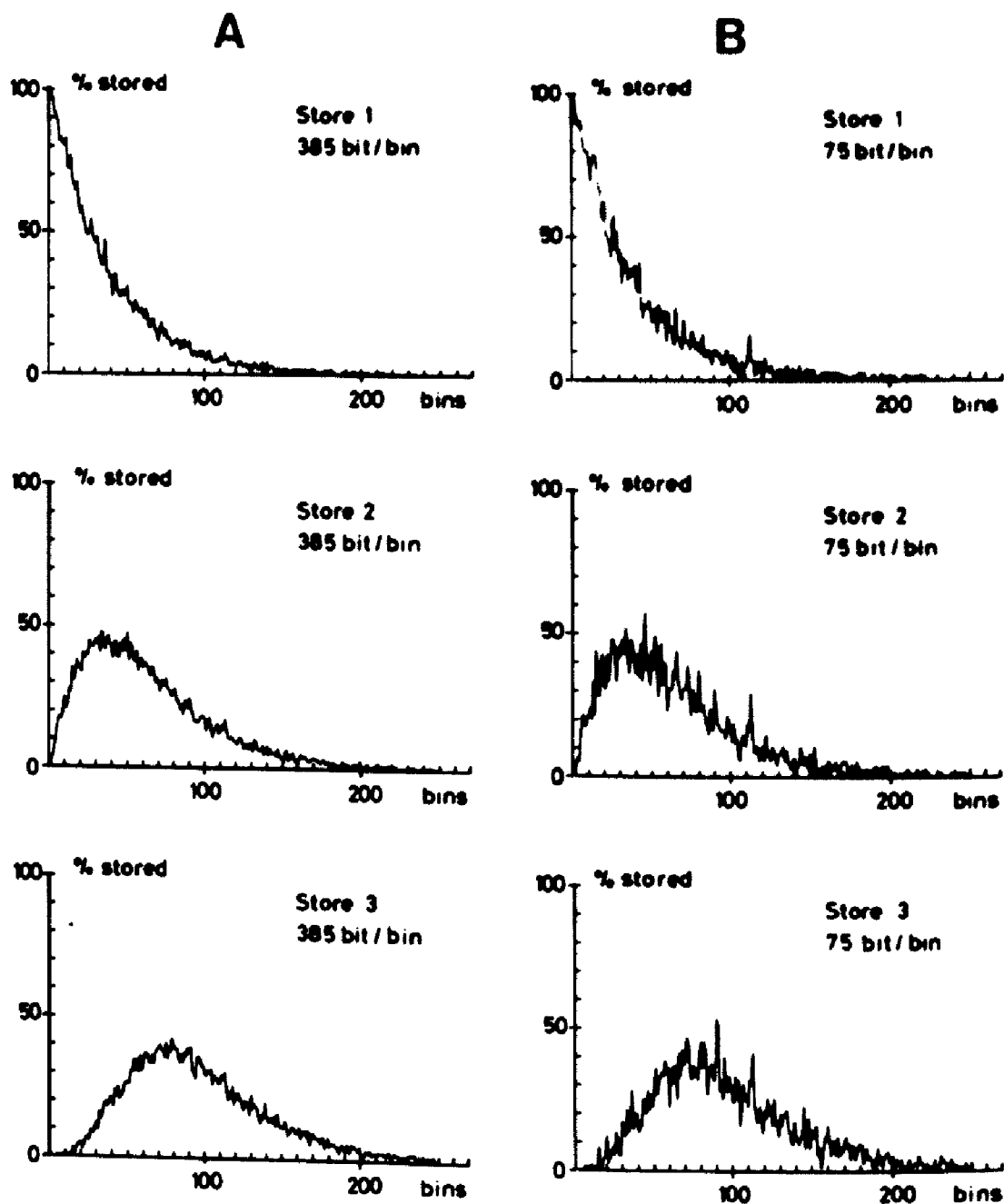
Fig. 8. "Sensitivity" curves obtained by the computer simulation outlined in Fig. 7 and described in the text. Abscissa: Number of bins of (A) 385 or (B) 75 bits of information. Ordinate: percentage of stored bits within each bin.

cleus rotundus, and at the termination of this visual projection, the ectostriatum of the telencephalon. The time at which degeneration occurred in the ectostriatum was just before the peak of the sensitive period for sexual imprinting. H.-J. Bischof and K. Herrmann (in preparation) demonstrated a similar time course in the development of sensory and motor

areas of the zebra finch by measurements of cell size, myelinization, and fiber development.

It is not intended here to discuss these details further, since the simulation was only provided to demonstrate that the above considerations lead logically to the proposed shape of the sensitivity curves. The simulation does not yet include parameters that are very important for the outcome of imprinting experiments, such as stimulus value, occurrence of different stimuli, or length of exposure (Bateson, 1978). Moreover, there may be neurons of different complexity in one neuronal area, as Hubel and Wiesel demonstrate for the visual cortex of the cat. These neurons may be differently accessible and alterable by external stimulation and thus complicate the mechanism and time course of storage.

However, it is tempting to speculate that by consideration of a storage process that is characterized by a limited store, a random access to the different elements, and the condition that "full" elements cannot be altered again, one gets curves like those obtained in the above physiological and behavioral experiments.

The mechanisms of storage modeled above cannot explain the apparent complexity of imprinting. As we have seen in Sections IVD and V, the process of self-termination might be affected by more global influences, such as motivation and arousal. These influences may select between stimuli on the basis of their arousal value or prevent access to the storage area (the animal is not motivated or ready to learn), and thus alter the time course of storage and the shape of the sensitivity curve in an essential way. However, as we have seen, the similar time course for many imprinting and plasticity phenomena may indicate that the influence of superimposed centers cannot fully suppress the basic features of this self-terminating process.

On the other hand, in normal development, gating mechanisms may play a much larger role than in the highly artificial experiments dealt with in the preceding sections. These experiments may demonstrate the limits of the sensitive periods rather than their normal shape and duration (Immelmann and Suomi, 1981). For example, observations of young ducklings in nature reveal that most of the time during which imprinting can occur they are beneath their mother (Sjölander, 1978); following behavior occurs only if there is some danger for the young due to predators or when the mother leads them to the water. Thus, imprinting mediated by following behavior can occur only in this comparatively short period of time. In these situations, however, it seems likely that the arousal level of the young is high compared with "normal" situations, and according to our view of the influence of arousal, imprinting can be done in these

short periods. Thus, in the natural environment, it might be very difficult to obtain time spans of sensitivity like those measured in the laboratory.

Another example may be the development of the zebra finch. Evaluating more carefully the influences of external stimulation on imprinting, one can see that not only the parents, but also the siblings of the young bird have an influence on the result of imprinting (K. Immelmann, in preparation) and that the first courting experience in some cases also has an influence. If one looks at the time course of sensitivity, it seems that the siblings have only a very small influence during the first 30 days of life, until the birds become independent. Thereafter the influence of the siblings will be a little bit greater, presumably because the birds no longer direct their attention exclusively to their parents, as they do during the phase in which they are dependent on feeding. Instead, with rising interest in social and sexual contacts, they will also attend to their siblings. However, there is no evidence that there may be two different sensitive periods underlying these influences of parents and siblings; it seems more likely that by shifting the attention to other objects additional features can be stored. The general time course of sensitivity does not seem to be affected.

K. Immelmann (in preparation) was able to demonstrate that in the first courtship sequence of a zebra finch male, the preference of the birds is eventually changed from the imprinted species to the species of the female that is present during the test situation. Thus, in the sexual contact of the birds sensitivity to the environment is enlarged to such an extent that eventually the formerly acquired preference fails to be exhibited. However, even in this case this does not mean definitely that information stored during the sensitive period is erased; as Bateson (1979b) points out, it may be that in this process of stabilization the previously acquired sensory image has to be matched to the motor output. If at the time when this should occur the right object is not at hand, some sort of emergency mechanism couples the motor output to an object that is available, and the imprinted feature is no longer used under normal circumstances. This view has much in common with that held in research on vocal development; in this case it is presumed that a sensory template acquired in early ontogeny has to be matched to the structures of the song system when adult song crystallizes (Konishi, 1965; Konishi and Nottebohm, 1969). As Marler and Peters (1982) demonstrate, the structure of the song system may provide further limitations on what can be uttered by the bird, since the plastic song has many more elements than the adult song in some species.

The main conclusions of this section are as follows. Imprinting and cortical plasticity are self-organizing and self-terminating processes. Storage of information lowers the probability for new information to be stored.

This process results in the sensitivity curves obtained in the laboratory experiments. Superimposed on this relatively simple process of self-termination are mechanisms that can guide the flux of information. In contrast to laboratory experiments, these superimposed mechanisms may have a large influence on the time course of sensitive periods. Thus, it may be that in more natural evaluations one could get very different sensitivity curves. The "natural" sensitive period may be much shorter or longer or even separated into several peaks due to the influence of the superimposed control mechanisms.

C. Learning in Adult Animals

The amount of plasticity that can be demonstrated by histological methods in the adult brain appears to be very small. Evidently adult learning cannot be explained solely by morphological changes, since its capability 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 the two age groups. Hebb's theory was developed for classical conditioning, and its applicability to cortical plasticity was demonstrated by Rauschecker and Singer (1981) and to imprinting by Bischof (1979). 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 (Section IIID) resonance effects within neuronal subsystems. By this resonance the pathways that 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 submicroscopic alterations of nervous tissue. The morphological changes observed in the young animal seem to be more stable than the purely submicroscopic changes in the adult. Therefore, information acquired in early stages may be irreversibly stored, while in adult animals the mechanism of permanent storage is not as effective (Singer *et al.*, 1982a,b).

From this point of view, imprinting does not involve a separate learning paradigm, but is an effect of age-dependent alterations on brain responsiveness to external influences. The more morphological changes can be observed as an 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, since there are many more already determined structures, which in turn should facilitate selection of stimuli leading to resonance (Campbell and Spear, 1972). As mentioned above, only the permanency of storage should be lower in older animals.

However, imprinting-like processes also may be observed in adults. There are at least two possibilities: if the brain connections are altered by lesions, rewiring may be accomplished by the same rules as govern the ontogenetic organisation of nervous connections (Singer, 1982). 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. The same may happen if already established connections are destroyed by normally occurring neuronal death (Wolff, 1981). It must be mentioned that this potency of morphological recovery differs among species: in lower species the degree of adult morphological plasticity seems to be larger than in higher animals (Jacobson, 1971).

On the other hand, there seems to be a small amount of neuronal tissue that remains susceptible to morphological changes throughout life. We cannot decide whether these neurons are evenly distributed over the brain or whether they are concentrated in higher order centers. The experiments of Nottebohm (1980) support the second view; he demonstrated a large amount of plastic changes even in adult birds in the hvc, but not in any other brain area. Some experiments demonstrate that this neuronal area behaves like embryonic tissue even in adult birds: contrary to the long established theory that in differentiated brains no new neurons can be developed, Nottebohm and Goldman (1983) demonstrated that in the n. hyperstriatum ventrale pars caudalis (hvc), neurons are proliferated from an ependymal zone even in the adult canary. Thus, it appears as if within these areas (perhaps by regulation of the above-mentioned gating mechanisms) an early stage of development is preserved in the adult brain.

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, most of the 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 accom-

plished 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 such as might occur, for example, in traffic accidents. "Breaking in" of horses or comparable animal training methods may provide further examples (Bateson, 1982a). The latter author states that there might be a linkage between stress situations and catecholamine production, which in turn has an influence on plasticity, as demonstrated in the cat visual cortex (Kasamatsu and Pettigrew, 1976, 1979).

An example of recovery of visual function in adult humans is provided by Zihl (1981). In man, lesions of the striate cortex lead to scotoma, a form of blindness within a limited part of the visual field. With extensive training it is possible to reduce the size of this scotoma and to restore visual functions in areas that were previously blind. The crucial point in the training procedure seems to be that the patient has to learn to direct his or her attention selectively to the function abolished by the lesion. Thus, attentional mechanisms again seem to play a major role in this recovery process. Since recovery occurs in the course of the experiment, which lasts for about 60 min, it is unlikely that regeneration of synaptic connections occurs; apparently intact but nonfunctional synapses are reactivated by this training procedure. Other examples of this kind are provided by Singer (1982).

It may be important to point our 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 should precede morphological alterations. 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.

D. Significance of Sensitive Periods and Imprinting for Adult Behavior

In the preceding sections it has been demonstrated that in very different phenomena sensitive periods exist in the course of which the organism is very vulnerable to external stimulation. It has also been demonstrated that these early influences can have large influences on the organization and behavior of the adult brain and that these influences are

difficult to erase later in life. Statements like this have often been strongly contested in the psychological and sociological sciences. Admittedly, the view that a child who fails to get the appropriate stimulation at the appropriate time will be damned to the consequences of this failure for its whole life would be horrible (Bateson 1979b, 1982a).

However, this rather deterministic way of interpreting sensitive periods is the result of some obviously misleading statements of researchers in the field, as Oyama (1979) points out, and does not represent the opinions of most of the scientists working in the field of sensitive periods and imprinting.

One of the misinterpretations is to see imprinting as a "single-shot" event (Scott, 1978) by which a "decision" is made that settles the future of the organism. In such a mechanism, a wrong decision could be catastrophic. However, as demonstrated in the preceding sections, sensitivity for external stimulation is high in all cases for a certain amount of time, and the result of the imprinting procedure is affected by each event and input occurring in this period. Moreover, constraints that raise the ability to learn the appropriate stimuli above the ability to learn others provide the animal with an additional security mechanism. Therefore, the possibility of an animal's being misimprinted by a single event is substantially diminished.

Much more important is the question of the extent to which the behavior of the adult animal really depends on the information acquired during the sensitive period. If there were no way to overcome the effects of imprinting, parents in most cases would not be able to provide the right stimulation for their offspring at the appropriate time.

There are two lines of argument that demonstrate that the influence of imprinting is largely overestimated by such a view. First, one has to take into account how many different things an animal has to learn during its sensitive period, and that it should not be of large effect if a few of the thousands and thousands of things that are to be stored are established wrongly. The other, more important argument is that in most cases of imprinting known to date, mechanisms have been evolved to overcome the effects of inappropriate establishment of synaptic connections during the sensitive developmental period. This ability to overcome the effects of early experience effects seems to differ depending on the organizational level of the system considered.

There is no doubt that squinting or other malfunction of the eyes has drastic effects on the development of binocularity, which is a prerequisite for depth perception. These effects can be demonstrated not only in the above-mentioned animal experiments, but also by clinical observations in man (Sireteanu, 1982). The only chance of avoiding the influence of

squint on binocular vision is to make appropriate corrections in early childhood. However, one can demonstrate that amblyopic patients without binocular vision can perceive depth to a certain degree, apparently by mechanisms that are not used by people with normal vision.

Similarly, the influence of imprinting on the choice of the object for the following reaction or courtship behavior can easily be demonstrated. However, in this case, where it is not a relatively small neuronal area, but a complex pattern of behavior that is imprinted, one can see that the animal is not really fixed to that imprinted stimulus: as stated above, the preference only comes to the surface in situations of choice; otherwise the birds can follow or court other, nonimprinted objects, and under certain circumstances even breed with birds to which they were not imprinted.

In mammals, influences of imprinting phenomena are even less obvious in some species. As mentioned in earlier sections, the influence of early experience, for example, in the Mongolian gerbil (Agren and Meyerson, 1979), is normally not detectable and comes to the surface only in extraordinary situations.

For humans, it is likely that in most cases influences of early experience are not detectable under normal conditions, and that these influences can be fully superimposed by other learning events (Bateson, 1982a). This theory was already proposed by Freud (1953). What remains, however, is the fact that these early influences do have a certain effect on adult behavior, and therefore that the period of development has to be carefully attended to even in humans.

VII. CONCLUSIONS

The comparison presented above demonstrates that there are in fact striking similarities between imprinting phenomena and the modifications of the visual cortex.

In both cases a sensitive period exists. In the course of the sensitive period information from the environment can be stored irreversibly. The shape of the sensitivity curve suggests that the process of storage is self-terminating: the more information is acquired, the less new information is capable of being learned and the longer is the time for a given portion of information to be stored. External influences reaching the organism beyond the sensitivity period can only be superimposed on the previously stored information, but cannot erase it. In older animals, information does not seem to be stored as stably as in the young; it can be forgotten. In both phenomena the storage process is influenced by some sort of ge-

netically influenced preorganization and by more global mechanisms such as attention, arousal, or motivation.

One can conclude that the two phenomena are not directly linked, but are two expressions of a developmental process that may be common for the organization of the connectivity of a single neuron as well as for complex neuronal networks as are likely to be involved in imprinting. One possible description of this basic process is based on the theory of learning proposed by Hebb (1949). According to this theory, learning occurs by changes of synaptic connectivity (stabilization or rejection of synapses) as a consequence of synchronous or asynchronous activation of pre- and postsynaptic elements.

Such a mechanism also may be involved in the above-mentioned examples of developmental plasticity and imprinting as in adult learning. The difference between learning in young and in adult animals thus may not be a difference in the acquisition process, but may depend on the developmental state of the animal.

In the younger animal the neuronal tissue seems to be generally more vulnerable to external stimulation; thus, external influences may lead to morphological changes of the neuronal connectivity. This vulnerability is essentially diminished in older animals. Therefore, excitation from the external world leads in most cases to solely biochemical or submicroscopic changes of synaptic connections, the morphological features remaining unaltered. Differences of the stability of storage of external influences may be explained by this difference in the overall amount of morphological alteration, which is large in the young, and small in the adult animal.

Thus, the difference between imprinting and other learning phenomena may not be dependent on different principles of acquisition, but may be a consequence of the different developmental states of the brain, or, speaking with more caution, the developmental state of the neuron that is affected by learning.

VIII.   ACKNOWLEDGMENTS

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