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Sexual imprinting as a two-stage process

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There is now a considerable literature concerning the phenomenon known as sexual imprinting and the mechanisms underlying it (for reviews see Bateson, 1966; Immelmann and Suomi, 1981; Kruijt, 1985), However, recent findings by Immelmann, Lassek, Pröve & Bischof (1991) and by Kruijt & Meeuwissen (1991) suggest that earlier concepts of imprinting-like learning have to be revised. In this chapter I will analyse this new evidence and discuss its implications for some of the presumed characteristics of imprinting, such as the existence of a sensitive period and the stability of preferences. Further, I will consider some important questions such as stimulus selection and the reasons for stability of preferences. Many of the ideas I will present here are speculative and have little experimental backing. However, they may help us discard some of the old ideas concerning imprinting and so allow for the generation of new ones.

I will start with a brief description of the findings which prompted this chapter. Then I will propose an interpretation of these findings in terms of a two-stage process. The period in early development where information about the appearance of the parents is stored is called 'acquisition phase' here. Subsequently, there is a 'consolidation process' which takes place when the animal becomes sexually mature. In the final section of this chapter, I summarize the main features of the two-stage process and try to evaluate how the ideas presented here can be generalized to other learning paradigms.

Sexual imprinting in zebra finches

Immelmann (1969) was the first to describe sexual imprinting in zebra finches. In his experiments, young zebra finches were cross-fostered by Bengalese finches, birds which readily adopt and rear young of other species. The song of cross-fostered adult zebra finch males resembled that of the Bengalese finch (Immelmann, 1968). Further, the males showed a strong preference for the foster species if tested in a simultaneous choice test, in which they could choose between a female of their own and of the foster species (Immelmann, 1969, 1972; Clayton, 1987a). Immelmann also presented evidence suggesting that sexual imprinting was possible only during a sensitive phase, which started at about 10 days. Imprintability was high until about 20 days and then decreased asymptotically to zero (Immelmann, 1972; Immelmann & Suomi, 1981).

Once a significant sexual preference was established, it was thought to be stable (Lorenz, 1935). Immelmann (1979; Immelmann &. Suomi, 1981) tested this hypothesis by exposing adult zebra finch males, which were raised by Bengalese finches and showed a sexual preference for the foster species, to a zebra finch female for 7 months or longer. The males courted these females irrespective of their previously shown preference for Bengalese finch females, and eventually reared clutches of young. However, when the birds were separated from the females, after some time they again preferred females of the species of their foster parents. Immelmann (1979) concluded from these results that imprinting on the foster parents was stable, and that the preference for the conspecific female was superimposed on the original preference, but did not erase it. However, there were some indications in his experiments that the pretest, which served to measure the initial preference of the bird, influenced the final results: if Immelmann omitted this test, some of the males developed a new and stable preference for zebra finch females. On the basis of these findings, I postulated a 'second sensitive period', in the course of which the final preference of the bird was established (Bischof, 1979).

Although at present I would not defend all of the features of the model that I presented in 1979, subsequent research by Immelmann *et al.* (1991) and Kruijt & Meeuwissen (1991; cf. Kruijt, 1991) confirmed the notion of a two-stage process. These authors reared male zebra finch young with Bengalese finch foster parents for 40 days and subsequently isolated them until day 100. Half of the males were then given a preference test and showed a strong preference for females of the foster species. All the birds then received breeding experience with a female of their own species for 7 months (Immelmann *et al.*, 1991) or 3 months (Kruijt & Meeuwissen, 1991). Thereafter, the birds were tested in two series of preference tests, one immediately after the end of the breeding experience, the other some months later (at different times in both studies). Although there were slight differences in design between the two experiments, the results were remarkably similar. Whereas in the group that received a pretest, most of the birds retained their original preference for the foster species, the majority of the males of the group without pretest preferred females of their own species. The second test, up to 1 year later, showed that this preference remained stable. This similarity of results in two independent studies shows that the effect of the pretests is very reliable.

The authors of both studies concluded that the initial preference which the bird acquires during the first 40 days of its life is not stable, but has to be validated by later experience. Immelmann *et al.* (1991), following Bischof (1979), described the effect as 'consolidation', presuming that under natural conditions the information which was acquired during the early sensitive period, and that which is stabilized or consolidated by the first sexual experience with a female of the parent species will be the same. Kruijt & Meeuwissen (1991), more exactly, point out that in the experiments described above, the effects of the original experience are modified if the first and the second experience differ. Thus, they claim that, depending on the similarity or dissimilarity of the two subsequent experiences, the process involved is described as 'consolidation' or 'modification', respectively.

In addition, both studies showed that the acquired preference remained stable for 7 months or more than a year, respectively. Besides these general findings, they reveal some details of the two-stage process. Immelmann et al. showed that the timing of the experiment is important for the final result: more of the animals exposed to the foster parents for 35 instead of 40 days showed a preference for their own species, irrespective of previous choice tests. Surprisingly, longer experience (50 days) with foster parents also diminished the consolidation effect. This may be due to the presence of conspecific siblings, which has been shown by Kruijt, ten Cate & Meeuwissen (1983) to affect later sexual preferences significantly. Kruijt & Meeuwissen (1991) showed, in addition, that the effect of the breeding experience on preferences is not due to physical interactions between the male and the female, nor is it dependent on breeding itself. The effect of keeping the experimental bird in visual contact with a female, but separated by wire, for 3 months was not different from that of keeping the male in direct contact with the female. The same was true for the preference tests: the stimulus females in both studies were separated by wire from the experimental male, showing that direct physical contact was not necessary for the stabilizing effect of the preference test.

Bischof & Clayton (1991), in an experiment similar to those described above, showed that at least in an experimental situation where the birds were isolated between day 40 and day 100, it was the first exposure to a female or 'the first courtship' which established the preference. They used a more balanced design where the birds were raised by Bengalese finch parents and isolated between day 40 and day 100, until they were exposed for 1 week to a Bengalese female, then for an equal time to a zebra finch female or vice versa. Whereas all birds which were first exposed to the Bengalese finch showed a 100 % preference for females of this species, the birds first confronted with zebra finch females showed preferences either for the one or the other species. Raising the birds with their own parents, however, resulted in all cases in a preference for zebra finch females, irrespective of the sequence of exposure to females as adults. Bischof & Clayton interpreted this result as suggesting an 'own species bias' in the formation of sexual preferences. However, the alternative explanation that differential social interactions with the parents (ten Cate, 1982) or the influence of siblings (Kruijt *et al.*, 1983) may contribute to the difference between Bengalese and zebra finch-reared animals cannot be excluded. In a recent study, Kruijt & Meeuwissen (1993), using a design similar to Bischof & Clayton (1991), compared the preferences of zebra finch males raised by conspecific parents with those of cross-fostered zebra finch males in their earlier study (Kruijt & Meeuwissen, 1991). The comparison did not reveal an asymmetry in the preferences of conspecific-reared and cross-fostered males. Because the main difference between the two experiments was the number of siblings with which the experimental males were raised (0–1 in the Kruijt and Meeuwissen studies, and 2–4 in the Bischof and Clayton experiment), this may be the crucial factor for the development of such asymmetries (see Kruijt & Meeuwissen, 1993, for further discussion).

Bischof and Clayton (1991) also showed that the outcome of the experiments depends on the interactions between the young and their parents, and the male and the female in the 'first courtship' situation, respectively. Comparing brothers within clutches, the one that begged and was fed more by its foster parents developed a stronger preference for Bengalese finch females. The more song phrases a male directed to the zebra finch female during the first exposure period after isolation, the stronger was the sexual preference for zebra finch females in the choice tests.

Although the experiments described above support the concept of sexual imprinting as a two-stage process, they provide relatively little information concerning mechanisms underlying it. The evidence suggests that interactions between the experimental males and their parents and also their mate, respectively, might be important. In the next section, I shall discuss some of the features of the phase during which the birds learn about the environment. I call this period, which is identical with the classical 'sensitive phase' of sexual imprinting, the 'acquisition phase'.

The acquisition phase

It is logical and generally accepted that sensitive phases for acquisition of external information cannot start before the sensory system has developed to a stage that sensory input can reach the central nervous system. The question is then which sensory systems are involved and at which time they become functional (Gottlieb, 1971; see also Balsam & Silver, this volume). Because in sexual imprinting the characteristics of the object for sexual behaviour are learned (Lorenz, 1935), it is useful to ask which sensory information is mainly used in courtship behaviour. For sexual behaviour in zebra finches, visual information seems to be the most important by far. Male zebra finches court stuffed dummies of zebra finch females, but do not respond with sexual behaviour to female calls, even if there is a chance for the male and female to communicate acoustically. However, the reaction to the visual image of a female is enhanced by acoustic cues. Most probably, acoustical features of the female arouse the male to a certain degree, but do not alone release courtship behaviour (Bischof, 1985a).

In the course of development, young zebra finches react with gaping responses to acoustic and mechanosensory cues from the time of hatching (Bischof & Lassek, 1985). Reactions to stuffed dummies are observed not earlier than day 10, although the eyes of the birds open at about 6 days. Thus, for the first few days the gaping reaction is elicited only by acoustical and mechanosensory cues, and these stimuli may, after the visual system starts to develop, help to guide the animal's attention towards the visual stimuli. The appearance of the first reaction to visual stimuli could be interpreted as showing that the sensitive phase for the acquisition of visual cues in zebra finches starts at about 10 days from birth. However, at 15 days of age, the young birds react to stuffed dummies with fear instead of gaping reactions. The birds obviously cannot differentiate between dummies and the parents (which had free access to the young except during experiments) earlier than this day. Thus, it is possible that the visual system needs another 5 days to allow the perception of complex stimuli, and one might therefore set the starting point for the sensitive phase at 15 days of age. The data from Immelmann's consecutive rearing experiments (see above) show that the truth lies somewhere in between. By 13 days of age, 10% of the birds have already acquired enough information about the parents to show a stable preference for them. However, if the parents are replaced by foster parents at 19 days of age, about 85% of the birds retain the initial preference. Therefore it appears as if, under normal conditions, most of the information is stored between 13 and 19 days of age (Immelmann & Suomi, 1981). However, the acquisition phase may be extended if, as mentioned above, the birds are not reared by their own parents. That raises the question of how the storage of information is accomplished, what factors are responsible for the acquisition of information, and what are the factors that end the acquisition period.

The first attempt to explain sensitive periods was a model in which the sensitivity to the environment was switched on and off, by an internal, perhaps genetically determined factor (e.g. Scott, 1962) At present, most theoretical considerations favour the view that a store of limited capacity is filled with information, starting at the time when the sensory system becomes functional. Information storage is fast at the beginning (but perhaps hindered initially by an incomplete development of the sensory system), and slows down dependent on the filling of the store (Bateson, 1981, 1987; Bischof 1983, 1985b; Boakes & Panter, 1985; Bolhuis & Bateson, 1990).

To prevent misinterpretations, it should be mentioned here that the notion of 'limited store' could be taken literally. That is, there may really be some limited space within the brain which is capable of storing the information which comes in during development. It is more probable, however, that the limitations are set by the information itself: if the bird has learned the main features of, say, its parents, there is little opportunity for acquiring new information. The storage process concerning the parents may come to an end because new features appear only very rarely. If at this time the foster parents are replaced by conspecific parents (or *vice versa*) the representation of the characteristics of the parent is already complete, but details of the 'new' parent image may be added. Ten Cate (1986a, 1986b) suggested that such consecutive rearing (as well as simultaneous rearing with two species) results in a mixed representation of both kinds of parent features. Our results (Bischof & Lassek, 1985) on the development of the gaping reaction suggest a third mechanism for limiting the acquisition of information. They show that acquisition of the parent features may simultaneously result in a development of fear towards other, new objects that prevents the birds, at least partly, from learning features other than those with which they are familiar already. This has often been mentioned as a factor limiting learning in filial imprinting (Sluckin & Salzen, 1961; Salzen, 1962; Hoffman & Ratner 1973; Bateson 1981).

However, if the fear reaction is overcome, acquisition of new information may be possible.

So far, nothing has been said about what kind of information is stored during the acquisition period. When sexual imprinting was supposed to be a one-stage process, it was thought that the bird acquired information about its later sexual partner. The problem with this idea was that the system selecting the input for the store had to 'know' at the time of input by what features such information is characterized. Because the bird at that time has no sexual experience, this could only be some sort of prefunctional knowledge about what might be relevant features for finding a sexual partner later in life.

The two-stage model offers another interpretation. It is conceivable that at the time of the aquisition phase the young bird does not know anything about sexual partners and sexual behaviour. However, there are other things which have to be learned, for example 'who is feeding me' or 'who is competing with me for food'. These are examples of acquisition processes that include interactions between the individual that learns and the object of learning. For filial imprinting there is some evidence that associative learning may be the basis for this kind of acquisition (for reviews see Hoffman & Ratner, 1973; Bolhuis, de Vos & Kruijt, 1990). On the other hand, zebra finches may learn about their inanimate environment, for example, without conventional reinforcement, as has been shown for filial imprinting (reviewed in Bolhuis, 1991). However, this issue will not be discussed here since other chapters in this volume (Clayton, ten Cate; see also Clayton, 1987b) deal with the factors influencing information storage in imprinting and song learning.

Whatever the mechanisms of acquisition may be, one can infer that some sort of internal representation – a 'neuronal model', as Salzen (1962) put it, or a 'template', as it is usually called in the song learning literature (Konishi, 1965) – is formed in the brain of the bird. This suggestion implies that the part of the brain or store which acquires information about the environment has to possess some sort of prestructured knowledge. Information about the inanimate environment, such as the walls of the nest box, is put in a different store from, for instance, information about the parents. On the other hand, if birds are reared consecutively by two species, a mixed representation of the features of both species is formed (ten Cate, 1986a, 1986b; see also Clayton, 1988). This means that the system has to 'know' which incoming information has to be stored where. As mentioned above, this could be accomplished by associative processes; for example, categories could be built like 'these are the subjects which are always feeding me' or 'these are subjects which are competing with me for food'. However, there have to be other ways of categorization; it is not easy to understand, for example, how information about the colour of the walls is put into an appropriate store.

It must be emphasized here that it is not only visual information that is stored during the acquisition period. The song learning literature shows that acoustic information is stored as well (e.g. Böhner, 1990). This storage may start even earlier than the storage of visual information. As described above, zebra finches react with gaping to acoustic stimuli from the first day of their life (Bischof & Lassek, 1985). It cannot be excluded that they can perceive acoustic information even in the egg, as has been shown for ducklings by Gottlieb and colleagues (Gottlieb, 1971).

Thus, although acoustic features are not the most important for the elicitation of sexual behaviour (Bischof, 1985a), there is no reason to believe that these features are not learned during development. It has been shown that features of the calls of zebra finches are learned, although the basic structure is inherited (Zann, 1985). It may then be possible that in cross-fostering experiments the birds learned acoustic features from their natural parents before the eggs or the very young hatchlings were transferred to their foster parents. This may also contribute to the apparent 'own species bias' which is observed in many experiments of sexual imprinting, and may also have implications for the consolidation process.

The consolidation process

Neural representations

At the end of the acquisition period, the bird has a set of neural representations of individuals which are important during this period of its life. It may already distinguish between father, mother, and siblings. The 'siblings' category is probably updated several times because the siblings grow older and change their appearance (Bateson, 1981). The 'sibling' category may later also be divided into several subdivisions, allowing the bird to identify each individual brother or sister.

The idea I wish to present here is that the information acquired in the course of the acquisition period is used also in situations other than those which led to its storage. In the experiments by Kruijt & Meeuwissen (1991) and Immelmann *et al*. (1991), the birds were, after reaching independence, isolated for about 60 days. If they are exposed to a female after this isolation period this is a new situation in two respects. First, the male zebra finch sees another bird after a long time of isolation, which may lead to high levels of arousal (Bischof & Herrmann, 1986), and second, the male has become sexually mature in the meantime.

It is therefore conceivable that the bird's attention towards the new stimulus animal(s) is very high. If there are two females from different species, as is the case in the choice test, the male most probably attends to the one similar to the birds to which it has been exposed previously. If there is only one bird, and this is not of the species with which he has been reared, he may nonetheless try to court it, probably because the strange bird shares some features, like having wings or the general shape of a bird, with his parents or siblings. On the other hand, he may court the strange female because his courtship motivation is so strong that he courts almost anything, or he may not court at all.

The two-stage hypothesis predicts what happens if the female that the young male sees first after isolation is of the species he was reared with. There is a stored representation which resembles closely the image of the female to which the male is exposed: that of the mother. Thus the male is familiar with this sort of stimulus and tries to direct the new behaviour which he has developed towards it. As a consequence of courtship behaviour directed towards the female and some contingent behaviour of hers, the young bird learns that the image in the store is good not only for getting food, but also for courtship behaviour. The new association of a stored representation and a new behaviour system (sex) is then stably installed (see also Hogan, 1988).

How can a fostered bird change its preference towards zebra finch females during the consolidation period? In this case no zebra finch representation would be stored, and this should result in a lack of interest in this species, as it is not known. There are different ways to explain this problem, and at present there is no possibility to decide which is the right one. The simplest solution would be to state that the acquisition phase has not yet ended. Immelmann & Suomi (1981) showed that, under certain conditions, the preference of a male zebra finch can be changed very late, an extreme case being reversibility after 70 days. This means that new features may be added to the recognition system even in late stages of development.

An alternative explanation for the shift towards a zebra finch preference is that there is already some representation in the recognition system. This may be some sort of predetermined structure, as I preferred to think (Bischof, 1979; Bischof & Clayton, 1991). However, the objections against such a view, formulated frequently by Kruijt and his colleagues, have somewhat changed my mind. It may well be that, for example, the presence of zebra finch siblings in the nest has affected the formation of a representation of zebra finch features (see Kruijt & Meeuwissen, 1993, for further discussion), or that the young birds, before being transferred to the foster parents, had acquired some acoustic features of their natural parents (see above). As in many other cases, both factors may be involved. Gottlieb (1971, 1981), for example, demonstrated that young ducklings need some sort of acoustic stimulation before hatching to develop a preference for the mother's call, but this does not have to be the call itself. Likewise, Horn and colleagues (e.g. Horn, 1985, 1990; Johnson & Bolhuis, 1991; cf. Bolhuis, this volume) showed that there is some sort of predetermined preference (a 'predisposition') for more natural objects such as a stuffed junglefowl in filial imprinting in chicks. Thus, a prefunctionally determined structure of the recognition system cannot be excluded.

Some of the arguments presented above can probably be tested. If there is no representation in the recognition system at the time where consolidation occurs and a new one can be added at this time, the zebra finch males should also be able to court a third species, for example silverbills (*Euodice cantans*), another finch species, and probably develop a stable preference for this species. If the representation stems from influence of siblings, the cross-fostered male should, given a choice between young and adult females, probably prefer the young one, and if the representation involves acoustic cues from the zebra finch parents, mute zebra finch females should not be courted.

Linking the appropriate behaviour

In any case, in the course of the consolidation process, one (or more) stored representations will influence sexual behaviour. Independently of my first account (Bischof, 1979) of the results discussed here (Immelmann *et al.*, 1991; Kruijt & Meeuwissen, 1991), Bateson (1981, 1987) developed a model of imprinting based on results of Immelmann (1969) and Cherfas & Scott (1981). As mentioned above, Immelmann found that male zebra finches that were reared early in life with Bengalese finches, and after a choice test were kept for 7 months with conspecifics, bred successfully with female zebra finches. However, in a subsequent choice test, the males courted Bengalese finches in preference to zebra finches. Thus, for the time of breeding with conspecific females the preference for Bengalese finch females was masked by a new one, but resurfaced when a choice was possible. Bateson stated that this could be explained by proposing two separate systems, a recognition system and an executive system (for example the one for sexual behaviour).

The recognition system, according to Bateson, is organized as presented above in this paper. Bateson suggested that the recognition system gains access to the executive system in the course of the sensitive phase. If more than one image (for example a zebra finch and a Bengalese finch image) 'captures' a behavioural subsystem of the executive system (for example sexual behaviour), the one which has stronger access controls the behaviour as long as the stimulus is available. However, if the bird does not have a choice, the other image can also control behaviour.

So far, this is very similar to the view presented here. In contrast to Bateson's proposals, however, it is assumed here that the acquisition process and the consolidation process are guided by different and independent mechanisms. Whereas, as outlined above, the recognition system is shaped during the 'classical' sensitive phase and does not have anything to do with sexual imprinting directly, the consolidation process takes place during the second stage, when connections are made with the executive system (Kruijt & Meeuwissen, 1991). The most important feature of this consolidation process is that it occurs only if sexual behaviour is performed and the validity of the learned image for sexual behaviour can be tested; thus, it depends on a certain sexual maturity of the bird.

First courtship attempts in young zebra finch males can be observed between 30 and 35 days of age (Kalberlah, 1980). At this time, there is a peak in plasma testosterone levels (Pröve, 1983). When this peak ends, the plasma concentration of 17β-oestradiol, which is the metabolite acting in the brain (e.g. Gurney & Konishi, 1980; Harding, 1983), is raised substantially (Pröve, 1983). If courtship is a necessary prerequisite for the consolidation process, it cannot occur earlier than 30 to 35 days. As the results of Kruijt & Meeuwissen (1991) and Immelmann *et al.* (1991) show, it can be delayed even until the bird is 100 days of age. However, it is conceivable that under natural conditions consolidation occurs earlier and that it may not be restricted to a single courtship bout.

Direct evidence that raised levels of testosterone are a prerequisite for consolidation has been provided by Pröve (1990). He reared zebra finch males with Bengalese finch parents until they were 35 days old. During this time the birds received silastic implants containing testosterone. From day 35 to 95 the birds were transferred to a zebra finch female. Half of these birds received silastic implants containing Cyproteronacetate (CyA), an antiandrogen which has been shown to suppress reversibly sexual behaviour (Pröve & Immelmann, 1982). Subsequent choice tests showed that the birds which had received CyA implants retained the preference towards the foster species, whereas the non-treated animals preferred their own species. Unfortunately, no observations of the behaviour of the birds were performed in these experiments. They suggest that stabilization occurs only if testosterone is available. It is conceivable, however, that because of the lack of testosterone, the birds did not court their cagemates between 35 and 95 days (cf. Bolhuis, 1991). In that case, the experiments would support the suggestion by Immelmann *et al.* (1991) that sexual behaviour is necessary to stabilize or modify the preference.

In the experiments performed by Immelmann *et al.* (1991) and Kruijt & Meeuwissen (1991), the birds appeared highly aroused. Observations by Bischof & Herrmann (1986), using ^{14}C-2-deoxyglucose (see also Bolhuis, this volume) may be relevant to this issue. These authors found that four areas of the forebrain of zebra finch males were activated strongly if the bird was aroused by chasing it round the cage, or under the same conditions that Immelmann *et al.* (1991) used in their experiments. It may well be that this high arousal level is a precondition for consolidation. This suggestion receives some support from anecdotal evidence presented by Bateson (1983).

We cannot define exactly what factors may contribute to the level of arousal. Obviously, the male is aroused by the appearance of the female. Probably, the behaviour of the female towards the male is an important factor. However, Kruijt & Meeuwissen (1991) have shown that a female separated from the test male by wire has the same effect as a female that can be accessed directly by the male. Bischof & Clayton (1991) demonstrated that the preference for the test female is greater when the male's courting activity is high. Whether this, in turn, depends on the behaviour of the female, cannot yet be decided. Both findings can also be interpreted as showing that the male's behaviour itself may be sufficient to stabilize his preferences. This idea has been put forward in filial imprinting, e.g. in the form of a 'law of effort' (Hess, 1973). Kruijt & Meeuwissen (1991) argued that the high level of arousal that the birds show in the given experimental situation may be dependent on the long period of isolation preceding exposure to a female. This is supported by findings of Bischof & Herrmann (1988), who showed that the activation of the four brain areas mentioned above, which was used as an indicator for arousal, was dependent upon the time of isolation preceding the experiment.

However, it is conceivable that under normal conditions the arousal level of a male is enhanced if a female appears. The enhancement may be small, but sufficient for consolidation to occur. According to this view, the experiments by Kruijt & Meeuwissen (1991) and Immelmann *et al.* (1991) did not measure an artifact, but drove one of the factors involved (namely the level of arousal) to its limits. To be really sure about the role of arousal, however, it is necessary to find ways to test this hypothesis more directly.

Conclusions

From the experiments described in this chapter, sexual imprinting can now be characterized as occurring in two stages: First, an 'acquisition phase' during which the bird learns about its environment, for example about its nest, its siblings, and its parents. When the bird is able to perform sexual behaviour, this previously acquired representation is used when choosing a sexual partner. If the representation matches the courtship partner, it is used for sexual behaviour subsequently. If it does not fit, the existing representation is altered or a new representation influencing sexual behaviour may be formed. In either case, the representation remains stable after the consolidation process.

It may be too early to generalize these ideas to other imprinting-like paradigms. However, as has been mentioned above (see also Clayton, ten Cate, this volume), song learning shares many features with sexual imprinting. It is generally accepted that song learning in birds is a two-stage process. With slight modifications, it is assumed by all authors working in this field that birds learn their song during early development in the course of a sensitive phase. The songs which are acquired during this sensitive phase are stored as a 'template' which can later be recalled. In the so-called 'sensorimotor phase', this template is used as a guide for the young bird to develop its own song by matching the own song output with the neuronal model stored in the template. As yet, it is not easy to decide whether the similarities end here and whether dissimilarities show up with closer examination. Further research may clarify this issue.

Comparisons with other imprinting paradigms are also difficult at this stage. Filial imprinting, for example, obviously does not have a time lag between acquisition and stabilization, although formally the two stages can be separated (Bischof, 1979). An idea that might be interesting to investigate is that each behaviour which is triggered by a releaser, the characteristics of which are learnt, is coupled to this releaser by a consolidation process. However, at present one can only speculate that the two-stage process that has been found in sexual imprinting may be a common feature of all imprinting-like processes.

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