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# MAMMALIAN SOCIALIZATION AND THE PROBLEM OF IMPRINTING

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Imprinting is a well documented phenomenon. The published literature is vast and variable. There exist, however, several comprehensive and/or critical reviews : Moltz (1960), Thorpe (1961), Hinde (1961, 1962), Fabricius (1962), Denenberg (1962), Scott (1962), Salzen (1962), Sluckin (1962, 1965, 1970), Etkin (1964), Bateson (1966), Klinghammer (1967), Immelman (1972), Connally (1972), Hess (1959 c, 1973).

Unfortunately, imprinting-like phenomena in higher mammals, especially in primates, have usually been referred to in passing only, or more frequently, completely omitted. Likewise, the perceptual prerequisites for imprinting have been singularly underemphasized. Furthermore, extrapolations from highly artificial experiments have too often been considered as equivalent, in terms of their implications, to naturalistic observations. This review has therefore been undertaken in an attempt to meet the afore-mentioned deficiencies.

Though imprinting classically deals with the acquisition of filial (1) and sexual behaviours, it is to be noted that early learning, especially when the result of a sensitive imprinting-like period, is of particular interest to those ecologists who wish to clarify the mechanisms determining the selection of habitat (Klopfer, 1962, 1970), of food choices and perhaps even of social communication signals (Hess, 1973).

## I. THE PROBLEM OF IMPRINTING

Lorenz (1935) was struck by the fact that incubator hatched goslings reacted to him as though he were the natural parent

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(1) Filial : The attachment or social relationship formed by an offspring or immature organism to its caretaker(s).

figure. That is : they followed him, tried to remain close to him and showed signs of distress if they could not. Moreover, adult jackdaws which he had reared by hand frequently attempted to court him. Obviously, something had gone wrong. A human being is an inappropriate maternal or sexual object for a bird. One implication of the « mistake » was that at least for certain species neither recognition of the mother nor choice of sexual partner was innate in the sense of « built in before birth ».

Naturalistic experiments indicate that goslings, ducklings and many other nidifugous species of birds have a propensity to follow the first moving object present after hatching. In the average expectable environment, i.e., the environment of evolutionary adaptedness (Bowlby, 1969), this moving object would most probably be the mother bird ; an egg which had not been incubated (by a hen) would not hatch, therefore, the presence of the hen at the time of hatching would be highly likely, if not inevitable, as far as most chicks, ducklings or the like are concerned. Laboratory hatched birds, by contrast, can be observed to follow and later in life to attempt to court such diverse objects as a ball, a cube, a wooden decoy, or similar inappropriate objects. Thus it appeared to Lorenz that the mere presence of a moving object was sufficient in itself for newly hatched birds to learn its characteristics and to become attached or imprinted to it.

In contrast to other types of learning, imprinting seemed to be the result of a process which, during a relatively brief period early in an organism's development, restricts social responses/preferences to that class of stimuli/objects first eliciting them. Imprinting could therefore be described poetically as a form of « acquired instinct », i.e., certain types of responses are built into an organism as a result of experience in a way such that once the « building-in » has taken place, it is impossible thereafter to distinguish them from responses inherited genetically. Imprinting would therefore be essentially different from ordinary learning in so far as it could neither take place just any time in an organism's ontogenesis, nor be forgotten. Unlike classical or operant conditioning, no practice was deemed necessary. Moreover, there was no reward in the conventional sense of the word. Instead, imprinting was assumed to be the direct result of an intrinsic propensity for young birds to follow a moving object. In fact, Lorenz considered the moving object to trigger an *Innate Releasing Mechanism* which elicits the following and brings about the preference for or bound to the object followed. Evolution was described as having provided *Sign-Stimuli* which, via the Innate Releasing Mechanism, release specific built-in responses in a way analogous to a key fitting into and opening a lock. Metaphorically, imprinting could be viewed as a form of phylogenetic adaptation, i.e. pre-adaptation on the ontogenetic level as

a result of species selection. In fact, Lorenz has listed four characteristics which he considered to be specific to imprinting : (i) it has irreversible effects, (ii) it takes place only during a critical period which is limited in time, (iii) it is supra-individual learning, and (iv) it influences patterns of behaviour which are yet to develop in an organism's repertoire. He was most specific however that imprinting involved the formation of « preferences » and not merely of behaviour (1).

Zoologists and psychologists the world over were impressed with the possible importance of Lorenz' theorizing, though many were highly critical of his experimental procedures, or what they considered to be a lack of them.

Therefore, laboratory experiments were undertaken in an attempt (i) to examine the actual parameters which influence imprinting, (ii) to determine the dimensions of the critical period, (iii) to assess the later or long term effects of the early experience in question, and (iv) to ascertain the generality of the phenomenon.

## II. EXPERIMENTAL MANIPULATION OF FILIAL AND OF SEXUAL IMPRINTING IN NIDIFUGOUS (PRECOCIAL) BIRDS.

When Ramsey and Hess (1954), compared the strength of imprinting and the effort expended by ducklings in following a wooden decoy, they discovered a positive relationship between strength of imprinting and amount of effort expended in following the object imprinted to. The harder a duckling « worked », the better it imprinted. Experimental birds were induced to run up inclined planes and to jump hurdles in order to keep in contact or proximity with a wooden decoy. Hess (1957, 1958, 1959 a, 1959c, 1962 a) formulated a « law of effort » which predicted the strength of imprinting to vary as a direct function of the effort expended during the critical period. He even hypothesized that it was effort on part of the subject which « caused » imprinting to take place.

Experiments by other researchers have not substantiated Hess's theorizing. To the contrary, Baer and Gray (1960), were able to imprint chicks to guinea pigs which were separated from the chicks by glass so that following was impossible. Moltz (1963) restricted the movements of ducklings by putting them in boxes ;

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(1) In contrast to other types of learning in which an organism changes the use or application of already existing structures, imprinting was considered to involve the formation of structures. In classical psychoanalytic language, it could be conceptualized either (1) as the formation of the Ego and above all of the process of cathexis in contrast to introjected objects and/or memories which later would be contained in the Ego, or (2) as the establishment of an « instinctual » object or « drive-object » and its mental representation (phantasy).

nonetheless, they still imprinted. Jaynes (1958 a), and Smith (1962) obtained similar results. Obviously, movement of the subject is not a sufficient factor. However, the fact that effort is not prerequisite does not affect the finding that it may aid or strengthen imprinting. What must be distinguished are the minimally sufficient and the optimal conditions for imprinting. Movement of the subject appears to be an optimal condition, whilst orientation of the subject the minimally sufficient condition.

As has been said, it was originally thought that imprinting could only occur if a moving object were present at the critical time (Lorenz, 1935). However, James (1959, 1960 a, 1960 b) and Smith (1960) were able to imprint newly hatched birds to intermittent stimuli which were two-dimensional. Moreover, Gray (1960) successfully imprinted chicks to a static figure. Compatible results were found by Sluckin (1960, 1962). Therefore, it can be concluded that neither real nor artificial movement of the object (i.e. stimulus to be imprinted to) is necessary. In other words, heterogeneously patterned stimuli constitute the minimally sufficient conditions for imprinting to take place as regards the environment. An intermittent source of light or an actual animal would, of course, provide more optimal environmental conditions. However, the mere presence of stimulation, of something to orientate to, seems to be enough.

Hinde (1961) listed the number and type of different objects which could be imprinted to. He emphasised that in the young bird there is « initially a weak tendency to respond to a fairly wide range of objects and sounds ». This tendency is then « primed by practice and conditioned to the characteristics of the particular objects which have elicited the response ». Initially, the tendency to flee is low, at the same time, the tendency to follow is strong. Later, when the tendency to flee becomes stronger, it is more likely that a new object will be run away from rather than approached. Hinde stressed that « imprinting to an object involves not only an increased specificity in responsiveness and an increased tendency to respond to the object when it is present, but also an increase in the intensity of appetitive behaviour shown when the object disappears ».

Tolman (1963) suggested that increased learning ability (as a basis for a sensitive period) in chicks may be due to increased arousal. He observed that wakefulness increased dramatically during the first 12 hours, after hatching. Further evidence comes from developmental changes in the electro-retinogram of chick embryos (Peters, Vonderahe and Powers, 1958). Thus Sackett (1963) hypothesized that, if vision is a prerequisite for minimal filial imprinting, then the sensitive period, as indicated by an increased readiness to learn, might be the result of the developing organization of the retina. In fact, Paulson (1965) has

offered electro-physiological evidence that the onset of the sensitive period for filial imprinting in ducklings comes as a result of the rapid development of the visual system.

Immelmann (1972) considered it possible that « the great sensitivity early in life and the great stability of early experience could be correlated with the formation of new synapses, and the end of the sensitive period could be associated with the end of mitotic activity ». A similar formulation comes from Hebb (1949), who contrasted primary learning and the formation of cell-assemblies with secondary learning.

Bateson (1972), obtained direct evidence for endogenous changes, i.e. maturation of the nervous system, as a general factor involved in the onset of imprinting in chicks. « RNA synthesis increases significantly from 21 days to 21½ days after the beginning of embryonic development. Over the same period the time before a chick approaches a flashing light significantly decreases. » Nonetheless, imprinting can occur prior to three weeks embryonic age if chicks receive appropriate visual stimulation (Haywood, Zimmerman, 1964 ; Diamond, 1968). Obviously, the development of the nervous and perceptual systems not only presupposes many general environmental variables but also can be (in)directly influenced by specific experimental variables.

Horn, Rose and Bateson (1973) offer experimental proof that the morphological, physiological and biochemical properties of the C.N.S. are modified by experience. The most striking results were obtained from imprinting of split brain chicks which had one eye covered during imprinting to an intermittent visual stimulus, thus only one half of the brain was « imprinted ». « Incorporation of [<sup>3</sup>H] — uracil into macromolecules was 15.2 per cent higher on the trained side of the forebrain than on the untrained side. No such differences were found in any other region of the brain » (Horn, Rose and Bateson, 1973). « The forebrain roof has been implicated not only as the site of rapid incorporation of uracil into presumed RNA during an imprinting procedure, but also as the region where the activity of RNA polymerase and incorporation of lysine into presumed protein first increases after imprinting » (Bateson, Horn and Rose, 1972 ; Haywood, Rose and Bateson, 1970).

In a second experience (Bateson, Rose and Horn, 1973), domestic chicks were trained on the first day after hatching for 20, 60, 120 or 240 minutes ; on the second day, all were retained for 60 minutes. « The greater the chick's experience on the first day, the lower the rate of incorporation of tritiated uracil into macromolecules in the anterior part of the forebrain roof on the second day. Such effects were not found in other brain regions, nor in any brain region of chicks that received similar treatment on the

first day but were not retrained on the second » (Bateson, Rose and Horn, 1973).

Obviously the onset of the sensitive period for filial imprinting must be at least in part accounted for in terms of both specific and general neurological and visual development.

Various theories have been proposed to explain the termination of the sensitive period for filial imprinting. Kaufman and Hinde (1961), have classified these into four categories :

- i) End of low anxiety state
- ii) Maturational end of sensitivity
- iii) Inhibition through socialization
- iv) Growth of timidity and/or fear

Moltz (1960), postulated newly hatched chick to be in a state of low anxiety which then becomes associated with a moving object. On the one hand, there is no empirical evidence that newly hatched chicks are in a state of low anxiety (Salzen and Tomlin, 1963). On the other hand, such an explanation is unnecessary, if not even untestable. Ultimately, it derives from an assumption that all learning must be reinforced or associated with drive-reduction. It is superfluous, however, to postulate hypothetical drives when none are evident. One of the salient characteristics of imprinting has always been the lack of rewards in the conventional sense.

Sluckin (1965), pointed out that if the concept of maturation is interpreted narrowly, it cannot be excluded as a general terminating or limiting factor. It is self-evident that no maturational period can be indefinitely extended. No higher organism is infinitely malleable. Thorpe (1961), for instance, has shown that the sensitive phase for learning of the species song in the chaffinch can end without imprinting having taken place. If, however, the concept of maturation is interpreted more widely, then it cannot be considered a sufficient factor. Studies by Guiton (1958, 1959), by James (1960 a, 1969 b), and by Moltz and Stettner (1961), offer clear evidence that the «period of responsiveness can be appreciably extended» by a variety of experimental manipulations. Obviously, it is not a question of either environmental influences or maturation but of an interaction of both.

Inhibition through socialization as a terminating factor implies that imprinting continues so long as no firm imprinting has taken place. This formulation can be only partially tenable. As quoted above, Thorpe (1961) demonstrated that the termination of a sensitive period could take place without the learning of an incompatible response. Nonetheless, it is obvious that the formation of «approach and following responses to any stimulus configuration tends to inhibit approach and imprinting to new figures » (Sluckin 1965). Like maturation, inhibition through socialization

can be said to contribute to the termination of the sensitive period in certain circumstances, though neither can be said to be a sufficient explanation in itself.

Scott's (1962) account for sensitive periods in terms of differentiation and organization is quite similar to the socialization hypothesis : « once a system becomes organized, whether it be the cells of the embryo that are multiplying and differentiating or the behavior patterns of a young animal that are becoming organized through learning, it becomes progressively more difficult to reorganize the system. That is, organization inhibits reorganization. Further, organization can be strongly modified only when active processes of organization are going on » (1).

It has long been accepted that fear of a figure inhibits approach. For this reason, fear has been widely accepted as a terminating factor (Hess, 1957, 1959 b ; Hinde, 1955 b). Brosset (1971) however, was able to produce imprinting in Galapagos turtle doves, a species which does not manifest « typical » fear responses. Therefore, it seems unlikely that fear can be considered as a sufficient factor to explain the termination of imprintability. First of all, fear is not a primary response. Moltz and Stettner (1961), have shown it to be dependent on, amongst other things, strangeness. Since it takes time for stimuli to become familiar it must also take time before non-familiar stimuli can be perceived as strange (Schaller and Emlen, 1962). « Whether maturation is or is not an important factor in the development of fearfulness, the tendency to flee from strange objects must be acquired in so far as "knowledge" of what is strange is acquired » (Sluckin, 1965). Strangeness or non-familiarity as such cannot account for « fearfulness » since Galapagos turtle doves are capable of discriminating between familiar and non-familiar and yet do not manifest fear. Therefore, in so far as fearfulness is dependent firstly on the development of the ability to discriminate strangeness and secondly on an attachment to or preference for the familiar, so can it be considered to be a special aspect of socialization : in other words, fear as determining factor is but a derived or special aspect of attachment. If, however, fear is considered to be a « motivational » factor, then it can be a secondary aspect of « general development ».

Be avoidance or flight taken as a criterion of fear, then birds can be experimentally imprinted to a « feared » object (Fabricius, 1951 a ; Jaynes, 1957 ; Weidmann, 1958 ; Guiton, 1959 ; Sluckin and Salzen, 1961). However, in the natural environment of evo-

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(1) Compatible neurological evidence comes from Spenelli, Hirsch, Phelps and Metzler (1972) who found that in the visual cortex of a kitten, once the receptive field of a neuron has been modified, it is not changed by subsequent visual experience.

lutionary adaptedness, fear definitely appears to contribute to the termination of the sensitive phase and to be paradoxically a result both of the familiarity and of the preference formed in that phase ; that is : fear is a result of and at the same time a factor contributing to the termination of imprinting.

A similar explanation has been put forward by Salzen (1962), and by Sluckin (1962), who suggest that « imprinting ends as a result of imprinting ». Though this statement may sound circular, the implication is that imprinting is, in the natural environment (i.e., environment of evolutionary adaptedness), an auto-terminating process. That is : there are an ensemble of events which tend to preclude the formation of alternative attachments ; these events are (i) the limitations of maturational flexibility, interacting with environmental influences, (ii) the awareness of novelty and the growth of fear, (iii) the difficulty of redirecting onto a strange and/or new object a response already exclusive in its orientation. In short, there appears to be « a gradual change in the probability that imprinting will occur, depending on the conditions of rearing » (Kaufmann and Hinde, 1961 ; King, 1968).

Vidal (1971 a) reared chicks with a hen for the first month, after which they were removed, isolated and given imprinting training. In the imprinting situation, the behaviour of these month old chicks resembled that of newly hatched : their following response and dependance on the model for thermal regulation seemed regressed to an « infantile » level. Since a bond between the chicks and the model was established in spite of the previous experience with a hen, Vidal concluded that month old chicks are still dependant on their environment for orientation of behaviour. The redirection of attachment, however, should not be confused with the formation of attachment. The later is presupposed by the former. Slazen and Sluckin (1959 b), observed that the duration of imprinted attachments were quite short under certain experimental circumstances. Jaynes (1958 a) also found this to be the case. Thus, Sluckin (1965) and Guiton (1961) concluded that « stability of attachment appeared to be a function of the extent of initial experience ». In other words, imprinting must be considered a more-or-less and not an all-or-nothing phenomenon and therefore not irreversible in the strict sense of the word, though frequently quite stable.

In a « natural » setting, nonetheless, filial imprinting appears to be extremely durable, firstly because the imprinted object is « appropriate » in terms of its evolutionary function, and secondly, because the stimulus parameters influencing « natural » imprinting are maximal or optimal in effect, whilst those influencing « experimental » imprinting are « minimal » and/or « artificial ». It should not be surprising therefore that arti-

fically induced filial behaviour is neither as complete as, nor as stable as « natural » filial behaviour.

Lorenz (1935) considered courtship fixations, like filial attachment, to be a result of an imprinting process. Immelmann (1972) has pointed out, however, that there is no justification for treating the data from experiments on filial imprinting as if they applied to sexual imprinting. Both Lorenz and Immelmann emphasized that in both filial and sexual imprinting a preference is acquired and not merely behavioural responses. Many researchers, however, have misinterpreted Lorenz' original formulation to imply that imprinting must result in an exclusive and invariable sexual response. Even though courtship fixations must be defined on the behavioural level and are reversible on that level (Guiton, 1962 ; Fisher and Hale, 1957 ; Wood-Gush, 1958), the behaviour in question may well be nothing more than the acceptance of substitute sexual objects. As is obvious, preferences cannot always be directly inferrable from overt behaviour, especially when there is no possibility of choice. If, for instance, a starving bird eats food which it would not otherwise touch, one has no legitimate bases for assuming that it has changed its food preferences.

Even when the existence of a sensitive period is either undelineated or even uncertain, the existence of a special, stable form of early learning can be legitimately inferred from cross-species fixations. Sexual attachments to humans are well attested for numerous nidifugous species : the lesser white fronted goose (Steven, 1955), the domestic turkey (Raber, 1948 ; Schein, 1963), the red jungle fowl (Hess, 1959 c), the domestic fowl (Fisher and Hale, 1957 ; Schein and Hale, 1959 ; Guiton, 1962), and the corn-crake (Heinroth and Heinroth, 1924-1933).

Painstaking experiments by Schutz (1963, 1965 a, 1965 b, 1968, 1970, 1971) have demonstrated that in ducks the sensitive period for sexual imprinting is temporally coincident neither with that for filial, nor with that for the formation of gender preferences. In the mallard, the onset of sensitivity for sexual imprinting is 5 to 9 days after hatching and lasts for about 50 to 70 days (Schutz, 1965 a). Beyond 80 days of age, most birds are no longer imprintable sexually. The sensitive phase for homosexual fixations (gender preferences) comes even later and may last for as long as three months.

Andrew (1966) was able to elicit copulatory movements to a human hand in 2 days old chicks. Vidal (1971 b), however, was able to elicit similar behaviour to a stuffed model of a conspecific only on the 4th day of after. Since isolated cockerel chicks were slower to manifest precocial sexual behaviour to the model, Vidal suggested that imprinting or fixation might be prerequisite for orientation of precocial copulatory movements. In the « natural »

environment, such behaviour is checked by the active avoidance of the sibling chicks towards whom it is directed.

In a subsequent article, Vidal (1973) noted that in chicks, some form of sexual fixation could be established during the classical period for releasing the following response. Thus he did not feel that the results of his particular experiment justified the separation of sexual and filial imprinting in chickens, though he emphasized that his experimental design was extremely different from that of Schutz'.

Experimentally induced sexual fixations may be long lasting, though are frequently not as stable as naturally occurring fixations. As one would expect, and as experiments have demonstrated, differing experimental conditions are associated with behavioural results correspondingly different from « naturally » occurring appropriate and/or fixated reproductive behaviour. Free-living or wild ducks are never minimally imprinted, whilst to the contrary, the majority of experimental birds are.

Sexual imprinting may be reversible or irreversible according to the criteria employed, according to the age of the bird when reversing is attempted, and also according to the reversing procedures undertaken. None the less, sexual preferences, even « abnormal », frequently tend to be stable in nidifugous birds.

It will be remembered that Lorenz proposed what he considered to be the four criteria definitive of imprinting. As has been shown, there is an empirically definable phenomenon which is now generally referred to as « imprinting » ; however, Lorenz' original criteria must be modified in light of the above-cited experimental evidence.

Firstly, the concept of irreversibility is applicable only in certain cases, i.e., imprinting is not irreversible as such. Nonetheless, imprinted choices frequently remain quite stable. Secondly, there is no *absolute* « critical » period as Lorenz had claimed, though most ethologists agree that there is a *sensitive* period. Hinde (1962), however, would consider it best to speak of the sensitive period as an « optimal » period. Moreover, there appear to be at least three sensitive or optimal periods. Sexual and filial imprinting, for example, are not temporally coincident as Lorenz had thought. Thirdly, concerning super-individual learning, it is obvious that sexual responses are directed to an entire species, whereas filial attachments are exclusively to one or two individuals and thus not supra-individual. No one can contest Lorenz' position that whilst a young bird is learning the characteristics of its individual parent(s), it is simultaneously learning the general characteristics of all members of the species to which the parents belong. Fourthly, Lorenz considered imprinting to influence responses yet to develop in an organism's repertoire. Though the formulation is defensible, it would be

better to revise it as follows : experience during a sensitive or optimal period constitutes the beginning of an ontogenetic process which will be influential in determining the manifest form that later behaviour will take.

### III. — FILIAL AND SEXUAL IMPRINTING IN ALTRICIAL BIRDS

It has been alleged that imprinting is difficult to produce in altricial birds, however, an inability to produce imprinting experimentally is no justification for concluding it does not function in the « natural » environment. The evidence of courtship fixation in several species would indicate that a similar process of socialization probably is taking place. Klinghammer (1967) lists 28 different species in which varying degrees and types of « imprinting » are documented :

TABLE I

#### *Altricial Birds in which Sexual Imprinting has been demonstrated*

Sexual fixations to humans have been noted for species whose vernacular name is followed by an asterisk \* ; where no published reference is available, the date given by Klinghammer has been put in parantheses.

| <i>Passeriformes</i>  |           |                    |                                       |
|-----------------------|-----------|--------------------|---------------------------------------|
| Lorenz                | 1935      | Jackdaws *         | <i>Corvus monedula</i>                |
| Nicolai               | 1956      | Bullfinch *        | <i>Pyrrhula pyrrhula</i>              |
| Immelmann             | 1965      | Zebra finch *      | <i>Taeniopygia guttata castanotis</i> |
| Kear                  | 1960      | Hawfinch *         | <i>Coccothraustes coccothraustes</i>  |
| Nicolai               | 1964      | Widow birds        | Viduinæ various sp.                   |
| Gwinner               | 1964      | Raven *            | <i>Corvus corax</i>                   |
| Klinghammer           | (1961)    | Crow *             | <i>Corvus brachyrhynchos</i>          |
| <i>Psittaciformes</i> |           |                    |                                       |
| Hellman               | 1954      | Budgerigar *       | <i>Melopsittacus undulatus</i>        |
| Lorenz                | 1955      | »                  | »                                     |
| Klinghammer           | (1964)    | Senegal parrot     | <i>Poicephalus s. senegalensis</i>    |
| <i>Ciconiformes</i>   |           |                    |                                       |
| Portielje             | 1921      | American Bittern * | <i>Botaurus stellaris</i>             |
| O. v. Frisch          | 1957      | Purple Heron *     | <i>Ardea purpurea</i>                 |
| Löhrl                 | 1961      | White Stork *      | <i>Ciconia ciconia</i>                |
| <i>Strigiformes</i>   |           |                    |                                       |
| Heinroth O. & M.      | 1924-1933 | Eagle Owl *        | <i>Bubo bubo</i>                      |
| <i>Falconiformes</i>  |           |                    |                                       |
| Waller                | 1942      | Peregrine Falcon * | <i>Falco peregrinus</i>               |
| Mohr                  | 1960      | Sparrowhawk *      |                                       |

### *Columbiformes*

|                       |           |                   |                                             |
|-----------------------|-----------|-------------------|---------------------------------------------|
| Craig                 | 1914      | Ring Dove *       | <i>Streptopelia risoria</i>                 |
| Whitman               | 1919      | Doves & Pigeons * | Columbidae                                  |
| Goodwin               | 1948-1958 | Pigeons & Doves * | Columbidae                                  |
| Warriner              | 1960      | King Pigeons      | <i>Columba</i> sp.                          |
| Heinroth K.           | (1961)    | Pigeon            | <i>C. livia</i>                             |
| Nicolai               | 1962      | Mourning Dove     | <i>Zenaidura macroura</i>                   |
| Lade & Thorpe         | 1964      | Doves             | <i>Streptopelia</i> sp.                     |
| Klinghammer<br>& Hess | 1964      | Ring Doves        | <i>S. risoria</i>                           |
| Klinghammer           | (1966)    | Pigeon            | <i>Columba livia</i>                        |
|                       |           | Mourning Dove     | <i>Zenaidura macroura</i>                   |
|                       |           | Grayson's Dove    | <i>Zenaida graysoni</i>                     |
|                       |           | Dwarf Turtle Dove | <i>Streptopelia</i><br><i>tranquebarica</i> |
|                       |           | Spotted Dove      | <i>S. chinensis</i>                         |

Whilst a newly hatched nidifugous chick is precocious, can see and follow, the reverse is the case with most nidicolous nestlings, which are altricial. As Klinghammer (1967) pointed out : « the adaptive requirements to which a newborn altricial bird is exposed and to which a particular species has become adapted during the course of evolution are substantially different from those that precocial animals encounter ».

If one accepts Bateson's (1966) definition of imprinting as a process (a) which « restricts social preferences to a specific class of objects » and (b) of which the behavioural manifestations « become restricted to the stimuli » first eliciting them, then there is no reason to consider socialization in altricial birds as categorically different from that in precocial already described. If the afore-mentioned contributions of Tolman (1963), of Peteres, Vonderache and Powers (1958) and of Sackett (1963) are relevant to the development of a sensitive phase for filial imprinting in precocial birds, then one would expect that differences in the level of visual and locomotor maturity of newly hatched non-precocial birds would account at least in part for corresponding differences in the ontogeny of socialization.

As is obvious, nidicolous birds do not usually leave the nest until able to fly, by which time socialization has definitely taken place. The lack of an easily observable behaviour such as following makes it difficult to discern the temporal limits of a sensitive period for socialization. Nice (1943, 1950), however, offers indirect evidence for a sensitive period in the socialization of the song sparrow. The newly hatched nestling is blind and almost naked. At 5 to 6 days, the eyes open, and a day or so later, the first fear reaction appears. Between 10 and 16 days of age, the young bird leaves the nest for the first flight. Nice found that the sparrow can form a social relationship to a human if it is taken from the nest at about or before 10 days of age, i.e. before

the fledgling stage. Similarly, Lorenz (1935) has shown that jackdaws will become strongly attached to human if hand-rearing begins just at the time when the bird is ready for flight.

In the ringdove, a period optimal for the formation of filial attachments to humans was discovered to lie between the 7th and 9th days after hatching (Klinghammer and Hess, 1964). Filial attachments in ravens, however, appear to be a function of mere exposure (Gwinner, 1964). Furthermore, experiments with bullfinches (Nicolai, 1956) and mourning doves (Klinghammer, 1967) indicate a sensitive period for the formation of sexual orientation in these species.

Brosset (1971) was able to demonstrate both filial and sexual imprinting in the ring- and mourning- doves (*Nesopelia galapagoensis*, *Streptopelia risoria*, *S. senegalensis*, *Zenaida macroura*). Though sexual responses were modifiable, the effects of early experiences were never completely eradicated. Homosexual pairing were also observed as a result of rearing conditions.

Obviously, species with different ontogenetic patterns manifest differences in the process of socialization on a phenomenological level.

#### IV. — FILIAL BONDING AND SEXUAL PREFERENCE IN MAMMALS

Hinde (1961) pointed out that in many aspects the development of the relationship between mammalian mother and infant resembles that occurring in birds; he stressed, however, that similarities are probably the result of similar selective forces, and not necessarily of similar mechanisms. Obviously, similar selective forces have undoubtedly « operated in groups other than birds ». In other words: « many of the characteristics of imprinting in birds can be understood in functional terms, and similar learning processes are found in functionally similar contexts in other groups ». Thus, Hinde (1963) demarcated certain similarities of development across species: first a general responsiveness, then a specific responsiveness to the parent or caretaking figure, next the emergence of fear and later aggression. He pointed out (1963) that the result of the filial imprinting process is that an immature organism « learns to recognise its mother as an individual, and [that] a number of discrete responses made by the young animal... become integrated onto one object ».

Obviously, it is fruitless to argue over the use of terms. Whether something *is* imprinting, or *is not*, can all too easily degenerate into a verbal argument. The label is not important. What is important is how two different species are similar and/or different as regards a particular behaviour or function. Hence it is best to consider socialization (both filial and sexual) via imprinting on the functional and phenomenological or naturalistic levels

as it occurs in birds if it is to be compared with socialization in mammals.

The first point to be emphasized is the difference observed between precocial and altricial birds : mammals as well are born at different stages of maturity/immaturity. In particular, it was noted that in altricial species, imprinting occurs without following. In other words, learning during following, and not following per se, is the essential factor.

Shipley (1963) has demonstrated that an imprinting-like process exists in guinea pigs, a precocial mammal. Piglets isolated from four hours after parturition followed a wooden block later on that same and subsequent days, whereas controls did not. Though Shipley did not delimit the boundaries of a sensitive period, it appears that experience before 5 days of age, though effective, is not sufficient, whilst after a month, socialization becomes more difficult to establish. As in precocial birds, the actual timing and nature of the early social experience correlates directly with the nature of and stability of later social choices.

Other researches with guinea pigs have yielded similar results (Beauchamp and Hess, 1971 ; Gaston, Stout and Tom, 1969 ; Harper, 1970 ; Sluckin, 1968 ; Sluckin and Fuller, 1969).

Kunkel and Kunkel (1964) found that hand-reared guinea pigs often directed sexual behaviour towards humans. Beauchamp and Hess (1971) noted that both male and female guinea pigs reared with chicks « preferred » the foster species to their own. At puberty, however, these male guinea pigs began directing their sexual responses towards females of their own species also, though still continued to court and mount chicks.

Beauchamp and Hess (1973) observed that male guinea pigs « weaned during the first week after birth were more likely to direct sexual responses to members of other species than were animals weaned later ». As would be expected, « social experience with a member of another species was usually necessary for individuals of that species to elicit sexual behaviour... » from the guinea pigs in question. A process in some way similar to sexual imprinting may be involved.

Scott (1945) reared a ewe from birth for 10 days. At three years of age this female still was unsocialized to her own species. Collias (1956) conducted experiments with sheep which indicated that « the critical period for socialization is short and sharply limited, but limited by the behavior of mother rather than that of the lamb ». Similar results were obtained by Herscher, Richmond and Moore (1963).

Evidence for inter-species fixations betraying sensitive periods in socialization also comes from other ungulates. Inter-species following in new born calves was recorded for bison (Garretson, 1938), for the African buffalo calf (Berger, 1910) for the zebra

and wildebeest (Heck, 1930), for various wild sheep (Hediger, 1950 ; F. G  the, 1939).

Hodge (1936) reported the hybridization of alpacas and vicu  as to be possible only by cross species fostering of a newborn vicu  a to an alpaca mother. Such a vicu  a, when adult, would then mate with alpacas, which otherwise would not occur. When Kuo (1938) reared kittens in the presence of rats, he discovered that the adult cats so reared did not become rat-killers. In short, no cat could be tempted to kill the same species of animal with which it has been reared. This finding as a result of cross fostering is more than vaguely reminiscent of imprinting.

Scott (1962) compared the ontogenesis of and socialization in puppies and in song sparrows (Nice, 1943), both of which are non-precocial :

TABLE II  
*Developmental periods in the puppy and the song sparrow*

| PUPPY              |                          |                  | SONG SPARROW        |                         |                               |
|--------------------|--------------------------|------------------|---------------------|-------------------------|-------------------------------|
| Name of Period     | Length Period of (weeks) | Initial Event    | Name of Period      | Length of Period (Days) | Initial Event                 |
| I. Neonatal ...    | 0-2                      | Birth nursing    | Stage 1 (nestling)  | 0-4                     | Hatching gaping               |
| II. Transition ..  | 2-3                      | Eyes open        | Stage 2             | 5-6                     | Eyes open                     |
| III. Socialization | 3-10                     | Startle to sound | Stage 3             | 7-9                     | Cowering-first fear reactions |
|                    |                          |                  | Stage 4 (fledgling) | 10-16                   | Leaving nest-first flight     |
|                    |                          |                  | Stage 5             | 17-28                   | Full flight                   |
| IV. Juvenile ....  | 10-                      | Final weaning    | Stage 6 (juvenile)  | 29-                     | Independent feeding           |

A neonatal puppy is capable of little more than reflex activity ; there is no true social behaviour. The first change towards socialization takes place at about 2 weeks of age, when a puppy's eyes open. Histological examination indicates that a pup's retina is undeveloped at this time and is not completely developed until 4 weeks or shortly there after (Parry, 1953) when tail wagging, an obvious social response, is first observed. At about the third week, when audition becomes functional, brain waves indicating a difference between sleep and alert wakefulness begin to appear, though the visual cortex of the brain does not assume adult form until 7 or 8 weeks.

Obviously, socialization is impossible until perception and

learning are functional. Physiological changes thus prepare the pup for socialization.

The experiments of Scott and Fuller (1965) indicate that the sensitive period for formation of social attachment in dogs lies between the 3rd and 7th weeks ; that is, coincident with the onset of perception, audition and the end of early rapid neuro-physiological development. The optimal period for socialization, however, appears to lie between the beginning of the 5th and 8th weeks, whilst a decline in the ability to socialize is found after that time, coincident with the onset of fear. Evidence for this sensitive phase is extrapolated from the results of intra-species fostering begun at various stages during ontogenesis.

Dogs reared in complete isolation from humans (Scott and Fuller, 1965) seem very wolf-like when adult. It is now even accepted that the dog is a domesticated relative of the wolf, domestication being possible as a result of sensitive periods which underlie socialization and which therefore make inter-species attachments possible. Supporting evidence of an anecdotal nature comes from the hand-rearing of wild canids (Fox, 1972).

Allyn (1948) recounted personal experiences with two pet red foxes, hand-reared from the neonatal period. Allyn and Allyn (1974) reported further observations on the two foxes in question :

« June and Junior were brought to us after their mother had been killed whilst raiding a hen-house. They were very small at the time and we had to feed them by hand with a baby bottle. Our dog, Peggy, a small shephard, had in her way adopted them. She played with them and they with her as if she were their natural mother. We have films of this. One in particular shows the foxes and Peggy running around in circles, and it is hard to tell whether the foxes are chasing her or she them.

« We kept both foxes together in the kitchen in a large box until they were old enough to be outside. We then let them run loose until they got destructive. Any item of cloathing laid on the back steps, they promptly took and hid. They ran through the gardens, knocking down plants, etc. They even chased away any strange dog wich happened onto the property, and they did this together. We finally had to put them on leads which they accepted.

« Eventually, we thought it best to give them to a small public zoo. We did not think it wise to turn them loose in the wild because *they had absolutely no fear of people* and really would have been killed before they would have learned to fend for themselves. They were well treated at the park, but some... man stuck his lighted cigar through the wire of the cage into Junior's eye. He was blinded and his trust in mankind was destroyed. From that time on, he stayed away from the fencing where people stood and snarled at them. A year after the "accident", your sister Alma went into the cage. Junior remembered her in spite of his bad experience. Alma put him on a lead and took him for a walk. »

From this description, it is safe to assume that like the wolf, taming of the fox is possible if begun early enough. Though

June and Junior were destructive in a « non aggressive » sense, they were manageable by humans, either through the use of the social bond, or through discipline. And it is to be noted that an animal will accept discipline only from its master, otherwise it reacts by defending itself.



Figure 1. — American gray fox nursing a bird dog.

When the author reared a red fox, he obtained similar results. The animal was hand fed from the neonatal period on, accepted the author as master, and, in a dog-like fashion, followed him around, waited for him by the gate when he went away, and even came voluntarily to sleep in his bed (which was forbidden), hiding under the bed when his mother's footsteps were heard coming up the stairs. The author « adopted » a grey fox as well (fig. 1). This latter animal was at first hostile to humans, though it had not yet been weaned when the author got it. After a few days of regular feeding and gentle handling, however, it became quite docile. One occasion before weaning, this grey fox discovered a bird-dog nursing her pups and advanced carefully ; when the bitch gave no opposition, it joined in. Both the grey and red foxes accepted the lead and enjoyed being played with. In fact, they « loved » human company and in many respects were more dog-like than fox.

The author's sister (pers. comm.) reared a raccoon, which when adult was turned loose and returned regularly from the forest to the family's hunting cottage, would play on the beds and

accept food. One summer, however, he did not return. No one knows why. He may have been killed.

Another raccoon was hand-reared by the Allyn family (Allyn and Allyn, 1974) and then given to friends. This animal remained playful and affectionate even as an adult and rode around on a wagon or tractor with the workmen of the estate belonging to the friends in question.

The author has had similar results with raccoons, American grey squirrels and skunks, all of which became attached to him personally, though, when adult, such animals might nonetheless become aggressive, sometimes even vicious, if the author attempted to put them in a small cage. In this respect, they differ from dogs who accept being caged, even though they do not enjoy it.

Whilst the author has conducted no formal experiments as such with either foxes, raccoons, squirrels or skunks, his personal experience in rearing many of these animals has convinced him that a process similar to socialization in dogs is involved. Of course, an animal must be taken very young. If, to the contrary, it is taken after weaning, then it will always remain wild and difficult to handle.

There are numerous anecdotal accounts of wild animals reared in captivity, as well as of domestic animals, which direct their sexual behaviour towards their human caretakers (Hediger, 1942, 1954 ; Fox, 1968 ; Hafez, 1962 ; Heinroth, 1970). Unfortunately, no systematic observations have yet been carried out. Nonetheless, it seems plausible that some process similar to sexual imprinting may be involved.

#### V. ONTOGENESIS AND AFFECTIONAL SYSTEMS IN HIGHER PRIMATES, INFRAHUMAN AND HUMAN

The primate parturate (1) is comparable in certain respects, to the altricial hatchling and follows a developmental sequence similar to that described for canines by Scott (1962).

Sluckin (1965) pointed out that a « baby-monkey's initial exposure to its mother ties it to her, much as the chicks early experience ties it to the mother hen », and that the « behaviour of a frightened cloth-mother attached monkey... is strikingly similar to that of a frightened moving-box imprinted chick ».

Harlow (1958) produced strong filial/social fixations in rhesus to inappropriate inanimate objects. When infant monkeys were given a choice between spending time on a lactation wire surrogate or on a non-lactating contact-comfort cloth surrogate, they all « preferred » the cloth to the wire. Obviously drive reduction

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(1) Parturate : a young organism immediately after or a few hours only after parturition.

or reinforcement would not be considered a sufficient concept to explain the attachment of an infant monkey to its mother or mother surrogate. Moreover, the surrogate later came to serve as a « secure base » when the young animal was frightened or anxious.

Every surrogate in question, with the exception of one, had been fitted with an artificial head containing monkey-like features. In the one case, however, the head had been left blank or featureless. When the faceless head was replaced with a faced head, the young monkey who had been reared with a faceless mother surrogate turned the features away from him, so that only the featureless back was visible (Harlow, 1958, 1959, 1960, 1961, 1962, 1963 ; Harlow and Harlow, 1962, 1969 : Harlow and Zimmermann, 1958, 1959). Thus it appears that monkeys become attached to conditions as specific as the maternal face in a way not dissimilar from the visual imprinting described by Thorpe (1961) (1).

According to Harlow, the first 15 to 20 days of a rhesus infant's life are dominated by reflex movement. At the end of this period, infants, when afraid, will run to and cling to the mother or mother surrogate. This use of another member of the same species or of a surrogate as a secure base can be interpreted as a manifestation of a social preference and thus as evidence that something like imprinting has already taken place. According to Harlow (1961, 1963) and Harlow and Harlow (1964) an infant rhesus does not manifest a lack of security, however, in the absence of its mother until 80 days of age, by which time attachment is well established and is synonymous with security. As Bateson (1965) points out, the end of a sensitive phase for learning-socialization does not necessarily mark the point at which learning-socialization is complete.

Mason and Kenney (1974) fostered infant rhesus monkeys to dogs and came to the conclusion that attachments formed during the first ten months to an adoptive mother by rhesus infants were strong, specific and exclusive, but could be redirected if the infant and original mother figure were separated and if a more or less appropriate alternative mother-figure substitute were available. Mason and Kenney emphasized « the fundamental importance of distinguishing between the attributes of strength, specificity, exclusiveness, and permanence (i.e., irreversibility) in discussions of attachment behaviour ». In fact, they felt that these afore-listed attributes vary independently.

As one would expect, the infant rhesus in the Mason-Kenney experiments always « preferred » a familiar dog to either an unfamiliar dog or an unfamiliar monkey. Filial attachments are always to a specific familiar figure and not to unfamiliar members

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(1) See page 249.

of the same species. Two peer-raised monkeys, in fact, « preferred » the dog with which they were living to the original cage mate. The meaning of this « preference », however, is ambiguous. The ontogenesis of the capacity to form attachment must not be confused with the focalization of that already formed attachment onto various or different figures. Studies by the Robertsons (1971) treat in detail the problem of attachment and its redirection.

Observations of stump-tail macaques by the author have convinced him that in that species, as soon as attachment is manifested in behaviour, « defenses » against separation, loss, etc are simultaneously observable. Thus, it is worth emphasizing that attachment and attachment behaviour are not identical. If attachment results from an imprinting-like process which builds in a preference, then this preference may conceivably remain invariable even though the attachment or social behaviour which results from it may vary.

Mason and Kenney did not feel that there was evidence for the hypothesis that the capacity to form *new* filial attachments diminishes sharply during the first two months and disappears by the seventh or eighth month. The essential point which remains to be confirmed empirically is whether there is a delimited sensitive period during which the capacity to form attachments *per se* develops.



Figure 2. — A young female Lowe's guenon suckling a bitch  
(From Bertrand and Bourlière).

Bertrand and Bourlière (in press, fig. 2 & 3) observed a young female Lowe's Guenon (*Cercopithecus campbelli lowei*) which had attached herself to a bitch. The dog allowed the monkey to nurse and cling. When the monkeys was separated from the adopted mother, even if it was placed among a wild troop of its own species, it immediatly rushed to its foster mother, sometimes over a distance of 50 meters, abandoning its own kind.

Bertrand (pers. comm.) reared a young male stumptail by hand for the first 3 months, after which time he was fostered by a pigtail female in the company of other juvenile stumptails. When this male was 6 months old, he exhibited most of the normal species specific social behaviour ; however, he also showed a strong attachment to humans, whereas a young female of same age and same species, though reared by her mother, yet always in the presence of humans, was mre wary of human, at times even fearful, and definitely neither attached nor socialized to humans.

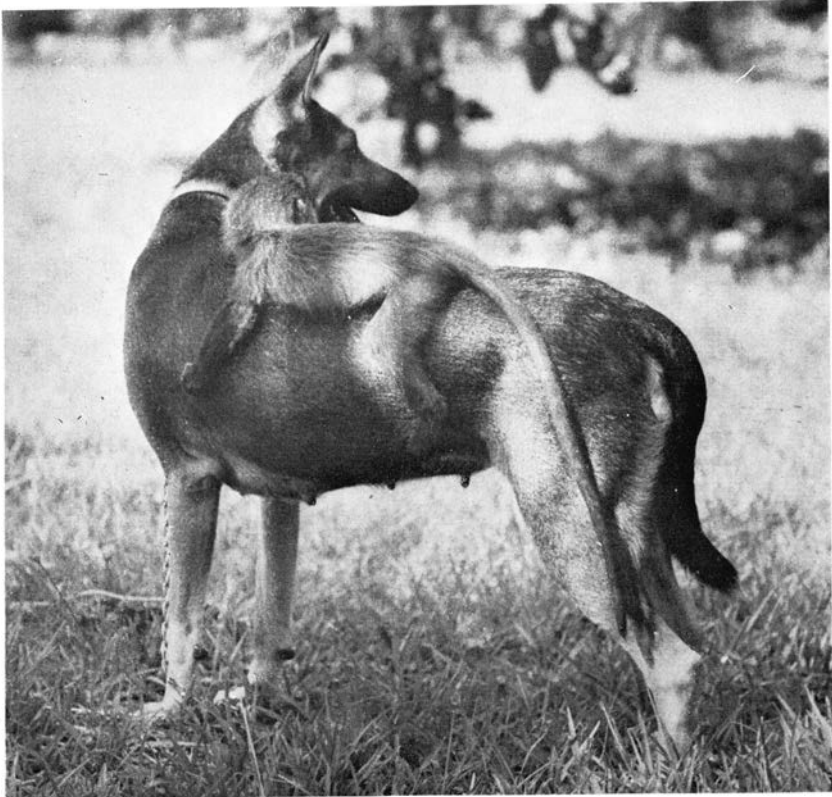


Figure 3. — The same female Lowe's guenon riding on the back of her adopted mother (From Bertrand and Bourlière).

In fact, the young male reacted to separation both from Bertrand and from the author in a way quite similar to the children described by the Robertsons (1971). Subsequently, when a modification of Ainsworth's (1969, 1971) and of Harlow's (1961, 1963) strange situation experiments was carried out with this animal, he used the author as a secure base, seemed to have no disturbance about being separated from his own species so long as the author was present, but when the author attempted to leave the room or was absent, the « little monkey » panicked, though upon the author's return came into his arms and immediately calmed down. When reunited with Bertrand after a separation of several months, this infant macaque appeared at first not to recognize her or even to ignore her ; however, after a couple of weeks, when the strange situation experiment was repeated, he used her likewise as a secure base in contrast to his animal keeper who was also present. It is to be emphasised that this infant stump-tail was, from the age of seven months, more frequently in contact with his animal keeper than with either Bertrand or the author ; nonetheless, even after long separations, this animal still used both Bertrand and the author as a secure base, and not his animal keeper.

Bertrand tamed another animal with similar results. From the age of 6 months, this female stumptail was in close association with humans and other sumptails. Now adult, she is socialized to her own species, though readily comes on the lap of or even in the arms of familiar humans. By contrast, another female of the same species was tamed by the author. This female was jungle born and bred, coming into contact with humans only at the age of 3 years or there about. She could only be approached if isolated from other members of her species and then with great difficulty. As a result of « taming », she is less aggressive to humans than before, though she will only present or come on the author's lap if there are no other stumptails present, with the exception of infants or one less dominant female. The moment she is with her own kind, she refuses to have anything to do with humans, the author included.

Sackett, Porter and Holmes (1965) consider that « a phenomenon perhaps related to imprinting may be operant in primate behaviour ». They showed that rhesus infants reared during the first month of life by humans and then subsequently isolated, « preferred » humans over their own species two to three years later.

Sackett (1970) was explicit that his data « strongly point to the existence of inborn and maturational perceptual and response mechanisms that support the acquisition of social approach behaviours in the absence of specific conditioning and reward factors ».

The possible sensitive period described by Sackett appears to last for months and is not absolute ; subsequent experience can definitely modify social behaviour. In other experiments with rhesus, (Sackett, 1966), evidence was obtained which could be interpreted as indicating the existence of an innate releasing mechanism.

Maladaptive sexual behaviour can also result from early experimental manipulations (Senko, 1966 ; Harlow, 1962). It appears that in primates, mother-infant attachments follow a course of development different from sexual and social, a finding congruent with Immelmann's and Schutz' differentiation of filial, sexual and gender imprinting. There is striking evidence, furthermore, that overly intense mother-infant relationships (fixations) may inhibit social and sexual development.

Chamove, Rosenblum and Harlow (1973) found that newborn infant rhesus monkeys which were reared continuously together manifest an « excessive » amount of clinging and reduced social play during the first 15 months of life. Infants reared for 8 months with a mother only, however, do not manifest this syndrome due to the mother's tendency to reject clinging with increasing frequency after the third month.

In a sister experiment, Chamove (1973) reared infants in pairs, some of which never varied, others of which did, i.e. the partner was changed, though a monkey was only and always with one other peer reared under similar conditions. Chamove observed that « self-play and social play increased and self-clinging and aggression decreased as an increasing function of the number of rearing partners » and that « social clinging was greatest in subjects, reared constantly with the same animal ». The active role of the mother figure is obviously requisit for the development of species-typical social behaviour.

Pets or experimental animals reared exclusively by humans frequently become attached to their caretakers. Such interspecies fostering are well documented for the patas monkey (Bolwig, 1963), the baboon (Rowell, 1965), the chimpanzee (Kellogg and Kellogg, 1933 ; Kohts, 1935 ; L. Hess, 1954 ; Hayes, 1951) and the gorilla (Martini, 1955).

Considering the ample and diverse evidence for sensitive phases which early in life influence the formation of filial and sexual preference in birds, and considering also evidence for similar phenomena in dogs, it would seem not unreasonable that similar processes are operant in higher primates, human included.

In spite of the obvious difference between higher mammalian species, e.g., humans, monkeys, cows, sheep, dogs, etc., there are in the environment of evolutionary adaptedness, nonetheless,

strikingly regular sequences in the development of social attachment comparable on the level of manifest behaviour (1) :

a) Social responses of every kind are first elicited by a wide array of stimuli and are later elicited by a much narrower array, confined after some months to stimuli arising from one or a few particular individuals.

b) There is evidence of a marked bias to respond socially to certain kinds of stimuli more than to others.

c) The more experience of social interaction an infantile organism has with another organism the stronger his attachment to that other organism becomes.

d) The fact that in certain species intra-species discrimination commonly follows a period of attentive staring and listening suggests that « exposure learning » (2) may be playing a part, as is definitely known to be the case for nidifugous birds.

e) It seems probable that there is a period early in life during which attachment behaviour develops most readily.

f) Initially, an infantile organism is socially unresponsive. Then after a certain time, he is not only responsive to familiar figures but more likely to respond to strange figures with fear ; thereafter, the development of attachment to a new figure becomes increasingly difficult.

g) Once an organism has become strongly attached to a particular figure, it tends to prefer that figure to all others, and such preference tends to persist despite separation.

Gray (1958) was the first to entertain the possibility of filial imprinting in humans. He considered socialization to be « essentially the same in most or all species where a social complex is an attribute of survival ». He was most emphatic that theorists should not ignore the « continuity of species » and thus see human development as unique.

Gray designated four periods in humans analogous to those found in birds :

- i) a *pre-learning period* ;
- ii) an *imprinting period*, which he defined as an innate disposition to learn the parent or parent-surrogate ;
- iii) a *period of infantile fear* ;
- iv) a *period of species learning*.

Gray's pre-learning period roughly corresponds to Scott's neonatal period ; the imprinting period is analagous to Scott's transi-

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(1) Adapted after Bowlby (1969).

(2) See page 251.

torial period and the first part of his socialization (1) ; whilst the periods of infantile fear and species learning subsume the rest of Scott's period of socialization.

Gray underlined the perceptual aspects of filial imprinting in contrast to the performance of overt motor responses. Furthermore, he considered the smiling response in human infants to be the motor equivalent of the following response in birds and infra-primate mammals. He speculated that a sensitive period for imprinting in humans begins at about 6 weeks, coincident with the onset of smiling and comes to a close at about six months with the first signs of fear towards strangers.

In a thorough review of Gray's paper, Ambrose (1963) criticized the former on the grounds that his conclusions presupposed more evidence than he was able to present. Nonetheless, Ambrose found a functional equation of smiling and following to be acceptable.

Likewise emphasizing the perceptual bases of imprinting, Ambrose considered the eyes to be « the first figural entity which is consistently perceived by the infant at a time when fixation first becomes possible ». He also stressed that eyes possess the best combination of qualities which attract an infant's attention : figure, albedo, movement and light-reflectance ». In short, he considered the human eyes (in particular, those of an infant's caretaker) to be a social releaser or sign stimulus, i.e. the human equivalent of the first moving object seen in the average expectable environment of a newly hatched bird. Furthermore, Ambrose made reference to Hinde et al. (1956) that « the apparently striking nature of the limitation of the following response to a particular sort of object is due merely to the fact that the animal has become familiar with that object by the time the fleeing response develops ». Ambrose was in agreement with those theorists who consider fear to contribute to the end of the sensitive period in so far as it elicits responses incompatible with following and orientating to the new stimulus. These incompatible responses are : searching, distress, flight and others forms of emotional behaviour.

Using smiling as a functional equivalent of following, Ambrose observed that infants do not consistently respond to a silent moving human face before eleven weeks or so. Three to four weeks later, the readiness to smile to all faces reaches a peak. The strength of this general or indiscriminate responsiveness soon takes a sharp decline, which change was interpreted as due to the beginning of the ability to discriminate strangers' faces from the mother's. With the onset of discriminative smiling, Ambrose designated supra-individual learning and therefore, by implica-

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(1) See pages 223-224.

tion, filial imprinting, to be at an end. That is : learning of the parents' general characteristics is simultaneously learning of the species' general characteristics and thus can be considered supra-individual learning.

Wolff (1963) observed smiling in home-reared American infants, though he made no specific reference to imprinting. He noted that during the first week « smiling could be elicited during

TABLE III

*The relationship between Ainsworth's, Sander's and Bowlby's descriptions of the early developmental sequences in humans is*

| NICE                                                               | SCOTT                                                | HARLOW                                                 |
|--------------------------------------------------------------------|------------------------------------------------------|--------------------------------------------------------|
| STAGE I<br>Nestling<br>Hatching gaping<br>0-4 days                 | PERIOD I<br>Neonatal<br>0-2 weeks                    | PHASE I<br>Reflex<br>0-15 or 20 days                   |
| STAGE II<br>Eyes open<br>5-6 days                                  | PERIOD II<br>Transitional<br>2-3 weeks               |                                                        |
| STAGE III<br>Cowering-first fear reaction<br>7-9 days              | PERIOD III<br>Socialization<br>3-10 weeks            | PHASE II<br>Comfort and Attachment<br>to 60 or 80 days |
| STAGE IV<br>(Fledgling)<br>Leaving nest first flight<br>10-16 days |                                                      | PHASE III<br>Security<br>60 to 80 days on              |
| STAGE V<br>Full flight<br>17-28 days                               |                                                      |                                                        |
| STAGE VI<br>(Juvenile)<br>Independant feeding<br>29 days           | PERIOD IV<br>Juvenile<br>(Final weaning)<br>10 weeks |                                                        |

irregular sleep and drowsiness by a variety of sounds » such as a high pitched brass bell, an Audubon bird whistle and a high pitched voice. By the second week, however, smiling is more effectively elicited by a voice than other stimuli. During the third week, infants give their first « social smile ». Though infants are now capable of smiling when bright eyed and alert, a human voice is still the most effective stimulus. It is only at about the

TABLE III cont'd

*compared below with that of Nice in the Song Sparrow, of Scott in dogs, and of Harlow in rhesus monkeys.*

| AINSWORTH                                                                                                                         | SANDER                                                                                                                                                    | BOWLBY                                                                                                                                             |
|-----------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------|
| <p>STAGE I<br/>(a) Neonatal Reflex<br/>0 to 4 weeks<br/>(b) Undiscriminating<br/>Social Responsiveness<br/>4 to 8 or 12 weeks</p> | <p>ISSUE I<br/>Initial Regulation<br/>0 to 3 months</p>                                                                                                   | <p>PHASE I<br/>Orientation and Signals<br/>without Discrimination<br/>of Figure<br/>0 to 8 or 12 weeks</p>                                         |
| <p>STAGE II<br/>Differential Responsiveness<br/>in Close Proximity to the<br/>Mother Figure<br/>8 or 12 to 20 or 25 weeks</p>     | <p>ISSUE II<br/>Reciprocal Exchanges<br/>in Interaction<br/>4 to 6 months</p>                                                                             | <p>PHASE II<br/>Orientation and Signals<br/>Directed towards One<br/>(or more) Discriminated<br/>Figure(s)<br/>2 or 3 to 6 months</p>              |
| <p>STAGE III<br/>Differential Responsiveness<br/>at a Distance<br/>20 or 25 to 30 or 35 weeks</p>                                 |                                                                                                                                                           |                                                                                                                                                    |
| <p>STAGE IV<br/>Active Initiative<br/>(with onset of locomotion)<br/>30 to 35 weeks on</p>                                        | <p>ISSUE III<br/>Infant's Initiative<br/>to Direct his Activity<br/>7 to 9 months</p>                                                                     | <p>PHASE III<br/>Maintenance of Proximity<br/>to a Discriminated Figure<br/>by Means of Locomotion<br/>as well as Signals<br/>6 or 7 months on</p> |
| <p>STAGE V<br/>Stranger Anxiety<br/>9 months on</p>                                                                               | <p>ISSUE IV<br/>Availability of Mother<br/>to Infant's Initiative<br/>10 to 13 months</p> <p>ISSUE V<br/>Self-Assertion of Infant<br/>14 to 20 months</p> |                                                                                                                                                    |

fourth week that visual stimuli begin to play a part in the eliciting of smiling. At about the same time, or shortly later, infants can be considered to focus on the eyes of an adult, i.e., to make true eye-to-eye contact.

Thereafter, smiling becomes a predictable and more selective response to a number of specific, highly articulated stimuli and achieved greater autonomy from organismic state. In other words, one month old infants can definitely respond socially to visual stimuli, whereas previously they could not. It is obvious, of course, that the ability to perceive a stimulus is prerequisite for imprinting to it.

Hunt (1970) underlined the attentional factors involved in imprinting. He pointed out that « under at least certain conditions, perceptual encounters with objects, patterns, and places lead to perceptual preference for these familiar objects, patterns, etc., before they lead to preference for what is unfamiliar or novel ». Moreover, he interpreted following behaviour to indicate that the object, pattern, etc. which is visually orientated to is « preferred ». However, Hunt was careful only to make a comparison between imprinting and other types of learning.

Ainsworth (1964) studied the development of attachments among the Ganda and subsequently (Ainsworth and Bell, 1970 a, 1970 b) among middle class white Americans. She noted an absence of social responsiveness during the neonatal period. An indiscriminating social responsiveness appeared at about one month. Infants smiled to any face in social interaction. By the third to the fourth month, social responsiveness became differential and preferential when an infant was in close proximity with his caretaking figure(s). Smiling, crying, and vocalisation were among the first responses to become differential and therefore to imply discrimination. A month or so later, an infant not only greeted his caretaker when she entered the room but also cried when she left, i.e., he could be considered differentially responsive at a distance. At around eight months, usually with the onset of locomotion, Ainsworth dated the first occurrence of active initiative on the part of the infant and a few weeks later, the onset of manifest stranger anxiety.

Sander (1962, 1964) regarded the mother-infant dyad as a unit of social interaction. He concerned himself not only with attachment behaviour but also with its reciprocal complement, caretaking behaviour. He considered the interaction between mother and infant in terms of « issues », the first of which centres around « initial regulation ». By about two and a half or three months, a mother and infant have usually got on some kind of schedule and a « reciprocal exchange in interaction » of a social nature becomes the second issue. At the end of the sixth month begins the third issue, which has as its focus an « infant's initiative

to direct his activity » and is followed at about ten months by the fourth : the « availability of a mother to an infant's initiative ». The last issue concerns an infant's « self-assertion ».

Bowlby (1962) distinguished four main phases in the development of human attachment behaviour. The first is characterised by an infant's indiscriminate orientation and responsiveness to social stimuli. At eight to twelve weeks the second phase begins with the appearance of discrimination of one or more persons. The third phase usually starts after the sixth month when an infant employs signals to remain in proximity to already discriminated persons. Once he can crawl, he also uses locomotion. (Somewhere after the end of the second year, an infant becomes capable of a reciprocal and insightful relationship with his caretakers. Bowlby designated his fourth phase as the « formation of a goal-corrected partnership ».)

#### VI. — THE DEVELOPMENT OF FILIAL ATTACHMENTS IN HUMAN PRIMATES CONSIDERED IN TERMS OF MINIMALLY SUFFICIENT EXPERIMENTAL CRITERIA FOR FILIAL IMPRINTING FOUND OPERANT IN BIRDS

To date, there is no uncountested evidence that the human neonate is capable of innate recognition of the human face or of any other pattern (1). Rather, he is differentially sensitive to certain classes of stimuli which frequently emanate from a human source (Wolff, 1963 ; Bowlby, 1969). The neonate can see, though his visual abilities are limited. Like many other « higher » mammals, especially other « higher » primates, he is unable to follow or cling. Therefore, in the environment of evolutionary adaptedness, he would most likely be almost continually held by his mother (or another caretaker), whilst in modern European society, he may either lie in a crib or be held.

The minimal experimental requirements for filial « imprinting » in the more general or extended sense of the concept have been seen to be (i) a naive subject (ii) capable of orienting to (iii) patterned stimulation (iv) which must be present (v) during an optimal period for learning.

(i) So far, there is absolutely no evidence that requires one to postulate innate ideas, nor innate recognition of, with or without response to a specific visual stimulus configuration. In short, there can be little doubt that the parturient is visually naive, a state which can be considered optimal for visual learning.

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(1) Hess (1973) claimed that « the human infant is born with a preference for the normal human face ». One of his students, Carolyn Jirari, found that infants 24 hrs old or younger visually followed a schematic face more markedly than a scrambled. This finding (C.G. Jirari, Unpublished Doctoral Dissertation, University of Chicago, 1970) is definitely at variance with those of the studies of Kagan, Henker, Hen-Tov, Levine and Lewis (1966) and of Wilcox (1969) to be quoted below.

(ii) The human parturate withdraws from overwhelmingly intense stimuli and, of course, does not even respond to stimuli above or below his thresholds of attention, but he can and does orientate to stimuli within a certain range, though not indiscriminately. Wolff (1963) has observed that a high pitched brass bell and an Audubon bird whistle are initially as effective as a human voice in eliciting smiling, and are more effective than fog horns. In fact it is quite certain that the « normal » full-term parturate is capable of orientating to sources of heterogeneous stimulation. The research of Fantz (1958, 1961 a, 1961 b, 1963, 1964, 1966) and of Bower (1965, 1966, 1969, 1971) presupposes just that ability to orientate.

(iii) Perceptual studies indicate that it is patterned stimuli which attract an infants attention (Fantz, 1958, 1961, 1963, 1966 ; Berlyne, 1958 ; Bruner, 1968). Moreover, there is an optimal level of complexity which infants « prefer » or fixate longer (Herschenson, Munsinger and Kessen, 1965 ; Thomas, 1965 ; Brennan, Ames and Moore, 1965 ; Caron and Caron, 1969 ; Moffett, 1969 ; Cohen, 1969 ; Haith, Kessen and Collins, 1969). Furthermore, a moving or varying stimulus, especially one which responds to an infant's own actions, appears to be more « attractive » than a static or unresponsive one (Caron, 1967 ; Rovee and Rovee, 1969). It does not need to be emphasized that the maternal face constitutes a relatively complex (though not too complex), intermittent responsive stimulus and therefore meets the requirements of the stimulus parameters to which a neonate can and does respond. Therefore, the task is to establish which specific stimuli are present and when.

Since the ability to orient is alone sufficient for visual imprinting to take place, the inability of the human infant to follow poses no genuine problem. The functional equation of following and smiling is therefore irrelevant. Neither movement of the subject nor of the object, though advantageous, is requisit. Thus, it appears possible to draw certain comparisons between the minimally sufficient conditions in newly hatched birds for imprinted recognition of a visual stimulus and the corresponding conditions under which a human infant grows responsive to or attached to the human facial Gestalt. The obvious differences between optimal conditions for the different species will not be stressed.

(iv) The parturate comes equipped with a fixed focal length of approximately nineteen centimetres on the average (Haynes, White and Held, 1964). Any stimulus which does not fall within the distance of 12 to 25 cm from a neonate's eyes will be more or less out of focus. Thus, objects or patterns at a distance of 65 cm or more do not exist in the practical sense of the word as far as the neonate is concerned. Moreover, very young infants appear to be able to resolve only strong contrasts of grey (Nelson,

1968). It is as though a neonate views the world through a lens which reduces patterns to flat areas of black and white. Stimuli which are too complex cannot be resolved and therefore are visually precluded. Furthermore, a neonate is incapable of scanning a stimulus. Rather, he picks out an attractive part, usually an angular element, on which he fixates (Salapatek and Kessen, 1966 ; Nelson and Kessen, 1969). Moreover, it appears that neonates are perceptually bound, that is : they are forced to look at something and cannot look away (Stechler and Lats, 1966), therefore no problem of divided attention or competing visual stimuli.

As is obvious, a neonate's potential experience is greatly restricted by his limited visual abilities. It would be poetically accurate to say that he cannot see more than he can understand, for there are only a limited number of stimuli which can initially impinge upon his naive visual awareness, a state optimal for learning.

Von Uexküll (1921, 1934) distinguished between the environment in which an organism is conceived to live and its Umwelt or phenomenal-subjective « world ». Though environments may overlap, Umwelten do not necessarily. In short, there is no single objective « world » in which all organisms live, for each particular Umwelt is a « world » created from the potential environment as a result of an interlocking of a species effector and receptor systems.

In higher organisms, one of the many possible, and perhaps the most important of Umwelten is visual. As von Uexküll emphasised, there can be little doubt that a visual Umwelt, for instance of either adult or infant human, has survival value and is the result of evolutionary selective forces. The question is, therefore, whether the restriction of a neonate's visual Umwelt has an evolutionary function.

It could be argued that the human infant is born premature and hence the restriction. However, the mechanisms underlying the restriction must not be equated with the function of the restriction. It could equally well be argued that prematurity had been selected because it ensured restricted vision, and thus indirectly favoured proper socialization via an imprinting-like process. The question therefore has to be re-phrased : Does the restriction of an infant's vision have survival value for the species ?

If attachment has the evolutionary function of ensuring survival of the species by decreasing the number of young that fall prey to predators (Bowlby, 1969), then there must be certain mechanisms to make it more likely that attachment takes place. These mechanisms would likewise have been selected phylogenetically for their contribution to the formation of the infant-mother bond.

An immature organism such as the human neonate presupposes an active caretaker who will feed, hold and care for him. The neonate is endowed with potentially social responses such as clinging, sucking, crying, smiling etc. Now, if a reflex social relationship is established before the onset of the sensitive period for socialization, then there is almost nil likelihood of « mal-imprinting », i.e., all infants that survive must be imprinted to some extent. On the one hand, the caretaker has become attached to the infant before the onset of the sensitive period, and the active reciprocal role of the caretaker in socialization/imprinting must not be underestimated. On the other hand, the infant's reflex, pre- or potentially-social responses are already focused on the proper stimulus-source/species-objects, i.e., the caretaker, otherwise he most probably would not have survived. Thus the neonatal phase appears to have the evolutionary function of ensuring that socialization has begun properly, before the onset of the actual sensitive phase during which social preferences are formed.

In the average expectable environment, the stimulus most constantly present in a neonate's visual Umwelt is the face of his caretaker. Spitz (1948, 1959), Ainsworth (1967), Wolff (1963), Sander (1962, 1964) etc., describe the frequency with which, and the way in which, a young infant responds to his mother in the midst of routine care and games (1).

As was indicated above, young infants « prefer » patterned stimuli to a homogeneous field, but they do not scan a figure. Instead, they appear to fix upon an attractive part. Moreover, they seem to have a predilection for stimuli which are intermediate in complexity and which move or vary. To be sure, the human facial Gestalt meets all of these criteria, including the criterion of « attractive » parts, namely : the eyes (Ambrose, 1963). Therefore, it comes as no surprise that the face is the first visual stimulus to which an infant responds most consistently and most vigorously with differential behaviour, and to which he shows the first signs of primitive recognition. By the fourth or fifth week, when an infant is capable of focally accommodating to changes in distance and of resolving subtler shades of grey, he gives definite evidence of having become familiar with the human facial Gestalt (Wolff, 1963 ; Griffiths, 1964).

Since a human neonate cannot approach or follow locomotorly, the restriction of visual stimuli to which he is exposed increases the probability that extraneous stimuli do not interfere with « exposure learning » until a reflexive or neonatal attachment has already been established.

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(1) It is to be noted that most mothers initially hold their own face about 13 to 26 cm from their infant's eyes when in direct face-to-face interaction.

That is : as a consequence of the initial limitations of an infant's visual system, it is statistically more likely that he will become familiar with and attached to or imprinted to the biologically appropriate class of visual stimuli via the mother's actual face. If looking is all an infant can do and if the basis of « exposure learning » or « imprinted recognition of and response to specific patterns of visual stimulation » is looking, then it is reasonable to assume some factor(s), presumably the result of evolutionary selective processes, which would limit the range of visual stimuli and thereby reduce the likelihood of maladaptation or fixation to biologically inappropriate objects. In short, if an infant is not to be overwhelmed by the complexity of the visual environment and if the mother's face is to enjoy primacy over other patterned stimulation in his visual experience, then not only must he be equipped with a « preference » for certain classes of stimulation which originate more frequently in the human face, but also must his visual experience be restricted in such a way that, in the average expectable environment, opportunities to perceive his caretaker's face would be facilitated whilst opportunities to perceive other classes of stimuli, equally preferable initially, would be reduced or even precluded (1).

Since the human neonate cannot cling, he would have to be carried or held in the environment of evolutionary adaptedness and he would usually be held in the arms, on the chest or strapped against the back. In the first case, perception of the mother's face would be possible, though not frequently optimal (except when she lowered her head) ; in the latter, it would be impossible. In short, a young infant would spend most of his time looking at and therefore becoming more familiar with stimuli other than his mother's face. When one considers that in the environment of evolutionary adaptedness, a mother would have to be involved with tasks of survival such as food gathering and vigilance for predators, it is obvious that her infant would not receive her exclusive attention and would more frequently be exposed to patterns other than her face if his vision were not restricted.

(v) Since the human infant, six months or younger, is prelinguistic in his verbalizations, it is impossible to ask him what he sees. Smiling or the looking response itself can, however, reveal much about an infant's visual world. Thus, it is possible to study the development of perception empirically, though the methodology and stimuli used in a given experiment will naturally influence the results.

Spitz (1946, 1948, 1965), Ahrens (1964) and Watson (1966)

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(1) It is interesting that some young infants appear to be attached to or « imprinted on » not only the mother's face but also on a teddy bear or on a mobile which has been present in the crib from the first weeks.

made inferences about perception from the way in which infants smile in response to a living human face and/or to schematic models of it.

According to Spitz (1946, 1948, 1965), the four to five months old infant does not respond to the human face as a face, but rather as a « privileged Gestalt... of forehead, eyes, and nose, the whole in movement ». He is most emphatic that both eyes (presumably open) plus the nasal and supraorbital structures must be present to form the « sign Gestalt ». In short, the head in profile is insufficient.

Ahrens (1954) observed that during the first weeks, only a dot or a primitive equivalent for an eye seems sufficient. However, the actual eye configuration plus nose and forehead becomes increasingly necessary especially by the third to fourth months. As stimuli, Ahrens used masks and marked cards, as well as actual faces, and found that at four months an infant can distinguish the two. In addition, he noted that a configuration of face with eyes evokes more smiling than that of one without. Artificial eyes worn on a real face evoke smiling from an infant up to 5 or 6 months, after which time they elicit negative responses.

Watson (1966) likewise used a living face as stimulus. He observed that thirteen to fourteen weeks old infants smiled most frequently to a face presented in the « natural » position (i.e. at zero degrees rotation). By contrast, smiling to a face presented sideways (i.e. at ninety degrees orientation) showed a peak at twenty weeks. The same infants were also tested with either a schematic face, a circle containing a dot or a circle containing a « T », the effects of orientation, however, appeared only for the schematic face.

Numerous other experimentors (Fantz, 1956 ; Thomas, 1965 ; Kagan and Lewis, 1965 ; Kagan and al., 1966 ; Wilcox and Clayton, 1968 ; Wilcox, 1969 ; Koopman and Ames, 1967) have used looking per se, rather than smiling, as the primary response from which perception is to be inferred. These experimentors have employed schematic faces, however, and not an actual living face.

Fantz (1956) published that infants aged two to six months « prefer » a properly arranged version or a schematic face either to a scrambled version of it or to a bull's eye. Thomas (1965) noted that infants aged four to six months fixated a schematic face longer than stripes, a checker-board effect or a drawing of a figure. Kagan and Lewis (1965) reported that six months old infants « preferred » photographs of face to a symbolic representation of a panda-bear.

Kagan, Henker, Hen-Tov, Levine and Lewis (1966) conducted two experiments in which 4 months old infants were presented with three-dimensional representations of a human face : Smiling

and decrease in heart rate were significantly more frequent to a natural face. Facial patterns containing eyes (either naturalistic or scrambled) tended to elicit longer fixation than faces without eyes.

Wilcox (1969), however, was unable to obtain differential fixation in response to various schematic and scrambled faces. Neither the presence nor absence of either eyes or nose or mouth was correlated with any change in visual behaviour. By 16 weeks, however, a photograph did elicit greater total fixation than the drawings.

Fantz (1966) warned that infant's reactions to a particular face-like patterns used in experiments « do not necessarily reflect the development of responsiveness to actual faces... lack of preference for the schematic face might mean not lack of discrimination but the ability to distinguish between a real and a simulate face ».

As is obvious, attachment to or preference for a specific caretaker or for a given species can be inferred from perceptual experiments with infants. In fact, Thorpe (1961) (1) argued that filial imprinting should be considered under several aspects, one of which was « imprinted recognition of and response to specific patterns of visual stimulation ». However, in so far as masks, drawings and other artificial stimuli have been used, so is one uncertain as to the implications of experimental results in terms of social development. Therefore, the author (Allyn, 1974) undertook the following series of experiments to investigate which parts of a *living* face must be present if it is to be fixated by an infant.

In the first experiment, 12 infants, aged 11 to 16 weeks, were allowed to fixate their own mother's face under various degrees of completeness. All showed differential fixation. A face without both eyes was fixated significantly less frequently than were both eyes only with or without other facial features and was also associated with a negative reaction of actively refusing to look. A full or complete face, however, was not fixated any more frequently than an incomplete which contained eyes.

In a second, though impromptu naturalistic experiment, a 16 weeks old infant was allowed to fixate a television monitor on which was presented either a human face or a complex test pattern. The author could manipulate at will the pattern to be presented. When the face was presented, the infant watched attentively. When the experimenter switched to the non-facelike pattern, however, the infant looked away. Whenever the infant glanced back, he would look away if the pattern was on. But

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(1) See below page 249.

if the face had been presented whilst he was looking away, then he would fixate the monitor so long as the face remained.

In a third experiment, 14 infants, aged 16 to 25 weeks, were allowed to fixate two television monitors on which were simultaneously presented filmed versions of a strange female face under various degrees of completeness. The first and third experiments yielded almost identical results. Again, the absence of both eyes was associated with a negative reaction.

The overall results of the third experiments, especially when compared with the results of the first (in which a real face was used as the stimulus) indicate that infants could be considered as responding to a televised face in a way which is undifferentiable in terms of amount of looking from the way in which they were shown to respond to a real or living face.

Above all, the negative reaction to both a real « face without eyes » and to a filmed version of it, but not to other conditions, is most striking support for an interpretation that infants 16 weeks or older can « recognise » a filmed or televised version of a face as « face-like ». Incidental qualitative observations indicated, however, that infants did distinguish real from filmed faces.

The refusal to continue looking at a « face without both eyes » can thus be interpreted as suggesting that infants had an expectancy of seeing eyes, perhaps as a result of association with surrounding facial features. In other words, infants of three to four months act as if they have either a primitive notion, internal representation or memory trace of certain configurations which belong together. Since infants also cried in response to a stimulus in which the expectancy of seeing eyes was appropriate but unfulfilled, it seems plausible that the absence of eyes is more than just an insufficient stimulus. To the contrary, it appears that a « face without eyes » is either disappointing or perhaps even terrifying. On the one hand, such an aversive reaction could be cognitive in origin, i.e. the result of a frustrated scan path (Noton & Stark, 1971) or an interrupted TOTE (1) (Miller, Galanter & Pribram, 1960) in which a « set » expectancy is not met. On the other hand, it could

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(1) The TOTE (Test-Operate-Test-Exit) sequence, proposed by Miller, Galanter and Pribram (1960) to replace the static notion of a reflex arc, presumes two reciprocally connected neuronal systems. The one, analogous to the intrinsic system of the brain, performs the test functions: when receptor inputs arrive, a search is made among the hierarchically arranged store of representations either of action systems (frontal portion) or of perceived objects and events and processes (posterior system) to find one that matches the input. When incongruity persists between input and representation, control is presumed to shift to the second, i.e., the extrinsic system, which then operates on either the receptor mechanism, on the environment, or on both, until the incongruities of the test are resolved. A similar formulation is given by Bernstein (1967). In very young infants, however, it is doubtful that such a shift to the extrinsic system could be completely effected.

be reaction of a fearful and/or anxious nature in response to either a « novel » and/or « horrifying » stimulus. Obviously, these alternatives are not mutually exclusive. Equally important is the appetitive aspect inferable from such a negative reaction. It will be recalled that one criterion for distinguishing an imprinted from a merely recognized object was the presence of an appetitive response to the former.

In an informal experiment the author asked a mother to get her 12 week old infant's attention and then to talk to him. The infant smiled to his mother's talking face even when nose and mouth were masked, but when both eyes were masked, the infant gave a definite impression of being « confused » or « perplexed » by the talking, eyeless face.

It will be remembered that Ahrens (1954) encountered a similar phenomenon in infants of five to six months : artificial eyes worn on a real face elicited negative responses, whereas previously they had evoked smiling.

In both the first and third of the author's experiments, the presence of eyes alone proved sufficient to elicit looking. This fact suggests that eyes are a necessary or even a central feature to which infants respond when scanning or focusing on a stimulus configuration which is potentially a facial Gestalt. Nonetheless, eyes plus some other part of the face, be it either « hair and forehead » or « nose and mouth », received more fixation than « eyes only ». Thus, eyes alone seem to constitute a minimally sufficient stimulus, though not an optimal one. Whilst a more complete face was fixated more frequently than a less complete, there is no evidence that a full or naturally complete face was looked at any more frequently than a partial face which contained eyes. In light of these findings, it is not possible to consider the face as a « privileged Gestalt » as far as looking is concerned. The present evidence suggests a heterogeneous summation effect centred around « privileged features », namely, the eyes. Both eyes are not necessary, however, one eye is sufficient. In fact, a « face with one eye only » was not fixated significantly more or less than were « eyes only » or a « face without outline », conditions which contain both eyes. Hence, it appears that the eye is to be considered as a structure « interesting » or « focal » per se and not as a paired or balanced part of a greater Gestalt.

The centrality of the eyes may be partially due to an innate attractiveness ; they are the most light reflective part of a natural face ; they contain great contrast within themselves and in relation to surrounding facial features ; they are in continuous movement ; and they are the most responsive part of the face, registering changes more quickly and more consistently than other parts.

Brackbill (1958) observed that once an infant had been conditioned to smile to a responsive adult face, he refused even to look

at that face during the extinction process when it no longer responded to his smiles. She described an infant's refusal to look as quite active. If he could not turn his head, then he would avert his eyes. The studies by Caron (1967) and by Rovee and Rovee (1969) offer evidence that infants four months and under become progressively more responsive to stimuli which change directly in response to their own behaviour. In other words, infants respond to feedback. Not only do they look more frequently at a responsive stimulus, but they also vocalize, laugh and wave their limbs excitedly. In short, infants appear to derive pleasure from a stimulus which responds to them. By contrast, infants reacted negatively to a previously « responsive » stimulus when it ceased to respond. Infants fretted, squirmed or even cried. Infant's negative reactions to the cessation of feedback clearly suggest that they have a definite expectancy of feedback, that this expectancy is appetitive in nature, and that whenever this expectancy is appropriate, the absence of feedback is experienced as frustrating. Thus it is tempting to speculate that an eyeless face is functionally similar to Brackbill's face which refuses to continue to smile.

## VII. — THE DEVELOPMENT OF ATTACHMENTS IN HUMAN PRIMATES : A RECAPITULATION AND SUMMARY

At the end of the first quarter, when an infant's visual system is roughly equivalent in function terms to an adult's, there can be little doubt that most infants respond differentially to and therefore can be said to recognize and to prefer their mother (Ainsworth, 1964, 1967 ; Sander, 1962, 1964 ; Ambrose, 1963, Wolff, 1963 ; Shaffer, 1971). Infants approximately sixteen weeks old smile, vocalise and laugh more frequently to, stop crying more readily for, and accept food more easily from a familiar caretaker than a stranger. Though few infants show fear of or anxiety to strangers at this time, many appear to be wary of them (Bronson, 1971). Infants of this age frequently watch television and are decidedly interested in mirrors. In fact, they smile, coo and wave their arms to multiple images of their own mother in a set of mirrors. This reaction demonstrates « that young infants can recognise features in recognising their mothers, but they recognise the mother as one of many identical mothers » (Bower, 1971). However, infants of twenty weeks or older become quite upset at the sight of more than one mother, which implies they « know they have only one mother ». In other words, they no longer identify objects with places but with features. Obviously, the stimulus characteristics of the mother's face have been internalized. The negative reaction to multiple images of one mother can be considered to betray an expectancy and an appetitive response comparable with the reaction to a face without eyes.

Nonetheless, attachment is not yet complete, even by approximately 7 or 8 months when infants begin to manifest exclusive and tenacious affective rapports.

Visual differentiation obviously presupposes recognition both logically and ontologically. An infant has to be able to recognize the general qualities of a facial Gestalt qua faceness as contrasted with other visual Gestalten before he can differentiate a particular facial Gestalt from others. Therefore, attachment can be said to presume both recognition and differentiation. In other words, individual learning and supra-individual learning are simultaneous and complementary.

As has been argued, imprinting of a young organism to its caretaker must not be confused with imprinting to sexual objects etc. Therefore, imprinted recognition of and reaction to a caretaker is to be seen to involve a socially appetitive and/or affective response system for a specific object and not for a class of objects ; nevertheless, the characteristics of the « class of objects » are learned and can be associated with fear. A young animal, either bird or human, becomes attached to the characteristics of a particular individual caretaker and not of the whole species, but he still responds to his own species differently from the way in which he responds to inanimate objects or other species. When an infant shows himself capable of recognising the human facial Gestalt and especially when capable of differentiating one such Gestalt from another, it can be inferred that « faceness », and in particular one person's face, has been « printed in » his « mind » as a standard with which he can compare external stimuli and which he can use as a goal in a search among them. Moreover, an infant's response to various combinations of facial features as face-like suggests a « stamped-in » or internalized standard, i.e., a face-schema, in terms of which incomplete facial features are recognised to be face-like. Further evidence for a « stamped-in » face schema is provided by the already cited negative reaction to a face without eyes.

A sixteen to twenty week old infant could in no way be considered visually naive for (i) he shows an ability to recognise and distinguish between human facial Gestalten, and (ii) his behaviour betrays a preference or « appetite » for certain facial Gestalt(en) and a wariness of others. Thus, it would appear that something functionally similar to imprinted recognition of and response to the facial Gestalt has taken place and that the optimal period for this kind of exposure learning is well on its way to termination, if not, at least in the case of certain infants, already terminated.

In summation : « The development of a human mother-infant relationship bears many similarities to the analogous process in birds » (Hinde, 1963). For instance : « the developmental sequence of first social response to the parent, then fear, and later aggres-

sion, is... similar in birds, anthropoids... and humans » (Hinde, 1961). In functional terms, « the result of the imprinting process is that the young bird [or human infant] learns to recognize its mother as an individual, and a number of discrete responses made by the young... become integrated on to one object » (Hinde, 1963).

The behaviour of a human infant which has become attached to his mother is comparable to the behaviour in nidifugous birds which is known to be a result of a specific, relatively limited sensitive period. Moreover, the ontogenesis of attachment in the human infant bears many striking similarities to that in certain altricial birds and dogs for which the relative temporal limits of such a sensitive period can be demonstrated experimentally. The human neonate responds reflexively to certain classes of stimuli ; by the age of 4 to 6 weeks he begins to respond socially and to prefer stimuli which emanate from a human source ; by approximately four months he begins to respond to his caretaker's facial Gestalt as a coherent visual pattern which can be recognised as facelike, even from only a few features ; moreover, his response at this time suggests organized memory traces or internalized schemata against which a potentially face-like stimulus is measured or judged to be face-like and with which are associated both positive and negative appetitive affects. Above all, the « inner face » can be considered to constitute a « set-goal » which is highly charged with emotion and in terms of which the environment is searched.

To conclude, the minimally sufficient experimental conditions for imprinting in nidifugous birds have been shown to be similar to the conditions present during the development of socialization in infra-human mammals and of a human infant's recognition of and attachment to the facial Gestalt of his mother/caretaker. These conditions are : (i) a naive subject (ii) capable of orientation to (iii) patterned stimulation (iv) which must be present (v) during an optimal period for learning.

It was argued (a) that a neonate is visually naive ; (b) that a naive state is an optimal state for learning ; (c) that a neonate inhabits a restricted visual Umwelt due to his limited visual abilities ; (d) that the restriction of visual stimuli occurs when the infant is naive ; (e) that as a consequence of the restriction there is a higher probability that exposure learning will occur to a biologically appropriate object than to an inappropriate ; (f) that a neonate has been equipped by evolution with an unconditioned response to orientate to patterned stimuli ; (g) that the optimal visual stimulus to penetrate into that restricted Umwelt is the human face ; (h) that the visual stimulus to penetrate most frequently into that restricted Umwelt is also the human face ; (i) that though a neonate shows no preferential response to the face before one month, he does so thereafter with increasing

intensity ; (j) that by four months, when an infant's visual system is functionally equivalent to an adult's he demonstrates differential responsiveness to and appetitive behaviour for a real face ; (k) that the differential response can be considered to indicate a « stamping-in » or internalization of a « face schema » in an infant's « mind » ; (l) that the socially appetitive nature of the response to the human face is different from most other forms of learning, though similar to imprinting ; (m) that from the fourth month on, an infant becomes progressively more responsive to particular face(s) ; (n) that as soon as or soon after an infant becomes responsive to particular faces, he differentiates those faces from other or non-familiar faces ; (o) that when a neonate can differentiate familiar from non-familiar faces, he reacts with wariness or fear to the latter.

#### VIII. — IMPRINTING COMPARED WITH OTHER FORMS OF LEARNING

Though Hinde advised that imprinting qua phenomenon is not categorically different from other forms of learning qua phenomena, it needs to be emphasised that the implications drawn by many ethologists are very different from those drawn from other forms of learning by behaviourists. However, if imprinting were to be compared phenomenologically with other forms of learning, Hinde would contend it best to postulate a continuum running from behaviour which is environmentally stable to behaviour which is environmentally labile. Imprinting would then be conceptualized as a form of learning which occurs during an environmentally labile period and which afterwards becomes relatively stable environmentally.

Whilst Hinde (1961, 1963) conceded that « all learning is more likely to occur at some stages in the life cycle than it is at others », he did not deem it useful to ask whether imprinting occurs in species other than birds, but he did consider it legitimate to ask whether a given type of learning occurs within a sensitive period, and if it does, what limits that period.

In contrast to Hinde, Thorpe (1961) proposed at least three types of imprinting :

a) Imprinted recognition of, and response to, specific patterns of visual stimulation ;

b) Imprinted recognition of, and response to, specific frequency patterns of auditory stimulation (fine periodicities or patterns ;

c) Imprinted recognition of, and response to, specific gross periodicities (rhythms) of stimulation.

Filial and sexual imprinting in the natural environment would be an example of types (a) and (b), i.e. visual and auditory

imprinting. In both cases, recognition is a prerequisite for and different from any imprinted preferences formed. The experimental findings of Smith (1960) and of James (1959), quoted above, are compatible with the notion that imprinting to only a visual stimulus can occur. Experiments by Thorpe (1956, 1958 a, 1958 b), Hinde (1958), Marler and Tamura (1964), Marler, Kreith and Tamura (1964) and by Nicolai (1973), offer evidence that in the chaffinch there is a sensitive phase for the acquisition of the species song, in other words, imprinting to auditory stimuli. Moreover, quieting to, recognition of and approaching a source of auditory stimulation have been frequently reported for ducks and chicks (Fabricius, 1951 a, 1951 b ; Collias, 1952, 1962 ; Collias and Collias, 1956 ; Sluckin and Salzen, 1961 ; Klopfer, 1959 a, 1959 b).

If, however, imprinting is considered not in terms of learning but in terms of socialization, then there are at least 3 separate « sensitive » phases, the first concerned with the formation of filial attachment ; the second, with that of sexual orientation to a given species ; the third, with that of gender preference, male or female (i.e., hetero- or homo-sexual) (Schutz, 1963, 1965 a, 1965 b, 1970, 1971 ; Immelmann, 1969).

Imprinting is always « early learning » and is presupposed by later learning from which it is different at least temporarily. Learning when an organism is immature, i.e. when an organism is malleable and in the process of rapid growth, is different from learning in a mature or already formed organism (Hebb, 1949). Since there are important anatomical differences between the brains of very young or immature and those of adult or mature organisms, it seems not unreasonable to suppose that the former differ from the latter in the way they learn (Russell, 1959 ; Sluckin, 1965). In other words, the formation of a brain is different from the use of that brain once formed. Supporting evidence comes from the work of Scott and Marston (1950), Biel (1940), Munn (1950), James and Binks (1963), Vince (1958, 1959, 1960, 1961), Peters, Vonderache and Powers (1958), Paulson (1965), Bateson (1972), Horn, Rose and Bateson (1973), Bateson, Rose and Horn (1973). In fact, « it is the general conclusion of students of animal learning that younger individuals are better learners than are older ones » (Thorpe, 1961).

Though there is little agreement among authors as to just what learning is, it can, for convenience sake, be defined as relatively lasting changes in behaviour resulting from experience. The lasting character of behavioural change as a definition of learning distinguishes it from changes associated with fatigue, stress, drugs, or the like. The experiential aspect of the definition precludes changes dependent on maturation or ageing.

Association, above all else, is held to be the salient criterion of conditioning (Morgan, 1961). But in all forms of conditioning « the pairing of stimulus and response is selective : either one out of a range of possible stimuli becomes associated with a given response, or one particular response becomes associated with some stimulus » (Sluckin, 1965). The behavioural aspect of filial imprinting, however, is characterised by a built-in, unconditioned orientation response to a source of stimulation and by an equally built-in, unconditioned approach response. In fact, an imprinted object can be used as an unconditioned stimulus in classical conditioning (James, 1959, 1960 a ; Abercrombie and James, 1961 ; Klopfer, 1959 b).

Classically conditioned responses extinguish when the unconditioned stimulus is removed ; operant responses decline in the absence of reinforcement. This is not true of imprinting ; imprinted responses never habituate and an important characteristic of anything that is learned (e.g. conditioned responses) is that it can be forgotten (Bühler, 1928). Moreover, avoidance conditioning of an imprinted response is impossible, i.e., once established, imprinting cannot be deconditioned by punishment or negative reinforcement. Thus, it is obvious that neither classical nor operant conditioning provide paradigms easily compatible with the phenomena of imprinting.

In imprinting there is no external reinforcement. Nor is there a conditioned stimulus. « The releasing stimulus itself is attractive from start and becomes more attractive as the organism continues to be exposed to it » (Sluckin, 1965). By contrast, an unconditioned stimulus does not become more attractive when paired with a conditioned stimulus. Likewise, a reinforcement does not become more reinforcing with training. Sluckin (1965) is explicit that « in so far as the term reinforcement implies or suggests external reinforcement, imprinting may be described as a form of non-reinforced learning ». Foss (1963) characterized imprinting as « a discriminated preference for one object developed in the absence of any conventional reinforcers ».

The ability to discriminate between familiar and novel or strange, which is a consequence of imprinting, appears to be acquired « not by conditioning but through perceptual learning » (Sluckin and Salzen, 1961 ; Sluckin, 1962 ; Gibson, 1969 ; Hunt, 1970). In this connection, Drever coined the expression « exposure learning » which specifies both « the perceptual registration by the organism of the environment to which it is exposed » and « the familiarisation of the organism with its environment » (Sluckin, 1965). In both classical and operant conditioning, a response, either elicited or emitted, becomes associated with a stimulus, be it a conditioned stimulus or a reinforcement, with which it was not previously associated. Above all, there is no

« selective pairing of stimuli and responses » in imprinting. The initial bond between eliciting stimuli and imprinted response, to the contrary, is strengthened with experience and becomes exclusive or is redirected, according to the intervening circumstances.

Since imprinting is thus a form of learning in which selection is impossible, it can be described as a form of non-associative learning, for association presupposes alternatives. In fact, Vince (1960) considers learning to be too crude a concept for developmental changes, one of which is imprinting.

Though the notion of an Innate Releasing Mechanism can be overstated, it is exactly the non-selective phenomenon of releasing stimuli which differentiates imprinting from associative learning. The first « object » presented is accepted as « absolute ». Conditioning always implies learning to respond to classes of stimuli, this is true of sexual and of gender imprinting, though not of filial.

In other words, it can be argued that imprinting *qua* imprinting is not *per se* a form of learning in the strict sense of the word. Whilst the characteristics of the parent object, etc. involve some type of (perceptual) learning, etc., the actual learning of the parent object is neither identical with nor equatable with the total phenomenon of imprinting. One must distinguish between « acquired » and « learned ». Even though imprinting involves an environmentally acquired modification of a pre-existent behavioural potentiality, its salient characteristic is the interaction of « innate », acquired and learned variables. « Learning of the characteristics of the environment need not... entail the formation of any attachments ». Weidmann (1956) observed that non-imprinted birds would follow only when hungry and showed no distress when left alone.

Imprinting is obviously not just « learning of characteristics of a parent-object » (Baer and Gray, 1960), it is also the development of appetitive responses to or « needs » for that object. It is precisely the socially appetitive aspects of imprinting which distinguish it from what is usually considered as learning.

Bowlby (1969) noted that when the term « imprinting » is used in a generic sense, it implies (a) « the development of a clearly defined preference », (b) « a preference which develops very quickly and usually during a limited phase of the life cycle », and (c) « a preference that, once formed, remains comparatively fixed ».

On the one hand, imprinting is foundation or primary experience, upon which other or subsequent learning rests. It is, moreover, an early acquisition limited to a relative brief sensitive or optimal period. On the other hand, it is the actualisation of

« desire » in the sense that a built-in response realizes the particular goal or object of an « instinctive » motivational system.

Scott (1962) emphasized that « the critical period for primary socialization constitutes a turning point. Experience during a short period early in life determines which shall be the close relatives of the young animal, and this, in turn, leads the animal to develop in one of two directions — the normal one, in which it becomes attached to and mates with a member of its own species, or an abnormal one, in which it becomes attached to a different species, with consequent disrupting effects upon sexual and other social relationships with members of its own kind ».

Hess (1973), however, does not regard imprinting simply as « primary socialization » but as a « particular type of learning process — that is, a tool (in the same sense as eating or breathing are tools), which may be used by a species for the formation of a filial-maternal bond, pair formation, environmental attachment, food preference, and perhaps other cases involving some sort of object relationship ». For Hess, imprinting is different from *other* forms of « learning » in so far as it is a « genetically programmed learning, with some species-specific constraints upon the kind of object that may be learned and upon the time of learning » ; in other words, it is a « genotype-dependant ontogenetic process », the most salient characteristics of which are a « critical » period and irreversibility.

Hess distinguishes between « critical », « susceptible » and « optimal » periods, a formulation reminiscent of Hinde's (1959) environmentally stable-labile continuum, though Hess considers these three types of sensitive periods or subdivisions of the aforementioned continuum to be categorically distinct. His criteria for a « critical » period are (i) extreme shortness in duration and (ii) irreversibility. Hess therefore argues for imprinting of mother sheep to their newborn, which type of imprinting process is « repeated at the birth of subsequent offspring ».

Vidal (1974) criticizes Hess on the grounds (i) that not only the findings of other authors, but even the results of Hess' own experiments contradict the notion of an extremely short « critical » period which is irreversible in its effects and which is exclusively dependent upon genetic control or physical maturation, and (ii) that his definition of imprinting is circular and without experimentally verifiable criteria.

It does appear that for Hess the term imprinting is equivalent to a critical period with irreversible effects.

Nonetheless, one can only agree with Hess (i) that imprinting involves not the acquisition of a response, but of an object (1) ; (ii)

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(1) A similar formulation is given by Salzen (1970).

that the majority of imprinting experiments have also entailed deprivation and hence have produced « abnormal » animals ; and (iii) that the newly hatched chick or duck is pre-programmed to react in such a way as to integrate certain aspects of his environment. One must ask, however, to what degree are the different aspects of imprinting directly (or indirectly) genetically controlled.

The question is, therefore : why are sexual and filial behaviour in vertebrates not controlled solely by genes ? In other words : why is experience necessary ?

If one stops to consider the femur and pelvis, the answer is obvious by analogy : there is always variation in living structures. An archetype is not a mold, but a tendency. When two entities must interact with each other, the statistical risk of malfunction is less if their ontogeneses are simultaneous and complementary in terms of reciprocal influence, otherwise « misfits » would be more probable (Waddington, 1969). Exclusive genetic control of complex interactive systems is probabilistically more dangerous than that of simpler systems. Filial and reproductive behaviour in vertebrates, especially in « higher » mammals, is not only extremely complex, but in essence reciprocal.

Bateson (1966) stressed that it is disadvantageous in a rapidly evolving species for the young to have a highly specific preference for parental characteristics that are subject to change. « The failure of the young to respond to the parent would detract from the selective advantage of changes in, say the plumage of the parent. Conceivably modifications in the genetic mechanisms controlling plumage characters could be linked with modifications in those controlling the preference for these characters. However, an initially unspecific preference subsequently refined by learning is a simpler solution to the problem, providing the chances of responding to anything other than the parent at the outset were low. Studies of imprinting under natural conditions indicate that they are. The young have ample opportunity to learn many of the characteristics of the mother before she leads them from the nest ; furthermore, the mother plays an active role in initiating imprinting and keeping the brood together (Gottlieb, 1963 a, b). »

Ewer (1959) suggested that imprinting is necessary since the sensory facilities of even precocial birds are inadequate at the time of hatching. Hinde (1961) modified and extended Ewer's position in his argument that « initially high selectivity of responsiveness could be disastrous if the young birds had not developed size and distance constancies which enabled them to recognize their parent under a variety of conditions. The mother might appear in many shapes, sizes and even colours according to her posture, distance, background and the light conditions ». Therefore, imprinting would be advantageous for the species because young birds must respond appropriately to their parents at an

age when perceptual constancies are presumed by Hinde not to have developed. Implied is the assumption that imprinting is to relatively unchanging (visual, auditory, etc.) aspects of the parent organism.

Imprinting can therefore be considered as a phylogenetic predisposition to acquire rapidly, in a relatively limited period of time, early in life, those essentials for social interaction which cannot be safely built-in genetically. In this light, imprinting can be viewed as an evolutionary compromise between the extremes of absolute control by genes (as is the case with hygienic behaviour in bees, cf. Rothenbuhler, 1964 a, 1964 b) and pure learning. The function of a developmental process such as imprinting, however, must not be confused with the causal and/or determining factors governing that process. As Bowlby (1969) emphasized : « the causes of any behaviour are those factors that activate that particular behavioural system : whereas the function of that behaviour derives from the structure of the system, which is such that, when it is in action in its environment of evolutionary adaptedness, a consequence that promotes survival [of the species] commonly follows ».

It is ultimately impossible to understand the ontogenesis of an individual organism without considering the evolution of its species in its environment of evolutionary adaptedness. For this reason, naturalistic observations are of variations in phenomena produced by evolutionary selection forces in their present and historic aspects, whilst observation resulting from experiments are of « contrived » or « artificial » phenomena. Naturalistic observations, however, allow little to be known directly of causal determinants, whereas to the contrary, experimentation does. But since by necessity, experimental parameters must replace natural environmental ones, the implicit organism-environment unity is changed to the degree that experimental parameters deviate from those of the environment of evolutionary adaptedness.

Aristotle's concepts of « potentiality » and « actuality » are essential if one is to understand laboratory experiments or « artificial nature » : potentiality is best considered as analogous to a given species genotype and actuality to the phenotype. Laboratory experiments can therefore be seen not to be concerned with the naturally occurring actuality of a given phenomenon, but with the potentiality in a phenomenological configuration. The experimenter, by manipulating environmental conditions, especially ontogenetic influences, plays the role of « god » or « selective forces » in the « natural » evolutionary process as manifested on an individual ontogenetic level.

Thus, there is a fundamental, perhaps even an insurmountable problem in developmental research : namely, the design of ontogenetic experiments. Be it true that there is a continuous

interaction between genetic and environmental variables, i.e., between the innate and learned (as there appears to be), then it is doubtful that one can consider observations made via experiments as equivalent to those made in the natural habitat.

Mechanisms which determine the behaviour of an organism under experimental conditions are not necessarily those which determine its behaviour under natural conditions. That is : experimental (or artificial) determinants of behaviour cannot be assumed ipso facto to be the same as those in the environment of « evolutionary adaptedness ». In experiments, one can only hope to attain minimal control of various determining parameters, whereas natural processes, by contrast, demonstrate optimal/maximal determinism (even multi-determinism).

In fact, Waddington (1969) has argued that one should consider epigenetic processes as an essential part of a greater evolutionary process, phenomenologically inseparable from the genetic factors contributing to the phenotype. In other words, genetic material is selected in terms of, and presupposes complementary developmental processes. The experiments of Levine (1962 a, 1962 b, 1968, 1969) testify to the parsimony of such an interaction : « the character of early experience is an... important determinant of individual differences in animals [...] Genetic determinants do not find expression except in interaction with aspects of the environment » (Levine, 1960).

Therefore, in so far as the paradigm of any development experiment interferes with the epigenetic requirements implicit in the development of a phenotype, so must it interfere with the phenotype likewise. Unfortunately, there is no way of knowing whether or not it interferes with the genotype as well. In a sense, an experimenter plays with the possible variation in phenotype (or actuality) in order to make hypothetical constructs about the genotype (potentiality).

If a dog is reared under condition X and a cat under Y, no one would dream of comparing the behaviour of those two animals when adults. Now if genotype A reared under conditions B produce an individual organism of phenotype C, and that same genotype A under conditions D produce an individual organism of phenotype E, then one is comparing two radically different organisms and not individual differences in the same type of organism as a result of different previous conditions. Developmental experiments in psychology and zoology are invaluable, but they can never shed light directly on a species genetic potential or programme.

In résumé : imprinting as a distinctive phenomenon in « higher » vertebrates can be characterized by an ensemble of twenty criteria.

*Imprinting as an Evolutionary Phenomenon Characteristic of  
« Higher » Social Vertebrates.*

- 1) Imprinting is a phenomenon occurring in social vertebrate species, the infantile organisms of which come equipped with « built-in » potentially-social or pre-social responses.
- 2) Though the infantile organisms of many higher vertebrate social species are initially unresponsive socially, the potentially-social or pre-social responses in question are first elicited by a wide range of stimuli and later on by a much narrower range.
- 3) Moreover, these potentially-social or pre-social responses are initially elicited with a greater frequency by certain stimuli than by others, these eliciting stimuli emanating most frequently from a social source, i.e., from an organism of the same species ; hence, it can be said that there is a species-specific constraint upon the type of eliciting stimuli possible.
- 4) Imprinting is thus a phylogenetic pre-disposition to acquire those essentials for social interaction which cannot be safely built-in genetically ; in other words, it is an ontogenetic and epigenetic process which is dependent on the genotype and which constitutes an essential and integral part of a greater evolutionary process.

*Imprinting as an Individual Ontogenetic and Epigenetic Process.*

- 5) As a process, imprinting is only one of many onto- and epigenetic processes undergone by social organisms.
- 6) It constitutes a turning-point in an organism's development; this process involves learning, though is not identical with it ;
- 7) The learned component can be considered as « exposure learning » and is non-associative in nature ;
- 8) The result of this process is best described as an « acquisition » in which learned and genetically programmed interact ;
- 9) This acquisition takes place in the absence of conventional reinforcers ;

*The Evolutionary Function of the Imprinting Process.*

- 10) The usual result of this process has an adaptive function in terms of species evolution ;
- 11) This process must take place within certain environmental limits (i.e. within an « average expectable environment », or the « environment of evolutionary adaptedness ») if the particular result of such an acquisition in an individual organism is to fulfill a species specific function ;
- 12) This function is the establishment of certain preferences ;

*Imprinting as Preference acquired during an Early Sensitive or Optimal Period.*

- 13) These preferences are appetitive in nature and are definitely social, frequently either filial and/or sexual ;
- 14) The acquisition of these preferences is begun early in life during a relatively limited « sensitive » or « optimal » period ;
- 15) The consolidation of these preferences is not accomplished during the « sensitive » or « optimal » period, but afterwards ;
- 16) These preferences cannot be equated with, nor are always directly inferable from manifest behaviour ;

*Variability in Imprinting as a Phenomenon and as a Process.*

- 15) Variations in experience during the « sensitive » or « optimal » period frequently correlate positively with variations in subsequent behaviour ;
- 17) Experience beyond the « sensitive » or « optimal » period, however, can well effect the stability of, as well as the actual manifest form of the behaviour considered to be dependent upon acquired or imprinted preference ;
- 19) In the natural habitat, the trend begun during the « sensitive » or « optimal » period is continued beyond that period, usually with only minor variations, and thus leads to extremely stable manifest behaviour ;
- 20) The degree to which « normal » ontogenesis is interfered with experimentally, so is subsequent social behaviour likely to be unstable, maladaptive, non functional and/or deviate.

IX. — AN APPENDAGE : SOME TENTATIVE SPECULATIONS

There can be little doubt that the absence or formation of attachment and its quality in infra-human and human primates is the result of early experience. To date, there is no direct experimental evidence for specific temporal limits of a sensitive period influencing the establishment of affective or sexual bonds in primates. Naturalistic observations, as well as extensive clinical evidence, however, have lead many ethologists, psychologists and psychotherapists, the author included, to consider the formation of social preferences in all primates to be associated with a sensitive period similar to, though obviously not identical with, that found in dogs and certain birds. The literature cited by Spitz (1945, 1946 a, 1946 b, 1947), Gray (1958), Ainsworth (1962), Broody (1956), Broody and Axelrod (1970), Sander (1962, 1964, 1969), and above all Bowlby (1969, 1973) is compatible with such a sensitive period hypothesis. The literature to be cited on autism is complimentary.

As has been shown, neither imprinting nor attachment is an all-or-none phenomenon, there are various degrees (as well as types) of both (Bowlby, 1969, 1973). The actual variants of experience during a sensitive period correlate significantly with the type and quality of behaviour likely under subsequent conditions. If one accepts the clinical observations of Winnicott (1958, 1965), Balint (1968), Tustin (1972) and Tinbergen and Tinbergen (1972), then it is possible that « autism » may result in part from what amounts to improper or even insufficient filial imprinting, in which case the social bond cannot be established because the onset of fear has taken place before there was an attachment or a « secure base » from which the child can explore the external world. Thus, for the autistic child, fear evoking stimuli are paradoxically the same as those which are usually social and which during the proper sensitive phase would have brought about attachment.

Psychiatrists and psycho-analysts, no matter of what school, are in basic agreement that in the human, the formation of the mother-infant relationship is different from the formation either of sexual identity or of sexual object choice, the two of which must not be equated. There are abundant clinical reports of human sexual fixations not dissimilar in certain general aspects to those found in birds and infra-primate mammals.

Clinical evidence suggests, moreover, that certain variations in human sexual behaviour are a direct result of experiences beginning usually not before the end of the second year, and well established usually by the end of the fifth year, i.e., long before the onset of puberty. By contrast, the mother-infant relationship is well established, though not complete, by the end of the first year.

The above mentioned experiments by Chamove, Rosenblum and Harlow (1973) and by Chamove (1973) demonstrate how social as well as sexual inhibitions and disfunctions similar to those found in humans can be produced experimentally in rhesus macaques by « over intense » attachments or « fixations », furthermore, there appears to be a temporal limiting factor.

Most male macaques exhibit overt homosexual behaviour. However, neither macaque hetero- nor homo-sexual practices are strictly comparable with either human hetero- or homo-sexuality, except on a behavioural level. Male macaques can be observed to masturbate, to felate or to attempt to mount anally another male, even in the presence of receptive females, but psychological preferences as such are difficult to infer since no stable pair-bond is formed. Macaques are erotic opportunists. Males give the subjective impression of being interested only in something to insert into, i.e., the nature of the erotic object appears important only in so far as it affords pleasure. Macaques are pure hedonists,

incapable of « love » in the human sense of the word. Doves and ducks, by contrast, show decided sexual preferences and do form lasting couples both hetero- and homo-sexual. It is to be noted that the existence of a homosexual bond is not dependent upon sexual gratification. In ducks, for instance, true mountings are never achieved, yet the couple remains stable. Macaques, to the contrary, have no stable pairs, whilst manifesting homosexual behaviour resulting in orgasm.

A theory postulating the origin of human homo- and heterosexuality in an imprinting-like situation would not be incompatible with contemporary psychoanalytic and psychiatric clinical literature, though such a theory would necessitate a distinction between true homosexuality in which the preference for the same sex is a result of imprinting, and reactive or displacement homosexuality in which the opposite sex is imprinted on, but turned away from because of « Oedipal », « incestuous » or similar reasons. As is well known, manifest behaviour is not always identical with preference. It must be added, furthermore, that either an imprinted or a reactive homosexual could be neurotic concerning his homosexuality, in which case the imprinted homosexual would then be clinically similar to the classic hysteric, now a rare patient on the couch.

All that can be legitimately said of imprinted homosexuality is that it is non-functional in terms of species reproduction, though it is now well established that reproduction is only one aspect of sexuality, in particular of primate sexuality.

Money, Hampson and Hampson (1955, 1956, 1957) have offered evidence that even the formation of gender identity may be acquired during special conditions which they considers to resemble the sensitive period for imprinting. But one must follow Hooker (1963, 1965) and distinguish homosexuality as a phenomenon of object choice from sexual or gender identity. Money (1965) presented evidence for transvestites who are not homosexual. The author was asked to make a diagnostic evaluation of a transvestite who was very heterosexual on the level of manifest behaviour and who showed absolutely no interest in sexual relations with men, nor in the possibility of a transsexual operation which was suggested to him by his personal physician.

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