

she goes and whenever she moves, are directed and confined to stimuli with which the young have specific appropriate experience at an appropriate time. The exact stimulus object to which the birds respond in this way maintains its capability of evoking the adient response (attachment) through much of the young animal's life. The innate social responses through the process of imprinting become altered, so that the originally great diversity of objects capable of eliciting attachment becomes restricted to only the class or classes of objects encountered during the limited acquisition period.

D. A. Spaulding (1954/1873), the first to describe the phenomenon, showed that the attachment need not be restricted to the mother, although it normally is. He noted that as soon as newly hatched chickens could walk, they would follow any moving stimulus. This promiscuity of following could be observed in visually naive chicks only during the first few days. He placed small hoods over their heads as soon as they hatched and removed them at different intervals. For up to three days the chicks would run to Spaulding, but the chicks whose hoods were removed after four days fled in terror.

The strength of the attachment can be seen in one or more of the following tests: (1) *recognition at reunion*, in which, after separation, more imprinted birds return to the imprinting stimulus than do control chicks; (2) *choice*, in which experimental and control birds are presented with a training and a control stimulus; (3) *distress at separation*; (4) *run to mother*, in which somewhat dispersed chicks are exposed to a novel, frightening stimulus, whereupon the imprinted but not the control chicks are expected to retreat to the training stimulus; and (5) *work for reunion*, in which the birds must perform an arbitrary response such as a bar press to obtain access to the training stimulus.

Lorenz and others distinguished imprinting from ordinary learning because: (1) imprinting can take place only during a limited critical period; (2) once imprinting is accomplished, forgetting does not occur; (3) conventional rewards are not necessary to imprinting; (4) certain responses to the imprinted stimulus may not appear until late in life, long after the imprinting took place; (5) imprinting occurs more readily when trials follow each other quickly than when they are widely spaced, contrary to most associative-learning experience; and (6) painful stimuli strengthen imprinting, whereas punishment usually results in the avoidance of the associated stimulus.

The term "critical period" has been weakened somewhat into "sensitive period," for the all-or-nothing character of the former term does not stand up to fact. Instead, there seems to be a quantitative rise and fall in the ease or strength of imprinting. Moreover, additional experiences may interfere with imprinting: communally reared chicks may imprint on one another and this fraternal imprinting may inhibit the maternal. Also, if fear responses develop naturally at a certain age to potential social stimuli, the termination of the sensitive period may be abrupt.

The belief that imprinting is irreversible is no longer widely held. It has been shown that attachment can be transferred to new stimuli. In addition, a number of species do not direct their adult social attachments strictly to the parental figure or to its species; again, the species of its broad companions may dominate. This observation is rather general, and is the rationale for having domestic fowl rear clutches of wild birds in wildlife refuges, the young of which eventually are released and, presumably, carry on a normal reproductive life. Perhaps one way of looking at the persistence of early attachments is to note that primacy may be more effective than recency in the formation of the association.

The fixed action patterns of species that are imprinted to unusual objects remain unchanged. A human-imprinted ring dove shows the typical courtship rituals that would normally be used in courting a member of the opposite sex.

Object imprinting may be sex-related. Females of many groups of closely related species are often similar, particularly if they are rather drab; males, in contrast, have rather conspicuous markings which can act as releasers. The similarity of the females (absence of releasers) implies ease in accepting

other species as sexual partners. The female is dependent with respect to her sexual behavior on the key sign stimulus of the male of her species. Accordingly, she is unlikely to court males of other species, even though she may have been raised with them.

Although much of the research on imprinting has been done with birds, a few observations suggest that similar processes occur in mammals. Sheep, horses, and other hooved animals can be imprinted to humans, if a person assumes the parental role shortly after birth. Dogs are known to form close attachments to persons who care for them between the fourth and the sixth week of life. The pattern of treatment, nurturant or punishing, seems to be of little importance.

In *A general introduction to psychoanalysis*, Sigmund Freud emphasized the importance of early childhood in the development of attachments. If these attachments fail to develop during the sensitive period, the child's well-being may be permanently impaired. Separation studies by R. A. Spitz (1945) and others have provided evidence for such irreparable damage.

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BEHAVIORAL GENETICS ETHOLOGY INSTINCTIVE BEHAVIOR LEARNING THEORIES

A. J. RIOPELLE

INBREEDING AND HUMAN FACTORS

Inbreeding is mating between genetically related persons, that is, persons who share genes derived from a common ancestor. The degree of inbreeding is a function of the number of common ancestors and the number of generations they are removed. Specifically, degree of inbreeding is expressed quantitatively as the average probability that the offspring will receive two of the same alleles (alternate forms of a gene) from the same ancestor. (The methods for determining this value for any given mating between relatives are explicated by Crow & Kimura, 1970, and A. R. Jensen, 1978.) Brother-sister and parent-offspring matings are the highest degree of inbreeding found in humans. Incestuous matings have been taboo in all human societies throughout history, probably because of the high frequency of genetically undesirable effects, both physical and mental, on the inbred offspring (G. Lindzey, 1967). Mating of first or second cousins, however, is still relatively common in some societies; the adverse effects on the offspring are much more subtle than in the offsprings of incestuous matings, but are nevertheless clearly detectable. The average risk of genetic defects, for example, is approximately doubled in the offspring of first-cousin matings as compared with the offspring of unrelated mates. (It is increased eightfold for brother-sister and parent-child matings.) For individuals born with rare genetic defects—particularly various forms of severe mental deficiency—the percentage of their parents who are first cousins is some 20–40 times as great as the percentage of first-cousin matings in the general population.

The effects of inbreeding are understandable in terms of genetic theory. Inbreeding simultaneously affects all traits, physical and mental, that are conditioned to any degree by genetic factors. Inbreeding does not alter gene frequencies, but changes the frequencies of various genotypes (i.e., specific combinations of genes). Inbreeding always increases the amount of homozygosity (the same alleles, e.g., AA or aa, at a given chromosomal locus), and decreases heterozygosity (different alleles, e.g., Aa at a given locus). A general consequence of this relative increase in homozygosity is an increase in trait variance; inbred offspring are more variable in every

trait influenced by segregating genes (i.e., genes with two or more allelic forms).

The one other effect of inbreeding—probably the most important—occurs when a trait involves dominant and recessive alleles. If, as is usually the case, the dominant alleles enhance the phenotypic expression of the trait and the recessive alleles diminish the trait, the overall effect of inbreeding is to diminish the expression of the trait in the inbred individual. The reason, essentially, is that inbreeding increases the chances that the recessive alleles will be paired with other recessives, thereby depressing the trait—an effect known as *inbreeding depression*. (The pairing of a dominant and a recessive allele produces the same phenotypic effect as the pairing of two dominant alleles, and therefore results in enhancement of the trait.) The probability of recessive mutant or deleterious alleles coming together is much greater in inbred persons. Since most deleterious characteristics are recessive, inbreeding increases the risk of genetic defects in the progeny. This is especially marked in the case of single-gene characteristics such as albinism, alkaptonuria, muscular dystrophy, congenital deafness, and causes of severe mental defect such as phenylketonuria, galactosemia, microcephaly, and Tay Sachs disease. The latter, for example, occurs with a frequency of about 1 in 40,000 births in the general population, but something between 11 and 40% of these cases result from first-cousin matings, varying in different populations.

But even nonpathological trait variation that involves some degree of directional dominance, as do height and intelligence, will show inbreeding depression. Offsprings of first- and second-cousin matings, for example, show similar degrees of inbreeding depression for height and I.Q., amounting to about 0.2–0.3 standard deviations (3–5 I.Q. points) for the Wechsler Full Scale I.Q., as compared with age-matched offspring of genetically unrelated parents who were statistically matched with the cousin matings on a number of I.Q.-related variables such as socioeconomic status (Schull & Neel, 1965). The amount of inbreeding depression shown on the various subtests of the Wechsler is significantly positively correlated with the subtests' *g* loadings (i.e., the correlation of the subtest with the general intelligence factor common to all the subtests). Inbreeding depression also showed up in scholastic achievement. A number of studies of the offspring of incestuous matings (reviewed by A. R. Jensen, 1978) show that this high degree of inbreeding results, in general, in a severe depression of I.Q.; about one-third of such children show marked defects and are placed in institutions for the retarded.

The effects of inbreeding on mental ability are virtually impossible to explain in environmental terms, but they are predictable from genetic principles not only in humans, but in all animals and plants that reproduce sexually. Studies of the effects of inbreeding in humans clearly indicate that genetic factors, including directional dominance, are involved in individual differences in mental abilities as well as in physical characteristics.

BEHAVIORAL GENETICS HERITABILITY

A. R. JENSEN

INCENTIVES

A *positive reinforcer* or a *negative reinforcer* serves two quite different functions in the control of behavior. On the one hand, such events are critical to learning, although the mechanism of this influence remains controversial. On the other hand, they are motivators. This latter role identifies the concept of *incentive*, the motivational value of a reinforcer. The *Crespi effect* provides a demonstration of the operation of an incentive at the level of the laboratory rat. At the human level, approval, reproof, and money are examples. In these cases, of course, the incentive value is learned.

One of the earliest and most appealing illustrations of the effectiveness of such acquired incentives were the studies of token rewards to chimpan-

zees. J. B. Wolfe's experiments (1936) were representative. The tokens were small disks similar to poker chips, to which the animals were originally quite indifferent. Preliminary training consisted of teaching the chimpanzees to insert tokens in the slot of a vending apparatus which automatically released a grape to the animal. After having learned the reward value of tokens, the chimpanzees were trained to perform simple instrumental responses to secure the tokens. One task required the lifting of a lever; another involved pulling in a small sliding tray by means of a cord. The animals would continue to work at these tasks for a number of tokens which could not be exchanged for food until later. In an extension of these experiments, J. T. Cowles (1937) found that the tokens could be used as incentives in the acquisition of simple position habits and visual discriminations. A position habit requiring as many as 20 trials could be completely learned in one session with tokens as the sole reinforcing agent, prior to any reception of food reward.

CLASSICAL CONDITIONING CRESPI EFFECT REWARDS

G. A. KIMBLE

INCEST

The term "incest" is broadly construed to refer to sexual behavior between individuals who are related in any fashion except directly by marriage. Beyond this consensus, definitions found in various state laws and those proposed by experts differ along two dimensions: specific behaviors involved, and specific relations of participants.

Some definitions list only vaginal and anal coitus as behaviors involved in incest, while others include oral-genital behaviors and even fondling or mutual exhibition of the genitalia. These differences, especially among surveys and other research reports, make it difficult to estimate the incidence of various types of incest, however defined. Furthermore, any collation of data is bound to be attenuated by a significant failure to report on the part of victims—a tendency that incest shares with rape. For this reason, it has been suggested that brother-sister incest occurs far more often than father-daughter incest, which has been traditionally regarded as the most common form. A comparison of recent surveys suggests that if incest is broadly defined to include casual types of sexual contact, and if a large unselected sample is surveyed, then sibling incest will be the most common with a reported incidence of 10–15%. However, intercourse or attempted intercourse will be reported in less than 2% of the cases. Examples of such survey reports are in Morton Hunt, *Sexual behavior in the 1970's*, and Davis Finkelhor, "Sex among siblings: A survey of prevalence, variety and effects."

On the other hand, if the researcher seeks out individuals who have already reported incest, then the father-daughter form is most common. Proportionately, coitus appears to occur more often in the father-daughter dyads than among siblings. The perennial belief that incest occurs primarily in lower class and rural communities is not supported by recent data such as that of Finkelhor (1980) and Hunt (1974). These investigations suggest that incest is somewhat more likely to occur in upper and middle-class communities. The fact that the lower-class offender is more likely to come in contact with law enforcement agencies has distorted the overall picture.

The impact of incest, especially its long-term effects, has been generally thought to be malignant. William Masters and associates (1982) suggest that incest can lead to "drug abuse, prostitution, suicide attempts, and a host of other problems [including] a variety of sexual problems." Recent data indicate that the effect of incest is not that simple. For example, Joan Nelson (1981) found that the long-term reaction was more likely to be untoward if the incest occurred prior to age 10, and might actually be benign if it occurred after age 13. Nelson also reported that a negative