

The shaping of animals' minds

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Mind is seen as a collection of abilities to take decisions in biologically relevant situations. Mind shaping means to form habits and decision rules of how to proceed in a given situation. Problem-specific decision rules constitute a modular mind; adaptive mind-shaping is likely to be module-specific. We present examples from different behaviour 'faculties' throughout the animal kingdom, grouped according to important mind-shaping factors to illustrate three basically different mind-shaping processes: (I) external stimuli guide the differentiation of a nervous structure that controls a given behaviour; (II) information comes in to direct a fixed behaviour pattern to its biological goal, or to complete an inherited behaviour program; (III) specific stimuli activate or inactivate a pre-programmed behaviour. Mind-shaping phenomena found in the animal kingdom are suggested as 'null-hypotheses' when looking at how human minds might be shaped.

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Human psychologists use the term mind for a collection of faculties, or mental capacities, involved in perceiving, remembering, evaluating, and deciding. To not just describe, but understand how the human mind is structured and why it is structured that way, an evolutionary view is necessary. Therefore we will have to consider non-human animals' minds. One may then wish to know more precisely what a mind is. Saidel (2002) convincingly argues that one should use a functional definition by postulating an ability that a mind has and ask if particular organisms have that ability. We here postulate as crucial for mind the ability to make biologically meaningful decisions (McFarland, 1977). They in turn have to be inferred from some overt behaviour that is then taken as a behavioural marker of mind. In non-human animals, meaningful decisions are mostly involved in solving problems of ecological relevance to a given species'

environment. In order to be understood as mind-related, a behaviour should then be relevant for helping an organism to survive and reproduce.

We will scrutinize this mind concept by presenting selected examples from different animals to stress the fact that perceiving, remembering and evaluating capacities necessary for making decisions may be correlated to events not only in a brain, but also in less centralized, functionally equivalent nervous systems of so-called lower animals.

Mind shaping may include some form of learning, be it trial-and-error-learning or social learning. Trial-and-error-learning requires that the learner exploits the feed-back of results achieved by his own goal-directed actions. Social learning needs some type of interaction with model individuals who in some way or another provide relevant information (Heyes, 1994). Learning is operationally defined as a change in an animal's behaviour that is caused by a specific experience, which is stored as information in long-term memory. But long-term mind-shaping is often accomplished without learning, based on other physiological mechanisms. Imprinting for instance, defined as a long-term effect triggered in a sensitive phase, may either be related to learning (cognitive imprinting) or result from other physiological processes (physiological imprinting; see below). While genetic programs offer similar problem-solving programs to individuals that belong to the same species and the same sex, individual experiences and learning enable an individual to find its own solutions to problems; the respective mental capacities may then well differ between conspecific individuals.

We do not intend a review paper but want to provide a guideline for comparing mind-shaping processes in animals. For the present purpose we will distinguish three different mind-shaping processes:

- (I) special stimuli direct, early in ontogeny, the structural differentiation of parts of the central nervous system that control a given behaviour;
- (II) information is added to complete or supersede a given behaviour program later in ontogeny;
- (III) defined stimuli activate or modulate an already pre-programmed behaviour; this may happen at any time during life.

(I) Parts of the nervous system are structurally differentiated by external stimuli

Mental capacities may develop under tight genetic guidance. Some genetically pre-programmed properties will always be a factor in an individual's

perception and decision making. In animals without genetic sex determination, environmental stimuli may determine the sex of the developing embryo, i.e. the development of its male or female morphology, physiology and sex-related behaviour, including the corresponding processes of perception, memory and decision making.

For some turtles, lizards and crocodiles incubation temperature is the decisive environmental stimulus for sex determination (Bull, 1980; Gans, 1988).

Of all reptile brains the crocodile brain is the most highly developed (Mertens, 1960), as is the sex-specific differentiation of behaviour. Female crocodiles build nests to shelter the eggs and remain close to the nest for several months to protect the eggs from predators. The female estuarine crocodile (*Crocodylus porosus*) builds a mound of mud and decaying plant material, in the centre of which are the eggs. With her tail she splashes water onto the nest, thus promoting the heat-generating process of vegetative decay. When ready to emerge, the young utter squeaking sounds whereupon the mother removes the debris and gently picks up the young with her powerful jaws and carries them in her mouth to near water. Male crocodiles on the contrary fight heavily for territories but catch and swallow baby crocodiles, even their own ones. The very different sexual behaviour repertoires of adult crocodiles are not determined in the egg, but develop according to the breeding temperature.

The same applies to some other reptiles. On top of this, breeding temperature may also decide upon more subtle sex role characteristics. In the leopard gecko (*Eublepharis macularius*) males are produced at temperatures between 30° and 32.5°C. Males that developed under a higher temperature are more aggressive and less sexually active than males that developed under a lower temperature. Furthermore, incubation temperature even influences behavioural plasticity in adulthood: heterosexual social experiences increase territorial behaviour (scent marking) and courtship behaviour (tail vibrations) in low-temperature but not in high-temperature males. These character differences arise during embryogenesis when temperature influences the differentiation of brain nuclei which are the neural mechanisms underlying aggressive and sexual behaviour (Coomber et al., 1997; Sakata & Crews, 2003).

In mammals a similar phenomenon can be found, mediated not by temperature but by hormones. In several rodents (house mice *Mus*, Mongolian gerbils *Meriones*, red-backed voles *Clethrionomys*) an individual's intra-uterine position between either two brother (2M) or two sister (2F) embryos profoundly affects the individual's subsequent behaviour and reproductive life history (Zielinski & Vandenbergh, 1991). This is caused by a prenatal suscepti-

bility to wombmates' hormones (Clark & Galef, 1994, 1995). 2M female house mice become more aggressive, less sexually active, have lower life-time fecundity but larger home ranges than 2F females. In *Meriones* gerbils 2M females will, as mothers, produce litters containing more sons than daughters. So their female embryos will also more likely have two male neighbours, to the same after-effect. That means, females acquire from their brothers, through a prenatal endocrine mechanism, a male-biased sex-ratio among their offspring; and those females' brothers enhance the production of their own nephews by an effect on their sisters (Vandenbergh, 1993; Vandenbergh & Huggett, 1994). An epigenetic mind-shaping effect on an individual's gender role behaviour can thus even be transferred into subsequent generations.

(II) *External information complements an inherited behaviour program*

In many animals various epigenetical — environmental and social — influences act at some point in ontogeny to shape an individual's mental capabilities. Genetic and epigenetic mind-shaping processes will then complement each other. The information required to complete a given behaviour program may concern the perception or the execution part of a behaviour; that is, it may be needed either (1) to correctly identify the target of a given behaviour, or (2) to develop a specific behaviour performance to perfection; and (3) some behaviours need improvement of both perception and execution.

(1) Target identification

a. Physiological imprinting on food types

'Imprinting' is an aspect of passive experience during a sensitive period, usually in the early stages of an animal's life. It provides an alternative to an innate recognition of important objects and has long-term effects on social relationships, food or habitat selection.

Some insect mothers deposit their eggs on a special substrate that serves as food for their developing larvae; a plant leaf in the case of some butterflies, a living caterpillar in the case of *ichneumonid* wasps. After pupation the emerging adult still remembers the substrate on which it developed and, if a female, will prefer that same type of substrate for her own egg deposition (Thorpe, 1956), thereby determining the same process for the next generation and potentially starting a new food tradition. The information acquired in the feeding context is transferred into the adult reproductive behaviour, directing egg-laying to its biologically meaningful target substrate. To do so, this information obtained by

the larva has to survive the profound reorganization (Breidbach, 1988) of the bodily structures during pupation of the larva into a flying insect.

b. Cognitive imprinting on social companion

Imprinting often serves to recognize species-specific characteristics. Individuals of various precocious bird species acquire the ability to identify a fellow-member of their species by an early posthatch exposure to the parent. This is proven by the fact that the young, if artificially misimprinted on an individual of a foreign species, will keep contact and consistently follow that pseudo-parent. A misimprinted male duckling will later in his life consort and try to mate with members of the wrong species (Lorenz, 1935), while in geese the misdirected preference is maintained only as long as the young need parental care.

A sensitive period for imprinting may also arise in relevant situations later in life. Instead of offspring becoming imprinted on their parents, in some cichlid fishes parents become imprinted on their offspring. If one replaces the very first brood of *Hemichromis* parents by that of a foreign species the parents will raise those foreign young. But thereafter the *Hemichromis* parents will care for young of that foreign species only and will swallow young that hatch from their own eggs (Myrberg, 1964).

c. Social learning about enemies

Cultural transmission of enemy recognition has been analysed in detail by Curio (1988). He showed that adult birds' conspicuous mobbing behaviour towards a visible predator attracts inexperienced individuals and serves to socially transmit recognition of local predators to them. In this critical experiment, naïve European blackbirds (*Turdus merula*) were exposed to some neutral object, for instance a multicoloured plastic bottle, while an experienced bird was tricked into mobbing a resting owl that was shielded from view of the naïve birds. So the naïve birds connected the predator harassment to the neutral object and from then on habitually mobbed this object. The pupil birds eventually turned into tutor birds passing this mistaken information on to their own offspring.

d. Social learning about food

Cross-generational transfer of food preferences, which has a long-term influence on the offspring's later food choice, can take place in different ways. Spiny mice (*Acomys*), for example, adopt maternal food preferences via nose-mouth contact with a feeding mother: the mother holds still with the mouth slightly open in a stereotypic posture (McFadyyn-Ketchum & Porter, 1989) which may

be interpreted as an initial step towards teaching. Weanling rats learn to prefer food eaten by their true as well as by foster-mothers, indicating that the preference transfer is non-genetic (Bronstein et al., 1975). Infant primates, too, tend to synchronize their feeding bouts with those of their mothers and feed on the same food items as their mothers (Hauser, 1994). Likewise, cultural transmission of new feeding techniques by observational learning has been observed in free living vervet monkeys (*Cercopithecus aethiops*) and chacma baboons (*Papio ursinus*) (Cambefort, 1981).

Rabbit embryos adopt their mother's food preferences even prenatally via odours associated with mother's diet. This process, that could well be interpreted as a case of imprinting, leads to enhanced, stimulus-specific sensitivity of the basic sensory mechanism, illustrating mind-shaping via an epigenetic social influence on a perception apparatus (Hudson & Distel, 1999).

Some free living birds establish feeding traditions not by becoming passively imprinted but by active social learning (Diamond, 1987). A young bird may closely follow its parents, intently observing their feeding and then trying to eat from the same spot. To become efficient foragers, the young of some finch species need more than one year of training about where to look for what kind of food (Werner & Sherry, 1987).

(2) Performance improvement

Examples in the preceding paragraph illustrate cases where information has to be acquired to direct a genetically fixed behaviour pattern to a biologically meaningful target object. On the other hand, information about the target object may be genetically provided while the corresponding behaviour pattern needs functional improvement.

a. Trial-and-error learning about food acquisition

The Galápagos woodpecker finch *Cactospiza pallida* is famous for using twigs or cactus spines which it holds in its beak to push, stab or lever arthropods out of tree holes and crevices. The bird varies the technique according to the particular task and modifies its tools by shortening too long ones and breaking off twiglets that would prevent insertion (Eibl-Eibesfeldt, 1961). All young woodpecker finches pick up and playfully manipulate twig-like objects and try to probe with them into holes. In areas with few holes but with otherwise easily accessible prey, individuals soon lose interest in twigs and will as adults not even try to use tools. Neither young nor adults learn from observing other birds using tools. However, young birds that start their lives in an environ-

ment with ample opportunity to find holes and insects in them, will by trial-and-error learning soon become skilled tool-users regardless of whether they had tool-using or non-tool-using parents. Effective tool-use thus has an innate component but also requires complementation by learned components from adequate interaction with specific environmental features (Tebich et al., 2001) to establish tool-using behaviour and to develop the necessary fine-tuned motor coordination, presumably by enhanced cerebellar synaptogenesis (Byers & Walker, 1995).

b. Social learning of birdsong

When they learn how to sing, most songbirds listen to adult tutors, keeping the songs in mind as acoustic templates, and then assimilate (emulate) their own vocalizations to the model sounds memorized from the first months of their lives. This “training phase” seems to be comparable to the babbling phase of human children (Marler, 1973). Song learning is the nearest known functional and evolutionary parallel to human language in the animal kingdom, encompassing the cultural tradition of the structure, semantic and syntax of vocal elements as a communication system (Salwiczek & Wickler, 2004), including the corresponding mind-shaping processes.

Strains of socially learned vocalizations tend to diverge due to cultural drift and give rise to local song dialects. Communication between representatives of the diverging strains may become increasingly difficult, rendering mating ever less likely. Where dialects in this way limit gene flow, genetic evolution becomes constrained by tradition, and culture starts to keep genes on a leash. Traditive (i.e. not genetically transmitted) elements, that shape minds accordingly and determine partner choice, may thus even direct ongoing genetic evolution (Salwiczek, 2001).

(3) Goal identification plus behaviour improvement

In some animal species, the growing individuals still need both information about important objects and about specific performances.

a. Social learning about both new food and feeding techniques

A well known example recorded since 1930 from several tit species in many parts of England is the habit to pierce the covers of milk bottles (Fisher & Hinde, 1949). Milk is not a normal source of food for these birds, but in some localities a few birds discovered how to drink milk from bottles delivered to doorsteps. Watching a companion feeding from a bottle raises interest in others who then

try by themselves. They thereby learn to recognise milk bottles as a potential supply of food and then attack the bottles within a few minutes of their being left at the door. Some parties of tits even used to follow the milkman's cart down the street, removing the caps from bottles in the cart.

In addition to socially learning about this new food and where to locate it, each individual bird has to find out by trial and error how to open a bottle. Accordingly, the method of opening varies greatly, and each individual may employ several techniques. A cap of metal foil can first be punctured by hammering with the beak and then the thin strips of metal can be torn off. Cardboard taps may be removed in total, or torn off layer by layer, or a small hole can be made in it. People of course tried to cover the tops of the bottles; but the birds even removed a flat stone from the top of a bottle or reached the milk in spite of a tea cloth spread over the bottle. It may thus make persistent attempts to reach the milk even though the top of a bottle is no longer visible (Fisher & Hinde, 1949).

A continuous cultural evolution of feeding techniques was reported by the late Eugène Marais (1971): *Chacma* baboons in South Africa in the midst of the nineteenth century discovered that milk could be found in the stomach of sheep lambs. They caught the lambs, tore open their entrails and ate the curdled milk. Within 80 years this habit spread and became a regular habit in the Central Cape Province. Next the baboons began to eat the flesh of the slaughtered lambs and to capture lambs for no other purpose. They also changed the killing method; originally they just tore open the entrails, but later they would stretch the lamb on its back, bite both jugular veins and leave the lamb until it was dead. Then the flesh was torn from the body and eaten. In the end the baboons began to slaughter large sheep too.

b. Social learning that establishes complex (proto-)cultures

Behavioural traditions play a vital role in primates, who in nature depend heavily on learning from conspecifics various details about their technical and social world. To achieve this they exploit past experiences of elders and pass on to their offspring skills and information that would be dangerous or arduous for them to acquire on their own (Tomasello & Call, 1997). Various traditive traits in chimpanzee behaviour have recently been summed up as 'chimpanzee cultures'; they include tool usage, nest-building, grooming and courtship behaviour, gestural communication, and knowledge about medicinal plants and their usage (Wrangham et al., 1994; Whiten et al., 1999). Clearly chimpanzees'

and other primates' minds are shaped like human minds by associative learning, active curiosity and social copying.

Socially transmitted packages of information that control behaviour are called 'memes' (Dawkins, 1989). They are mind shaping by definition; influencing decision-making evaluations, and overt behaviour in various ways. Socially acquired preferences may guide food preferences, nest site selection, communication style, mate choice, etc. Memes not only shape minds but can install complete new behaviour programs already in animals. In humans memes form the set of cultural instructions people carry in their brains; memes are evidenced as ideas (neural codes) as well as associated overt behaviour patterns, language included. There are cases of important coevolution of memetic and genetic traits in humans (Durham, 1991) and birds (Salwiczek, 2001). But because there is no reason why successfully spreading memes should be connected to an individual's genetic success, memes can as well function like parasites in the hosting human or non-human organism (Dawkins, 1982; and see the next section).

(III) External stimuli switch on or off a pre-existing inherited program

Overt perception, memory as well as evaluation, and in turn decision making may be inclusively manipulated by external stimuli which selectively block or activate complete behaviour programs.

(1) gender role activation

Individuals of various animal species have their genetic sexual predisposition epigenetically modulated by social stimuli which can act on different physiological levels. Social sex determination and social mind shaping in the sexual context (expressed in partner choice, memory for social interactions in dominance situations, evaluating options for successful reproduction, and deciding between alternative behaviours) are found in sequential hermaphrodites, who undergo change of sex and gender role as adults, either once and for good, or repeatedly.

Some labrid fish species are peculiar in that they have three types of sexuals: initial females and initial males, both genetically determined, and supermales who arise either from sex change in an initial female, or from role change in an initial male (reviewed by Grober, 1998). In *Thalassoma bifasciatum* initial males and females are of similar yellow colouration, while supermales have blue heads, a black-white-black banding behind the head, and green bodies. Super-

males are highly aggressive and defend breeding sites where they gain exclusive access to females and may mate with up to 100 females per day. Initial males do not defend breeding sites, are less aggressive and mate in large aggregations of about 50 males per female; they also try to sneak mate with a supermale/female pair. Should the supermale from a social group disappear, the largest initial stage individual, either male or female, will within minutes increase aggression towards similar-sized individuals and direct courtship towards females. It thereby gains social dominance at once, while gonadal sex change needs 7–10 days. The physiological background of these changes in behaviour and responsiveness is as follows: Sex reversal is blocked in individuals by the presence of a dominant male. Decreases in the amount of aggressive behaviour received by the largest individual result in rapid changes in brain peptid expression, allowing for higher rates of male-typical behaviour. This triggers changes in the hypothalamic-pituitary-gonadal system, in coloration, endocrinology, gonad anatomy and physiology, and in overt behaviour (Grober, 1998).

Social dominance, which in turn depends upon differences in relative body size between group members or pair mates, is the key factor in the inhibition of sex or role changes in subordinate individuals, in vertebrates and invertebrates. This is most apparent in species whose individuals can change sex more than once. While in the labrid fish *Thalassoma* sex change is irreversible, the closely related cleaner fish *Labroides dimidiatus* may change sex repeatedly: If a male is kept together with a larger female both will change sex (Kawamura et al., 2002).

Neither *Thalassoma* nor *Labroides* care for the brood. But the mind-shaping effects of socially-mediated sex reversal become particularly obvious in complex behaviour changes of species with brood care. In the gobiid fish *Trimma okinawae* (Sunobe & Nakazono, 1993) males occupy a spawning site in a hole or under a rock which they defend aggressively against other males. Towards a female they show a specific courtship behaviour, hopping towards her, swimming round her, and leading her to the spawning site. After spawning the male cares for the eggs until they hatch. Female-typical behaviour is limited to visiting the territories of nearby males, thereby starting male courtship, and then attaching the eggs to the ceiling of a male's home. As in *Labroides*, individuals can change from one sex role to the other and back; their overt behaviour repertoire change as does the corresponding specific attention to social and environmental stimuli, including those coming from their own eggs.

Similarly, sex and behaviour can change in the marine polychete worm *Ophryotrocha diadema*, which forms stable monogamous pairs, one individual

acting as male, the other as female. During synchronizing courtship both engage in extensive rubbing of their bodies against each other and form a mucous tunnel, in which one lays eggs and the other fertilizes. The egg cocoon is cared for by the partners taking turns. Either parent may leave the tunnel for some time and then come back to the eggs. Interestingly, both partners in a pair tend to simultaneously change sex after one, or a few, spawnings, and they repeat this regularly every 3–4 days. The reason is that some 80% of the physiological reproductive effort is allocated to the female functions and females therefore are soon drained of resources. They then change to the less costly male role, and males thus become more apt to function as females. Furthermore, male reproductive success drops with increasing size because females prefer to mate with small males to avoid a costly conflict over sex (Premoli & Sella, 1995).

The fish species mentioned are called sequential hermaphrodites because their complete physiological (including gonadal) sex and sex role reversal takes some time (up to 10 days). The *Ophryotrocha* worm can change sex roles between successive spawnings within 3 days. While sequential hermaphrodites can only act either as male or as female at any one time, simultaneous hermaphrodites are constantly ready for both gender roles. Simultaneous hermaphrodites are common among many lower animals (worms, snails, and seastars) but also occur among fishes. Here social stimuli determine an individual's sex for just a momentary social interaction. Consequently, pair mates have to arrange who is male and who is female at a given moment. Such opportunistic switching between roles requires persistent decision-making; it may be understood as 'open-mindedness', as opposed to a shaped mind which should keep its shape for some sizeable time span.

As an example we mention the black Hamlet *Hypoplectrus nigricans*, a serranid coral reef fish. A pair could finish spawning within a few minutes if at first one partner ejected all its eggs, the other fertilized them, and then both changed roles. However eggs are costly in production, while an individual has enough sperm to fertilize the eggs of several mating partners. The fertilizing individual of a pair therefore, instead of offering its own eggs in return, might withhold its eggs and leave to search for other egglayers. Understandably any individual will prefer the male part for reproduction which in turn leads to subtle behavioural negotiations and so-called egg-trading between mating individuals. As a counter measure, the egg-laying individual of a mating pair will only offer a small portion of their available eggs for fertilization and will then wait for the partner to reciprocate (Fischer, 1981). Under egg parcelling a cheater could win only a small portion of eggs 'unpaid', and the partner would

still have enough eggs to remain a preferred mating partner. This, together with an estimate of costs for cheating (how long it takes to find a new partner, with how many eggs) keeps the action going, though over a seemingly unnecessary long time (Friedmann & Hammerstein, 1991).

(2) Heteronomous mind-shaping

Many animals have some of their own genetically pre-determined species-specific behaviour programs untimely unlocked, and their minds 'mis-shaped', from modulating influences from foreign species. Mind-shaping parasites of all types can, to their own benefit, manipulate the decisions, and activate specific behaviours, of their hosts to the benefit of the parasite. This is an often neglected factor that shapes the minds of host animals. The rabies virus for instance causes foxes to stop caring for their family and instead roam about to bite, rather indiscriminately, other animals (including humans). This behaviour clearly is detrimental for the fox but beneficial for the virus who rides in fox saliva into new hosts. Some parasites castrate their host and stop its interest in sexual rivalry and costly reproductive behaviour, thus enhancing the chance for the host to survive as a resource for the parasite (Baudoin, 1975). Other parasites as larvae turn an intermediate host's negative phototaxis into a positive one such that the host, instead of hiding from predators, presents itself in the open and falls easy prey to a predatory animal which in fact is the parasite's final host. A more intricate mind-shaping is executed by the larva of the liver fluke *Dicrocoelium*. When adult it lives in sheep and related ruminants. Fluke eggs, dispersed in the host's faeces, are finally eaten by ants. Inside the ant, a fluke's metacercaria larva enters a specific area of the ant's lower oesophageal ganglion. From there it changes — as a 'brain-worm' — the ant's sleeping behaviour to the effect that the ant, at night, no longer returns to the subterranean ant colony but instead climbs a grass stem and spends the night firmly bitten to a grass tip. Early in the morning when the ant hangs numb, grazing ruminants will swallow it and become infected with the liver fluke (Hohorst & Sprengel, 1972). We need not expand further on that topic. A breathtaking survey of parasites' tricks is given by Zimmer (2000).

Conclusions

Zoologists invited to give a lecture at a Making Mind conference will invariably compare human and non-human animals. The benefits of such cross-taxa

comparison are gratefully acknowledged in medicine, but when it comes to comparing cognitive abilities there is a strong tendency to view animals as separate, special, creations and man even more separate and more special, or even to make humans incomparably unique by definition. We think the uniqueness of any species must not just be conceived but has to be shown to exist, and this can only be done by thorough comparisons. Mind-shaping phenomena found in the animal kingdom could, on the other hand, be used as 'null-hypotheses' when looking at how human minds might be shaped.

We understand 'mind' as some abstract organ which is involved in perceiving, remembering, evaluating, and making biologically relevant decisions. Under the premise that decision-making has to be inferred from an individual's overt behaviour, the mind-concept can in a meaningful way be applied to non-human animals. Mind shaping then means to form habits and decision rules about how to proceed in a given situation; it commits the individual to follow a decision rule for that situation. The re-appearance of that situation is mandatory for us to identify a decision rule. On the other hand, it is only in the case of a re-occurring situation that it pays for the individual to form a decision rule at all. The 'shape' in question, then, should outlive the time span necessary for repeated appearances of that situation.

Mind shaping concerns different behaviour 'faculties' in animals. The need to solve problems of different kinds will require different special-purpose programs, each with its own situation-specific decision rules. Those different programs or abilities would constitute a modular mind (Barkow et al., 1992), and an adaptive mind shaping then is likely to be module-specific. A migratory bird will be genetically determined to decide when and where to fly, may be imprinted to recognize conspecifics and enemies, will socially learn how to communicate, and will by trial-and error acquire specific feeding techniques. Complex cultural traditions will be similarly based on quite different mind-shaping processes.

So far no thorough studies are available that show how many behaviour faculties can be influenced by mind shaping in a single species. It may well be that humans are peculiar in the range of mind-shaping effects upon all levels of behaviour organization. On the other hand, because the ability to take decisions has to be inferred from functional behaviour, one has to take interrelated functions into consideration when looking for a corresponding mind module that may have been shaped. If a female mouse uses a larger home range, is less sexually active, but is a more effective mother compared to other females, she — while still in her mother's uterus — may have just a mind module shaped

that is responsible for agonistic decisions, perhaps based on a critical threshold for attacking or avoiding conspecifics.

Depending on the species, various influences of environmental or social origin may be involved in forming habits and decision rules. Whether to behave in a female or male way is environmentally determined via breeding temperature in reptiles, but is socially determined by dominance situations in some worm and fish species. Knowledge about where to lay the eggs is ecologically mediated via larval feeding substrate in some insects. Social transmission of knowledge about what to eat can take very different ways: it is mediated in bees by their dancing communication system, in some rodents by physiological imprinting, and in baboons by imitative learning.

Learning is a well-known process in habit formation, be it by trial-and-error learning, where an individual itself strives to solve a problem, or by social learning, where the key information to solve the problem is taken from a tutor individual. Both processes require an active interest from the learner individual. When learning by trial-and-error, the individual displays an amazing perseverance despite a series of failures; a goal-directed fervour prevents it from being discouraged and giving up after initial fruitless efforts. During social learning the individual exhibits a special curiosity in others' actions (e.g. thoroughly watching its feeding parents; Werner & Sherry 1987) and may even solicit lessons from a tutor; young songbirds for instance during the song-learning phase may prod an adult male to sing.

On the other hand, we selected examples from throughout the animal kingdom to point out that learning need not be involved in epigenetic mind shaping in animals. Instead an individual's mind can be passively (and unavoidably) shaped by external stimuli. This happens in reptiles whose brain nuclei, responsible for activities in social situations, become sex-specifically organized by the incubation temperature, and some rodents undergo an intra-uterine establishment of food preferences and hormonally induced gender-role expression. These processes may be called 'physiological imprinting', as opposed to 'cognitive imprinting' — as a case of (in principle avoidable) borderline-learning — which would apply to those situations where the learner has to join another individual's activities to become imprinted, for instance on the biologically correct social companions, as in the following reaction in waterfowl, on locally important enemies, as in mobbing behaviour, or on maternal food preferences, as in synchronously feeding near the mother's mouth.

Our examples illustrate different mind-shaping processes: An external stimulus may guide the basic differentiation of a nervous structure that con-

trols a given behaviour. In various vertebrates brain areas differ in size and anatomical structure between sexes and in the behavioural consequences of brain sex (Gahr, 1994, 1996). These brain differences develop under the influence of hormones. Hormone functions in their turn are often genetically determined, but can also be causally related to epigenetic factors, as exemplified by the intra-uterine influences on rodent females' expression of social behaviour. Environmental factors like breeding temperature can yield the same result as described for the differentiation of brain nuclei underlying the behavioural plasticity of the male gecko.

Another type of mind-shaping compensates for a lack of information. Gathering information by trial-and-error-learning is decisive for the woodpecker finch to develop and improve basic behaviour elements into functional tool-use. Socially provided information may be needed to direct a fixed behaviour pattern to its biological goal if the individual is, for instance, inherently able to eat, walk or be aggressive or fearful, but needs information about what to eat, and whom to follow or treat as a predator. Baboons need information about both new behaviour tactics and the targets for special ways of foraging. Likewise chimpanzees, in order to acquire a cultural habit, need information about which things to handle as well as tactics about how to handle them.

And finally, mind-shaping may operate via specific stimuli to activate or inactivate a pre-programmed behaviour. In cases of long-term or short-term sex reversal a male or female set of reproductive activities is triggered mainly via a change in relative social dominance.

All mind-shaping parasites, too, activate part of the host-specific behaviour repertoire. The liver fluke larva elicits a sleeping behaviour characteristic for solitary *hymenoptera* (Kaiser, 1995), the ants' phylogenetic ancestors. Although no longer shown by socially living ants, they still harbour the dormant program. A host whose life is driven by a parasite will not show part of the parasite's behaviour. And instead of prying into the intricate physiology of a complex host organism it will be more economic for a parasite to exploit the host's own decision-making, by manipulating the evaluation functions by way of disinformation (from the host's point of view). A parasite for instance, that needs a longlived caterpillar to live in, may reinforce the production of some kind of juvenile hormone, thereby persistently 'convincing' the host that he is still too young for pupation into a flying insect and consequently he continues growing with ever more moulting cycles. Thus a host's mind, which is manipulated by a parasite, still makes meaningful decisions, though biologically mean-

ingful for the parasite. Needless to say that this is the same way how memes can influence an individual's mind.

All things considered, an individual's learning history may only to some degree explain the making of its mind. In humans, too, mind-shaping ranges from the foetus being passively influenced (or even imprinted), e.g. by hearing specific voices (Kolata, 1984), to perinatal food-related chemosensations and childhood eating experiences that establish culture-typical foods, up to curiosity-driven learning and incorporating culturally transmitted assumptions about the existence and particular — even counter-intuitive — causal powers of supernatural entities and agencies. We suggest using mind-shaping phenomena found in the animal kingdom as a 'null-hypotheses' when looking at how human minds might be shaped.

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References

- Barkow, J. H., Cosmides, L., & Tooby, J. (1992). *The adapted mind*. Oxford: Oxford University Press.
- Baudoin, M. (1975). Host castration as a parasitic strategy. *Evolution*, 29, 335–352.
- Breidbach, O. (1988). *Die Verpuppung des Gehirns*. Köln: Universitätsverlag.
- Bronstein, P. M., Levine, M. J., & Marcus, M. (1975). A rat's first bite: the nongenetic, cross-generational transfer of information. *Journal of comparative and physiological psychology*, 89, 295–298.
- Bull, J.J. (1980). Sex determination in reptiles. *Quarterly Review of Biology*, 55, 3–21.
- Byers, J.A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *American Naturalist*, 146, 25–40.
- Cambefort, J. P. (1981). A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon *Papio ursinus* and the vervet monkey *Cercopithecus aethiops*. *Folia Primatologica*, 36, 243–263.
- Clark, M. M., & Galef, B. G. (1994). A male gerbil's intrauterine position affects female response to his scent marks. *Physiology and Behavior*, 55, 1137–1139.
- Clark, M. M., & Galef, B. G. (1995). Prenatal influences on reproductive life history strategies. *Trends in Ecology and Evolution*, 10, 151–153.
- Coomber, P., Crews, D., & Gonzalez-Lima, F. (1997). Independent effects of incubation temperature and gonadal sex on the volume and metabolic capacity of brain nuclei in

- the leopard gecko (*Eublepharis macularius*), a lizard with temperature-dependent sex determination. *Journal of Comparative Neurology*, 380, 409–421.
- Curio, E. (1988). Cultural transmission of enemy recognition by birds. In T. Zentall, T. & B.G. Galef, B. G. (Eds.), *Social learning: psychological and biological perspectives* (pp. 75–97). Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Dawkins, R. (1982). *The extended phenotype: the gene as the unit of selection*. New York: W. H. Freeman.
- Dawkins, R. (1989). *The selfish gene (new edition)*. Oxford: Oxford University Press.
- Diamond, J. M. (1987). Learned specializations of birds. *Nature*, 330, 16–17.
- Durham, W.H. (1991). *Coevolution*. Stanford California: Stanford University Press.
- Eibl-Eibesfeldt, I. (1961). Über den Werkzeuggebrauch des Spechtfinken *Camarhynchus pallidus* (Slater und Slavín). *Zeitschrift für Tierpsychologie*, 18, 343–346.
- Fischer, E. A. (1981). Sexual allocation in a simultaneously hermaphroditic coral reef fish. *American Naturalist*, 117, 64–82.
- Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds*, 42, 347–357.
- Friedman, J.W., & Hammerstein, P. (1991). To trade or not to trade; that is the question. In R.Selten (Ed.), *Game equilibrium models. I. Evolution and game dynamics* (pp. 257–275). Berlin: Springer Verlag.
- Gahr, M. (1994). Brain structure: causes and consequences of brain sex. In R.V. Short & E. Balaban (Eds.), *The Differences between the Sexes* (pp. 273–299). Cambridge: Cambridge University Press.
- Gahr, M. (1996). Die sexuelle Differenzierung von Gehirn und Verhalten. *Habilitationschrift*. München: LMU.
- Gans, C. (Ed.) (1988). *Biology of reptilia. vol. 18, Ecology B*. New York: Alan R. Liss.
- Grober, M. S. (1998). Socially controlled sex change: integrating ultimate and proximate levels of analysis. *Acta ethologica*, 1, 3–17.
- Hauser, M. D. (1994). The transition to foraging independence in free-ranging vervet monkeys. In B. G. Galef, M. Mainardi & P. Valsecchi (Eds.), *Behavioural aspects of feeding* (pp. 165–202). Chur, Switzerland: Harwood Academic Publishers.
- Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*, 69, 207–231.
- Hohorst, W., & Sprengel, T. (1972). Entwicklungszyklus des Kleinen Leberegels (*Dicrocoelium dendriticum*). *Publikationen zu wissenschaftlichen Filmen*, Film D 1081. Göttingen: Institut für den Wissenschaftlichen Film.
- Hudson, R., & Distel, H. (1999). The flavor of life: Perinatal development of odor and taste preferences. *Schweizerische Medizinische Wochenschrift*, 129, 176–181.
- Kaiser, W. (1995). Rest at night in some solitary bees — a comparison with the sleep state of honey bees. *Apidologie*, 26, 213–230.
- Kawamura, T., Tanaka, N., Nakashima, Y., Karino, K., & Sakai, Y. (2002). Reversed sex-change in the protogynous reef fish *Labroides dimidiatus*. *Ethology*, 108, 443–450.
- Kolata, G. (1984). Studying learning in the womb. *Science*, 225, 302–303.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie*, 83, 137–413.
- Marais, E. N. (1971). *My friends the baboons*. London: Anthony Blond Ltd.

- Marler, P. (1973). Speech development and bird song: are there any parallels? In G. A. Miller (Ed.), *Communication, language, and meaning* (pp. 73–83). New York: Basic Books, Inc..
- McFadyen-Ketchum, S. A., & Porter, R. H. (1989). Transmission of food preferences in spiny mice (*Acomys cahirinus*) via nose-mouth interaction between mothers and weanlings. *Behavioral Ecology and Sociobiology*, 24, 59–62.
- McFarland, D. J. (1977). Decision making in animals. *Nature*, 269, 15–21.
- Mertens, R. (1960). *The world of amphibians and reptiles*. New York: McGraw-Hill.
- Myrberg, A. A. (1964). An analysis of preferential care of eggs and young by adult cichlid fishes. *Zeitschrift für Tierpsychologie*, 21, 53–98.
- Premoli, M. C., & Sella, G. (1995). Sex economy in benthic polychaetes. *Ethology Ecology & Evolution*, 7, 27–48.
- Saidel, E. (2002). Animal minds, human minds. In M. Bekoff, C. Allen, & M. Burghardt (Eds.), *The cognitive animal* (pp. 53–57). Cambridge Mass./ London: The MIT Press.
- Sakata, J. T., & Crews, D. (2003). Embryonic temperature shapes behavioural change following social experience in male leopard geckos, *Eublepharis macularius*. *Animal Behaviour*, 66, 839–846.
- Salwiczek, L. (2001). Grundzüge der Memtheorie. In W. Wickler & L. Salwiczek (Eds.). *Wie wir die Welt erkennen. Erkenntnisweisen im interdisziplinären Diskurs* (pp. 119–201). Freiburg / München: Verlag Karl Alber.
- Salwiczek, L. H., & Wickler, W. (2004). Bird song: an evolutionary parallel to human language. *Semiotika*, 151.
- Sunobe, T., & Nakazono, A. (1993). Sex change in both directions by alteration of social dominance in *Trimma okinawae* (Pisces: Gobiidae). *Ethology*, 94, 339–345.
- Tebbich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society London B*, 268, 2189–2193.
- Thorpe, W. H. (1956). *Learning and instinct in animals*. London: Methuen & Co.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York/Oxford: Oxford University Press.
- Vandenbergh, J. G. (1993). And brother begat nephew. *Nature*, 364, 671–672.
- Vandenbergh, J. G., & Huggett, C. L. (1994). Mothers' prior intrauterine position affects the sex ratio of her offspring in house mice. *Proceedings of the National Academy of Science*, 91, 11055–11059.
- Werner, T. K., & Sherry, T. W. (1987). Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin's Finch” of Cocos Island, Costa Rica. *Proceedings of the National Academy of Science USA*, 84, 5506–5510.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399, 682–685.
- Wickler, W., & Salwiczek, L. H. (2003). Foreign-language phenomena in birds: means to understand the evolution of high level acoustic communication. In R. Ahrens (Ed.), *Europäische Sprachenpolitik / International Language Policy* (pp. 395–412). Heidelberg: Universitätsverlag Winter.

- Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., & Heltne, P. G. (1994). *Chimpanzee cultures*. Cambridge, Mass. / London: Harvard University Press.
- Zielinski, W. J., & Vandenberg, J. G. (1991). Effect of intrauterine position and social density on age of first reproduction in wild-type female house mice (*Mus musculus*). *Journal of comparative Psychology*, 105, 134–139.
- Zimmer, C. (2000). *Parasite rex*. New York: The Free Press.

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