

# Structure and development of behavior systems

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Behavior systems are particular organizations of cognitive structures that are called behavior mechanisms: perceptual, central, and motor. Thus, behavior systems are defined here in structural terms and not in terms of their functional characteristics. In young animals, behavior mechanisms often develop independently of functional experience, though specific types of experience are usually necessary for integrated systems to develop. These concepts are illustrated here by the dustbathing, feeding, aggressive, and sexual systems of the fowl, which are considered to be typical of behavior systems in other species. Aspects of neural development are examined and found to facilitate our understanding of a wide range of developmental phenomena, such as critical periods and irreversibility. Finally, various examples of classical conditioning and instrumental learning are analyzed in terms of the type of structures involved, and they are related to general developmental processes.

The postulation of behavior systems is one attempt to reduce the complexity of naturally occurring behavior. In this paper, I will first define what I mean by a behavior system, and then provide some examples of how such systems develop. I will use the dustbathing and feeding systems of the fowl as my primary examples, but will also briefly discuss the aggressive and sexual systems. These systems are considered to be typical of behavior systems in other species (see Hogan, 1988). Finally, I will discuss whether it is possible to extract some general principles from the data. One such principle is that learning, as studied by experimental psychologists, is but one aspect of the processes underlying behavioral development.

## WHAT IS A BEHAVIOR SYSTEM?

I have proposed motor, central, and perceptual mechanisms as the basic units of behavior (Hogan, 1988). These entities are viewed as corresponding to structures within the central nervous system. They are conceived of as consisting of some arrangement of neurons (not necessarily localized) that acts independently of other such mechanisms. They are called behavior mechanisms because their activation results in an event of behavioral interest: a specific motor pattern, an identifiable internal state, or a particular perception. Behavior mechanisms are cognitive structures, and thus, this conception can also include entities such as ideas, thoughts, and memories. It should be noted that although I define behavior mechanisms as structures in the nervous system, this definition does not imply that the study of behavior involves

neurophysiology. The study of behavior is the study of the functioning of the nervous system and must be carried out at the behavioral level, by using behavioral concepts: our major concern is the *output* of the nervous system, manifested as perceptions, thoughts, and actions (see Hogan, 1994a).

Behavior mechanisms can be connected with one another to form larger units called behavior systems, which correspond to the level of complexity indicated by terms such as feeding, sexual, and aggressive behavior (Baerends, 1976; Hogan, 1988). The organization of the connections among the behavior mechanisms determines the nature of the behavior system. Thus, a behavior system can be considered a description of the structure of behavior. It can be defined as any organization of perceptual, central, and motor mechanisms that acts as a unit in some situations (Hogan, 1971; Hogan & Roper, 1978). A pictorial representation of this definition is shown in Figure 1. It can be noted that this definition is quite similar to Tinbergen's definition of an instinct: "a hierarchically organized nervous mechanism" (1951, p. 112). The activation of an instinct produces instinctive behavior, and the activation of a behavior system produces behavior. In both cases, behavior is the expression of the activity of structures in the nervous system. This definition is also similar in many respects to McDougall's (1928) conception of an instinct. McDougall, however, insisted that the essence of an instinct is its goal (1928, p. 119), which raises a number of problems that are beyond the scope of this paper; one of these problems, however, is discussed in the next paragraph.

In the context of this symposium, I should point out that my definition of a behavior system in terms of its structure is different from Timberlake's (1983, 1994) definition. Timberlake defines a behavior system in terms of its functional characteristics. There may often be a close correspondence between systems defined in

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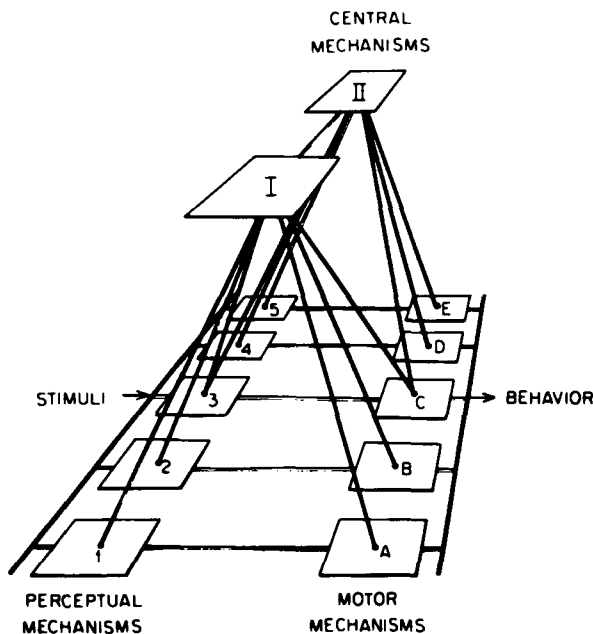


Figure 1. Conception of behavior systems. Stimuli from the external world (including stimuli produced by the behavior) are analyzed by perceptual mechanisms. Output from the perceptual mechanisms can be integrated by central mechanisms and/or channeled directly to motor mechanisms. The output of the motor mechanisms results in behavior. In this diagram, Central Mechanism I, Perceptual Mechanisms 1, 2, and 3, and Motor Mechanisms A, B, and C form one behavior system; Central Mechanism II, Perceptual Mechanisms 3, 4, and 5, and Motor Mechanisms C, D, and E form a second behavior system. 1-A, 2-B, and so on can also be considered less complex behavior systems. From "Cause and Function in the Development of Behavior Systems," by J. A. Hogan, in *Handbook of Behavioral Neurobiology* (Vol. 9, p. 66), ed. by E. M. Blass, 1988, New York: Plenum Press. Copyright 1988 by Plenum Publishing Corp. Reproduced by permission.

structural and functional terms, but this is by no means always the case; and it is very easy for confusion to arise. For example, a structural definition of sexual behavior would include a description of the perceptual mechanisms that analyze stimuli and activate a central sexual coordinating mechanism plus a description of the motor patterns that occur when the central mechanism is activated. A functional definition of sexual behavior would emphasize reproduction—that is, those behaviors that lead to successful propagation of the species. It should be clear that many animals, including humans, engage in sexual behavior by the structural definition when that behavior definitely will have no reproductive function. Further, courtship behaviors in many species are necessary for successful reproduction, even though the courtship behaviors themselves can be considered to belong to nonsexual behavior systems such as fear and aggression (Baerends, 1975; Tinbergen, 1952). This distinction between structure and function will continue to be an issue throughout this paper.

## DEVELOPMENT OF BEHAVIOR SYSTEMS

Development implies changes in the structure of behavior. The study of development comprises (1) describing the changes in the organization of the behavior mechanisms themselves as well as changes in the connections among the behavior mechanisms, and (2) investigating the causes of those changes (Hogan, 1988). This view of development is a generalization of a proposal by Kruijt (1964), who suggested that the motor components of behavior often function as independent units in young animals, and that only later, after specific experience, do these motor components become integrated into more complex systems, such as hunger, aggression, and sex. In looking for the causal basis of developmental changes, I have found it convenient to make use of the concept of *prefunctional* (Hogan, 1988; Schiller, 1949/1957). If a behavior mechanism develops prefunctionally, this means that functional experience (or practice) is not necessary for normal development to occur. It should be stated that there is no implication about the role of other kinds of experience. I make this distinction because most people assume that experience means functional experience and that cause and function go hand in hand. As mentioned above, however, this is not always the case.

### Dustbathing

Dustbathing in the adult fowl (and many other bird species) consists of a sequence of coordinated movements of the wings, feet, head, and body that serve to spread dust through the feathers. It occurs regularly, and bouts of dustbathing last about half an hour (Vestergaard, 1982). When dust is available, dustbathing functions to remove excess lipids from the feathers and to maintain good feather condition (van Lier & Bokma, 1987).

The sequence of behaviors in a dustbathing bout begins with the bird pecking and raking the substrate with its bill and scratching with its feet. These movements continue as the bird squats down and comes into a sitting position. From time to time, the bird tosses the dusty substrate into its feathers with vertical movements of its wings and also rubs its head in the substrate. It then rolls on its side and rubs the dust thoroughly through its feathers. These sequences of movements may be repeated several times. Finally, the bird stands up, shakes its body vigorously, and then switches to other behavior.

Dustbathing can also be described as a behavior system, as shown in Figure 2. A perceptual mechanism analyzes stimuli from the substrate; a central mechanism integrates information from the perceptual mechanism with various internal factors and controls the timing and duration of dustbathing; and motor mechanisms coordinate the individual behavior patterns. This figure depicts the structure of the dustbathing system in the adult fowl. However, dustbathing does not appear fully formed

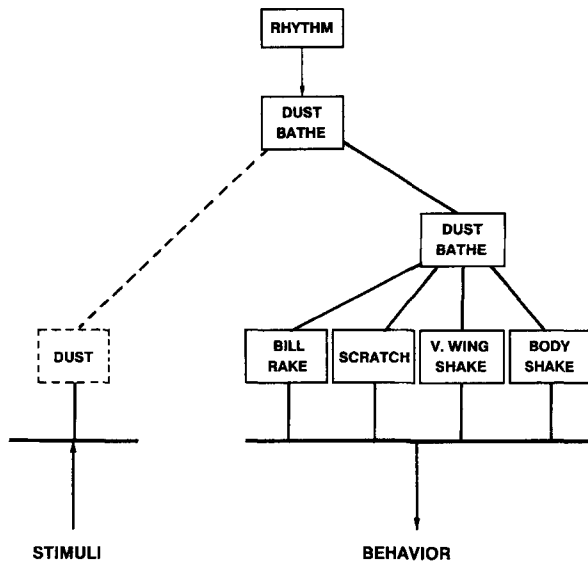


Figure 2. The dustbathing behavior system of a young chick. Boxes represent putative cognitive (neural) mechanisms: a perceptual mechanism responsible for recognizing dust, a central dustbathing mechanism responsible for integrating input from the perceptual mechanism and other internal influences as well as for coordinating output to the motor mechanisms, and several motor mechanisms responsible for the various motor patterns constituting dustbathing. Solid lines indicate mechanisms and connections among them that develop prefunctionally. Dashed lines indicate mechanisms and connections that develop as the result of specific functional experience. From "The Development of a Behavior System: Dustbathing in the Burmese Red Junglefowl: I. The Influence of the Rearing Environment on the Organization of Dustbathing," by K. Vestergaard, J. A. Hogan, and J. P. Kruijt, 1990, *Behaviour*, 112, p. 100. Copyright 1990 by E. J. Brill. Reproduced by permission.

in the young animal. Rather, individual elements of the system appear independently, and only gradually do these elements become fixed in the normal adult form. Pecking is seen on the day of hatching, but the other motor components appear gradually over the first 10 or 12 days posthatch. We have carried out a number of experiments to determine what causal factors are necessary for this behavior to develop. We have looked at the development of the motor mechanisms and their coordination, the central mechanisms, and the perceptual mechanism for the recognition of dust.

According to Kruijt (1964), most of the dustbathing "movements are, at their first occurrence after hatching, immediately shown in their characteristic form, even though the chick has not had any opportunity to practice their function" (p. 23). Vestergaard, Hogan, and Kruijt (1990) asked whether the rearing environment influenced the organization of the motor components. They observed small groups of chicks that were raised either in a normal environment containing sand and grass sod or in a poor environment in which the floor was covered with wire mesh. A comparison of the dustbathing motor patterns of 2-month-old birds raised in the two environments showed surprisingly few differences. The form

and frequency of the individual behavior patterns as well as the temporal organization of the elements during extended bouts of dustbathing developed almost identically in both groups (see Figure 3). There were some differences in the microstructure of the bouts that could be related to the presence or absence of specific feedback (see also van Liere, 1992; van Liere, Kooijman, & Wiepkema, 1990), but the motor mechanisms and their coordination developed essentially normally in chicks raised in a dustless environment. Clearly, the experience of sand in the feathers removing lipids or improving

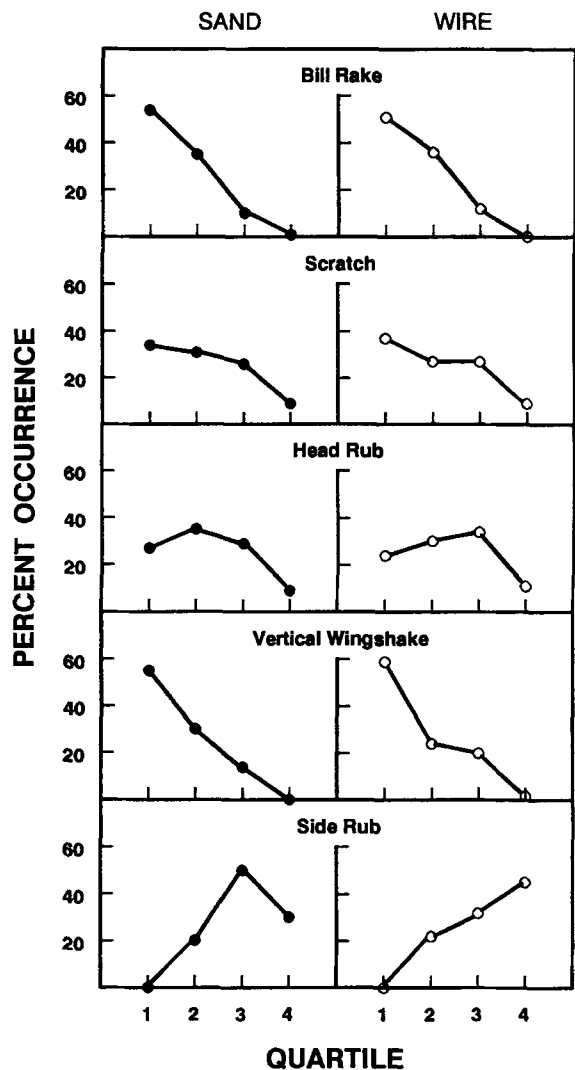


Figure 3. Percent of total occurrence of each of five components of dustbathing during successive quarters of a bout on a sand substrate or a wire mesh substrate. A bout was defined as beginning with the first vertical wingshake and ending with body shaking. All subjects were raised in the environment in which they were tested. From "The Development of a Behavior System: Dustbathing in the Burmese Red Junglefowl: I. The Influence of the Rearing Environment on the Organization of Dustbathing," by K. Vestergaard, J. A. Hogan, and J. P. Kruijt, 1990, *Behaviour*, 112, p. 108. Copyright 1990 by E. J. Brill. Reproduced by permission.

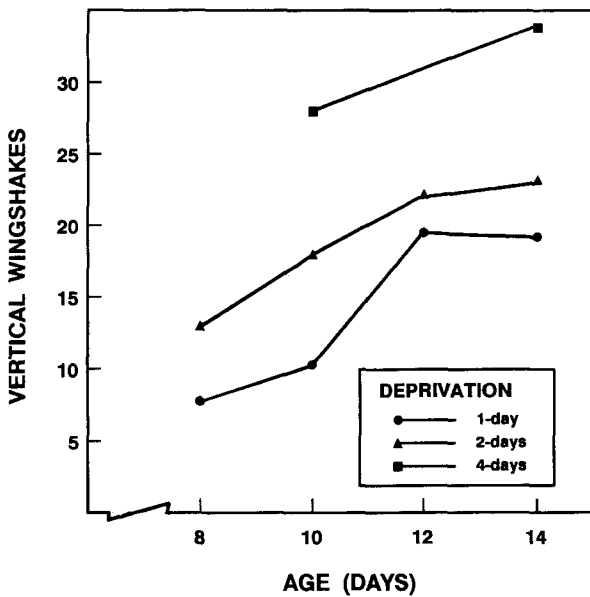


Figure 4. The amount of dustbathing (mean number of vertical wingshakes per chick) seen during a 1-h test on sand as a function of age and length of dust deprivation (chicks were held on wire mesh between tests). Each line represents data from a separate group of chicks. Chicks in the 1-day deprivation group were exposed to dust for 1 h on odd-numbered days, but their behavior was not recorded on those days. From "Development of a Behavior System: Dustbathing in the Burmese Red Junglefowl (*Gallus gallus spadiceus*): II. Internal factors," by J. A. Hogan, G. I. Honrado, and K. Vestergaard, 1991, *Journal of Comparative Psychology*, 105, pp. 271. Copyright 1991 by the American Psychological Association. Reproduced by permission.

feather quality is not necessary for the integration of the motor components of dustbathing into a normal coordinated sequence.

In adult fowl, the occurrence of dustbathing varies directly with the length of time a bird has been deprived of the opportunity to dustbathe; it also occurs primarily in the middle of the day (Vestergaard, 1982). In young

chicks, as soon as dustbathing behavior is seen, at about 1 week of age, it is controlled by the effects of dust deprivation. Hogan, Honrado, and Vestergaard (1991) found that deprivation effects could be demonstrated at as early as 8 days of age and that they did not change over at least a 4-week period (see Figure 4). (It should be noted that once a chick has experience at dustbathing in sand, longer periods of dust deprivation are necessary before it will show "vacuum" or "sham" dustbathing on wire mesh.) No specific experience seemed to be necessary for the motivational factors associated with dust deprivation to gain control of dustbathing, which suggests that the central mechanism and the connections between it and the motor mechanisms develop prefunctionally.

Similarly, Hogan and van Boxel (1993) found that a daily rhythm, with most dustbathing occurring in the middle of the day, was seen in chicks at least as young as 14 days of age (see Figure 5). The occurrence of dustbathing, however, was not as strongly restricted to the middle of the day as in adults, and the length of dustbathing bouts was also shorter in the young birds. This study was not designed to test whether the daily rhythm controlled dustbathing prefunctionally, but the results are consistent with such an interpretation.

Functional experience does play an essential role in the development of the perceptual mechanism for recognizing dust and the connection between it and the central mechanism. Young chicks can be seen engaging in dustbathing movements on almost any surface that is available, ranging from hard ground and stones to sand and dust. In fact, Kruijt (1964) found that making the external situation as favorable as possible for dustbathing was insufficient for releasing the behavior. This result implies that early dustbathing may be controlled exclusively by the internal factors mentioned above. With respect to the behavior system model of dustbathing (Figure 2), it implies that the connection between the dust-recognition perceptual mechanism and the central mechanism is not formed

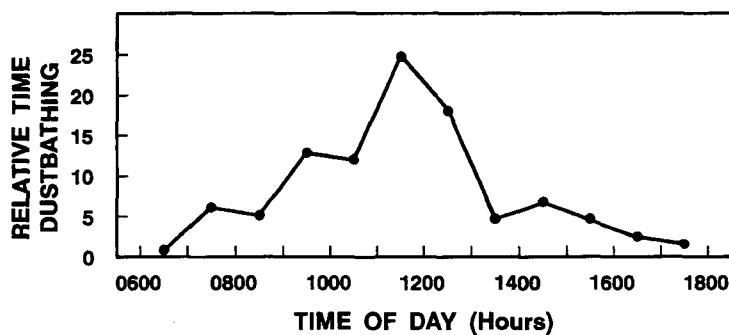


Figure 5. Percent of total daily dustbathing per hour for chicks with continuous access to dust during the 3rd week after hatching. Chicks were kept on a 12:12-h light:dark cycle. From "Causal Factors Controlling Dustbathing in Burmese Red Junglefowl: Some Results and a Model," by J. Hogan & F. van Boxel, 1993, *Animal Behaviour*, 46, p. 631. Copyright 1993 by Academic Press. Adapted by permission.

until well after the motor and central mechanisms are functional.

Some evidence is available for how the dust-recognition mechanism itself develops. The stimulus properties of a substrate constitute one important factor. For example, Vestergaard and Hogan (1992) found fine black coal dust to be much preferred to white sand, and Petherick and Duncan (1989) and van Liere (1992) found dark peat to be much preferred to sand and wood shavings. In the case of peat, the preference developed gradually, which implies that some aspect of the experience during dustbathing was crucial. It remains to be determined whether removal of lipids, the sensory feedback from the substrate in the feathers, or facilitation of the dustbathing behavior itself is the crucial factor. Other evidence from the same studies shows that early experience can lead to stable preferences for normally nonpreferred stimuli. As an extreme example, Vestergaard and Hogan (1992) raised birds on wire mesh but gave them regular experience on a substrate covered with coal dust, white sand, or a skin of junglefowl feathers. In choice tests given at 1 month of age, some of the birds that had had experience with junglefowl feathers were found to have developed a stable preference for dustbathing on the feathers. This example is important because it shows how a system can develop abnormally. It also suggests that the pecking associated with dustbathing may be a cause for "feather pecking," a common pathological condition in which some hens pull out the feathers of their cage mates, which is seen in many commercial groups of fowl (Vestergaard, Kruijt, & Hogan, 1993).

Overall, a general conclusion from all these studies is that particular classes of stimuli are more efficacious than others for the development of the perceptual mechanism for the recognition of dust. This conclusion is similar to that reached in studies of the development of perceptual mechanisms for the recognition of conspecific song in some species of song birds (e.g., DeVoogd, 1994; Marler, 1987) and perceptual mechanisms for the recognition of conspecifics in imprinting studies in various avian species (Bischof, 1994; Bolhuis, 1991; Ten Cate, 1994).

### Hunger

The hunger system of an adult chicken consists of various perceptual mechanisms that serve a food-recognition function, motor mechanisms that function to locate and ingest food, and a central mechanism that integrates signals from the physiological mechanisms concerned with nutrition and modulates signals from the perceptual mechanisms and to the motor mechanisms. A diagram of the hunger system of a young chick is shown in Figure 6.

As with dustbathing, both the individual motor mechanisms of the system (pecking, ground scratching, walking) and the integration of these mechanisms into effective foraging behavior appear prefunctionally. Unlike with dustbathing, however, the integration of the motor mechanisms disintegrates in the absence of effective

functional experience (Hogan, 1971). Hogan (1988) suggested that new connections were formed between the central hunger mechanism and individual motor mechanisms on the basis of the specific experience of the individual chick, and that these new connections effectively blocked the expression of the original prefunctional connections (see Figure 6).

Another difference between the dustbathing and hunger systems is that the central mechanism for hunger does not immediately control the motor mechanisms of the system. A chick begins pecking within a few hours of hatching, but its nutritional state does not influence pecking until about 3 days of age (Hogan, 1971). Early experiments showed that some kind of pecking experience is necessary for this change in control to occur (Hogan, 1973a), and further experiments led to the hypothesis that it is the experience of pecking followed by swallowing that causes the connection between the central hunger mechanism and the pecking mechanism to be formed (Hogan, 1977). In other words, it appears that a chick must learn that pecking is the action that leads to ingestion; once this association has been formed, nutritional factors can directly affect pecking (see Figure 6). Subsequent experiments have shown that the association of pecking with ingestion is, indeed, the necessary and sufficient condition for pecking to become integrated into the hunger system (Hogan, 1984).

The development of the perceptual mechanism for recognizing food and of the connection between the food-recognition mechanism and the central hunger mechanism requires functional experience, and is similar to the development of the corresponding structures of the dustbathing system in this way. The putative food-recognition mechanism in newly hatched chicks must be largely unspecified because of the very wide range of stimuli that are characteristic of items that chicks will come to accept as food. Although certain taste and tactile stimuli are more acceptable than others, these stimuli can be effective only after the chick has the stimulus in its mouth. Chicks learn to associate the visual characteristics of an object with its taste and tactile characteristics as early as 1 day of age, and they treat such objects as food or nonfood before nutritive factors gain control of pecking on Day 3 (see Hogan, 1973b, for review). This means that the food-recognition mechanism is independent of the central mechanism of the developing hunger system. Other evidence shows that the long-term effects of ingestion can also affect the development of the food-recognition mechanism, but only after the chicks are 3 days old (Hogan-Warburg & Hogan, 1981).

The existence of a connection between a perceptual mechanism and a central mechanism can be inferred by demonstrating the existence of "priming" or "incentive" effects (Hogan & Roper, 1978, pp. 231–232). For example, presentation of food may make an animal hungrier, or presentation of a sexual stimulus may increase its sexual appetite. There is evidence in young chicks that food particles develop incentive value between 3 and 5 days posthatch based on the long-term effects of ingestion

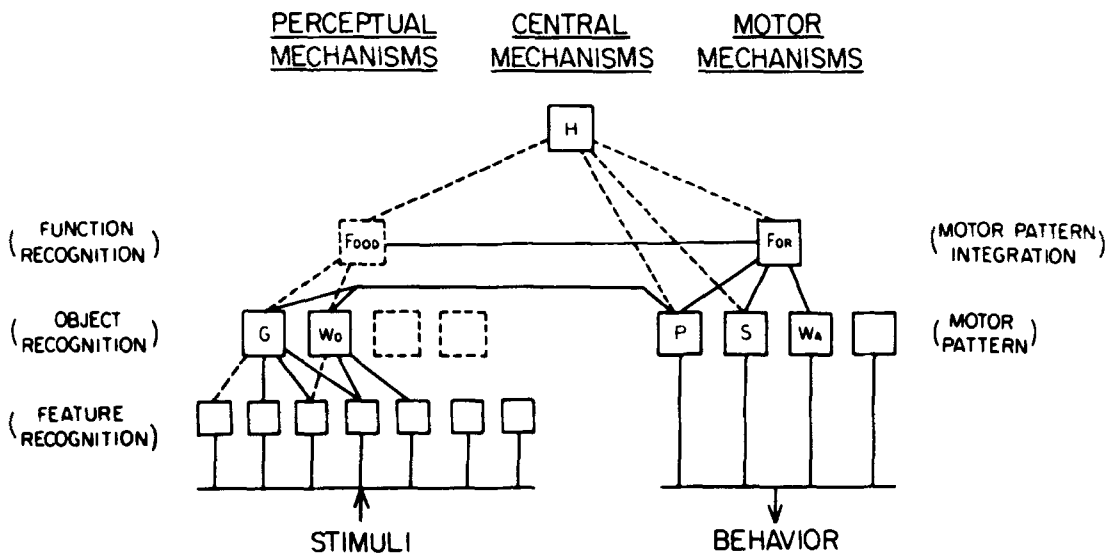


Figure 6. The hunger system of a young chick. Perceptual mechanisms include various feature recognition mechanisms (such as of color, shape, size, and movement), object recognition mechanisms (such as of grainlike objects [G], wormlike objects [Wo], and possibly others), and a function recognition mechanism (Food). Motor mechanisms include those underlying specific behavior patterns (such as pecking [P], ground scratching [S], walking [Wa], and possibly others) and an integrative motor mechanism that could be called foraging (For). There is also a central hunger mechanism (H). Solid lines indicate mechanisms and connections among them that develop prefunctionally. Dashed lines indicate mechanisms and connections that develop as the result of specific functional experience. From "Cause and Function in the Development of Behavior Systems," by J. A. Hogan, in *Handbook of Behavioral Neurobiology* (Vol. 9, p. 83), ed. by E. M. Blass, 1988, New York: Plenum Press. Copyright 1988 by Plenum Publishing Corp. Reproduced by permission.

(Hogan, 1971; Hogan-Warburg & Hogan, 1981). This would then be the time when the connection between the food-recognition and central hunger mechanisms develops (see Figure 6). Hogan (1988) has discussed in detail the evidence on which these conclusions are based and has reviewed similar evidence for the development of a hunger system in rat pups and kittens (see also Baerends-van Roon & Baerends, 1979; Blass, Hall, & Teicher, 1979; Hall & Williams, 1983).

### Aggression and Sex

The aggression system of an adult chicken consists of perceptual mechanisms that serve an "opponent" recognition function, various motor mechanisms that are used in fighting (including those that control threat display, leaping, wing flapping, kicking, and pecking), and a central mechanism that is sensitive to internal motivational factors (such as testosterone) and that coordinates the activation of the motor mechanisms. Kruijt (1964) showed that fighting develops out of hopping, which is a locomotory pattern that is not initially released by or directed toward other chicks. While hopping, chicks sometimes bump into each other by accident, and in the course of several days, hopping gradually becomes directed toward other chicks. Frontal threatening then starts to occur, and by the age of 3 weeks, pecking and kicking are added to aggressive interactions. Normal, well-coordinated fights are not seen until 2–3 months.

The sex system of a normal adult rooster consists of perceptual mechanisms that serve a "partner" recognition function; motor mechanisms for locomotion, copulation (which includes mounting, sitting, treading, pecking, and tail lowering), and various courtship displays, such as waltzing, wing flapping, tidbitting, and cornering; and a central mechanism that is sensitive to internal motivational factors such as testosterone and that coordinates the activation of the motor mechanisms. In small groups of junglefowl, Kruijt (1964) saw mounting and copulatory trampling (treading) on a model in a sitting position as early as 3–4 days, but such behavior was not common until weeks later. Full copulation with living partners did not occur before the males were 4 months old.

As in the dustbathing and hunger systems, the motor mechanisms and their coordination in the aggression and sex systems develop essentially normally even in animals that have been raised in social isolation. Several lines of evidence suggest that the neural circuits for the motor mechanisms in both systems are organized at least as early as 2 or 3 days after hatching and that the expression of aggressive and sexual behavior requires only the proper motivational state (Andrew, 1966; Evans, 1968; Hogan, 1988). Under normal circumstances, a sufficient level of external and internal causal factors is not reached until weeks or months after hatching.

Connections between the central coordinating mechanism for aggression and the motor mechanisms for ag-

gressive behavior patterns develop prefunctionally. Although some aspects of the development of fighting under normal social conditions would allow a role for operant conditioning, Kruijt (1964) also found that junglefowl chicks raised in social isolation showed full-fledged fighting when confronted with each other at 1 week of age—that is, 2–4 weeks earlier than fighting is seen in group-raised chicks. Social experience thus seems to inhibit the expression of aggressive behavior. The situation for the sex system is somewhat different. The copulatory motor patterns seem to be connected to the central mechanism prefunctionally, but the courtship displays of waltzing and tidbitting are seen first in other contexts, and only gradually come to be controlled by the sex system as a result of specifically sexual experience. Here an operant conditioning model fits the data well (Hogan, 1988; Kruijt, 1964).

Finally, the perceptual mechanisms for recognizing the “opponent” or the “partner” develop to a certain extent prefunctionally, although both are also influenced by functional experience. For example, the chicks mentioned above that were raised in social isolation for a week recognized other chicks as “opponents” prefunctionally. Nonetheless, isolated chicks of the same age can also direct aggressive behavior toward a light bulb hanging in the cage; and older isolated cockerels are often seen to direct aggressive behavior toward their own tails (Kruijt, 1964). Development of the perceptual mechanism for “partner” recognition seems to be even more dependent on functional experience. For example, junglefowl chicks become sexually dimorphic at about 1 month of age. By about 2 months, young males begin to show incomplete sexual behavior toward conspecifics, but such behavior is directed equally often toward males and toward females. Only gradually, as a result of specifically sexual experience, does sexual behavior become directed exclusively toward females (Kruijt, 1964). The development of the partner recognition mechanism has also been intensively studied for many years in the context of filial and sexual imprinting, and there is extensive evidence documenting the influence of both prefunctional and functional factors (Bischof, 1994; Bolhuis, 1991; Lorenz, 1935/1970). Some of these studies are discussed below.

## SOME PRINCIPLES OF DEVELOPMENT

### Development of the Nervous System

Changes in neural structure and/or in connections between neurons must be the cause of behavioral development. It is therefore useful to consider what is happening at the neural level during development. Those processes can give us some insight into corresponding changes in behavior. Brown, Hopkins, and Keynes (1991) have divided brain development, at the cellular level, into four major stages: (1) genesis of nerve cells (proliferation, specification, and migration); (2) establishing connections (axon and dendritic growth, and synapse formation); (3) modifying connections (nerve cell death and

reorganization of initial inputs); and (4) adult plasticity (learning and nerve growth after injury). Stages 3 and 4 are the most relevant to our question.

During fetal development, many more nerve cells are formed than will be found in the adult brain. These nerve cells all send out axons and establish connections with target cells (other neurons and muscle cells), but a large proportion of them die before the synapses become functional. The mechanism underlying this process involves electrical activity in the nerve cells and their targets, but it is still not fully understood (see Oppenheim, 1991). It is thought that neuronal death may serve to eliminate errors in the initial pattern of connections. The axons of the cells that remain are often found to have more extensive branches and to contact more postsynaptic cells than they will in the adult. The mechanisms that bring about axonal remodeling—that is, the elimination and reorganization of these terminal branches—also involve activity in the neurons. In brief, it has been shown that specific spatial and temporal patterns of electrical activity in both the nerve cells and their target cells are necessary for functional connections to form between them: “cells that fire together wire together” (Shatz, 1992, p. 64).

The process of axonal remodeling occurs both pre- and postnatally, but it is essentially irreversible. Once the axons have established functional connections with other neurons or muscles, those connections appear to be a permanent part of neural organization. The mechanisms that are responsible for adult plasticity involve facilitation or inhibition of synaptic transmission and the growth of dendritic spines which presumably correlates with the formation of new synapses (Bolhuis, 1994; Brown et al., 1991; see also DeVoogd, 1994, for a discussion of neurogenesis in adult birds). Whether these changes are reversible remains a matter of conjecture.

The work of Hubel and Wiesel established that visual stimulation plays a vital role in the development of the mammalian visual system (see Blakemore, 1973, and Wiesel, 1982, for reviews). They showed, for example, that normal development of the connections between cells of the lateral geniculate nucleus and the visual cortex in the cat requires binocular visual stimulation soon after the kitten’s eyes open. Allowing a kitten to see with only one eye at a time during the critical period results in most cortical cells’ being responsive to stimulation from one eye only, whereas binocular stimulation results in most cortical cells’ being responsive to stimulation from both eyes. These results were interpreted in terms of the eyes’ competing for control of cells in the cortex and are an example of axonal remodeling. They were important because they showed that the organization of a sensory system was actually driven by stimulation from the environment. They also provided a model for how the perceptual mechanisms underlying bird song learning and filial and sexual imprinting might develop (see Bischof, 1994; Bolhuis, 1994; DeVoogd, 1994).

The neural activity responsible for axonal remodeling in the visual cortex is triggered by stimuli originating in

the environment after the kitten is born and has opened its eyes. More recently, other investigators have asked whether neural activity is also necessary for neural connections to form in utero, and, if so, how this activity is instigated. Shatz (1992) and her collaborators, for example, have looked at axonal remodeling in the lateral geniculate nucleus of the cat, which occurs before birth. They found that the same kind of action-potential activity is necessary for developing normal connections from the retina to the lateral geniculate as is later necessary for normal connections to form in the cortex. Rather than being instigated by stimulation from the external world, however, the neural activity was caused by patterns of spontaneous neural firing. How these waves of activity are generated remains to be discovered.

These two cases of axonal remodeling illustrate the difference between development based on functional experience (organization of the visual cortex) and development that occurs prefunctionally (organization of the lateral geniculate nucleus). What is important in the present context, however, is that the mechanisms for synaptic change are the same before and after birth, and it is irrelevant for the connection being formed whether the neural activity arises from exogenous or endogenous sources. In fact, the same connection can be formed in either way. Some behavioral examples will be used to illustrate this point in the next section.

### **Critical Periods, Irreversibility, and the Concept of *Prefunctional***

Groothuis (1992, 1994) found that the oblique posture in the black-headed gull developed normally when a gull was reared either in social isolation or in large social groups, but that it sometimes developed abnormally when a gull was raised with only two or three peers. One can suppose that under circumstances of social isolation, endogenously produced patterns of neural firing provide the information necessary to develop the normal connections in the motor mechanism responsible for the form of the display, prefunctionally. When peers are present, functional social experience provides the information. Performance of precursors of the display often leads to reactions by the other gulls. These reactions, in turn, provide additional neural stimulation which could interfere with endogenously produced patterns and thus lead to different (abnormal) connections' being formed in the motor mechanism. If these connections require repeated stimulation to form, the probability that the average experience will be "correct" is greater in a large group than in a small group, where the effects of the behavior of one abnormal individual companion would be relatively greater. This line of reasoning suggests that functional and prefunctional "experience" provide alternative routes for the control of behavior system development, a suggestion that can also account for some of the results for the development of the aggression system in chickens reviewed above.

Individuals of most species of song birds require exposure to the species' song when young in order to be able

to develop the species-typical song when adult. The early phase involves development of a perceptual mechanism, often called a template, and the later phase involves development of the motor mechanism responsible for the production of the song (DeVoogd, 1994; Marler, 1976). One of the interesting aspects of the perceptual phase of song learning is the very large differences among species with respect to what kind of experience is needed for an adequate template to develop. At one extreme, a male cowbird, raised in social isolation, will develop a normal species' song (King & West, 1977), whereas a chaffinch or white-crowned sparrow, raised similarly, will develop a song that at best contains only a few species-specific elements (Marler, 1976; Thorpe, 1961). On the other hand, the time at which hearing the species' song is effective for learning is much more restricted in the white-crowned sparrow than it is in the chaffinch. Likewise, if socially isolated males are played variants of the typical species' song, or indeed songs of other species, or even pure tones, some species are able to learn only the song of their own species, whereas other species are able to learn a much wider range of sound patterns. Similar species differences are also characteristic of the range of stimuli to which young birds will imprint and the time at which these stimuli are effective (Lorenz, 1935/1970). In all cases, however, a perceptual mechanism develops that serves a species-recognition function.

One way to understand how so many apparently different ways can lead to a similar functional outcome is to suppose that once certain kinds of structural change have occurred in the development of a perceptual mechanism, further change is no longer possible (crystallization, consolidation, irreversibility). It then follows that the timing of triggering events becomes crucial in determining which events will affect development. In a particular species of songbird, for example, one can imagine that, if genetically triggered events occur in the perceptual mechanism for song recognition before the young bird can hear, then the perceptual mechanism is fixed, prefunctionally, in that species, and posthatching experience can no longer have an effect. If the triggering events are delayed, however, the posthatching experience of the bird can provide the trigger. In this way, the same type of perceptual mechanism can be used for either "innate" or "learned" song recognition.

The timing of events that trigger irreversible changes in developing behavior mechanisms can also explain some apparent differences between perceptual and motor mechanisms. It is noteworthy that, without exception, the motor mechanisms of the behavior systems discussed above all develop prefunctionally, whereas all the perceptual mechanisms require at least some functional experience in order to achieve the normal adult form. This fact might suggest that there are some fundamental differences in the causal factors responsible for the development of perceptual and motor mechanisms. Such a conclusion is unlikely to be true because, in both cases, the organization of neural or neuromotor



connections depends on particular spatiotemporal patterns of neural activity that can be generated either endogenously or exogenously. Prior to birth, most of the causal factors would be endogenous, although external stimulation may play a role in some cases (e.g., the auditory system in ducks: Gottlieb, 1978). After birth, both internal and external factors could be important. The fact that most of the motor mechanisms we have considered develop prefunctionally very likely reflects the fact that motor mechanisms generally become organized earlier in development than perceptual mechanisms (Hogan, 1994b).

It is tempting to speculate that development of behavior mechanisms that involves the elimination and reorganization of terminal axon branches (axonal remodeling) is essentially irreversible. The critical period then becomes the time at which the axonal remodeling occurs; it would depend on all the factors that can affect the timing of the remodeling. The production of new synapses continues to occur throughout life and could modulate the structure of behavior mechanisms after the critical period has passed. (Some readers will note that these ideas have some similarities to a proposal by Greenough, Black, and Wallace (1987) that different neural mechanisms have evolved for brain systems that serve different functions. They distinguish between experience-expectant and experience-dependent neural systems. However, as I have discussed in detail elsewhere (Hogan, 1994b), their view proposes a functional explanation for a causal phenomenon (see also Bolhuis, 1994). My proposal is considerably broader and is congruent with the putative neural mechanisms underlying it.)

Finally, it must be clear that I use the word *prefunctional* in many places where others would say *innate*. It is logically consistent to talk about behavior development that is prefunctional (or innate) versus behavior development that is learned when the criterion is the absence or presence of functional experience. (I prefer the word *prefunctional* because *innate* has too many additional meanings.) I think it is important to show how behavior that can be classified as prefunctional still presents interesting developmental problems that can be investigated in a causal framework. Nonetheless, it should be emphasized that any particular structural change could be triggered by genes or by the experience of reinforcement. The change itself cannot be classified as innate or learned because it could have been triggered either way, and it does not matter which way actually occurred.

### Learning and Development

The changes in the structure of behavior that occur as the individual goes from a fertilized egg, to birth, to maturity, and finally death are brought about by the complex effects of genes and the environment on the developing organism. Learning, as studied by experimental psychologists, is one of the processes that causes changes in behavioral structure, but there is no generally accepted conception of how learning differs from other

developmental processes (see Balsam & Silver, 1994; Shettleworth, 1994). We have seen above that the biochemical processes responsible for synapse strengthening are basically the same for all aspects of development ("cells that fire together, wire together"), and that these processes are all determined by "experience" that can originate either internally or externally. Thus, events at the cellular level provide no theoretical basis for separating learning from other developmental processes.

Nonetheless, as discussed in the previous section, most examples of what the majority of people (including psychologists) would consider learning fall into the category of changes in the structure of behavior due to *functional* experience. In this context, the phrase *functional experience* means all experience directly relevant to the change in behavior being considered. It thus includes habituation, sensitization, and Pavlovian conditioning, as well as instrumental, goal-directed learning.

If we accept this definition, we can go one step further and ask whether the structures that are changing might not provide a good basis for classifying different types of learning. That is what I will do in this last section. The structures that change as the animal develops are the perceptual, central, and motor mechanisms and the connections between them. I will first consider the perceptual mechanisms, then the motor mechanisms, and finally various connections among the behavior mechanisms.

Development of perceptual mechanisms has been studied most intensively in the ethological literature with respect to imprinting and song learning. In both cases, exposure *per se* to an appropriate stimulus leads to the formation of a "schema" (Lorenz, 1935/1970), or a "template" (DeVoogd, 1994; Marler, 1976), respectively. There is evidence that external factors such as social interaction can influence what is learned (see Clayton, 1994; Ten Cate, 1994), but de Vos and van Kampen (1993) have suggested that social interaction is a special case of directing the attention of an animal toward particular stimuli. In the psychological literature, it has been suggested that exposure to a stimulus (situation) can lead to the formation of "cognitive maps" (Tolman, 1948), "cell assemblies" (Hebb, 1949), and "neuronal models" (Sokolov, 1960). All these perceptual mechanisms are supposed to form because different aspects of the stimulus always have the same relationship to each other, and repeated experience of these relationships leads to the formation of a neural representation (e.g., Hebb, 1949). A modern "connectionist" model of how such representations could form has been proposed by McLaren, Kaye, and Mackintosh (1989; see also McLaren, 1994). This conception can also be applied to the formation of "memories" and "ideas," which are also examples of perceptual mechanisms.

Development of motor mechanisms proceeds somewhat differently. In one of the best studied examples, song learning, the bird learns to adjust its motor output to match the image (template) it has previously formed. Auditory feedback is essential for this adjustment, because deafened birds never learn to produce any song

that approaches normal song (Konishi, 1965). Hinde (1970) suggested that sounds produced by the bird that matched the image would be reinforced, whereas other sounds would extinguish. In this way, a normal song could develop in much the same way as an experimenter originally "shapes" a rat to press a lever (Skinner, 1953). It seems likely that the learning of skilled movements proceeds similarly, with the feedback from the instructor providing the reinforcement. It should be noted that in these cases reinforcement selects out bits of motor behavior, but that the actual formation of the motor mechanism requires repeated experience of sequences of those bits: Practice makes perfect.

Most cases of operant conditioning do not involve the shaping of a response (formation of a motor mechanism). Rather, motor mechanisms that already exist become attached to specific central mechanisms. For example, reinforcing a keypeck with food leads to a connection of the motor mechanism for pecking with the hunger system, while reinforcing with water leads to a connection with the thirst system. Schiller (1949/1957) reported the results of studies of problem solving by chimps. He noted that many of the behavior patterns used by his chimps to procure food that was placed out of reach were the same manipulative patterns that had first appeared spontaneously and prefunctionally. He suggested that these patterns could be considered operant responses that were used to solve the problem, and that they were reinforced when the chimp was successful. In the terminology used here, we could say that the originally independent motor mechanisms responsible for the various observed behavior patterns became connected to the hunger system as a result of operant reinforcement. The function of the reinforcer in all these cases is to activate the central mechanism so that it and the motor mechanism are active at the same time; under these conditions, a connection between the central and motor mechanisms can form.

Classical conditioning generally involves the development of a connection between a perceptual and a central mechanism. There are numerous examples of complex, species-typical behaviors that become released by previously neutral stimuli that develop their effectiveness by means of a classical conditioning procedure. For instance, Adler and Hogan (1963) paired the presentation of a weak electric shock with a mirror to a male Siamese fighting fish and showed that full aggressive display could be conditioned to the shock. In a similar way, Farris (1967) conditioned the courtship behavior of Japanese quail to a red light; this situation has now been examined much more extensively by Domjan (1994). These and many other cases exemplify the development of a connection between a perceptual mechanism and a set of behaviors as a result of a classical conditioning procedure. They do not, however, distinguish between a connection between a perceptual mechanism and a central mechanism or directly between a perceptual mechanism and a complex motor mechanism.

There are some cases in which a connection between a perceptual mechanism and a central mechanism is directly implicated. For example, Wasserman (1973) looked at the behavior of young chicks tested in a cool environment. The chicks were trained by being exposed to a lighted key for several seconds and then to presentation of heat from a heat lamp. After several pairings of the light and the heat, the chicks began to approach the key when it lighted up and showed pecking and snuggling movements to it. These behaviors were never shown to the heat lamp itself (which was suspended above the chicks, out of reach). Pecking and snuggling movements are behaviors that belong to the filial system of a young chick, and are shown when the chick solicits brooding from a mother hen (Hogan, 1974). Wasserman's results thus imply that the perceptual mechanism for the lighted key became connected to the filial system in the young chick, and that the presentation of this stimulus to a cold chick elicited brooding solicitation movements. Other similar examples are discussed by Hogan (1988).

Modern accounts of association learning posit that certain temporal relationships between two events lead to an association between the two events (Dickinson, 1980). One event is usually the occurrence of a neutral stimulus, while the other event is the occurrence of some salient stimulus. The salient stimulus is generally salient because it is already connected to some central mechanism. Although it is generally assumed that it is the representations of the two events that become associated, it is also possible that the representation of the neutral event becomes associated with (attached to) the central mechanism that makes the second event salient. Which connection is formed may lead to different predictions of experimental outcomes. For example, van Kampen (1993) has presented data on filial imprinting suggesting that the formation of the object-recognition perceptual mechanism depends on simple exposure to the stimulus. The perceptual mechanism can become attached to the central filial mechanism only when the filial mechanism is active (i.e., when the chick is in the motivational state for imprinting). His results suggest that blocking and overshadowing, two phenomena typical of association learning, are seen in the formation of the perceptual-central connection, but not in the formation of the perceptual mechanism itself. It seems quite possible that typical association learning phenomena are in general seen only in perceptual-central connections, and that other phenomena may be typical of other types of connections.

In conclusion, I would maintain that an understanding of the phenomena of learning can be reached only when the type of structures involved in the learning are specified. Traditionally, distinctions between types of learning have been made in terms of the experimental procedures used rather than the structures and processes that actually control performance. Recent accounts of instrumental learning, however, posit specific behavioral

structures (representations) and interpret results in terms of connections (associations) formed between these structures (e.g., Colwill & Rescorla, 1986; Dickinson & Balleine, 1994; Rescorla, 1994). Although some of these ideas date back to Tolman (1949a, 1949b), it is only recently that they have been incorporated into contemporary learning theory. Most of these behavioral structures have direct counterparts with the structures depicted in Figure 6 in this paper, and I have made some suggestions for the interpretation of certain learning phenomena in my terms. Further exploration of the mutual implications of these various formulations should prove highly fruitful, and could lead to a much more comprehensive theory of changes in behavior due to specific experience.

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