The purpose of this chapter is to present a general framework for studying the development of behavior. The thesis to be defended here is that the building blocks of behavior are various kinds of perceptual, central, and motor components, all of which can exist independently. The study of development is primarily the study of changes in these components themselves and in the connections among them.

I begin the chapter by explaining my conception of a behavior system. The basic concepts that I use are generally derived from classical ethological theory as set forth, for example, by Tinbergen (1951). There are, however, a number of differences in the way I define and use these concepts, and these differences are discussed where appropriate. The bulk of the chapter is devoted to the presentation and discussion of examples showing how behavior systems develop. Many of these examples are based on my own work on chickens, but I also show how the behavior systems of chickens can be considered to be typical of behavior systems in other species. One such system is the language system in humans, and one section of the chapter is devoted to showing how the general framework presented here can be applied to the development of human language. Finally, I discuss a number of general issues, including the distinction between causal and functional classification of behavior systems, the relevance of functional considerations to causal analyses, and whether any general principles of development emerge from the data.

The Conception of a Behavior System

No two occurrences of behavior are ever identical, and it is therefore necessary to sort behavior into categories in order to make scientific generalizations. These categories can be defined in different ways (e.g., structurally, causally, or functionally; cf. Hinde, 1970, Ch. 2; Hogan, 1994a) and at different levels of complexity (e.g., individual muscle movements, limb movements, or acts; cf. Gallistel, 1980). The concept of a behavior system is defined here structurally, and the level to be analyzed corresponds to the complexity indicated by the terms *feeding behavior, aggressive behavior, play behavior,* and so on. These terms can be considered names for behavior systems as a whole, but our analysis begins with a consideration of the parts of which these systems are constructed.

Three kinds of parts can be distinguished: motor parts, perceptual parts, and central parts. All of these parts are viewed as corresponding to structures within the central nervous system. For this reason, the word *mechanism*[1] is used in the rest of this chapter in references to these parts. Each motor mechanism, perceptual mechanism, or central mechanism is conceived of as consisting of some arrangement of neurons (not necessarily localized) that is able to act independently of other such mechanisms. These mechanisms are here called *behavior mechanisms* for two reasons. First, the actual neural connections, their location, and their neurophysiology are not of direct interest in the study of behavior. Second, the activation of a behavior mechanism results in an event of behavioral interest: a particular perception, a specific motor pattern, or an identifiable internal state.

Behavior mechanisms can be connected with one another, and the organization of these connections determines the nature of the behavior system. In order to make the discussion more concrete, I shall use the feeding system of a chicken as my example.

Motor Mechanisms

We say a chicken is feeding when it walks about looking at the ground, when it scratches at the substrate, and when it pecks and swallows small objects. Walking, scratching, pecking, and swallowing are all easily recognizable motor patterns and can be viewed as reflecting the motor mechanisms of the feeding system. Three points here are worthy of mention.

First, although the behavior patterns of walking and so on are easily recognizable, there is considerable variation between different instances of the "same" pattern. In a practical sense, this variation does not usually interfere with the identification of a pattern, and that is sufficient for our present purpose. The second point is essential. What we observe is only a reflection or manifestation of the motor mechanisms of the system. The motor mechanisms themselves are groups of neurons located inside the central nervous system of the animal; activation of a motor mechanism is responsible for coordinating the muscle movements that we actually see. Finally, the concept of a motor mechanism is clearly related to the ethological concept *Erbkoordination* (Lorenz, 1937) or *fixed action pattern* (Hinde, 1970; Tinbergen, 1951) but is meant to be much broader in scope and to encompass all types of coordinated movements.

Perceptual Mechanisms

Corresponding to the motor mechanisms on the efferent side of a behavior system are perceptual mechanisms on the afferent side. Perceptual mechanisms solve the problem of stimulus recognition and are often associated with particular motor mechanisms. In the feeding system of a chicken, there must be perceptual mechanisms for recognizing the objects at which the bird pecks, for what it swallows, and for the type of environment in which the bird scratches. There must also be perceptual mechanisms that are sensitive to changes in the chick's internal state consequent to its behavior. Particular perceptual mechanisms may be restricted to a single sensory modality, but frequently integrate information from several modalities.

Perceptual mechanisms are inherently more difficult to study than motor mechanisms because the output of a perceptual mechanism can be "seen" only after it has activated some motor mechanism. Thus, there are always more steps where variation can occur. The general method used to study perceptual mechanisms is to present stimuli that vary along different dimensions and to ascertain which combination of characteristics is most effective in bringing about certain responses.

The concept *perceptual mechanism* is clearly related to concepts such as *releasing mechanism* (Baerends and Kruijt, 1973; Lorenz, 1937; Tinbergen, 1951); *Sollwert*, or *comparator mechanism* (Hinde, 1970; von Holst, 1954); *cell assembly* (Hebb, 1949); and *analyzer* (Sutherland, 1964). However, as with the term *motor mechanism, perceptual mechanism* is meant to encompass all types of stimulus recognition mechanisms, including such "cognitive" mechanisms as *ideas,* and *memories* (see Hogan, 1994a).

Central Mechanisms

The final part of a behavior system to be considered is the central mechanism. This part is responsible for integrating the input from various perceptual mechanisms and coordinating the output to the various motor mechanisms associated with it. In many cases it is also responsible for the timing and activation of the whole behavior system. It is the central mechanism that usually corresponds to the name we give to a behavior system: a hunger mechanism, an aggression mechanism, a sexual mechanism, and so on. The concept *central mechanism* is clearly related to the neurophysiological concepts *central excitatory mechanism* (Beach, 1942); *central motive state* (Stellar, 1960) or *neural center* (Doty, 1976), but it will be used here in a still more general sense. Central mechanisms do not differ in any basic way from motor or perceptual mechanisms; they are distinguished separately because of their function of coordinating motor, perceptual, and motivational mechanisms.

Behavior Systems

We can now return to the concept *behavior system* and define it as an organization of perceptual, central, and motor mechanisms that act as a unit in some situations. A pictorial representation of this definition is shown in Figure 1.

The first part of the definition is structural and is basically similar to Tinbergen's definition of an instinct (1951, p. 112); it is also similar to the *functional* organization of von Holst and von St. Paul (1960). Hierarchical organization is also implied in this part of the definition, and it is thus related to conceptions of Tinbergen (1951), Baerends (1976), and Gallistel (1980); see also Hogan (1981). Further, as we shall see, there are various levels of perceptual and motor mechanisms, and the connections among them can become very complex. A diagram such as Figure 1, if expanded to encompass all the facts that are known, would soon become unmanageable. In the extreme, it would become congruent with a wiring diagram of the brain. The main function of such a diagram—and of the concept of a behavior system—is to direct our thinking into particular pathways.

The second part of the definition of a behavior system is causal: at present, the only method for determining behavioral structure is through causal (or motivational) analysis. In discussing the development of behavior systems, we shall be interested in both structural and causal (motivational) aspects.

The Development of Behavior Systems

In a very real sense, the development of behavior begins at conception and continues until death. Nonetheless, much can be understood about the development of behavior systems by considering only the period between birth (hatching) and maturity, and that is what I shall do here. The thesis of this chapter is that perceptual, central, and motor mechanisms are the building blocks out of which complex behavior is formed, and that a developmental analysis requires looking for the factors causing the development of the building blocks themselves, as well as for the way connections among these building blocks become established.

In some cases, the building blocks and/or their connections appear for the first time "prefunctionally" (Schiller, 1949); that is, functional experience is not necessary for their development. A building block (e.g., the pecking motor mechanism) is functional when its associated response (i.e., pecking) occurs in its adaptive context (i.e., grasping small objects). If the pecking response occurs in its normal form before the chick has ever grasped an object, the development of the pecking motor mechanism can be said to occur prefunctionally: experience grasping an object is not necessary for the development of a normal pecking response.

It should be noted that saying that a behavior mechanism develops prefunctionally implies only that particular kinds of experience play no role in its development; there is no implication about the role of other kinds of experience. For example, the development of the pecking motor mechanism in the chick may well be influenced by events associated with beak movements that occur in the egg before hatching or with head and beak movements that occur during hatching. The pecking motor mechanism would nonetheless still be regarded as appearing prefunctionally. This concept is discussed in greater detail later.

Even in cases in which behavior develops prefunctionally, developmental questions arise. I begin with an example of such a system. I then consider several examples of how individual behavior mechanisms develop, and, finally, some examples of the development of more complex systems.

The "Gustofacial Reflex": A Prefunctionally Developed System

Steiner (1979) showed that newborn human infants have at least three gustofacial reflexes. A sweet stimulus to the tongue elicits a "smile" reaction, a sour stimulus elicits a "pucker" reaction, and a bitter substance elicits a "disgust" reaction. The identification of these reactions by even inexperienced observers is highly reliable. In terms of the concepts discussed above, we can posit that the newborn infant has three perceptual mechanisms for particular tastes (a sweet, a sour, and a bitter mechanism) and three motor mechanisms (a smile, a pucker, and a disgust mechanism). These mechanisms and the specific connections between them are formed prefunctionally, that is, before the consequences of ingesting sweet, sour, or bitter substances have been experienced and before any social (or other) reactions to these facial expressions can have been perceived. Nonetheless, there are many questions of developmental interest that can be asked about these results.

With respect to the motor mechanisms, there is a large literature on the form and development of human facial expressions. Ekman and Friesen (see Ekman, 1982) have devised a facial action coding system which analyzes all human adult facial expressions as combinations of about 50 basic action units, and Oster (1978) has reported that almost all of these discrete action units can be identified in the facial movements of newborn infants. In this system, the smile, pucker, and disgust patterns discussed by Steiner consist of particular combinations of the basic action units. One can ask how these motor patterns are organized, how they change as the infant grows older, and what experience is necessary for the changes to occur. Thelen (1985) has used this framework of hierarchical organization of coordinative structures for understanding the development of motor mechanisms in general, and I return to some of her ideas in a later section.

The perceptual mechanisms that recognize sweet, sour, and bitter are probably the basic perceptual units, and developmental interest would focus on connections between them and other behavior mechanisms rather than on the development of the perceptual mechanisms themselves. Some of these connections develop before birth, and may depend on specific experiences of the fetus. These would include possible effects of tasting and swallowing amniotic fluid or feedback from movements of facial or other muscles. We are not concerned in this chapter with such prenatal experiences, but it is important to realize that there is a complex developmental history before the emergence of even a prefunctionally developed system.

Other connections develop after birth. For example, many adults will smile at the taste of coffee (a bitter substance). In such a case, presumably neither the perceptual nor the motor mechanism has changed over time. What has changed is the connection between them. Further, the change is not simply one in which the bitter mechanism becomes attached to the smile mechanism, because other bitter substances still elicit a disgust expression. Identification of the changes that occur and the experience that is necessary requires experimental analysis (see Rozin, 1984), but this type of formulation of the problem makes that analysis easier to tackle.

A related question has to do with connections between the motor mechanisms and higher level coordinative structures. People smile not only in response to sweet tastes, but also in response to a wide range of stimuli associated with the hunger, sexual, parental, and other systems. How does the smile mechanism become attached to these various systems? This question also requires experimental analysis (e.g., Blass, Ganchrow, and Steiner, 1984), and several examples of this type are considered below.

Development of Perceptual Mechanisms

Two of the most studied examples of behavior development, song learning and imprinting in birds, are both cases that involve a perceptual mechanism that develops independently of connections with central and motor mechanisms. Several aspects of these studies seem worthwhile to mention here. The development of food recognition mechanisms serves as a final example.

Song Recognition Mechanisms. Some time ago, Thorpe (1958, 1961) showed that the male chaffinch, *Fringilla coelebs*, had to learn to sing its species-specific song, and that this learning occurred in two stages. First, the young bird had to hear the normal song (or, within limits, a similar song); later, it learned to adjust its vocal output to match the song it had heard when it was young. Similar results have also been found for the white-crowned sparrow, *Zonotrichia leucophrys* (Konishi, 1965; Marler, 1970a), though not necessarily for other species of song birds (Hultsch, 1993; Logan, 1983; Marler, 1976). The first, or memorization, stage of learning involves the development of a perceptual mechanism, and that is discussed here; the second, or selection, stage involves the development of a motor mechanism, and that is discussed later. There have been many reviews of the bird song literature (e.g., Nelson, 1997; DeVoogd, this volume; West and King, this volume), and only highly selected aspects are mentioned in this chapter.

Konishi (1965) and Marler (1976, 1984) proposed that the results of studies of song learning imply the existence of an auditory template, which was conceived of as a sensory mechanism that embodies species-specific information. The normal development of the template requires auditory experience of the proper sort at the proper time. In our terms, the template becomes a song-recognition (perceptual) mechanism that is partially formed at hatching. One question that has been asked is whether there is one or many templates. Originally it was thought that the young bird memorized a single song and that later variation in produced song came about because of mismatches during the selection stage. More recently (Marler & Peters, 1982; Nelson, 1997), it has become clear that the bird memorizes a variety of species-specific songs when young, but only one (or one subset) of these is selected later for production. How this choice is made is not known, but it now appears that the template used in the development of song production is stored in a different part of the brain from the other song memories (Jarvis and Nottebohm, 1997; Bolhuis, Zijlstra, den Boer-Visser, and van der Zee, 2000).

A second question concerns constraints on the kinds of experience that can affect development. Thorpe (1961) found that chaffinches would learn to sing normal or rearranged chaffinch songs heard when young, but exposure to songs of other species resulted in songs no different from those sung by birds raised in auditory isolation. The range of stimuli that affect development turns out to depend crucially on such factors as the species, the age at which the bird is exposed, the previous experience of the bird, and the conditions under which the bird is exposed (Nelson, 1997). There are no easy causal generalizations.

A third question concerns the processes that are involved in development. In the memorization stage, it is often assumed that mere exposure to an adequate stimulus is sufficient for perceptual learning to occur. In a restricted sense this is probably true, but what makes a stimulus adequate often depends critically on the conditions under which the bird is exposed: For example, in many cases memorization is more likely to occur when exposure occurs during social interaction with another bird (Baptista and Petrinovich, 1984; Baptista and Gaunt, 1997; Clayton, 1994; Nelson, 1997), though the mechanism through which social interaction has these effects remains an open question (Houx and ten Cate, 1998, 1999).

Parent and Partner Recognition Mechanisms. Many species of birds do not recognize conspecifics on the basis of their song. These species have analogous perceptual mechanisms that analyze visual or other sensory input. The development of such perceptual mechanisms has usually been studied in the context of imprinting. This concept, as originally elaborated by Lorenz (1935/1970), was primarily concerned with the process by which early experience affects development. Lorenz proposed that "through imprinting, the bird acquires a schema of the conspecific animal…"(p. 133). He also noted that the young of some species such as the curlew (*Numenius arquata*) require no visual experience in order to recognize members of their own species, whereas the young of other species such as the greylag goose (*Anser anser*) direct all their species-typical social behaviors to the first moving object they see. Imprinting was relevant only to the acquired aspects of the schema. In our terms we would say that most, and perhaps all, species have a preassigned perceptual mechanism that serves a species recognition function. In a species such as the curlew, this perceptual mechanism develops prefunctionally. In a species such as the greylag goose, this perceptual mechanism requires various kinds of experience for its development. Recently, Bolhuis (1996) and van Kampen (1996) have also analyzed imprinting with an emphasis on the development of perceptual mechanisms. The question of whether there is a single perceptual mechanism for species recognition or independent mechanisms for parent recognition, partner recognition, etc. will be considered in the general discussion.

It turns out that all the problems relating to the development of song recognition mechanisms mentioned above are also applicable to the development of the perceptual mechanisms studied in imprinting. For example, work of Horn and his colleagues has shown that there are two independent perceptual mechanisms involved in parent recognition in young chicks. One, called a learning mechanism, is concerned with specific details of the imprinting stimulus while the other, called a predisposition, responds to generalized characteristics of fowl such as the head and eyes (see Bolhuis, 1991; Bolhuis and Honey, 1998; Horn, 1965 for reviews). The outputs of these two mechanisms must summate, perhaps in a higher level perceptual mechanism, to determine whether a particular object is recognized as the parent.

A related example comes from the work of ten Cate (1986) who demonstrated a case of double imprinting. Young zebra finches, *Taeniopygia guttata*, that are exposed early in life to both zebra and Bengalese finches, *Lonchura striata*, may later court both species. A stable preference is formed for both these species over other similar species, to which the zebra finches were not exposed when young. Further experiments (ten Cate, 1987) investigated what kind of internal representation (perceptual mechanism) is necessary to account for this phenomenon. Ten Cate found that doubly-imprinted males courted a zebra finch/Bengalese finch hybrid female more than they courted pure bred females of either species. He concluded that a single, combined representation is sufficient to account for a male's courtship preferences.

The problem of constraints on what experience can be effective and at what stage of development of a perceptual mechanism has been studied extensively in the imprinting literature, and the general conclusions are the same as for memorization of songs (see Bolhuis, 1991, 1996; ten Cate, 1994). The case of the developing predisposition is especially interesting because it illustrates an important aspect of prefunctionality. Young, dark-reared domestic chicks have a predisposition to approach objects resembling adult conspecifics, but only if they receive certain kinds of nonspecific experience such as an opportunity to run in a wheel (Johnson and Horn, 1988); and, this nonspecific experience must occur during a restricted time after hatching to be effective (Johnson, Davies and Horn, 1989). Thus, the predisposition develops prefunctionally because the chick approaches specific visual stimuli even though it has not had any visual experience; nonetheless, this effect is not seen if the chick does not have other kinds of experience. A similar example is provided by the development of the auditory recognition mechanism of the species' maternal call in Peking ducklings (Gottlieb, 1980).

The problem of the processes through which experience has its effects has also received much attention. As with song memorization, simple exposure to an adequate stimulus can be sufficient for imprinting to occur, but social interaction with the imprinting stimulus can enhance its effects (ten Cate, 1984). More recently, van Kampen and Bolhuis (1991) have shown that simultaneous exposure to an auditory stimulus and a visual stimulus results in enhanced learning about each stimulus separately. Further experiments by Bolhuis and Honey (1994) supported the conclusion that conjoint exposure to a visual and auditory stimulus leads to the formation of an integrated memory of them.

Food Recognition Mechanisms. The work of Steiner (1979) suggests that newborn infants have well-developed perceptual mechanisms for recognizing sweet, sour, and bitter. Most substances that humans (and other animals) treat as food, however, are recognized on the basis of more complex properties and require specific experience for recognition to develop (see Hogan, 1973; 1977 for reviews). I will here discuss two examples of how food recognition mechanisms develop in chicks and cats. I should emphasize that I am considering "recognition mechanisms" in a strictly (behaviorally) causal sense. That is, stimuli that activate a food recognition mechanism, for example, are those stimuli that the animal treats as food. We infer that an animal is treating a stimulus as food from the occurrence of behavior that belongs to the hunger system. Such stimuli may or may not be nutritious and could even be poisonous.

Newly-hatched chicks peck at a wide variety of objects, although, even at the first opportunity, certain colors and shapes are preferred (Fantz, 1957; Hess, 1956). These preferences need not be a reflection of an undeveloped food-recognition mechanism, however, for at least two major reasons. First, pecking is a component of aggressive, sexual, and grooming behavior as well as of feeding behavior, and the stimuli that release and direct pecking in these various contexts are quite different. Second, chickens continue to peck a wide variety of objects throughout their lives, even after the objects toward which they direct their feeding, grooming, aggressive, and sexual behavior have become quite specific. Thus, one could view these early preferences as being due to a perceptual mechanism directly connected to the pecking mechanism in the same way that the various taste mechanisms are connected to specific motor mechanisms in infants. This "independent" pecking might be regarded as serving an exploratory function, and it also has many of the characteristics of play.

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. Certain taste and tactile stimuli are more acceptable than others (see Hogan, 1973, for review), but these stimuli can be effective only after the chick has the stimulus in its mouth. In some cases, taste and tactile feedback seem to be sufficient to cause an item to become recognized as food. For example, as early as 1-2 days of age, a chick that has eaten one mealworm will treat all subsequent mealworms as food. Presumably, the taste of the mealworm is sufficient for subsequent visual recognition to occur because a second mealworm will be accepted immediately after the first, and thus long before any effects of digestion could be expected to play a role (Hogan, 1966). Taste is also sufficient for a chick to develop visual recognition of a stimulus to be rejected: a 1-day-old chick will learn to reject a distasteful cinnabar caterpillar in just one trial (Morgan, 1896; see also Hale and Green, 1979). The fact that mealworms can come to be recognized as food (i.e., are avidly ingested) and other insects can come to be rejected as food before nutritive factors gain control of pecking on day 3 (see below) is evidence that the food recognition mechanism is independent of the central mechanism of the developing hunger system.

The food recognition mechanism also develops under the influence of the long-term (1-2 h) effects of ingestion. Experiments by Hogan-Warburg and Hogan (1981) provide evidence that chicks gradually learn to recognize food particles as a result of the reinforcing effects of food ingestion. In these experiments, visual stimuli from the food gained significant control over the chicks' behavior after one substantial food meal, though oral stimuli gained control of ingestion more slowly.

The development of food recognition in young kittens is similar in many ways to that in chicks (Baerends-van Roon and Baerends, 1979). Kittens begin ingesting their first solid food at about 4 weeks of age. Some items are immediately recognized as food, whereas others require various kinds of experience before being accepted (or rejected) as food. Fish odor appears to be attractive to all cats, even those with no experience of fish. Fish is ingested as early as a kitten is able to eat solid food, but the main problem for the kitten is learning how to catch a fish. This topic is discussed in the next section. Mouse odor, on the other hand, does not appear to have an inherent attractiveness for cats. Mice become recognized as food only after a kitten has eaten a mouse. This can happen if a mother cat presents a dead (and opened) mouse. It can also happen if a kitten attacks and bites a live mouse by itself. It is not yet possible to say whether the taste of the mouse is sufficient experience for its subsequent recognition as food (as in the chicks) or whether nutritional effects of digestion are necessary. The Baerendses did observe that a shrew may be caught and ingested by a naïve kitten, but it is vomited within 15-20 min. Thereafter, kittens may catch and "play" with shrews, but they never ingest them. This finding suggests that the effects of digestion may be the critical experience for food recognition to develop. Such observations also indicate considerable independence of catching and eating behavior, a topic discussed later.

In a functional sense, the nutritional effects of ingestion should be the ultimate factor determining which objects are recognized as food. But sometimes, other factors override the effects of nutrition and lead to the development of a food recognition mechanism that is maladaptive. Two observations made on chicks' food preferences are relevant here (Hogan, 1971). First, many chicks that were fed mealworms on the first few days after hatching died at about 6 or 7 days. These chicks could generally be characterized as mealworm fanatics because of their excited, positive behavior toward mealworms. These mealworm fanatics never learned to eat the regular chicken food that literally surrounded them, and they apparently died of starvation. Second, many chicks that were raised on a mixture of chicken food and aquarium gravel also died at about 6 days of age, also apparently of starvation. In this case, the gravel seemed to be an exceptionally good releasing stimulus for pecking and swallowing. Both these examples suggest that factors other than the nutritional effects of ingestion can play an important role in the development of food recognition.

Discussion. The development of perceptual mechanisms illustrates most of the problems encountered in the development of behavior systems in general. First, the postulation of a template or schema implies a kind of modularity in the brain in that a certain part of the brain is preassigned a specific function. Second, there are constraints on the kinds of experience that can affect development and on the age or stage of development at which this experience can be effective. Third, there is the problem of developmental processes: Are the effects of experience direct or indirect? Is mere exposure sufficient, or is some sort of reinforcement necessary? Finally, there is much variability between species in the role played by experience and the types of constraints encountered. These problems are all interrelated, and I return to them in the general discussion.

One generalization about perceptual mechanisms per se is that the evidence supports their existence in at least three functional levels of organization: feature recognition, object recognition, and function recognition. Feature recognition mechanisms discriminate among various sizes, shapes, colors, smells, tastes, and so on. This is presumably the level at which the gustofacial reflex is organized in human infants. The reason for distinguishing between object recognition and function recognition is that objects with similar properties, such as food crumbs and sand, mealworms and cinnabar caterpillars, or mice and shrews, are easily recognized (after appropriate experience) as being food or nonfood, whereas other objects with greatly disparate properties, such as grain, insects, fish, and the leaves of various plants, are easily included in the food category. Similarly, a mockingbird, *Mimus polyglottos*, mimics very accurately the songs of many different species (Baylis, 1982). Therefore, it must have a number of perceptual mechanisms for recognizing each different song. Further, the various songs that the mockingbird has learned are combined into an overall song that has species-specific characteristics (Logan, 1983), so there must also be an additional perceptual mechanism at a higher level of organization. Ten Cate's (1994) imprinting results with zebra finches tell the same story.

Development of Motor Mechanisms

Many motor mechanisms develop prefunctionally. For instance, young chicks show normal locomotion and pecking movements almost immediately after hatching. And, within the next few days, ground scratching and various grooming movements appear. Kruijt (1964) showed that the proper functioning of these and other movements in the posthatching situation is not a necessary causal factor for their development. Of course, prehatching conditions obviously influence the development of these movements, though the processes responsible for behavioral organization remain largely unknown (Oppenheim, 1974). Studies of the responses of young rat pups to electrical stimulation of the medial forebrain bundle provide an additional example (review in Moran, 1986). Three-day-old rat pups show a number of organized behavior patterns such as licking, pawing, gaping, and lordosis in response to such stimulation. These patterns are not seen in their normal functional context until later in development. Thus, these motor mechanisms must also be organized prior to their functioning.

It should be emphasized here that, although motor patterns are visible to an observer, motor mechanisms are not. An example should make this point clear. Kuo (1967) noted that chicks that developed with their yolk sac in an abnormal position were often crippled when they hatched. He interpreted these results to mean that the development of normal walking movements required functional experience in the egg: the legs had to push actively against the yolk sac for normal development to occur. Such experience is indeed necessary for the development of normal joints (Drachman and Sokoloff, 1966), and without properly functioning joints, a chick cannot move normally. Nonetheless, the movements of a crippled chick cannot provide evidence for whether or not the motor mechanism for walking has developed normally. Such evidence certainly does not contradict the conclusion of Hamburger (e.g., 1973) that the neural patterning underlying the walking movements of a chick develops without functional experience (cf. Lehrman, 1970). (For a related example concerning human locomotion, see Thelen and Fisher, 1982.)

Perhaps the best studied case of how a motor mechanism develops on the basis of functional experience is the development of bird song, and this provides my first example. I then consider the development of some displays in birds; experience is effective in a surprising way in this example. Finally, I discuss aspects of the development of behavior sequences in dustbathing of chickens, grooming in rats, and prey catching in cats. These examples all give insight into the development of more complex behavior systems.

Song Learning. As we have seen above, the young bird, in many species, forms an auditory image of the song it will learn to sing. Learning to sing the song does not happen until later, when the internal state (e.g., the level of testosterone) is appropriate. At this point, it appears that the bird learns to adjust its motor output to match the image it has previously formed. This adjustment must involve the bird's hearing itself because deafened birds never learn to produce any song that approaches normal song (Konishi, 1965).

Experiments by Stevenson (1967) showed that hearing its species-specific song could serve as a reinforcer for an operant perching response in male chaffinches. On the basis of these results, Hinde (1970) suggested that song learning might involve matching the sounds produced by the young bird with the stored image: sounds 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 trains a rat to press a lever (Skinner, 1953).

In most species, three stages in the production of song can be distinguished: subsong, plastic song, and crystallized song (Thorpe, 1961). During the subsong phase, the bird essentially babbles, and slowly adjusts its production to match phrases and songs it heard during the memorization stage; it may also invent new combinations of phrases during this phase. These changes presumably come about in the manner suggested by Hinde. In the plastic song phase, the bird may be singing a number of songs that resemble songs it previously heard. Which of these songs becomes chosen as the crystallized song depends, in many species, on the songs it hears from other birds at this time. In some species it selects a similar song (which probably accounts for the occurrence of local dialects) and in other species it selects a dissimilar song. In either case, a selection is made from songs already developed (Marler & Peters, 1982; Nelson, 1997). The selection process presumably also involves some kind of reinforcement, often provided by the behavior of conspecifics. A particularly interesting example is the song of the brown-headed cowbird, *Molothrus ater*. Males of this species increase their performance of those songs that are associated with a wing stroke display given by the females (West and King, 1988).

Displays. A display is a behavior pattern that is adapted to serve as a signal to a conspecific (Tinbergen, 1952). The mechanism controlling the display is thus the motor counterpart of species-recognition perceptual mechanisms discussed above. Displays are often complex, yet they typically develop prefunctionally. For example, waltzing is a courtship display in chickens that essentially involves the male's circling a female in a characteristic posture. Kruijt (1964) showed that the form of this display can be derived from components of behavior that belong to the aggression and escape systems, and that these systems are activated when waltzing first appears. Nonetheless, waltzing appears even in animals that are reared in social isolation, so social experience cannot be a necessary causal factor in its development.

One example of a display in which social experience has been implicated as a causal factor in its development is the "oblique posture with long call" of the black-headed gull, *Larus ridibundus*. Groothuis (1992) raised gulls to the age of 1 year either in social isolation, in small groups of 2-4 individuals, or in large groups of 12. Black-headed gulls are colonial breeders, and large groups are the normal social environment for the developing young. All the birds raised in large groups, 50% of the birds raised in small groups, and 35% of the birds raised in social isolation developed the normal display in the first year. Of particular interest is that about 40% of the birds raised in small groups developed an aberrant display in which the head was held in an abnormal posture. Further experience in large groups for more than a year had no effect on the form of this aberrant display. This result contrasts with the finding that all of the isolated and other birds that originally showed only fragmentary forms of the display subsequently developed a normal display when placed together in a large group. A separate experiment (Groothuis and Meeuwissen, 1992) showed that isolated birds that were injected with testosterone at 10 weeks of age all developed a normal display within a few days of injection.

One process underlying the development of this display may be the same as that suggested by Hinde for the development of bird song. There may be some sort of template sensitive to proprioceptive feedback from the display that selects out the correct forms from all the transitional forms that normally occur. Such a cognitive structure that recognizes proprioceptive feedback has been proposed to explain the results of experiments on imitation by human infants (Field, Woodson, Greenberg, and Cohen, 1982). Nonetheless, the results from the testosterone experiments, in which essentially no transitional forms were seen, do not support such a process in the gulls. Further, the fact that many isolated birds developed a normal display means that social experience cannot be a necessary causal factor for normal development. However, the aberrant displays that developed in some birds raised in small groups suggest that social interactions can be of importance in special circumstances. Groothuis (1992, 1994) discusses several hypotheses to explain these results, one of which is that abnormal experience encountered in the small groups could have distorted normal development. I return to this idea in the discussion.

Dustbathing and grooming. Dustbathing in the adult fowl 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 Liere & 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. A diagram of the dustbathing behavior system is shown in Figure 2.

Dustbathing does not appear fully formed 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 7 or 8 days posthatch (Kruijt, 1964). 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. There were some differences in the microstructure of the bouts that could be related to the presence or absence of specific feedback, but the motor mechanisms and their coordination developed essentially normally in chicks raised in a dustless environment (see also van Liere, 1992). Clearly, the experience of sand in the feathers removing lipids or improving feather quality is not necessary for the integration of the motor components of dustbathing into a normal coordinated sequence.

More recently, Larsen, Hogan, and Vestergaard (2000) studied in detail the development of dustbathing behavior sequences in chicks from hatching to three weeks of age. They found that the individual behavior elements, as soon as they appeared, were incorporated into the normal adult sequence structure; this occurred even though the form of the elements themselves is not yet fixed. These results support the conclusion that separate mechanisms are responsible for the form of the individual behavior elements and for the organization of these elements into recognizable sequences as shown in Figure 2. A similar conclusion was previously reached by Berridge (1994) on the basis of results on the development of grooming sequences in young mice (Fentress, 1972) and young rats and guinea pigs (Colonnese, Stallman, and Berridge, 1996). In fact, Berridge and Fentress (1986) called certain sequences of grooming movements “syntactic chains” to emphasize the rules controlling natural action sequences (see also Fentress, this volume). I return to these ideas in the section on human language.

Prey catching. My final example of the development of sequences of motor patterns is the prey-catching behavior of cats (Baerends-van Roon and Baerends, 1979). Locomotion, pouncing, angling (with one paw), and biting are the basic motor patterns out of which effective prey-catching develops, and all these behaviors can be seen, prefunctionally, by the time the kitten is about 4 weeks old. The way these behaviors become integrated depends primarily on the type of prey being caught. If a mouse is the prey, locomotion and biting are sufficient to catch and kill, whereas with larger prey, pouncing is necessary in addition. If a fish is the prey, angling and biting are the necessary motor patterns. The evidence suggests that the “correct” behavior sequences are selected on the basis of the effects of the behavior. In other words, an operant shaping process can account for all the results, with the proviso that the basic elements—locomotion, pouncing, angling, and biting—are not themselves shaped. This conclusion is supported by the fact that the course of development can vary considerably among individuals even though the final result is quite stereotyped.

An important difference between prey-catching sequences and many of the other examples discussed above is that prey-catching sequences in cats do not “crystallize.” That is, functional experience continues to be effective in shaping new sequences. For example, kittens that have developed proficient fish-catching behavior can subsequently learn to catch mice, although there is some interference from the previous learning in that such kittens take longer to learn to kill the mouse with a bite than naïve kittens. Learning to catch a fish after the kitten has already developed mouse-catching behavior turns out to be considerably more difficult. The primary problem here is that older kittens have a stronger tendency to avoid getting wet than younger kittens. If the fear of water can be overcome, the fish-catching sequence can be easily acquired. This last example indicates an important problem in the study of development: It seems that certain cases of learning may be irreversible when, actually, indirect factors (such as fear of water, in this case) obscure the fact that functional experience can still have direct effects on development.

Discussion. The development of motor mechanisms illustrates the same problems previously discussed with respect to perceptual mechanisms: modularity, constraints, processes, and species differences. The emphases are somewhat different in that most motor mechanisms (with the notable exception of bird song) and even many motor sequences (such as dustbathing in chicks and grooming in rats) develop prefunctionally, whereas almost all perceptual mechanisms are directly influenced by functional experience. Further, when functional experience is relevant, mere exposure is probably sufficient for perceptual mechanisms, whereas some sort of reinforcement is usually necessary for motor mechanisms and motor sequences. These topics are considered again in the general discussion.

Another similarity between perceptual and motor mechanisms is the existence of different functional levels of organization. In the case of motor mechanisms there is the level of the individual motor pattern and the level of motor pattern integration. The results reviewed above for dustbathing, grooming, and prey catching all provided evidence that these levels are independent. In many ways the level of motor pattern integration is especially interesting because it provides the basis for the temporal patterning, or syntax, of functionally related behaviors. As Lashley (1951) pointed out, all skilled acts, including human language, seem to involve the same problems of serial ordering. In a later section, I will attempt to show how the framework developed here can be useful in understanding the development of human language.

In a recent discussion of motor development, Thelen (1995) proposes a dynamic theory in which “repeated cycles of perception and action can give rise to emergent new forms of behavior without preexisting mental or genetic structures….”(p. 93). She opposes her theory to one in which the brain matures and movements appear when the appropriate level of maturity is reached. Although I would maintain that there are always preexisting structures, in some ways her approach is similar to the one taken in this paper; for example, we have seen that feedback from the performance of a song or display can affect the form of future performances. What is very different is that her basic units of action lie at a lower functional level of organization than is considered here, and she explicitly considers factors that I call prefunctional and do not analyze further. With respect to the latter, her analysis is similar to Kuo’s analysis of walking in chicks discussed earlier.

Development of Connections between Central and Motor Mechanisms

We can say that a central and a motor mechanism are connected when the occurrence of a behavior varies directly with the presence of factors known to affect the central mechanism. Consider the behavior of pecking and the central hunger mechanism in a chicken. If the amount of pecking varies directly with the amount of food deprivation, then we have evidence that hunger and pecking are connected. On the other hand, if variations in food deprivation have no effect on the amount of pecking, we have evidence that hunger and pecking are not connected, that is, are independent mechanisms. The developmental problem is how we get from the state of independence to the state of connectedness. There are many examples of situations in which a motor mechanism becomes connected to a particular central mechanism, including examples from the operant conditioning literature. I shall discuss some of these later, but I begin with some examples of the development of normal feeding behavior.

<u>Hunger</u>. A surprising fact about the feeding behavior of many neonatal animals is that their early feeding movements are relatively independent of motivational factors associated with food deprivation. Hinde (1970, p. 551ff.) reviewed a variety of evidence from studies on kittens, puppies, lambs, and human infants that show that the amount of suckling by a young animal is very little influenced by the amount of food it obtains. More recently, a series of studies on the development of feeding in chicks and in neonatal rats has been published, and these are reviewed briefly here.

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). When chicks were 1 or 2 days old, 5 h of food deprivation did not influence the subsequent rate of pecking at food, whereas, by the time the chicks were 4 or 5 days old, 5 h of food deprivation led to a large increase in pecking at food. A very similar change in the control of feeding has been found in rat pups (Blass, Hall, and Teicher, 1979; Cramer and Blass, 1983; Hall and Williams, 1983). Before the age of about 2 weeks, the occurrence of behaviors such as nipple search and nipple attachment, as well as the amount of suckling itself, was not influenced by food (i.e., maternal) deprivation of as long as 22 h. After 2 weeks, however, deprived pups attached to the nipple more quickly and suckled longer than nondeprived pups. Similarly, when tested in a spatial discrimination task in a Y maze, nutritive suckling provided a greater incentive than nonnutritive suckling only after the pups were older than 2 weeks (Kenny, Stoloff, Bruno, and Blass, 1979).

The developmental question, with respect to these results, is: How do the motivational factors associated with food deprivation come to control feeding behavior? For chicks, early experiments (see Hogan, 1977, for a review) 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. In other words, 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. 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). Experiments on the development of pecking in ring doves (*Streptopelia roseogrisea*) also indicate that experience is necessary for hunger to gain control of pecking; though, in this case, the necessary experience apparently involves interaction with the parents, as well as with food (Graf, Balsam, and Silver, 1984; Balsam, Graf, and Silver, 1992; Balsam and Silver, 1994).

Similar experiments with rat pups have not been done, though the problem with mammals, in general, is more complex because the suckling response drops out altogether at weaning and is replaced by different behaviors (cf. Hall and Williams, 1983). Hall and his colleagues have shown that, under special conditions, rat pups ingest food away from the mother very soon after birth, but these experiments have not asked the same questions being asked here (see also Johanson and Terry, 1988). In the study by Kenny, *et al*. (1979), the infant rats received their nourishment through intragastric feeding between days 12 (before their ingestion was influenced by hunger) and day 17. When tested at day 17, motivational control of their ingestion was the same as in normally reared pups, which implies that experience eating solid food is not necessary for motivational control to develop. However, there are some results from guinea pigs that are also relevant (Reisbick, 1973). Guinea pigs normally begin ingesting solid food within a day of birth, and Reisbick found that experience of ingesting and swallowing was necessary before the guinea pigs showed evidence of discriminating between nutritious and nonnutritious objects. These results are very similar to the results from the chicks and have been discussed in more detail elsewhere (Hogan, 1977).

Operant Conditioning. A second source of evidence for the development of connections between central and motor mechanisms is the operant conditioning literature. The process of reinforcement, in general, can be regarded as influencing the development of connections between central and motor mechanisms. For example, the response of lever pressing is an easily recognizable motor pattern in a rat. Reinforcing lever pressing with food leads to a connection of the motor mechanism for lever pressing with the hunger system, and reinforcing with water leads to a connection with the thirst system.

Schiller (1949) 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 apparently the same manipulative patterns that had first appeared spontaneously and prefunctionally. The patterns included “weaving,” “poking and sounding,” and “joining sticks.” Schiller 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 test for “connection” here, as elsewhere, is to see if the occurrence of a behavior varies directly with the presence of factors known to affect the central mechanism: Do hungry chimps engage in these behaviors more than sated chimps? Schiller’s results suggest that they do.

One question that arises from these results is whether any motor mechanism can be attached to the hunger system using food reinforcement. Rice (1978) tried to affect the occurrence of shrill calls and twitters in young chicks by using food reinforcement, but he was unsuccessful. Shettleworth (1975), using golden hamsters (*Mesocricetus auratus*), also asked whether various behavior patterns could be influenced by food reinforcement. In one set of experiments, she observed animals in their home cages and in an unfamiliar environment both when deprived and when not deprived of food. In another set of experiments, she reinforced animals with food when they performed various behavior patterns, including scrabbling, digging, rearing, face washing, scratching, and scent marking. She found that food reinforcement was effective in increasing the occurrence of scratching, digging, and rearing, but that it had very little effect on the occurrence of face washing, scratching, and scent marking. The first three patterns all increased in frequency in hungry hamsters, and the latter three decreased in frequency. Thus, behavior patterns that belonged to the hamster's hunger system—when the criterion used is a positive correlation with food deprivation—could be influenced by food reinforcement, whereas behavior patterns that belonged to other systems could not. These results all indicate a considerable degree of inflexibility with respect to which motor patterns can become connected to which central mechanisms.

Development of Connections between Perceptual and Central Mechanisms

We can say that a perceptual mechanism and a central mechanism are connected when a stimulus that activates the perceptual mechanism can lead to the occurrence of the set of behaviors known to belong to the central mechanism. For instance, an egg recognition mechanism is connected to the incubation system in many birds because the presentation of an egg (or other appropriate stimulus) can lead to approach, retrieval, and settling on the nest. The evidence necessary to show that a perceptual mechanism is, in fact, connected to a central mechanism is to show that the presentation of an adequate stimulus has the same effect on the central mechanism (priming effects—Hogan and Roper, 1978, p. 231) as a direct manipulation of the relevant internal factors, for example, by deprivation or the injection of hormones.

Dustbathing. Functional experience plays an essential role in the development of the perceptual mechanism for recognizing dust and of the connection between it and the central mechanism (dashed lines in Figure 2). Evidence for the role of experience in the development of the dust recognition mechanism itself is reviewed by Sanotra, Vestergaard, Agger and Lawson (1995). Factors responsible for the connection between the dust-recognition mechanism and the central mechanism are reviewed here.

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 internal factors (see below). It also implies that the connection between the dust-recognition perceptual mechanism and the central mechanism is not formed until well after the motor and central mechanisms are functional.

Vestergaard and Hogan (1992) found that early dustbathing is most likely to occur in whatever substrate is pecked at most. They point out that pecking is a movement that functions as exploratory, feeding, dustbathing, and later aggressive behavior. They suggest that perceptual mechanisms specific to each system develop gradually out of exploratory pecking on the basis of functional experience. 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 shows that early experience can lead to stable preferences for particular stimuli (Petherick, Seawright, Waddington, Duncan, and Murphy, 1995; Vestergaard and Baranyiova, 1996). 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, and Hogan, 1993; Johnsen, Vestergaard, and Nørgaard-Nielsen, 1998).

Hunger. The results with the chicks discussed above show that a mealworm recognition mechanism can become connected to the motor mechanism for pecking at least one day before nutrition (i.e., the central "hunger" mechanism) gains control of pecking. The evidence indicates that the ingestion of mealworms remains semi-independent of hunger, probably throughout life: satiated chicks avidly ingest many mealworms, and the ingestion of a substantial number of mealworms, at least in the first week after hatching, has no effect on the amount of other food subsequently ingested (Hogan, 1971). This semi-independence of mealworm ingestion and hunger is probably the same phenomenon as the semi-independence of suckling and hunger in rats and prey catching and hunger in cats and most other predators.

Evidence that a food recognition mechanism becomes connected to the central hunger mechanism comes from the fact that food particles develop incentive value between 3 and 5 days posthatching (Hogan, 1971); development of incentive value probably reflects the same process involved in the development of food recognition discussed above (Hogan-Warburg and Hogan, 1981). More direct evidence of perceptual mechanisms' becoming connected to central mechanisms is provided by several examples from the learning literature.

Classical Conditioning. There are now 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 (*Betta splendens*) 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 (*Coturnix japonica*) to a red light. Moore (1973) showed that a small lighted key followed consistently by food elicited a food peck in a pigeon; when followed consistently by water, it elicited a drinking peck. Blass *et al*. (1984) were able to condition the ingestive behaviors of head orientation and sucking in human infants (which are unconditioned responses to the oral delivery of a sucrose solution) to gentle forehead stroking. These and many other cases exemplify the development of connections 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 also cases, however, where a connection between a perceptual mechanism and a central mechanism is directly implicated. 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 shown by young chicks when soliciting brooding from a mother hen (Hogan, 1974). Wasserman's results imply that the recognition mechanism for the lighted key becomes connected to a thermoregulatory system in the young chick (cf. Sherry, 1981), and that the presentation of this stimulus to a cold chick elicits brooding solicitation movements.

More recently, similar examples have multiplied. The systems include hunger, aggression, sex, and fear, in species ranging from insects through fish and birds to mammals including humans (see Domjan and Holloway, 1998; Fanselow and De Oca, 1998; Timberlake, 1994 for reviews). What many of these examples show is that previously neutral stimuli can, as a result of classical conditioning procedures, develop control of entire behavior systems. The studies by Fanselow and his colleagues, using the species-specific defense reactions of rats as their behavior, have even shown that the conditioned stimulus has its effects through the same neural structures as the unconditioned stimulus.

Development of Connections among Perceptual, Central, and Motor Mechanisms

The previous sections have presented evidence about the effects of various kinds of experience on the development of connections between pairs of building blocks. The principles of development that emerge from those results are sufficient to allow us to understand much of the development of more complex systems. As we shall see, however, some new principles seem also to be involved in these more complex cases. A review of some examples of the development of dustbathing, hunger, aggressive, sexual, and play systems will illustrate how these principles operate, and the final section will consider how they could be applied to the study of human language acquisition.

<u>Dustbathing</u>. The dustbathing system of an adult chicken consists of a perceptual mechanism that recognizes dust, a central mechanism that integrates internal motivational factors with signals from the perceptual mechanism and a circadian clock (Hogan, 1997), and controls the motor mechanisms that constitute dustbathing (Figure 2). As we have seen above, the perceptual mechanism itself and its connection with the central mechanism require specific functional experience for their development, whereas the motor components of dustbathing as well as the temporal organization of those components develop prefunctionally. Some evidence is also available for the development of the central mechanism.

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 is seen, at 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 as early as 8 days of age (the age that complete dustbathing bouts first appear) and that they did not change over at least a 4-week period. No specific experience was necessary for the motivational factors associated with dust deprivation to gain control of dustbathing (see also Vestergaard, Damm, Abbot, and Bildsøe,1999). 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. These results suggest that the central mechanism for dustbathing and the connection between the central mechanism and the motor mechanisms also develop prefunctionally.

<u>Hunger</u>. 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 (Figure 3). We have seen above how the perceptual mechanisms develop and what experience is necessary for the central mechanism to develop its modulating function. With respect to motor mechanisms, the previous discussion has focused entirely on pecking. There

are, however, several other motor mechanisms that are normally associated with the hunger system, such as those controlling ground scratching and locomotion. As with dustbathing, both the individual motor mechanisms of the system 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) reviewed the evidence that suggests that new connections are formed between the central hunger mechanism and individual motor mechanisms on the basis of the specific experience of the individual chick (dashed lines between 'H' and 'P' and between 'H' and 'S' in Figure 3), and that these new connections effectively block the expression of the original prefunctional connections.

The general picture that emerges from all the data is summarized in Figure 3. A young chick has a number of feature-recognition perceptual mechanisms, an undeveloped food-recognition mechanism, an independent central hunger mechanism, an integrated complex of motor mechanisms, and some connections between the perceptual and motor mechanisms; these mechanisms are available prefunctionally. The food recognition mechanism develops (perhaps simultaneously with a number of object recognition mechanisms) under the influence of experience with certain tastes or positive nutritious aftereffects of ingestion. The food recognition mechanism probably has connections to the motor mechanisms prefunctionally. A connection between the central hunger mechanism and the complex of motor mechanisms develops as a result of the experience of pecking followed by swallowing, and between the central hunger mechanism and the food recognition mechanism as a result of experience of the nutritive aftereffects of ingesting particular particles (the incentive value of food crumbs). More specific connections develop between the central hunger mechanism and particular motor mechanisms on the basis of nutritive feedback as well. These specific connections are in evidence especially when the chick is hungry, but the original prefunctional connections among perceptual mechanisms and motor mechanisms remain operative and can be seen especially when the chick is not hungry.

It should be noted that the picture for the development of prey catching in kittens is not essentially different from the picture just presented for chicks. Although the individual behavior patterns used in prey catching (pouncing, angling, biting) are originally independent in the sense that the precise ordering of components is not determined, nonetheless these behavior patterns do not occur at random. The specific patterns of these components that develop with respect to particular stimuli can be considered subsystems of the sort that chicks develop with respect to mealworms or to grainlike objects. These subsystems in kittens—a mouse-catching system or a fish-catching system—also have a relationship to the central hunger mechanism that is very similar to the relationship between hunger and pecking or ground scratching in chicks.

A final point is that the development of a hunger system can be greatly influenced by factors that are basically irrelevant to feeding or nutrition. The factor that has been mentioned here is fear, with respect to both the development of recognition of mealworms as food in chicks and the development of fish catching in kittens. A chick that is too afraid of a mealworm will never pick one up (Hogan, 1965), and a kitten that is too afraid of water will never learn to catch a fish. Such indirect motivational factors play an even more important role in the development of social behavior, as will be seen below.

Aggression. 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 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 to 3 months.

The various behavior patterns comprising adult fights can be seen to occur, independently, in the 1- to 2-week-old chick, well before their integration into fighting behavior. This means that functional social experience could be a necessary factor guiding development. This is, however, not the case. In other experiments, Kruijt (1964) raised chicks in social isolation for the first week of life and then placed them together in pairs. Many of these chicks showed aggressive behavior toward each other within seconds. Further, the fights that developed were characteristic of the fights of 1-month-old, socially raised chicks. Such results suggest that the organization of the motor components of the aggression system as well as the connections between the central and motor mechanisms develop prefunctionally, and that the occurrence of aggressive behavior requires only the proper motivational state. Similar results and conclusions apply to the development of aggressive displays in gulls (Groothuis, 1994). In this way, the aggression system is more like the dustbathing system than it is like the hunger system.

Whether functional social experience ever affects the organization of the motor mechanisms of the aggression system in chickens, as it does in gulls, remains an open question. Males raised by Kruijt in social isolation for more than a year still showed reasonably normal aggressive patterns, and the abnormalities that were seen could be accounted for in terms of interference from other systems such as fear. Nonetheless, social experience could be necessary for fighting to develop a high degree of effectiveness. One method of testing this idea is to see whether chickens can be "trained" to fight by appropriate tutors. Kuo (1967) reported that such methods are effective in training various breeds of dogs to fight.

The opponent-recognition perceptual mechanism must be partially formed prefunctionally because a chick as young as 2.5 days old will respond with frontal threat and aggressive pecks to the stimulus of a 6-cm green wooden triangle moved directly in front of it (Evans, 1968). Likewise, socially isolated chicks showed fully coordinated aggressive behavior when confronted with another chick at the age of 1 week. But isolated chicks of the same age can also direct aggressive behavior to a light bulb hanging in the cage. And older isolated males often come to direct their aggressive behavior to their own tails (Kruijt, 1964). Presumably the complete development of the perceptual mechanism depends on the proper experience at the proper time (just as the templates for song learning in many species), but the experiments necessary to explore this idea have not yet been done.

The development of normal aggressive behavior in kittens does require specific functional experience. Baerends-van Roon and Baerends (1979) described early attack behavior, which included most of the same behavior patterns previously discussed with respect to prey catching, including pouncing and biting. These patterns are apparently the same when originally directed to either a prey or another kitten, but they become modified in different way as a result of feedback from the opponent. In particular, the force of the pounce, the extension of the claws, and the strength of the bite all become reduced after a nestmate responds in kind. The occurrence of "play" behavior, especially in the period from 4 to 8 weeks, seems to provide the kitten with essential experience for the development of normal social behavior. Two kittens that were raised in social isolation (after weaning at 7 weeks) showed either unrestrained attack or total avoidance when confronted with a normally reared cat at the age of several months. These two cats also showed abnormal maternal behavior when they later had their own litters. The Baerendses suggested that normal development requires a proper balance of attack and escape motivation.

Sex. 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 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.

Many of the components of the copulatory sequence, including mounting, sitting, and pecking, are seen independently in young chicks, and there is ample opportunity for social experience to influence the occurrence and integration of these components. As with aggression, however, several lines of evidence suggest that the motor mechanisms are already organized soon after hatching, and that their expression merely requires a sufficiently high level of motivation. For example, Andrew (1966) was able to elicit well-integrated mounting, treading, and pelvic lowering in socially isolated domestic chicks as young as 2 days old by using the stimulus of a human hand moved in a particular manner. Andrew also found that injection of testosterone greatly increased the number of chicks that responded sexually in his tests during the first 2 weeks (see also Groothuis, 1994, for similar evidence on the expression of sexual displays in gulls, and Williams, 1991, for evidence on the expression of sexual behavior in rat pups). Further, junglefowl males that had been raised in social isolation for 6-9 months copulated successfully with females within so few encounters that it was clear that the motor mechanisms had been integrated before testing (Kruijt, 1962).

The occurrence of the courtship displays presents a somewhat different picture. For example, waltzing is first seen at 2-3 months of age, when it always appears in the context of fighting. As already mentioned, the form of the display seems to develop independently of social experience. The factors controlling the occurrence of waltzing, however, seem to be largely determined by social experience. Waltzing to a female often has the effect that the female crouches, and a crouching female is the signal for mounting and copulation. Experiments reported by Kruijt (1964) showed that the frequency of waltzing increased when mating was contingent on its occurrence and decreased when mating was not allowed. This finding suggests that, in normal development, the switch that is seen from the occurrence of waltzing in a fighting context to a sexual context may require the experience of the display followed by copulation. This interpretation is also supported by the behavior of the males that were socially isolated for 6-9 months. These animals did not show waltzing (or the other displays) before mating with the female, but they often showed displays before attacking her. Thus, copulation seems to be the reinforcer that causes the motor mechanism for waltzing to become attached to the central coordinating mechanism for sex.

Tidbitting is a display that consists of ground pecking directed to edible or inedible objects and/or ground scratching, accompanied with high, rhythmically repeated calls. It develops out of the pecking and calling that accompany “food running” (Kruijt, 1964), which can be seen in young chicks as early as 2 days. Tidbitting is especially interesting because it serves a courtship function in males but a parental function in females. In all three contexts, it serves to attract conspecifics from a distance: food running chicks attract other chicks and the mother hen, tidbitting males attract females, and food-calling (tidbitting) mother hens attract their chicks. As with waltzing, the form of the tidbitting display does not depend on social experience because it is seen in both chicks and adults that have been raised in social isolation. The causal factors controlling food running are complex and include escape, hunger, and possibly aggression (Hogan, 1966). Andrew (1966) reported that testosterone injections did *not* increase the occurrence of “juvenile tidbitting,” whereas they did increase copulatory behavior. Nonetheless, in adult males sexual factors play a primary role in the occurrence of tidbitting (Kruijt, 1964; van Kampen, 1997), and in adult females, parental factors play a primary role (Sherry, 1977). Somewhat surprisingly, sexual factors are not implicated in the response of females to a tidbitting male (van Kampen, 1994). All these results imply that the motor mechanism for tidbitting develops new connections with central mechanisms in the course of development. Unfortunately, there have been no experiments to determine what kind of experience is necessary for the switch in causal factors to occur (but see Moffatt and Hogan, 1992).

The development of the perceptual mechanisms of the sex system and their connections to the central sex mechanism seems to be much more susceptible to the effects of experience than the development of the motor mechanisms. 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 other animals, but such behavior is directed equally toward males and females. Only gradually, as a result of specifically sexual experience, does sexual behavior become directed exclusively to females (Kruijt, 1964). As we have seen above, the development of the partner recognition mechanism has been studied intensively for many years in the context of sexual imprinting, and there is extensive evidence documenting the influence of both prefunctional and functional factors (Bischof, 1994; Bolhuis, 1991).

It should be mentioned here that much of the work of Harlow and his students and of Hinde and his students on the development of social behavior in rhesus monkeys (*Macaca mulatta*) is also relevant to this discussion (see, for example, Harlow and Harlow, 1965; Hinde, 1977; Sackett, 1970). The parallels between the development of chicken behavior and monkey behavior are remarkable, and many of the points made in the previous discussion could have been illustrated just as easily by reference to the monkey results. There are also important parallels between the work discussed above and the development of human social behavior (see, for example, Rutter, 1991), but a discussion of these is beyond the scope of this chapter.

Play. The topic of play has been discussed extensively in the context of development. Here, I briefly present some ethological ideas about the causation of play, and I show how they complement the behavior system framework. A more general treatment of play that includes a discussion of problems caused by the confusion of cause and function is given by Martin and Caro (1985) and by Burghardt (Chapter XX).

The first important idea was expressed by Lorenz (1956): “It seems characteristic of ‘play’ that instinctive movements are thus performed independently of the higher patterns into which they are integrated when functioning ‘in serious’” (p. 635). In other words, the motor mechanisms are activated independently of an activation of the central mechanisms. Insofar as Kruijt's analysis (1964) of junglefowl development is correct, this is precisely the case in newly-hatched chicks. As the animal grows older, and causal factors for the central mechanisms grow stronger, the independence of motor and central mechanisms decreases, and one might expect the frequency of play to decline, which generally happens. Nonetheless, the analysis of the hunger system suggests that, even when particular motor patterns such as pecking and/or ground scratching become integrated into the system, these same movements can occur independently, especially when the causal factors that activate the central mechanism (i.e., the level of hunger) are weak.

Similar results have also been seen in other species. Lorenz (1956) described the behavior of a young raven that showed a wide array of "playful" movements toward a strange object when not hungry, but that immediately tried to eat such an object if it was hungry. Likewise, Schiller's chimpanzees (1949) showed a playful manipulation of objects, especially when not hungry. The motor patterns of the raven and the chimps under these circumstances could be recognized as being similar to motor patterns belonging to various adult behavior systems.

Once various behavior systems have developed, it may be that play ceases. This, of course, is not true in many species. Morris (1956) suggested that play occurs when central mechanisms are switched off: "The mechanisms of mutual inhibition and sequential ordering mechanisms are not switched on and as a result there is no control over the types and sequences of motor patterns in the usual sense" (p. 643). Switching off central mechanisms would effectively return the animal to a very early stage of development, in which the appearance of play would again be expected. A more elaborate version of this idea was suggested by Baerends-van Roon and Baerends (1979) and was based on their observations of kittens. They proposed that, in cats at least, a central play mechanism exists that, when activated, inhibits other central mechanisms, and "play" could thus appear. Thus, species-typical patterns of play can be understood as being due to a differential inhibition of central mechanisms. Further, when play occurs, its causation remains the same as Lorenz originally suggested: the independent activation of motor mechanisms.

Human Language. In this section, I hope to show how it is possible to consider human language to be a behavior system that is similar in many respects to the behavior systems we have already considered. Human language, of course, is vastly more complex than dustbathing or feeding in chickens, but, as a biological system, both the organization and development of language should share many of the principles governing these simpler systems. There is an enormous literature on language and its development, and only very restricted aspects can be considered here.

To begin, it is necessary to identify the building blocks of the language system: What are the perceptual, motor, and central mechanisms comprising the system? As we shall see, which building blocks are chosen depends on one's definition of language. For my present purposes, I will start with the perceptual and motor mechanisms that recognize and produce the sounds in a language. I will also restrict my discussion to specific speech sounds (i.e., phonemes) as opposed to other vocal aspects of language such as prosody (see Locke, 1993; 1994; Locke and Snow, 1997).

It has been known for some time that human infants as young as 1 month are able to perceive phonetic distinctions categorically in a similar way to normal adults (Eimas, Siqueland, Jusczyk and Vigorito, 1971; Eimas, Miller and Jusczyk, 1987). More recent evidence demonstrates that these perceptual categories can be altered by linguistic experience. For example, in a cross-cultural study of 6-month-old American and Swedish infants, Kuhl, Williams, Lacerde, Stevens and Lindblom (1992) found the two groups exhibited a language-specific pattern of phonetic perception to native- and foreign-language vowel sounds. Of particular interest is that these effects of experience are seen by 6 months of age, that is, before the infant itself begins producing speech sounds. Further, by 1 year of age, infants no longer respond to speech contrasts that are not used in their native language, even those that they did discriminate at earlier ages (see Werker and Tees, 1992). Thus, the perceptual mechanisms responsible for speech perception in infants are both highly structured at birth and highly malleable in that they are shaped, instructively and selectively, by exposure to the linguistic environment (Kuhl, 1994).

Normal infants begin to babble between 6 and 10 months (see Locke, 1993, for review). The initial sounds produced by the infant are species specific (i.e., are similar in infants raised in different linguistic environments), and include phonemes not found in its native language. As the child grows older, the distribution of sounds comes more nearly to approximate the distribution in its linguistic environment, and the non-native sounds drop out. The mechanism by which these changes occur has not really been adequately analyzed, but it presumably involves a process of matching vocal output to the previously developed perceptual mechanisms (templates) by auditory feedback (Marler, 1976).

These results for the development of the perceptual and motor mechanisms that recognize and produce speech sounds involve the same problems of modularity, constraints, and processes that we have seen before, especially with respect to the changes that occur in the development of bird song. These parallels have been noted for many years now (e.g., Lenneberg, 1967; Marler, 1970b), and continue to provide mutual insights into the development of both systems at both a behavioral and neural level (Hauser, 1996; Snowdon and Hausberger, 1997; Doupe and Kuhl, 1999).

Speech sounds, however, are only one aspect of normal spoken language. Sounds become combined into words (morphemes: units of meaning), and one can ask whether the phonemes or the morphemes are the basic units of the language system. Words can always be broken down into their constituent sounds, but there is now considerable evidence that infants learn utterances (words or short phrases) as a whole during the first two years with respect to both perception and production (Jusczyk, 1997; Locke and Snow, 1997). It is only later that children are able to break utterances down into smaller sound packets. For these, and other, reasons, Locke (1994) argues specifically that phonemes are not the basic building blocks of human language. We might then conclude that words are the basic unit of the language system, but first we must consider what the words represent.

Birds do not sing randomly. They sing when the appropriate internal and external factors are active. In most cases this is when the sexual and/or aggression behavior systems are activated.[2] Humans speak in comparable circumstances, but the range of circumstances in which humans speak is very much broader. In fact, cognitive psychologists (Shelton and Caramazza, 1999) have proposed that humans possess a semantic system that receives input from spoken and written words (phonological and orthographic input lexicons) and responds with output of spoken and written words (phonological and orthographic output lexicons). Our speech (or writing) thus expresses the state of our semantic system. Of course, our semantic system is much more complex than the sexual and aggression systems of songbirds (and much of the field of cognitive psychology is devoted to understanding the organization of the semantic system and the mechanisms of lexical access to it), but it seems certain that the principles of organization and development are similar. In the present context, some of Shelton and Caramazza's conclusions are particularly interesting. They reviewed studies of language processing following brain damage and found results that "broadly support a componential organization of lexical knowledge—the semantic component is independent of phonological and orthographic form knowledge, and the latter are independent of each other." (1999, p. 5) In my terms, their language system can be considered to have a central semantic mechanism with perceptual mechanisms for recognizing words and motor mechanisms for producing words.

One important component of language still has not been discussed: Words can be combined into sentences, and it is at this level of analysis that the concepts of grammar and syntax are generally used. It is also this level of organization to which the concept "language instinct" (Pinker, 1994) has been applied. The operation of grammatical structures is not normally apparent until some time after the age of 2 years, when words become recombined into novel utterances that follow particular rules (Locke and Snow, 1997). One set of rules, called Generative Grammar, was proposed by Chomsky (1965). These rules have been reasonably successful in describing the types of sentences produced by native speakers of English, but there has been great controversy about how these rules develop in the child, particularly whether specific kinds of linguistic experience are necessary (see, e.g., Tomasello, 1995). The details of this controversy need not concern us here except to say that most of the issues are the same as we have already met in describing the development of grooming (Berridge, 1994) and dustbathing (Larsen, *et al.*, 2000) sequences, some of which are considered further in the general discussion.

As a final point, there is a long history of authors' proposing uniqueness for the human species on the basis of aspects of the syntax found in our language. In a recent discussion of this issue, Kako (1999) continues this debate. He points out that in its "most generic form, syntax is defined as a set of rules for assembling units of any type into larger units." (p. 1) He then discards this definition because he finds it too broad, and proposes instead a set of four structural properties that define the core of syntax. Once again, the details of his proposal need not concern us here. It is my opinion, however, that the generic definition has many advantages if one is interested in looking for the similarities, rather than the differences, among systems (cf. Lashley, 1951). It must be true, by definition, that human language is unique, because all species are unique, as are the specific behavior systems possessed by each species.

These results suggest that the human language system comprises three basic sets of components at two major levels of organization, and that these components develop largely independently. The sensory-motor components correspond to the perceptual and motor mechanisms depicted in Fig. 1 (with additional connections between them and the central mechanisms), whereas the semantic (meaning) and syntax components correspond to two separate central mechanisms.

This general conception is also supported by the results of studies of deaf children. For example, deaf children born to deaf parents who communicate using sign language do not babble vocally; rather, such children babble with their hands (Pettito and Marentette, 1991). Manual babbling occurs at about the same age that vocal babbling occurs in children with normal hearing who have been raised in a vocal environment. Further, the development of sign language proceeds in much the same way as the development of vocal language, with respect to both structure and use. Goldin-Meadow (1997) has found that the same general rules apply and that they appear at the same age. These results all suggest that the language system can use auditory-vocal units or visual-manual units equally well. Studies of the neural organization of language (Hickok, Bellugi and Klima, 1998) are also consistent with this interpretation.

One can ask, finally, whether this conception of human language as a behavior system actually furthers our understanding of language and its development. I think it does in at least two important ways. First, by breaking the system up into its components, the study of the pieces becomes more tractable. There has already been considerable success in comparing the development of bird song and human speech (Doupe and Kuhl, 1999), and the development of grooming sequences may provide a useful model for some aspects of the development of syntax. Further, insofar as these components are the "natural" pieces of the system, it becomes easier to understand how the system could have evolved (cf. Pinker, 1994; Hauser, 1996). A second important reason is that development of all three sets of components requires both functional and non-functional experience, and involves the same problems of modularity, constraints, and processes that have appeared before: Solutions to these problems in one system should easily generalize to other systems.

Development of Interactions among Behavior Systems

A basic tenet of ethological theory is that various behaviors of an animal—and often the most interesting ones—are the expression of the activation of not just a single behavior system, but of the interaction of two or more systems that are activated simultaneously. This conflict hypothesis was proposed by Tinbergen (1952), and has been discussed by Kruijt (1964), Baerends (1975), and Groothuis (1994). There have been two major studies that have directly addressed the development of interactions among systems—those of Kruijt (1964) in chickens and Groothuis (1994) in black-headed gulls. I will restrict my discussion here to the behavior of chickens.

Kruijt's results (1964) show that the major behavior systems of escape, aggression, and sex develop in chickens in that order. Further, activation of a system already developed inhibits the expression of systems that are just beginning to develop. Thus, a young chick that shows frontal threatening and jumping to another chick may immediately stop this early aggressive behavior if it bumps into the other too hard. As the chicks grow older, and the causal factors for aggression become stronger, however, such escape stimuli no longer stop aggressive behavior. Rather, attack and escape begin to occur in rapid alternation, and various irrelevant movements start to appear during fighting. Likewise, early sexual behavior is immediately interrupted if either the attack or the escape system is activated, but later, behavior containing components of attack, escape, and sex can be seen simultaneously. As we have seen above, there is evidence that the basic organization of these major systems is formed prefunctionally, and that their expression merely requires a sufficiently high level of causal factors. The gradual appearance of more complex interactions can be interpreted as reflecting changes in the strength of causal factors (i.e., motivational changes) rather than changes in the connections among central mechanisms (i.e., developmental changes).

The fact that another member of the species is the adequate stimulus for activating the escape, aggression, and sex systems means that all these systems must normally be activated when a conspecific is present. Kruijt (1964) points out that the precise state of activation of these systems at any moment depends on the previous history of the male and on the appearance, distance, and behavior of the other bird. He suggests that the appearance of smooth, typical, adult courtship behavior depends on an increasing activation and mutual inhibition of the attack and escape systems, and the relationship between attack and escape is stabilized by the activation of the sexual system. He posits a stabilizing factor in order to explain why the adult animals do not constantly switch quickly from performing one type of behavior to performing another.

The stabilizing influence of sex on the agonistic systems of escape and aggression is not merely a consequence of increasing hormone levels as the animals grow older. Experience also plays a major role. Kruijt (1964) found that junglefowl males reared from hatching in social isolation for more than 9 months showed serious and apparently irreversible abnormalities in their courtship and sexual behavior. To a large extent, these abnormalities could be characterized as switching too quickly among escape, aggressive, and sexual behavior. In other words, the stabilizing influence of sex was present only after experience of the sort that would occur during normal early development. Kruijt also found that as little as 2½ months of normal social experience immediately after hatching was sufficient to obviate the effects of subsequent social isolation for periods of at least 16 months. These results are difficult to interpret because during the first 2½ months of life chicks show essentially no sexual behavior. Thus they could not be learning anything specific about sexual behavior. Instead, it would seem that the experience a chick gains during normal encounters early in life provides the information necessary for it to stabilize its agonistic systems, and that normal sexual behavior can only occur if the agonistic systems are already stabilized.

Results of the Baerendses, mentioned above, also support this interpretation. Their kittens that were raised in isolation from peers showed either unrestrained attack or complete avoidance when confronted with a normal kitten, and this pattern was also seen later in a sexual situation. Rhesus monkeys that were raised in isolation from peers also showed inadequate sexual behavior when adult (Harlow and Harlow, 1962). However, in both the cats and the monkeys, a particularly “good” partner was able to compensate for the behavioral deficiency in the isolation-reared animals (Harlow and Suomi, 1971; Novak and Harlow, 1975). The description of these encounters suggests that the sexual behavior system itself had not developed abnormally, but that abnormal fear or aggression interfered with the performance of sexual behavior. The conclusion that can be drawn from these studies is that well-integrated interactions among behavior systems are necessary for the normal, well-coordinated behavior we see in adult animals, and that functional experience is necessary for such integration to occur.

How a stabilizing influence develops has not been studied. We have seen that some of the experiences of a normally-raised young chick, such as bumping into other chicks or being pecked at as a result of pecking another chick, are not necessary for normal aggressive behavior to develop. Such early social experiences might, however, be crucial for developing a normal attack-escape relationship. I shall return to this problem in the discussion.

General Discussion

Structure, Cause, Function, and Development

In this chapter I have defined a behavior system in terms of its structure. Other investigators define a behavior system in terms of its functional characteristics (e.g., Timberlake, 1994). There may often be a close correspondence between systems defined in structural and functional terms, but this is by no means always the case; 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 the 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). Another example would be the language system which could be defined in terms of its communication function (Hauser, 1996). It should be emphasized that one type of definition is not inherently better or worse than the other type: which type is most useful depends on the questions being asked (see Hogan, 1994a).

Development implies changes in the structure of behavior, both changes in the organization of the behavior mechanisms themselves as well as changes in the connections among behavior mechanisms. To this point I have only considered the causes of changes in behavioral structure. In this section I will briefly discuss some examples of functional questions. Since I believe that there is no necessary relation between cause and function (Hogan, 1994a), it might seem that there is nothing to be gained toward understanding causal mechanisms by asking functional questions. In theory, this should be true. In practice, however, the problems that an animal must solve in order to survive provide the selection pressures that are responsible for evolution by natural selection. And, it turns out that the evolutionary solutions to these problems sometimes use causal mechanisms that are related to the function that the behavior serves. I shall consider first some examples of functional questions that do not increase our understanding of development, and then some examples that do.

Is Development Selected? It is almost a truism that natural selection should operate at all stages of development, and not only on the adult outcome, because any developmental process that reduces the probability of reaching adulthood will be very strongly selected against—all other things being equal. Nonetheless, a genotype with advantageous consequences at a particular stage of development can be selected for only if its consequences in the adult do not reduce the fitness of the individual possessing it. What this means is that, at any particular stage of development, behavior may be far from optimal: it need only be good enough to bring the animal to adulthood.

This line of reasoning also leads to other conclusions. For example, it seems intuitively obvious that the best mechanism for regulating a particular outcome would be one that is directly sensitive to the outcome. Thus, the best mechanism for regulating nutrition, say, would be one that could directly sense the state of nutrition. This is another way of saying that an optimal mechanism should be based on a simple, direct relationship between cause and function. But as we have seen, development is an extremely complex process and one in which optimal solutions may be the exception rather than the rule. It follows that development is opportunistic in the sense that any available means will be used to produce an acceptable end. Two examples should make this point clearer.

We have seen above that pecking in newly hatched chicks is not controlled by factors related to nutrition. When it became clear that experience was necessary for nutritional control to develop, it seemed reasonable to look at the effects of various kinds of nutritional experience on the occurrence of pecking. That approach turned out not to be the key to solving the puzzle because the necessary experience was not nutritional, but an association between the act of pecking and the effects of swallowing any solid object. These results were surprising (and took a long time to discover) because of our preconceptions about the relationships between the causes and functions of behavior. We intuitively feel that, when behavior changes in an adaptive direction, the cause of the change should be related to factors associated with the adaptation. Thus, when pecking changes in such a way that relatively more nutritive items are ingested, we infer that something about nutrition was responsible for the change. But in this case, our inference was wrong. Pecking behavior to food and sand during the test changes for reasons that are completely unrelated to nutrition.

A second example is provided by the analysis of Hall and Williams (1983) of the relationship between suckling and other ingestive behavior in rats. Suckling and eating are both behaviors that function to provide nutritive substances to rats—suckling normally for the first 3 weeks after birth and eating thereafter. In their search for the causal mechanisms underlying ingestion, Hall and his colleagues originally assumed that these mechanisms would be similar in both newborn and older animals. In fact, after many years of work, their results showed that the causal mechanisms controlling suckling are largely independent of the mechanisms controlling eating. Their analysis suggests that both systems coexist simultaneously, and that only one system is expressed at a time. Hall and Williams (1983, p. 250) concluded: "Such findings for suckling illustrate the general difficulty in determining the relationship between adaptive behavior of infancy and functionally similar representations in adulthood." Subsequently, Hall and Browde (1986) made similar studies of infant mice and discovered that the causal factors underlying eating are considerably different from those in rats. Thus, the study of the development of feeding behavior in chicks, rats, and mice shows that mechanisms for change have evolved that lead to an adaptive result, but that these mechanisms often bear little resemblance to our prior ideas of what they should be.

Adaptations for Development. The problems that an animal has to solve for survival put selection pressures on the causal mechanisms for the behavior that can evolve. It is for this reason that functional thinking can help us to understand causal mechanisms that we have discovered, and in some cases, it may direct out attention to seeking causal mechanisms that we would not otherwise have thought of. Oppenheim (1981) has provided many examples and an excellent discussion of this issue. Here, I shall make a few functional comments about the case of nutrition, which we have already considered from a causal perspective.

In almost all species of animal, the method of acquiring nutrition changes—willy-nilly, at least once, and often two or more times—in the course of the animal's lifetime. In mammals, for example, nutrition is provided to the fetus via the placenta and, after birth, first by suckling and later by eating. Suckling, as a motor mechanism, exists before birth and after weaning, but it is not expressed then. Thus, at some stage in development, suckling must be "switched in" to provide nutrition, and later, it must be "switched out." Similarly, in birds, the yolk sac provides nutrition in the egg and for some time after hatching; then the young bird may receive food from its parents by gaping, and finally, it feeds itself using some sort of pecking movement. Here, too, something must regulate when gaping is used, and when pecking is used. This, then, is the problem the animal must solve. How does it do it?

The causal answer to this question is probably different for every species. We have seen at least a partial causal answer for chicks in the results we have obtained from pecking. But these results raise several obvious functional questions, two of which can be considered here. First, why should pecking not be controlled by nutritional factors at hatching? Second, why should experience be necessary for pecking to become integrated into the hunger system?

One can imagine that, if pecking were originally controlled primarily by the chick's nutritional state, pecking might not occur at all until the yolk reserves were exhausted. Such a chick would not have as much experience with its world as a chick that had engaged in exploratory pecking during the first few days. Given that the control of pecking must shift sometime between hatching and the time when pecking is necessary for providing nutrients, there is no particular reason that experience should not provide the timing of the shift. On the other hand, there is one important reason that experience should provide the timing: Birds can hatch early or late with respect to their overall stage of development (and mammals can be born prematurely or past term). Endogenous timing of the switch in causal factors to or from pecking or suckling would be disastrous if, for example, a 1-week premature baby could not suckle in its first week, or if a baby could not be weaned early if its mother's milk supply were interrupted. In general, it seems certain that experiential factors provide a more reliable timing cue than endogenous factors could provide in most cases where a switch between methods of acquiring nutrition occurs.

In this context, it is useful to return to the concept of a play system and to consider what function it may serve. We have seen that the essence of the concept is that motor mechanisms have a chance to be "free" of influence from central mechanisms. Such freedom may give the motor mechanisms an opportunity to become incorporated into other central mechanisms. One can imagine that such a flexible system would be useful during development, especially in cases where something may have gone wrong, and in which the so-called normal connections would not function optimally. Similar functions for play have been suggested before, but one problem with such explanations is that adult behavior develops equally well in individuals that vary greatly in the amount of play they exhibit (cf. Martin and Caro, 1985). Here we can see a function for the developmental situation described by Groothuis (1994). Endogenous factors are sufficient to determine the development of particular behavior systems (or particular motor mechanisms), but during development the possibility exists for experience to bring about a somewhat different outcome. Under normal conditions of development, either endogenous factors or play could provide alternative pathways to reach the same result. Only under special conditions (such as those provided to the gulls by Groothuis) would the different pathways lead to different results.

The Concept of Prefunctional. It should be clear by now that it is quite possible to discuss the causal development of behavior without using the word *innate*. Nonetheless, it must also be clear that I have used the word *prefunctional*, defined as developing without the influence of functional experience, in many places where others would have said *innate*. In some ways, this is how Lorenz (1961, 1965) suggested the term *innate* be used, though he was not always consistent in his use (cf. Lehrman, 1970). Nonetheless, there are still some problems with using a functional definition, and I shall briefly mention two of them here. But first, it may be useful to indicate why I think the concept *prefunctional* is necessary at all.

Lehrman (1970) pointed out that one important reason for the controversy between him and Lorenz was that the two were interested in different problems: Lehrman was interested in studying the effects of all types of experience on all types of behavior at all stages of development, whereas Lorenz was interested only in studying the effects of functional experience on behavior mechanisms at the state of development at which they begin to function as modes of adaptation to the environment. In other words, Lehrman used a causal criterion to determine what was interesting to study, whereas Lorenz used a functional criterion. These two criteria are equally legitimate (cf. Hogan, 1994a), but the functional criterion used by Lorenz corresponds to the way most people think about development. In fact, 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* to the word *innate* because the latter 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. That is one of the things I have tried to do in this chapter.

It is also important to see some of the difficulties inherent in using a functional definition. Perhaps the most important of these is that the function of a behavior is not always obvious. For example, if the function of pecking is viewed as being to provide nutrition, pecking becomes integrated into the hunger system prefunctionally; if the function of pecking is viewed as being to bring about ingestion, then pecking becomes integrated into the hunger system through functional experience. In either case, the causal process is the same. Similar problems arise when there are alternative routes to reaching the same end, as in the development of the oblique posture in the black-headed gull.

A related problem is that the function of behavior can change over the course of time. Sometimes, this change is due to changes in the environment and sometimes to changes in the behavior mechanisms themselves. This means that, at best, the concept *prefunctional* is only relative: It can usefully be used to describe situations with respect only to the particular function that the investigator has in mind.

Some Principles of Development

The process of development is extremely complex, to a large extent because so many interdependent events occur simultaneously (cf. Hogan, 1978; Kuo, 1967). Unfortunately, it is not possible to comprehend all the important variables at the same time, so that various sorts of distinctions and simplifications must be made in order to further our understanding (cf. Bateson, 1999). The basic simplification that has been made in this paper is that of describing behavior in terms of motor, central, and perceptual mechanisms and the connections among them. These mechanisms are conceived of as structural units of behavior of a particular magnitude and complexity. Development is viewed as changes in these underlying behavioral mechanisms, and their connections. This conception makes it possible to see a clear analogy between behavior development and the development of specialized cells and tissues in the embryo (e.g., Waddington, 1966; Slack, 1991). I begin this section with a brief overview of the development of the nervous system, and then discuss the problems of modularity, constraints, and processes that have been identified above. Finally I consider some special aspects of the development of social behavior.

Development of the Nervous System. 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 mechanisms underlying this process involve electrical activity in the nerve cells and their targets, but they are 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, and 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 dentritic spines which presumably correlate 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 of the early work). 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. These results 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 section on processes.

Modularity. An important assumption made in this chapter is that particular parts of the central nervous system subserve particular functions, and that, by the time behaviorally interesting events are occurring, these parts, or modules, are preassigned. This means that, at the particular stage of development under consideration, the range of possibilities for further development of a particular behavior mechanism are so restricted that only special (i.e., already determined) kinds of experience can have a developmental effect on that mechanism. In practice, this means that, by the time of birth (or hatching), the central nervous system is already highly differentiated, with the general organization of pathways and connections already determined. By this stage of development, reversing the functions of major parts of the brain is generally impossible in the sense just discussed. Under these circumstances, it seems justified to speak of the song-recognition perceptual mechanism or the ground-scratching motor mechanism or the aggression central mechanism as prefunctionally developed units of behavioral structure subject to further (but quite restricted) differentiation on the basis of subsequent experience.

It should be realized, however, that, if we follow the development of any behavior mechanism backward in time, we can always find a stage in which the nerve cells making up the behavior mechanism could have subserved a different behavior mechanism under somewhat different conditions. If we go back still further, we will find a stage when the cells could have become something other than nerve cells, and so on. At the time of birth—an arbitrary time I have chosen for convenience—a particular set of nerve cells may have differentiated to the point where they, if they survive, will be the cells that mediate mate recognition, and in this sense, they are preassigned that function. But they are preassigned only from the point of view of future development. There has been much recent discussion about the meaning of modularity with respect to higher cognitive functions (e.g., a language module). This is not the forum to comment on this issue except to say that the principles involved are the same as I have just discussed (see Karmiloff-Smith, 1992, 1998).

Constraints. Constraints on development actually arise as an interaction between the structures (modules) available at any given time and the processes that can lead to changes in those structures. Two such constraints that are ubiquitous in discussions of development will be considered here: irreversibility and critical periods.

Insofar as behavior mechanisms can be regarded as preassigned, they illustrate the problem of the irreversibility of development. When Waddington (1966) discussed the question of whether the differentiation of cells is reversible, his answer was that “it depends.” It depends on what cell, in what animal, at what stage of development, and so on. This is already an important point because similar reasoning shows that it is nonsense to ask a question such as: Is imprinting irreversible? One can only begin to answer such a question after specifying the species, the particular imprinting procedures, the stage of development, and so on.

More important, Waddington specified some of the processes that are responsible for the irreversibility of cell differentiation. For example, some or all of the genetic material may have been "used up" or may have otherwise disappeared in the course of the development of the cell; or the genetic material may still be present, but for various reasons, it cannot be accessed. The most frequent reason for irreversibility, however, seems to be that

> development involves such a complicated network of processes that it would be an extremely long and tricky process to unravel them. On could, in theory, take an automobile, dismantle it, and build the pieces up again with a little modification into two motorcycles, but it wouldn't be easy; and it is something like this that we are asking a differentiated cell to do when we try to persuade it to lose its present differentiation and develop into something else. (Waddington, 1966, pp. 54-55)

Processes with similar characteristics seem certain to underlie cases of behavior irreversibility.

The best documented cases of total irreversibility involve motor mechanisms for bird song—as exemplified by the "crystallization" of song in the chaffinch (Thorpe, 1961) and the white-crowned sparrow (Marler, 1970a). The perceptual mechanisms, or templates, on which these songs are based are probably also fixed irreversibly once they have developed, although here the evidence is somewhat controversial (cf. Baptista and Gaunt, 1997; Nelson, 1997). Many of the courtship and agonistic displays seen especially in birds, such as waltzing in chickens (Kruijt, 1964) or the oblique posture in the black-headed gull (Groothuis, 1994), are probably also fixed irreversibly once they have developed. These cases probably all involve axonal remodeling and are analogous to the case of cell differentiation, in which the genetic material either disappears or becomes inaccessible during the course of development.

Here it is useful to emphasize the distinction between perceptual and motor mechanisms themselves, and the various connections that may exist between them: Even though a perceptual or motor mechanism has crystallized, there are still possibilities for alternative pathways among them. The concept of imprinting, for example, implies a change in a perceptual mechanism as a result of experience. In some species, such a change may be irreversible, but subsequent experience may lead to additional pathways being formed between other perceptual mechanisms and the sexual behavior system, and these new connections may mask the original imprinting. A rather difficult experimental analysis would be necessary to investigate this possibility. We have seen, however, a case such as this on the motor side of the hunger system in chickens: An original connection between pecking and ground scratching was masked, but not destroyed, by later experience.

The most common reason that behavior changes are apparently irreversible is probably the same reason that most cell differentiation is irreversible: So many events would have to be undone (or compensated for) that change becomes almost impossible. A very simple case, where changes could still be made, was training a kitten to catch fish after it had already learned to catch mice (Baerends-van Roon and Baerends, 1979). Here there were two problems. One was an indirect, motivational problem: A fear of water inhibited any attempt to catch the fish. Once the fear of water could be overcome, the kitten faced a direct, developmental problem: rearranging motor mechanisms in a different sequence. In this case, rearrangement was possible, although with some interference from the original learning.

A more complex case is the sexual behavior of male junglefowl raised in social isolation. Here, subtle aspects of the integration of the aggression and escape systems seem to be permanently missing. Because this integration plays a determining role in permitting sexual behavior to occur, these effects of social isolation are effectively irreversible, even though the copulatory motor patterns remain intact. The fact that some consequences of normal social experience during the first few weeks of life are sufficient for the development of relatively normal adult behavior implies that axonal remodeling-type processes are involved. In effect, it could be that various perceptual neurons are competing for connections with the attack and escape systems, and that a stable attack-escape balance depends on the pattern of connections that finally develops. This is a speculative suggestion, but it does fit in well with what is known about the development of neural connections at earlier stages. Such a suggestion also implies that no new principles of development are required to understand the development of behavior system interaction. It remains to be seen whether some sort of “therapy” could be devised to cope with this problem—as was possible in the cats and monkeys raised in social isolation—but that is an empirical matter.

The fact that development is not reversible (except as discussed above) means that constraints of various sorts are inherent in development systems. The most commonly discussed constraint is a “critical” or “sensitive” period that corresponds to the embryological concept of competence (Waddington, 1966). In essence, these concepts refer to the fact that the developing system is especially susceptible to particular external influences at particular stages of development. This topic has often been a matter of controversy, especially with respect to the factors responsible for the beginning and the end of the period (see Bateson and Hinde, 1987, for an excellent discussion of sensitive periods). Nonetheless, the previous discussion should make clear that probably all aspects of development are associated with critical periods. At each stage of development, the animal is different from what it was; it is only to be expected that the effects of the “same” experience will be different in the different stages (cf. Schneirla, 1956; Schneirla, Rosenblatt, and Tobach, 1963). The factors that are responsible for the beginning and ending of these periods are probably different in every case.

Processes. What are the processes of behavior development? There is not yet any answer to this question, but I think several points are worth making. To begin, it seems very unlikely to me that the biochemical processes responsible for altering the structure of behavioral mechanisms and their connections are different before and after a particular behavior begins to function. If this is indeed the case, a number of results I have discussed become more easily understandable.

A first example is provided by the results of Groothuis (1992, 1994). He 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 that 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 (cf. results from groups of song birds raised in isolation from adult song—Marler, 1976). 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, and for the results of play in several species (cf. Martin and Caro, 1985).

As a second example, one of the interesting aspects of the perceptual phase of song learning in birds 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 and 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 wide 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). 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, 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, with the exception of bird song and human language, 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.

These ideas have some similarities to proposals by Bateson (1987) and by Greenough, Black and Wallace (1987), though there are some important differences as well. The latter authors distinguish between experience-expectant and experience-dependent information storage based upon the functional requirements of particular brain systems:

> Experience-expectant information storage refers to incorporation of environmental information that is ubiquitous in the environment and common to all species members, such as the basic elements of pattern perception…. Experience-dependent information storage refers to incorporation of environmental information that is idiosyncratic, or unique to the individual, such as learning about one’s specific physical environment or vocabulary. (p. 539).

They also suggest that experience-expectant processes depend on selection or pruning of overproduced synaptic connections (i.e., axonal remodeling, as discussed above), while experience-dependent processes depend on formation of new synaptic connections.

With respect to the type of environmental information stored, the development of all the perceptual and motor mechanisms we have described would be classified as experience-expectant, and therefore, according to Greenough, *et al.*, dependent on synapse pruning. As we have seen above, however, the mechanisms responsible for axonal remodeling are the same regardless of whether the information comes from the environment or from endogenous processes. Thus, the word experience would have to be used broadly so as to include all information originating outside the specific brain structure itself (see Schneirla, 1965; Lehrman, 1970). It does not seem that this use of the word was intended. A further problem with this classification arises with respect to the environmental information stored during imprinting, which is common to all members of the species in the natural environment. As Bolhuis (1994) discusses, the development of perceptual mechanisms during imprinting must also involve experience-dependent processes.

Greenough, *et al.* also suggest that their categories offer a new view of phenomena that have previously been labeled critical or sensitive periods. Instead of viewing these phenomena as due “to the brief opening of a window, with experience influencing development only while the window is open,” their approach “allows consideration of the evolutionary origins of a process, its adaptive value for the individual, the required timing and character of experience, and the organism’s potentially active role in obtaining appropriate experience for itself.” (p. 539). This view proposes a functional explanation for a causal phenomenon, which leads to all the problems discussed above (see also Hogan, 1994a). The proposal I have made above includes all experience-expectant processes, but is considerably broader and becomes congruent with the putative neural mechanism underlying it.

Finally, if it is true that the processes responsible for altering the structure of behavioral mechanisms and their connections do not differ before and after a particular behavior begins to function, it follows that the processes responsible for learning are no different from the processes responsible for development in general. In other words, the same structural change can be triggered by different events, for example, by genes or by the experience of "reinforcement." The important point is that the change itself cannot be classified as genetic or learned because it could have been triggered either way. I have discussed elsewhere (Hogan, 1994c) how a consideration of the structures that are changing can provide a good basis for classifying different types of learning.

The Role of Early Social Experience. In a recent discussion comparing the development of social and non-social behavior systems (Hogan, 1994b), I concluded that both kinds of systems develop according to the same rules, and that there appear to be no systematic differences between them. The question then arises why topics such as imprinting and bonding have assumed such an important role in the developmental literature. My answer is that this interest is related to Lorenz's original conception of imprinting. He defined imprinting as "the acquisition of the object of instinctive behavior patterns oriented towards conspecifics." (Lorenz 1935/1970, p. 124). In terms of the concepts used in this chapter, we would say that imprinting refers to the development of a perceptual mechanism (or schema) that is responsible for species recognition, and that is connected to all (or many of) the social behavior systems in the animal. The reason imprinting is so important is that Lorenz's definition implies that a single perceptual mechanism serves a number of different behavior systems, and that this perceptual mechanism develops irreversibly very early in life.

Current evidence from imprinting studies is usually interpreted to mean that the object-recognition mechanisms for filial and sexual behavior develop separately (Bolhuis, 1991, 1996). Lorenz himself showed in his studies of jackdaws that the objects of the various functional systems he discussed (infant, sexual, social) might be different, and might develop at different periods in the animal's life. Thus, the implication of Lorenz's definition may generally not be true. Nonetheless, the idea that early experience has far-reaching, general effects on later social behavior has remained influential, and is supported by a wide variety of evidence (e.g., Bowlby, 1991; Hofer, 1996; Rutter, 1991). The question is, how do these effects come about if the perceptual mechanisms of the various social behavior systems develop independently?

One recent suggestion is likely to be widely applicable. Hofer (1987, 1996) and his colleagues have studied the processes of early social attachment in young rats and their responses to separation from their mothers. Their results show that separation has extensive effects on the young rats' behavior, similar to (though not as dramatic as) the effects of maternal separation on the behavior of young rhesus monkeys (Harlow & Harlow, 1962; Hinde, 1977). Hofer analyzes these effects into two components. The first involves the formation of an attachment system, which has similarities to the one proposed by Bowlby (1991) for human infants and to the filial system implicated in imprinting studies in birds. This system develops as the young rat learns the characteristics of its mother; when the infant is separated from her it shows distress reactions, and shows relief when it is later returned to her. If one substitutes an alternative "caregiver" for the mother, such as an inanimate object or another rat pup, Hofer's results show that the attachment system still seems to function normally.

The novel aspect of Hofer's analysis is the second component: the behavioral and physiological effects that occur during long-term separation from the mother are shown to depend on specific aspects of the mother-infant interaction. Hofer has isolated a number of regulators including body warmth, tactile and olfactory stimulation, stimulation peculiar to the suckling situation, etc. Many of the specific effects of these factors have been described by Fleming & Blass (1994). A real mother provides all the necessary regulators, but alternative caregivers do not. Under such circumstances, various behavioral and physiological abnormalities will develop.

Kraemer (1992) has interpreted the development of primate social attachment in similar terms to those of Hofer. He points out that a young rhesus monkey may become attached to an abusive mother or to a peer, and that such young monkeys can be seen in many ways to have a normally-developed attachment system. But such monkeys also develop abnormally in many other ways. Kraemer provides evidence that absence of an adequate caregiver leads to aberrant development of brain biogenic amine systems which are implicated in the control of sensorimotor integration and emotion: “If the attachment process fails, or if the caregiver is incompetent as a member of the species, the developing infant will also fail to regulate its social behavior and may be dysfunctional in the social environment.” (p. 493). It seems likely that similar processes determine the attack-escape relationship with respect to the development of sexual behavior in chickens as discussed above: A young chick can become imprinted on an inanimate object and develop a normal filial system, but the inanimate object does not provide the conditions for normal agonistic behavior to develop.

Lorenz’s and Hofer’s theories are the same in that both postulate that a representation of the imprinting object or caregiver (perceptual mechanism) is formed early in ontogeny. In Lorenz’s theory, that representation controls a number of social behavior systems; and long-term effects are seen because each system matures at its own time in the life of the animal. In Hofer’s theory, the representation controls only the attachment system; long-term effects are seen because the object to which the animal is attached provides the necessary conditions for various biochemical and neural changes that are indispensable for normal development of other systems.

Conclusions

The development of behavior systems is a very complex process, involving intricate interactions of external and internal causal factors with the genes and their products at every stage. Yet the principles involved in this process seem relatively simple. Specific patterns of neural activity are responsible for the formation of the basic behavioral mechanisms and many of the connections between them, probably through the mechanism of synapse pruning or axonal remodeling. Later stimulation causes the formation of new synapses which probably underlie the modification of behavioral mechanisms and the formation of new connections between them; new synapses are probably also important in the development of new representations (cognitive structures). These neural processes are, in fact, sufficient for understanding a wide range of developmental phenomena including critical periods and irreversibility. Yet understanding the neural mechanisms that determine development tells us nothing about how a particular system will develop in a particular animal. The development of any specific system and of its interactions with other systems will need to be studied in each case.

One of the remarkable things about development is how normal most individuals become in spite of large variations in the experiences to which they are exposed. Waddington (e.g., 1966) coined the term *canalization* to express this fact with respect to the morphology of the animal, and we have seen a similar picture with respect to behavior. The basic structure of the perceptual, central, and motor mechanisms, as well as the basic interconnections among these units, develops, by and large, prefunctionally. The experience of the individual is, of course, important, often in very unexpected ways, but typically, the basic structure of behavior is extraordinarily stable. Nonetheless, development, especially of social behavior, sometimes goes seriously wrong. Such disturbed development can often be traced to peculiarities in the social experience of the young animal, especially to periods of social deprivation. In general, the development of non-functional behavior is due to a combination of structural and motivational causes.

Structural causes for abnormal behavior include the development of aberrant behavior mechanisms and the development of anomalous connections among behavior mechanisms. For example, a chick that is force-fed and is not allowed to peck in its first 2 weeks after hatching is later unable to peck at food when hungry, presumably because the motor mechanism for pecking remains independent of the central mechanism for hunger (see Hogan, 1977). Or, the partner recognition mechanism may develop with the image of the wrong species or of a member of the same sex, and interspecific courtship or homosexual behavior would be seen. However, structural aberrations probably account for only a small proportion of developmental problems. Most disturbed development probably results from motivational causes such as an abnormally high activation of particular behavior systems or atypical interaction among behavior systems. For example, excessively fearful animals have general difficulties in learning new tasks, as the older kittens learning to catch fish, and in expressing normal social behavior; and the inadequate integration of fear and aggression is probably the main reason for problems in the expression of sexual behavior, as seen in isolated roosters, cats, and monkeys. In all these cases, the basic behavioral structure is present, but the more subtle interactions among behavior systems are missing. It is, of course, sometimes difficult to distinguish between structural and motivational aberrations. Nonetheless, the causal analysis of the development of behavior systems, as discussed in this chapter, provides a framework within which to attack these problems.

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Footnotes

1. The word *mechanism* usually connotes analysis at a molecular level. Nonetheless, as I have discussed in detail elsewhere (Hogan, 1994a, pp. 9-10), the dictionary definition of mechanism merely implies cause, and is agnostic with respect to the level of analysis. I use the word mechanism to emphasize the fact that the perceptual, motor, and central units that are discussed in this chapter are causal concepts at the behavioral level.
2. Note that this interpretation assumes that the perceptual and motor mechanisms for song have become attached to the sexual and aggression systems. We have not considered these systems in a song bird, and have not asked how these connections develop.

Figure legends

Figure 1. Conception of behavior systems. Stimuli from the external world 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 Hogan (1988).

Figure 2. The dustbathing 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; several motor mechanisms responsible for specific actions as well as a higher level motor mechanism responsible for the patterning of individual actions during dustbathing bouts. 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. Adapted from Vestergaard, *et al*. (1990). Copyright by E. J. Brill. Reproduced by permission.

Figure 3. 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 that develop prefunctionally; dashed lines indicate mechanisms and connections that develop as the result of specific functional experience. From Hogan (1988).