Revista Mexicana de Análisis de la Conducta,
1984, Vol. 10, Núm. 2, págs. 161-174

The integration of pecking into the Hunger System in Young chicks[1]

La integración del picotear al sistema de hambre en pollitos

Jerry A. Hogan

Department of Psychology, University of Toronto

ABSTRACT

Pecking is not controlled by nutritional state in a newly hatched chick, but by 3 days posthatch it is. This paper reviews evidence showing that the experience of pecking followed by swallowing is both necessary and sufficient for pecking to become integrated into the hunger system. Some implications of these results for ideas concerning the development of behavior systems are discussed, as are possible functions of such a mechanism of development. It is concluded that the function of a behavior may not be related to its causes.

DESCRIPTORS: motivational systems, development, pecking, chicks.

RESUMEN

Los picotazos de un pollito que recien ha salido del cascarón no están controlados por su estado nutricional, aunque tres días después si lo están. Este artículo revisa la evidencia que demuestra que la experiencia de picotear seguida por deglución es necesaria y suficiente para que el picotear se integre al sistema de hambre. Se discuten algunas de las implicaciones de estos resultados en las ideas relacionadas con el desarrollo de sistemas conductuales y las posibles funciones de tal mecanismo de desarrollo. Se concluye que la función de una conducta puede no estar relacionada con sus causas.

DESCRIPTORES: sistemas motivaciones, desarrollo, picotazos, pollos.

A surprising fact about the feeding behavior of many neonatal animals is that their early feeding movements are relatively independent of motiva-

[1] The research reported here was supported by a grant from the Natural Sciences and Engineering Research Council, A-0140. Reprints may be obtained from the author, Department of Psychology, University of Toronto, Canada M5S 1 A 1.

tional factors associated with food deprivation. Hinde (1970, p. 551f) has reviewed a variety of evidence from studies on kittens, puppies, lambs, and human infants that show the amount of suckling by a young animal is very little influenced by the amount of food it obtains. More recently, Hall and his colleagues have published a series of papers on the development of feeding in neonatal rats (see Hall & Williams, 1983, for a review). They have determined that suckling, defined as attaching or detaching from a nipple, has essentially no internal controls before the rat pup is more than two weeks old. Pecking in young chicks illustrates the same principle: 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).

In this paper, I ask how the motivational factors associated with food deprivation come to control the feeding behavior of young chicks. A number of early experiments showed that some kind of pecking experience is necessary for this change in control to occur (Hogan, 1973a). This led to a series of experiments designed to elucidate the role of experience. I review these experiments here and then discuss the implications of these results for our understanding of behavior development.

The general methods used in all the experiments were very similar and can be summarized briefly. Chicks of the Burmese red junglefowl (*Gallus gallus spadiceus*) were used as subjects. They were hatched communally in a darkened incubator and were removed, about 24 hr after hatching, to individual cages, 50 x 40 x 40 cm, with bare metal floors. Water was always available, but food was available only when specified. Chicks were given various kinds of experience for various lengths of time at various ages but were always tested at about 72 hr posthatch for 10 min. In all tests, the floor of the test cage was completely covered with the appropriate stimulus, either food (commercially obtained chick starter crumbs) or sand. An observer recorded the chick's behavior using a 20-button keyboard.

Some typical results are shown in Figure 1. This figure depicts data from six separate groups of chicks that were raised and tested as indicated. It can be seen that the two groups of chicks without pecking experience (empty floor condition) showed equal pecking rates whether tested on sand or on food, whereas the groups of chicks with experience pecking either sand or food showed higher rates of pecking when tested on food than when tested on sand. Differential pecking was not immediate, however. During the first two minutes of the test, pecking at sand or food was equal. Only later did the pecking rates begin to diverge. One additional effect is the large influence of experience on the absolute level of pecking: Chicks with experience pecking food pecked more at both test stimuli than did chicks with experience pecking sand.

It should be emphasized that all the differences in pecking seen in Figure 1 and other figures discussed in this paper are based on one-stimulus tests. Without further experience, a chick would not show any signs of differential pecking at food and sand if these two stimuli were offered simultaneously

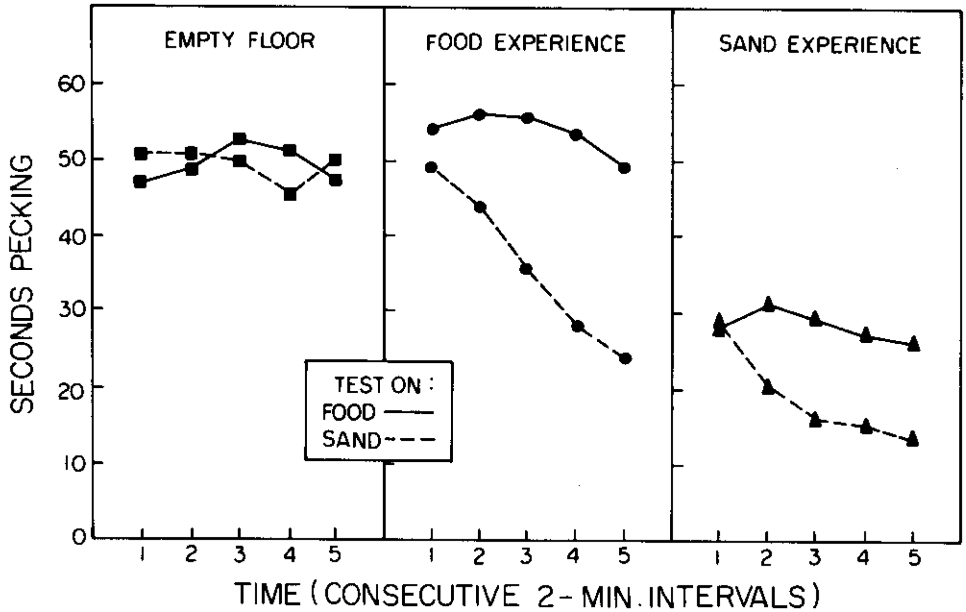

Fig. 1. Mean time spent pecking the stimulus in a 10-min test. Each curve presents data from a separate group of 3-day-old chicks. Each group had the indicated experience for either 19 hr (on day 3) or for 67 hr (on days 1 to 3), though similar results are typical of chicks with as little as 10 min experience on day 3. Data from Hogan (1975, 1977b).

(e.g., Hogan, 1973a, Experiment 1). This means that the differences in pecking considered here cannot be based on visual or gustatory aspects of the test stimuli: Both of these aspects of the stimuli are present either before the chick starts pecking or immediately after it starts, and neither the appearance nor the taste of the stimuli changes significantly during the course of the test. It seems likely that the changes in pecking rate that occur during the course of the 10-minute test are based on feedback that develops two to three minutes after ingestion. The changes in the absolute level of pecking as a function of previous experience are presumably due to the effects of digestion. It should be noted that chicks can learn to discriminate between chick crumbs and sand on the basis of vision and taste. The conditions necessary for this to happen have been investigated by Hogan-Warburg & Hogan (1981), and will be mentioned briefly bellow.

One way to understand these results is in terms of the conceptualization shown in Figure 2. At hatching (Time-1), a chick has a functioning hunger system and a functioning pecking system, but these two systems are functionally independent. Some time later (Time-2), after the appropriate experience, a "connection" is formed between the hunger system and the pecking system such that factors that control the hunger system become additional controlling factors for pecking. The hunger system comprises the physiological mechanisms that are responsible for regulating the level of

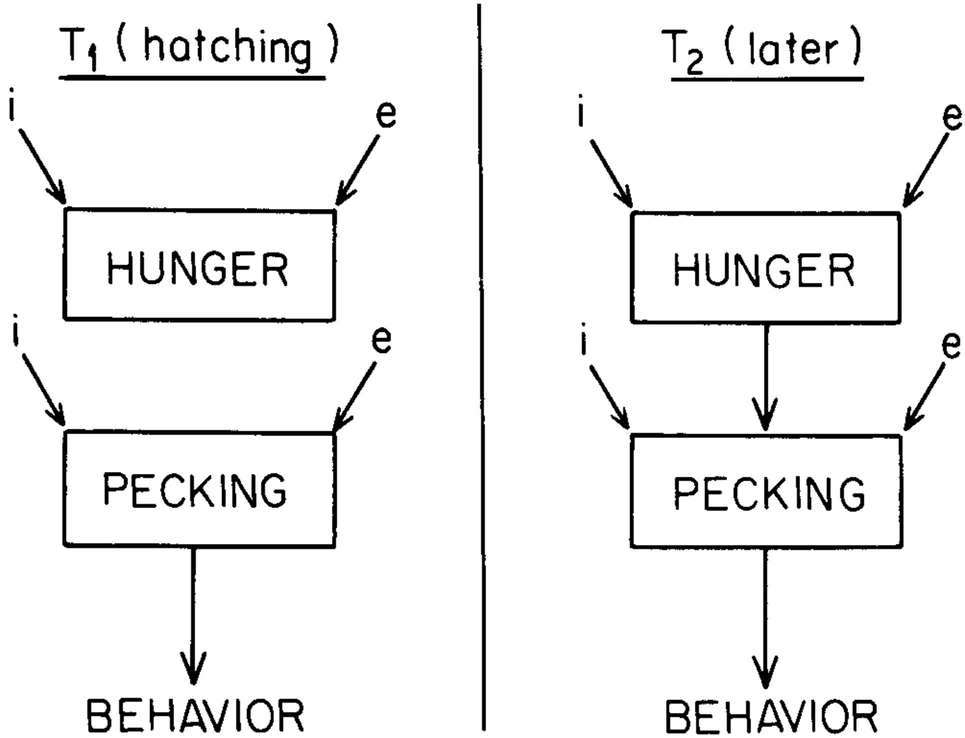

Fig. 2. A diagram summarizing one interpretation of the experimental results. The boxes represent the neural coordinating mechanisms of the hunger and pecking systems. At Time-1 (hatching), both systems are influenced by internal (i) and external (e) factors, but hunger has no influence on pecking. At Time-2 (later, and after the appropriate experience), both systems are still influenced by the same internal and external factors, but hunger has also developed control over pecking.

nutrients in the blood; these include receptors for various nutrients as well as autonomic reactions. The pecking system comprises perceptual mechanisms for recognizing particular stimuli, internal motivational factors, and the neural coordinating mechanisms for the pecking response itself.

Results such as those in Figure 1 imply that there are some similar effects of previous experience pecking food and pecking sand that are absent if the chick has had no previous experience pecking as in the empty floor condition. One similarity between pecking food and pecking sand is that in both cases the chick pecks and swallows a small particle. I have suggested (Hogan, 1977a, b) that it is this experience of pecking and swallowing that causes the connection shown in Figure 2 to be formed. In other words, it appears that what a chick must learn is that pecking is the action that leads to ingestion, once this association has been formed, other (nonlearned) processes are automatically responsible for the differential pecking rates to food and sand that develop during the 10-minute test.

There are several implications of this interpretation of these results. For example, if pecking followed by swallowing is the crucial experience, pecking and swallowing any substance should be sufficient for the connection between the hunger system and the pecking system to form, whereas pecking without swallowing or swallowing without pecking should not be sufficient. Further, once the connection is formed, all the factors that influence hunger should immediately affect pecking without any further experience being necessary. I shall present here the available evidence that is relevant to these implications in order to show that my interpretation is in fact well supported.

Pecking followed by swallowing. Under natural conditions, newly hatched chicks peck and swallow a variety of small objects. Such chicks are able to peck differentially at food and nonfood items by three days of age (see Hogan, 1973b). The same result has been obtained under the more restricted conditions of the present experiments. For example, chicks with experience pecking and swallowing only chick crumbs or only sand peck differentially at both these stimuli as shown in Figure 1 (Hogan, 1975). In this case, of course, the stimulus the chick has had experience with is the same as one of the two test stimuli. Stronger support for my interpretation would be provided by cases in which the chick has experience with a stimulus that is much different from either of the test stimuli. Results are available for two such stimuli. One is mealworms (Hogan, 1977a). Mealworms are nutritive, but differ from chick crumbs in size, shape, texture, and taste. The other is sawdust (Hogan, 1984a), with is nonnutritive and differs from sand especially in texture. Further, unlike sand or small stones, sawdust appears to be uncomfortable for chicks to swallow.

Some data are shown in Figure 3. The chicks with mealworm experience were allowed to peck and swallow 7 mealworms on two occasions, once on the afternoon of day 2 and once on the morning of day 3. The chicks with sawdust experience had 10 minutes exposure to sawdust about 2 hours before testing on the afternoon of day 3; only chicks that swallowed at least a criterion amount of sawdust were tested. It can be seen that for both groups of experimental chicks, differential pecking at food and sand developed over the course of the 10-minute test, whereas both groups of control chicks pecked equally at food and sand. These results for chicks with mealworm and sawdust experience are thus the same as the results for chicks with chick crumb and sand experience and therefore give strong support to the statement that pecking followed by swallowing any solid substance is sufficient for a connection between the hunger system and the pecking system to be formed. It is worth noting that all the chicks in these experiments had experience drinking on the first three days. Drinking, of course, involves swallowing, but it does not seem to influence the connection between hunger and pecking.

Pecking without swallowing. Young chicks that are held on an empty floor for the first three days posthatch do peck quite a bit. They peck at

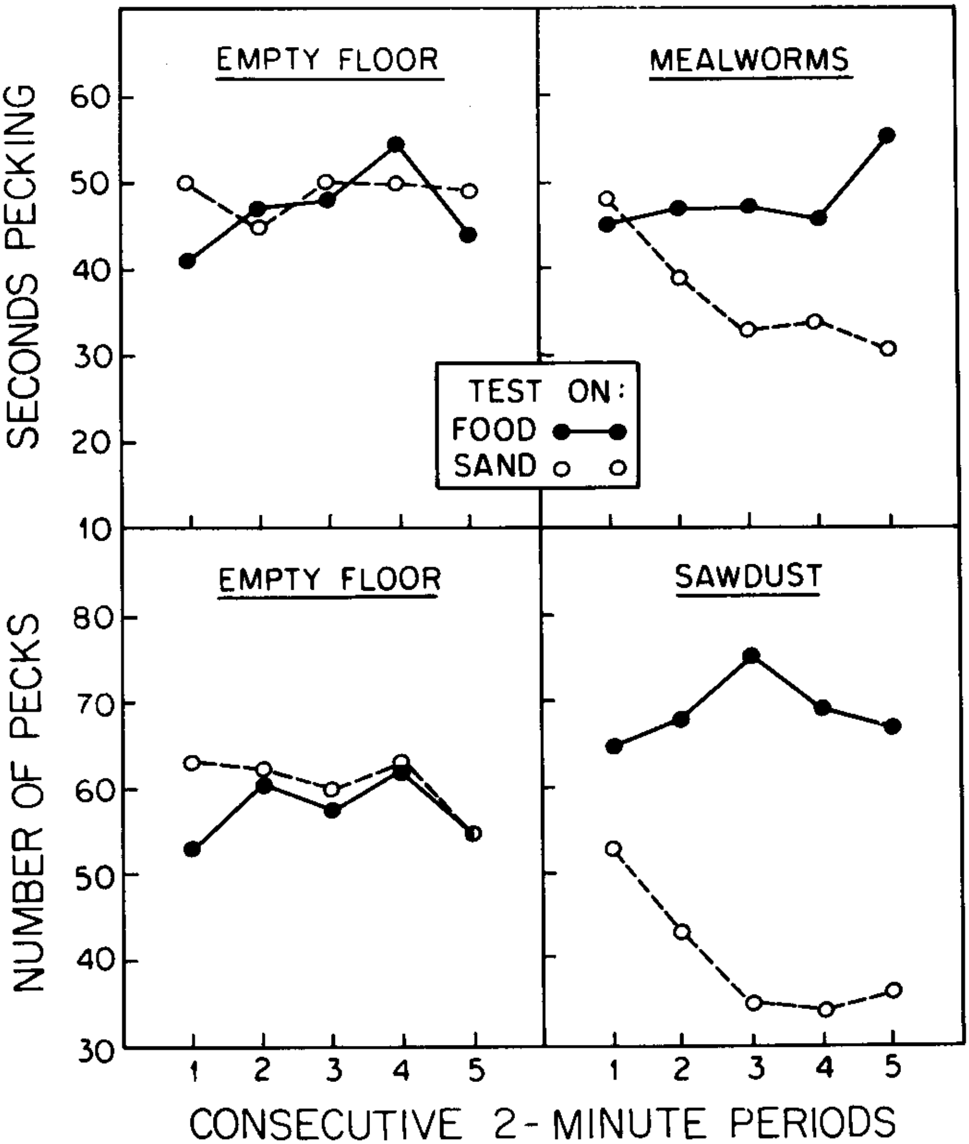

Fig. 3. Mean time spent pecking or mean number of pecks to either sand or food for chicks with the indicated experience. Each curve presents data from a separate group of 3-day-old chicks. Upper panels, data from Hogan (1977a); lower panels, data from Hogan (1984a).

small spots on the walls and floor, and they peck at their own body. Usually nothing is swallowed during these episodes, though occasionally they actually swallow a small particle of dirt or a piece of down. All this pecking, with an occasional swallow, does not seem to be sufficient, however, for a connection to be formed between hunger and pecking. Experimental evidence on this point would be desirable as well, but it has been difficult to collect because for a long time we were unsuccessful in devising a situation in which chicks would peck at a high rate for several minutes at a stimulus that could not be swallowed. We recently succeeded by constructing a floor that was covered with sand that had been embedded in clear plastic. The sand in plastic was not totally covered so that the chick could partially grasp individual grains, but could not remove them. We were then able to carry out the following experiment (Hogan, 1984a).

Three-day-old chicks were given 10 minutes of experience on a floor covered either with sand or with sand embedded in plastic about two hours before being tested. Pecking was measured during the period of experience, and only chicks that met a criterion of at least 25 pecks in the first two minutes and at least 100 pecks in the total period were tested later. The results are shown in Figure 4. It can be seen that the chicks with experience pecking sand showed the expected differences in pecking at sand and food during the test (although the absolute size of the difference was larger than usual due to the surprisingly high rate of pecking at food). Chicks with experience pecking at the glued-down sand showed an increase in pecking to both food and sand during the test, but the difference between pecking at food and sand was not significant. These results support the statement that pecking without swallowing is insufficient for a connection to be formed between

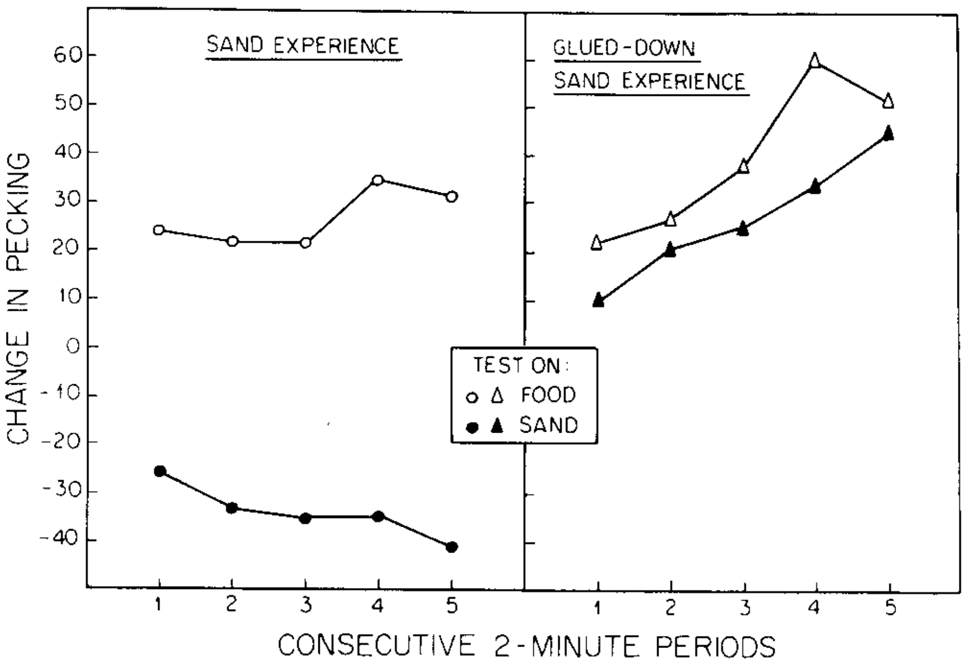

Fig. 4. Mean change in pecking (number of pecks in test minus number of pecks during experience) for chicks with the indicated experience. Each curve presents data from a separate group of 3-day-old chicks. Data from Hogan (1984a).

hunger and pecking, and are thus in accord with my general interpretation.

Swallowing without pecking. In nature, it seems highly unlikely that a chick would ever have an opportunity to swallow without pecking. (It should be noted, however, that the young of altricial species, which have a gaping response and are fed by their parents in the nest, normally swallow without pecking.) Nonetheless, it is possible that my interpretation is incorrect, and that, for example, the act of swallowing switches on the mechanism by which chicks can discriminate between nutritive and non-nutritive substances. The evidence, however, suggests that swallowing by itself is not sufficient. A number of experiments have been done in which two kinds of forced feeding techniques were used to introduce food into a chick's throat, which then elicited a swallowing reflex.

In one type of experiment, chicks were forced to ingest liquid food, a puree of regular chick crumbs and water (Hogan, 1977a). This was done by gently pushing the bill of the chick into the liquid food. This elicits a bill opening response which allows the liquid food to enter the mouth. When the chick is released, it lifts its head and swallows. This procedure was repeated 8 times which meant that the chick ingested about the same amount of food as it would ingest if it pecked for 10 minutes. Some results from one such experiment are shown in the upper portion of Figure 5. It can be seen that experience ingesting liquid food raised the absolute pecking rate of the chicks by about 25%, but that the pecking rate at food and sand did not differ (the slight difference seen in the figure was not significant).

In the previous experiment, chicks swallowed liquid food which would be expected to pass easily through the digestive system. The substances swallowed by a normally raised chick tend to be solid and hard, substances such as dry chick crumbs, various grains, sand, and small stones, for example. It is possible that swallowing such substances without pecking would give different results. Therefore, an experiment was done in which chicks were force fed sand (Hogan, 1984a). This was accomplished by holding a chick in one hand and gently prying open its bill with the end of a small spoon on which a small amount of sand was placed. The sand was tipped onto the back of the tongue which elicited a swallowing reflex. This procedure was also repeated 8 times. The results are shown in the lower portion of Figure 5. It can be seen that force feeding sand had no effect on the absolute rate of pecking, and that pecking at sand and food did not differ.

It is not possible, of course, to prove the null hypothesis that a particular kind of experience has no effect on development. Nonetheless, the results from these experiments, taken together, make it seem likely that the experience of swallowing, by itself, is not sufficient for discrimination between food and sand to occur. Once again, these results give support to the general interpretation that I have proposed.

Causal factors for hunger. According to my interpretation, once a chick has learned that pecking is the action that leads to ingestion, all the factors that normally influence the hunger system should immediately influence

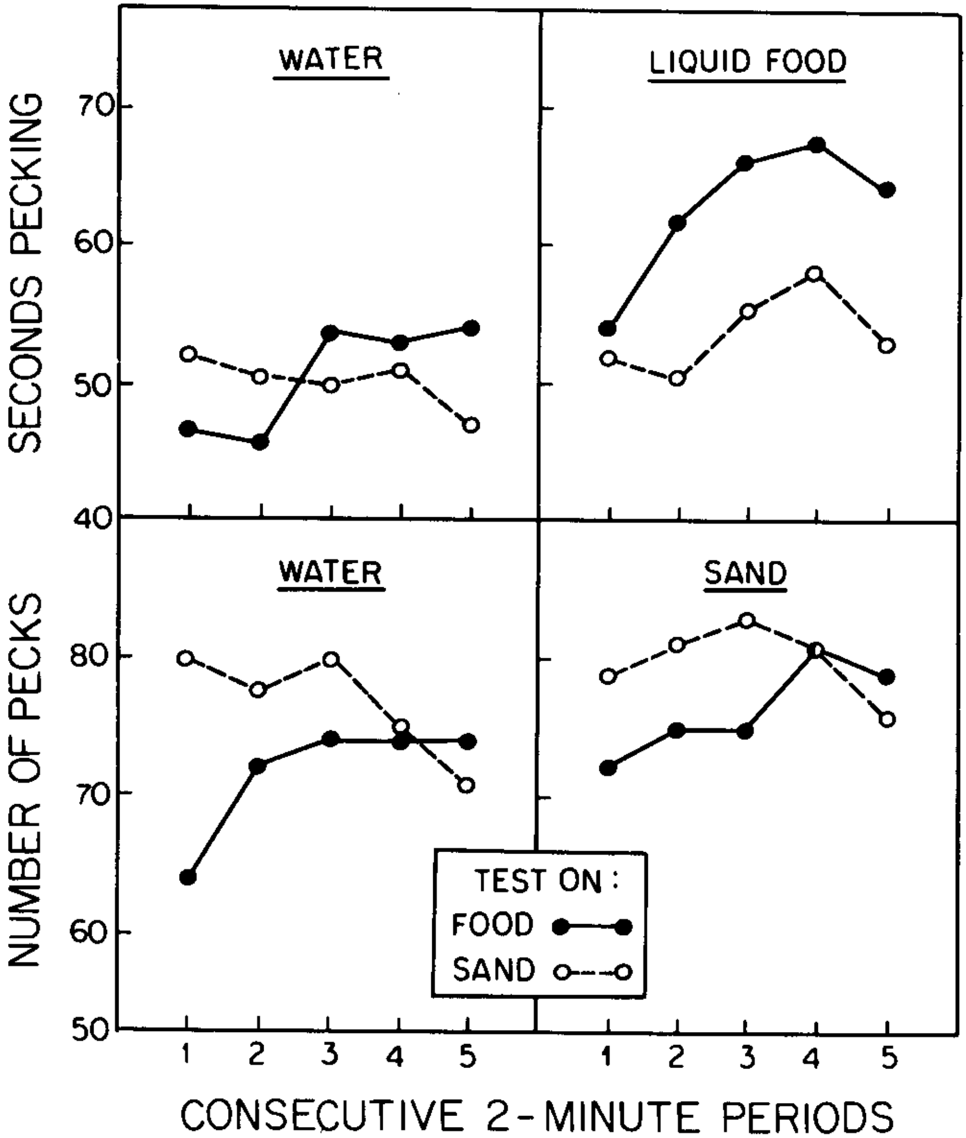

Fig. 5. Mean time spent pecking or mean number of pecks to either sand or food for chicks with the indicated experience. Each curve presents data from a separate group of 3-day-old chicks. Upper panels, data from Hogan (1977a); lower panels, data from Hogan (1984a).

pecking. One such factor is the feedback produced by the passage of nutritive or nonnutritive substances through the gastrointestinal tract. Puerto, Deutsch, Molina, & Roll (1976) found evidence for nutrient receptors in the upper gastrointestinal tract of rats, and it seems quite possible that similar receptors exist in chicks. I have suggested (Hogan, 1977a) that such receptors may provide signals that are responsible for the change in pecking rates that occurs during a 10-minute test session in chicks that have experience pecking. The output of these putative receptors could be the same whether or not the chick has had experience pecking and swallowing; only when the hunger system and pecking system become connected, however, can these signals affect the occurence of pecking.

Another factor that affects the hunger system is the change brought about by food deprivation. If chicks that have been raised on an empty floor are tested on a floor covered with a peckable stimulus, the absolute rate of pecking gradually increases with age. Maximum rates of about 40% to 50% of the time are reached between 3 and 4 days of age, and then decline (Hogan, 1971, 1973a). The increase in pecking rate with age most likely reflects a general increase in vigor as a result of growth. It might reflect effects of food deprivation, but this is not likely because pecking rates are remarkably stable between about 60 and 90 hours posthatch. This stability of pecking rate in naive chicks is in marked contrast to the very large changes in pecking rates in chicks with various kinds of experience. Two experiments suggest that food deprivation affects pecking in a major way only after chicks have had experience pecking and swallowing.

In the first experiment (Hogan, 1975, Experiment 4), a chick had either food experience or sand experience for 10 minutes on day 3, and then was tested either $1^1/2$ hours later or 5 hours later on either food or sand for 10 minutes. In the second experiment (Hogan, 1984a), a chick, once again, had either food experience or sand experience for 10 minutes on day 3, but was then tested either immediately, $1^1/2$ hours later, or 5 hours later on the same stimulus for only 2 minutes. Results from both experiments are shown in Figure 6. After $1^1/2$ hours the typical result can be seen of increased pecking after food experience but decreased pecking after sand experience. But $3^1/2$ hours later (5 hours after the pecking experience), pecking has increased for all chicks and by more than 50% for the chicks originally given experience pecking sand. These changes are far greater than any changes in pecking that would be seen in a 5 hour period in naive 3-day-old chicks. A simple explanation of these changes that is in good accord with my general interpretation is that the effects of food deprivation influence pecking only after the chicks have had pecking experience and the hunger system has become connected to the pecking system.

General Discussion

Pecking in newly hatched chicks, like the early feeding movements of many neonatal animals, is relatively independent of motivational factors associated with food deprivation. By the time chicks are three days old, under natural conditions, pecking is influenced by such motivational factors. Early experiments showed that some kind of pecking experience is necessary for this change in control to occur. The evidence reviewed above suggests

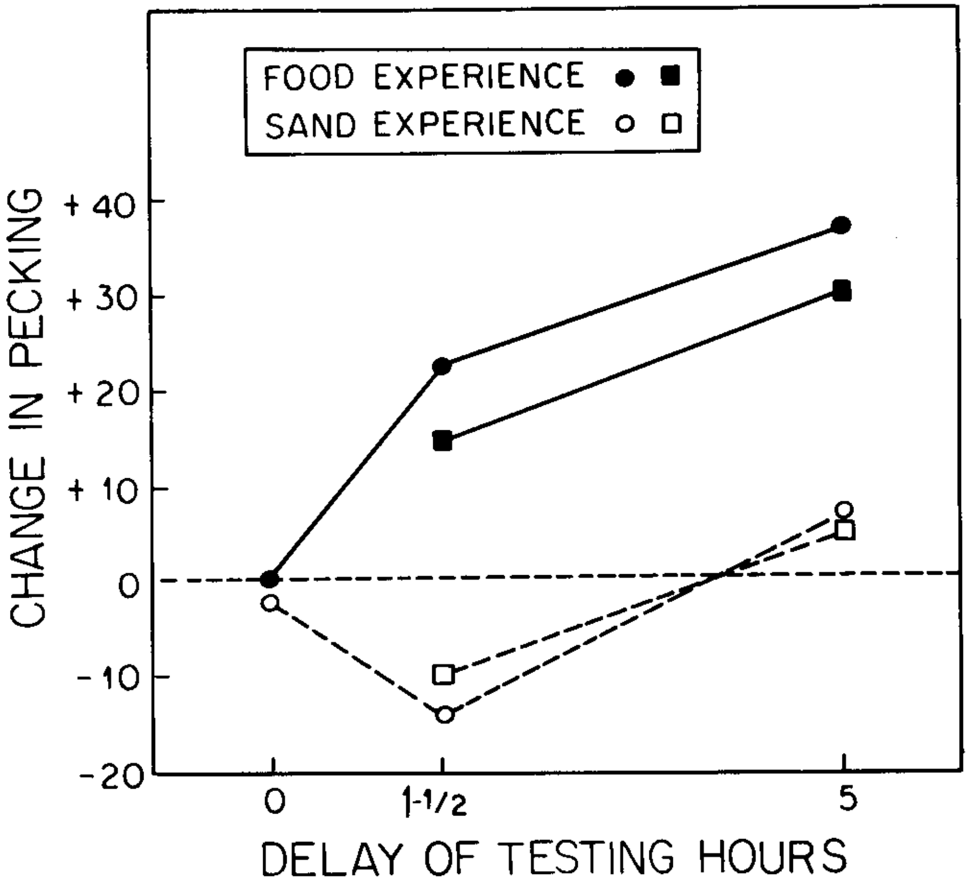

Fig. 6. Mean change in time spent pecking or number of pecks to the stimulus between original experience and test. Each point gives data for a separate group of 3-day-old chicks. Squares (■ □), data from Hogan (1975); circles (● ○), data from Hogan (1984a).

very strongly that it is the experience of pecking followed by swallowing that is both necessary and sufficient for pecking to become integrated into the hunger system. These results raise many questions, including the ones of development and function that will be discussed here.

The fact that experience is necessary for pecking to become attached to the hunger system, leads one to wonder whether behaviors other than pecking could also become attached to the hunger system in the same way. For example, if a chick were raised so that pecking never led to ingestion, but that it was force fed liquid food every time it scratched the ground or preened, would the chick show increased ground scratching or increased preening whenever it was hungry? This is basically an operant conditioning study, and it would not be especially surprising if chicks did increase their ground scratching or preening under such conditions. It would be surprising, however, if a chick that was force fed sand every time it ground scratched showed an increase in ground scratching whenever it was hungry. Such a result would not be in accord with principles of operant conditioning, but would be consistent with the results for pecking presented in this paper.

The general interpretation I have proposed of these experimental results is presented in terms of the concept of behavior system. A behavior system is any organization of perceptual, central, and response units that itself acts as a unit in some situations (see Hogan & Roper, 1978, p. 226). Behavior systems can exist at various levels of complexity as implied in Figure 2. One model of the development of such systems that seems compatible with most of the available data was originally proposed by Kruijt (1964). He suggested that the various activities seen in neonates occur relatively independently of each other, that is, they have few causal factors in common. As the animals grow older, many of these activities begin to occur in clusters and vary together. In other words, they become integrated into more complex motivational systems. Kruijt's work on the development of social behavior in chickens implicated a variety of ways in which experience affected the development of systems such as escape, aggression, and sex. My work on the development of a hunger system in chicks (Hogan, 1971) and the work of Baerends-van Roon & Baerends (1979) on the development of a prey catching system in kittens also provided evidence of the complex ways in which experience affected development.

A behavior system framework emphasizes the organization of behavior and the existence of different levels of units. If one conceives of learning as a process that changes the connections between units (Hogan, 1971; Hogan & Roper, 1978; Gallistel, 1980), then it is not surprising that a specific learning experience may have very diverse consequences. Thus, after a few pairings of pecking and swallowing, the pecking response of the young chick becomes controlled by a host of causal factors that it has never had experience with, such as feedback from nutritive substances passing through its gastrointestinal tract and factors associated with food deprivation. Many of the anomalous results of certain learning experiments can also be understood in this way. Timberlake (1983) has recently successfully analyzed several of them in some detail from this point of view.

One final point about development should be made here. Once a chick has learned that pecking leads to ingestion, it can then learn to recognize food on the basis of visual cues (Hogan-Warburg & Hogan, 1981). Learning to recognize food visually seems to follow the expected rules for learning, including the need for repeated pairings of a stimulus (chick crumbs) with a response (pecking) followed by reinforcement (nutrition). Very young chicks can also learn to approach or avoid (visual) stimuli that are associated with particularly attractive tastes such as mealworms (*Tenebrio* larvae) or repulsive tastes such as feces or certain kinds of caterpillars, respectively (see Hogan, 1973b). Further, very young chicks also learn to peck differentially at stimuli that are pecked at by a mother hen (Turner, 1964; Suboski & Bartashunas, 1984). Nutritional reinforcement seems to be unnecessary in these latter cases. Thus, newly hatched chicks possess a variety of relatively independent mechanisms by which they develop the functional ability to ingest the nutrients they need for growth. In this way, the development of food recognition provides a good illustration of Waddington's (1966) concept of canalization which refers to the tendency of a developing system to attain its normal end result even when one or more of the normal causal factors in development is upset.

Many functional questions are also raised by the results of the experiments described in this paper. The two most obvious are 1) why should pecking not be controlled by nutritional factors at hatching? and 2) why should experience be necessary for pecking to become integrated into the hunger system? The answer to these questions is not obvious, and must lie in the nature of developmental mechanisms. It can be noted that, prior to hatching, nutrients are provided by the yolk and not by pecking, and this state of afairs continues for several days after hatching. 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, it seems possible that experience provides the timing of the shift. These suggestions are quite speculative, but are consistent with what is known about the normal course of development.

Finally, I would like to comment on why the results of these experiments were surprising. I think they were surprising because of our preconceptions about the relationships between the causes and functions of behavior (cf. Hogan, 1984b). 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 to occur. But, with respect to the results shown in Figure 1, our inference can be wrong: Pecking behavior to food and sand during the test changed for reasons that are completely unrelated to nutrition. And such incorrect inferences are undoubtedly much more common than we realize. As Hall & Williams (1983) conclude: "Such findings for suckling illustrate the general difficulty in determining the relationship between adaptive behavior of infancy and functionally similar representations in adulthood." Study of the development of feeding behavior both in chicks and in rats 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.

REFERENCES

BAERENDS-VAN ROON, J. M., & BAERENDS, G. P. (1979). The morphogenesis of the behaviour of the domestic cat, with a special emphasis on the development of prey-catching. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde, Tweede Reeks* [Proceedings of the Royal Netherlands Academy of Sciences, Section Physics, Second Series], part 72.

GALLISTEL, C. R. (1980). *The Organization of Action.* Hillsdale, N. J.: Erlbaum.

HALL, W. G., & WILLIAMS, C. L. (1983). Suckling isn't feeding, or is it? A search for developmental continuities. *Advances in the Study of Behavior,* 13, 219-254.

HINDE, R. A. (1970). *Animal Behaviour.* New York: McGraw-Hill.

HOGAN, J. A. (1971). The development of a hunger system in young chicks. *Behaviour,* 39, 128-201.

HOGAN, J. A. (1973a). The development of food recognition in young chicks: I. Maturation and nutrition. *Journal of Comparative and Physiological Psychology,* 83, 355-366.

HOGAN, J. A. (1973b). How young chicks learn to recognize food. In R. A. Hinde, & J. G. Stevenson-Hinde (Eds), *Constraints on Learning* (pp. 119-139). London: Academic Press.

HOGAN, J. A. (1975). Development of food recognition in young chicks: III. Discrimination. *Journal of Comparative and Physiological Psychology,* 89, 95-104.

HOGAN, J. A. (1977a). Development of food recognition in young chicks: IV. Associative and nonassociative effects of experience. *Journal of Comparative and Physiological Psychology,* 91, 839-850.

HOGAN, J. A. (1977b). The ontegeny of food preferences in chicks and other animals. In L. M. Barker, M. Best, & M. Comjan (Eds), *Learning mechanisms in food selection* (pp. 71-97). Waco, Texas: Baylor University Press.

HOGAN, J. A. (1984a). Pecking and feeding in chicks. *Learning and Motivation,* 15, 360-376.

HOGAN, J. A. (1984b). Cause, function, and the analysis of behavior. *Mexican Journal of Behavior Analysis,* 10, 65-71.

HOGAN, J. A., & ROPER, T. J. (1978). A comparison of the properties of different reinforcers. *Advances in the Study of Behavior,* 8, 155-255.

HOGAN-WARBURG, A. J., & HOGAN, J. A. (1981). Feeding strategies in the development of food recognition in young chicks. *Animal Behaviour,* 29, 143-154.

KRUIJT, J. P. (1964). Ontogeny of Social behaviour in Burmese Red Junglefowl (*Gallus gallus spadiceus*). *Behaviour, Supplement 12.*

PUERTO, A., DEUTSCH, J. A., MOLINA, F., & ROLL, P. L. (1976). Rapid discrimination of rewarding nutrient by the upper gastrointestinal tract. *Science,* 192, 485-487.

SUBOSKI, M. D., & BARTASHUNAS, C. (1984). Mechanims for social transmission of pecking preferences to neonatal chicks. *Journal of Experimental Psychology: Animal Behavior Processes,* 10, 182-194.

TIMBERLAKE, W. (1983). The functional organization of appetitive behavior: Behavior systems and learning. In M. D. Zeiler, & P. Harzem (Eds), *Advances in analysis of behavior. Vol. 3: Biological factors in learning* (pp. 177-221). Chichester: Wiley.

TURNER, E. R. A. (1964). Social feeding in birds. *Behaviour,* 15, 284-318.

WADDINGTON, C. H. (1966). *Principles of development and differentiation.* New York; Macmillan.