Behavioural Processes 117 (2015) 105–113

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

A framework for the study of behavior

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ARTICLE INFO

Article history:
Available online 22 May 2014

Keywords:
Tinbergen's questions
Behavior systems
Relation of cause and function

ABSTRACT

Behavior is defined as the expression of the activity of the nervous system. The basic units of behavior are perceptual mechanisms, central mechanisms, and motor mechanisms. These units can be organized into more complex units called behavior systems such as hunger, sex, aggression, fear, etc. Perceptual and central mechanisms include cognitive mechanisms such as ideas, beliefs, memories, intentions, and cognitive modules. Behavior can be analyzed at genetic, physiological, whole organism, and population levels, and the concepts used to analyze behavior should be appropriate to each level. One can ask causal, structural, and functional questions about current behavior, ontogeny, and phylogeny. Causal and functional questions are independent of each other and should not be confused. There has been much confusion and disagreement about the relation between cause and function, and several examples are analyzed.

This article is part of a Special Issue entitled: In Honor of Jerry Hogan.

1. Introduction

What I am planning to do in this paper is develop a framework into which all aspects of behavior can be discussed using similar concepts. In the mid-twentieth century several general frameworks were proposed that became widely used (e.g., Skinner, 1938; Tinbergen, 1951). But as many studies of behavior became more molecular (behavioral physiology, behavioral genetics) or more molar (behavioral ecology, evolutionary psychology), new concepts evolved and many old concepts were discarded. Further, in both the older and the newer fields, new questions about behavior were being asked. A major result of this expansion was that scientists in one field often found the work being done in related fields to be irrelevant or even misguided. I hope to show that, insofar as one is actually interested in behavior, a common set of concepts can be used to understand and discuss issues in all these fields. There will be two parts to my argument. The first will discuss units of behavior and also deal with levels of analysis. The second will analyze the questions that can be asked about behavior. I will finish with a discussion of teleology and the relations between cause and function.

2. What is behavior?

I will begin by stating what I mean by behavior. One definition that is used by some behavioral scientists, and corresponds in many ways to common sense, is that which an animal does; what it does consists of muscular contractions and glandular secretions. This definition, however, does not include many phenomena, such as perceptions and feelings that intuitively belong in the concept. Another definition brings in the concept of mind, because mind does include all the phenomena one expects. Although I am sympathetic to this solution, I prefer a more corporeal concept. I define behavior as the expression of the activity of the nervous system, which may be manifested as activity in muscles and glands (Hogan, 1984, 1994) (For a different approach to the problem of definition, see Levitis et al., 2009.).

An important point to be made about this definition is that it does not imply that the study of behavior involves neurophysiology. The study of behavior is the study of the functioning of the nervous system and must be carried out at the behavioral level, using behavioral concepts (cf. Von Holst and von St. Paul, 1960). Physiology and neurophysiology in particular may provide useful insights into the functioning of the nervous system, but the major concern of behavioral science is the *output* of the nervous system, manifested as perceptions, thoughts, feelings, and actions. I discuss aspects of this definition in the next section and throughout the paper.

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http://dx.doi.org/10.1016/j.beproc.2014.05.003
0376-6357/

2.1. Units of behavior: behavior systems

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, functionally, historically: Hinde, 1970, Chapter 2) and at different levels of complexity (e.g., individual muscle movements, limb movements, acts: Gallistel, 1980). I will develop the concept of a behavior system using structural categories at a level of 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 my 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, and I will refer to them as *mechanisms*. The word *mechanism* usually connotes analysis at a molecular level, and might seem to imply that behavioral analysis should occur at a neural level. The *American Heritage Dictionary* (1969), however, defines a mechanism as "the arrangement of connected parts in a machine" or "any system of parts that operate or interact like those of a machine". It defines a machine as "any system. . . formed and connected to alter, transmit, and direct applied forces in a predetermined manner to accomplish a specific objective". This definition 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 of behavior systems are structural concepts arrived at by causal analysis at the behavioral level, as I discuss below.

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. I call these parts *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. This conception can also include entities such as ideas, thoughts, and memories, which are cognitive structures proposed by many psychologists. 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, but the concepts apply to all behavior systems in all species including human language (Hogan, 2001).

2.1.1. 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 most purposes. 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 and glandular secretions that we actually observe. Finally, the concept of a motor mechanism is clearly related to the ethological concept *Erbkoordination* (Lorenz, 1937) or *fixed action pattern* (Tinbergen, 1951; Hinde, 1970), but is meant to be much broader in scope and to encompass all types of coordinated movements.

2.1.2. 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 they 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 generally only be 'seen' after it has activated some motor mechanism. However, in some cases, modern imaging technology allows more direct observation of perceptual mechanisms, and it will undoubtedly become even more useful as the technology becomes more precise. In any case, 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* (Lorenz, 1937; Tinbergen, 1951; Baerends and Kruijt, 1973); *Sollwert*, or *comparator mechanism* (Von Holst, 1954; Hinde, 1970); *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. It also includes the neural circuits that underlie such 'cognitive' mechanisms as *representations*, *ideas*, *feelings* (LeDoux, 2012) and *memories* (Frankland et al., 2013; Akers et al., 2014) that may or may not be expressed by activation of motor mechanisms.

2.1.3. 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 is used here in a still more general sense that would also include the *modules* posited by many cognitive psychologists (Barrett and Kurzban, 2006). 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 and perceptual mechanisms.

2.1.4. 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 Fig. 1.

The first part of the definition is structural and is basically similar to Tinbergen's (1951, p. 112) definition of an instinct, but it is not