Animal Behaviour 78 (2009) 103–110

Contents lists available at ScienceDirect

Animal Behaviour

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

Behavioural biologists do not agree on what constitutes behaviour

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ARTICLE INFO

Article history:
Received 10 February 2009
Initial acceptance 12 March 2009
Final acceptance 23 March 2009
Published online 3 June 2009
MS. number: AE-09-00083

Keywords:
behaviour
definition
level of organization
philosophy of science

Behavioural biology is a major discipline within biology, centred on the key concept of 'behaviour'. But how is 'behaviour' defined, and how should it be defined? We outline what characteristics we believe a scientific definition should have, and why we think it is important that a definition have these traits. We then examine the range of available published definitions for behaviour. Finding no consensus, we present survey responses from 174 members of three behaviour-focused scientific societies as to their understanding of the term. Here again, we find surprisingly widespread disagreement as to what qualifies as behaviour. Respondents contradict themselves, each other and published definitions, indicating that they are using individually variable intuitive, rather than codified, meanings of 'behaviour'. We offer a new definition, based largely on survey responses: behaviour is the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes. Finally, we discuss the usage, meanings and limitations of this definition.

The biological study of behaviour has grown tremendously over the last half century. *Biosis Previews* tags 42 286 items published in 2007 with the Concept Code 'behavioral biology'. Dozens of scientific societies, journals, courses, textbooks, etcetera are organized around the central concept of behaviour. While behavioural biology interacts with a wide range of other disciplines, the unifying concept in behavioural biology is, as the name implies, behaviour. But while our understanding of behaviour has advanced tremendously since Tinbergen (1955, page 2) defined it as 'the total movements made by the intact animal', our formal definition has failed to keep pace with this progress.

What do we mean by this word, 'behaviour'? There are numerous published definitions, and for many biologists the meaning is simply and clearly intuitive. However, satisfying definitions of this word, in the context of modern biology, are hard to find. Many definitions are so vague as to be impossible to apply. Others are crafted around a particular taxon such that members of other taxa by definition cannot behave (e.g. the definition 'Behavior involves the interaction between an animal's machinery, its bones, muscles, nervous system, etc. and its outside world, such as its food, enemies and social practice' (Hall & Halliday 1998, pp. 6–7) by necessity excludes non-animals and those animals that lack 'muscles, nervous system, etc.' (Hall & Halliday 1998, pp. 6–7)). Still other definitions make distinctions that exclude phenomena widely considered to be behaviours or that fail to exclude phenomena most biologists would agree are not behaviours. Many sources, including textbooks on the topic of behaviour (e.g. Wilson 1975; Alcock 2005), fail to define their subject matter, assuming that the reader knows what is meant.

In science, precise definitions are important. As a new discipline develops, it is healthy for relevant definitions to evolve as understanding progresses. But available definitions of behaviour are generally both contradictory and imprecise. Can only animals behave, or can any living thing? Is intentional inactivity, or failure to do something (e.g. forage or reproduce) behaviour? Can groups behave, or is behaviour strictly an individual-level phenomenon? Must behaviours involve motion? Can developmental changes in response to stimuli be considered behaviours? None of these questions is resolved by a review of existing biological definitions of behaviour.

Much of behavioural biology focuses on what have come to be known as Tinbergen's (1963) 'four questions'. Each of these questions highlights a different way of answering how or why behaviours are the way they are. In this framework, 'there are four different levels of analysis: evolutionary origins, functional consequences, ontogenetic processes and mechanisms; the latter includes both cognitive processes and physiological processes' (Sherman 1988, page 616). Two of these levels, evolutionary origins and functional consequences, are easily distinguished from

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0003-3472/$38.00
doi:10.1016/j.anbehav.2009.03.018

behaviours because they are not traits but explanations of how traits evolved. The other two, ontogenetic processes (e.g. development and ageing) and mechanisms (e.g. physiology and information processing) are like behaviours in that they are traits of the organism and, therefore, can be more difficult to differentiate from behaviours. Is risk of confusion greater in conflating behaviour with development, cognition and physiology, or in drawing distinctions between these intimately linked processes?

Individually we may all think we know what is meant by behaviour, even if there is no agreed-upon definition within our field. Justice Potter Stewart (1964, page 184) wrote of pornography, 'I shall not today attempt further to define the kinds of material I understand to be embraced within that shorthand description; and perhaps I could never succeed in intelligibly doing so. But I know it when I see it'. When it comes to behaviour, do we know it when we see it, or is there significant disagreement and inconsistency about what to include?

Why Discuss What Behaviour Means?

Practically speaking, one rarely finds oneself uncertain of whether to refer to a particular phenomenon as 'behaviour'. The biology may not be in dispute, whatever the epistemology may imply. There has been no popular outcry for a more sophisticated definition. Why then do we bother to point out the lack of an operational consensus? A comparison with the great debate on the meaning of the word 'species' may be useful. Systematists widely discuss their disagreement as to what a species is (deQuieroz & Donoghue 1988; Templeton 1989), while behavioural biologists mostly act as though we all agree on what constitutes behaviour. A systematist regularly needs to decide where species boundaries lie. Similar boundary arguments have pervaded ecology, another relatively new discipline. When do behavioural biologists have occasion to discuss where behaviour is conceptually bounded?

Any behavioural biologist is likely to need to consider the definition of behaviour when teaching a behaviour course, organizing a behaviour-related job search, writing a book on behaviour, or constructing an ethogram. While these examples are prosaic and epistemological, scientific questions of significant moral and emotional import often cannot be answered for lack of a good definition. Whether dolphins are sentient cannot be determined without an operational definition of sentience, and whether it is overly anthropomorphic to describe animals as having language depends on the definition of language. Whether we classify the movements of plants as behaviour may seem arbitrary, but whether or not we think of plants as behaving may influence the light in which botanists view those movements, public attitudes towards conservation of rare plant species, as well as our thinking about the evolution of behaviours. Without an operational definition, we have no reasonable way of deciding whether a plant behaves.

The existence of ethograms, behaviour-focused symposia and animal behaviour courses point to a practical need to define behaviour. If it is useful to treat 'behaviour' as a cohesive field that bears thinking about as a discrete major concept, it is because we seek to think clearly and broadly about behaviour as a class of biological phenomena. To do so, we must know what phenomena we are referring to. If those writing about the genetic basis of behaviour and those studying behavioural plasticity mean different things by behaviour, much time may be wasted on semantic confusion before an integrated understanding can be achieved. We should not wait for that confusion to become an impediment before we move to alleviate it. Although the term behaviour has itself been the subject of relatively little definitional effort, other terms within the field of behavioural biology, such as 'fixed action pattern' (Dewsbury 1978) and 'tool use' (Pierce 1986) have been the subject of definitional papers after controversies arose that required clear definitions for their conclusion.

Finally, there is the traditional, and we believe correct, belief that intellectual rigour and scientific inquiry require the definition of terms, whether we perceive opportunity for confusion or not. Scientists simply should define their terms, while recognizing that definitions are not permanent or absolute, but simply reflect current understanding or practise. More specifically, we believe that scientists should provide definitions that meet certain criteria. These are similar to, although distinct from, the classical Aristotelian criteria (see Joyce 1926, page 159), and are based on our perceptions of the ways in which many existing scientific definitions fail. Throughout this paper we judge each definition based on whether it is operational, essential, widely applicable and succinct, as follows.

Operational definition

An 'operational definition' identifies specific characteristics that allow one to decide whether particular items or phenomena do or do not qualify under that definition (Tuckman 1978). A definition that gives the sense of a word but does not give the key discriminating characteristics is of limited value. For example, the definition of behaviour as 'what animals do' operationally suggests that development, respiration, thinking and death are all behaviours, and only clearly establishes that non-animals cannot behave.

Essential definition

An 'essential definition' is essential in that it means what we understand it to mean. An operational definition is of little use unless it excludes those items that we think should not qualify and includes those items that we think do qualify. For example, the definition of behaviour as 'the movements of organisms' excludes cognition but includes orbiting the sun, and therefore may not convey our understanding of what is and is not behaviour.

Widely applicable definition

A 'widely applicable definition' is widely applicable in that researchers in different areas should be able to apply the same definition, and phenomena are not excluded purely because they occur in a context different from that in which the definers work. For example, the definition of behaviour as 'how humans respond to their environment' or 'the responses of an amoeba to stimuli' can only be applied to specific taxa.

Succinct definition

A 'succinct definition' is succinct in that the definition is free of descriptive or explanatory elements that do not aid in the operational interpretation of the definition, and does not have so many clauses, caveats and modifiers as to encumber usage. For example, the clause 'behaviour is subject to natural selection' does not help us to agree upon what is or is not behaviour.

In this paper we examine opinions of practitioners in the field of behavioural biology to assess whether existing definitions are consistent with each other and with our understanding of what the word 'behaviour' means. Using survey responses from associates of three behaviour-focused scientific societies, we assessed (1) the degree to which individual scientists agree with themselves, with each other and with published definitions as to what constitutes behaviour, (2) the extent to which these perceptions vary between affiliates of different professional societies, (3) the effect that the level of expertise has on these issues and (4) what phenomena generally are thought to be behaviours. We then synthesize this information into a proposed definition of behaviour.