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.

METHODS

Existing Definitions

We gathered biological definitions of the word behaviour through the following means.

(1) Examination of the glossaries and texts of books on behaviour and related topics, books containing chapters on behaviour and related topics, dictionaries and other texts that seemed likely to contain relevant definitions.

(2) Searches of online bibliographical databases (e.g. Biosis, Web of Science, Google Scholar) for papers possibly containing relevant definitions.

(3) Searches through the online archives of relevant journals, such as Philosophy of Science.

(4) Consulting potentially fruitful papers listed in the references section of those sources.

Survey Methodology

We then used this list of definitions to formulate a series of potentially diagnostic statements about behaviour. This list went through two rounds of refinement. The first revision followed discussion with our behaviourist colleagues at the University of California (UC) Berkeley. The second set of refinements was based on an earlier version of the survey described below, sent to students in five undergraduate biology classes at UC Berkeley. Based on 63 student responses, we made minor edits to that list based on what we interpreted as possible respondent confusion over wording. Although the preliminary responses did not differ substantially from those presented in this paper, we excluded them here because of several minor differences in methodology. These two rounds of refinements led to the following list of posited statements about behaviour that were intended to reveal what biologists perceive as the essential features of behaviour (see Appendix).

(A) 'A developmental change is usually not a behavior.'

(B) 'Behavior is always in response to the external environment.'

(C) 'A behavior is always an action, rather than a lack of action.'

(D) 'All behaviors are directly observable, recordable and measurable.'

(E) 'People can all tell what is and isn't behavior, just by looking at it.'

(F) 'Behavior is always influenced by the internal processes of the individual.'

(G) 'Behavior always involves movement.'

(H) 'Behaviors are always the actions of individuals, not groups.'

(I) 'Behavior is something whole individuals do, not organs or parts that make up an individual.'

(J) 'A behavior is always in response to a stimulus or set of stimuli, but the stimulus can be either internal or external.'

(K) 'Behavior is something only animals (including people) do, but not other organisms.'

(L) 'In humans, anything that is not under conscious control is not behavior.'

(M) 'Behavior is always executed through muscular activity.'

Next we generated a list of phenomena that may or may not be behaviours, depending upon one's understanding of what constitutes behaviour. We here list those phenomena, followed in parentheses by the letters of those definitional statements above whose legitimacy is tested by the examples given. Example number 3 served as a 'control' in that it did not contest any of the posited statements.

(1) Ants that are physiologically capable of laying eggs do not do so because they are not queens (C, G).

(2) A sponge pumps water to gather food (B, M).

(3) A spider builds a web.

(4) A rabbit grows thicker fur in the winter (A, G, I, M).

(5) A plant's stomata (respiration pores) close to conserve water (I, K, M).

(6) A plant bends its leaves towards a light source (K, M).

(7) A person's heart beats harder after a nightmare (B, I, L).

(8) A person sweats in response to hot air (G, I, L, M).

(9) A beetle is swept away by a strong current (F, M).

(10) A rat has a dislike for salty food (B, C, G, J, M).

(11) A person decides not to do anything tomorrow if it rains (B, C, G, J, M).

(12) A horse becomes arthritic with age (A, B, E, G, M).

(13) A mouse floats in zero gravity in outer space (E, F, G, M).

(14) A group of unicellular algae swim towards water with a higher concentration of nutrients (F, H, K, M).

(15) A frog orbits the Sun along with the rest of the Earth (F, M).

(16) Flocks of geese fly in V formations (H).

(17) A dog salivates in anticipation of feeding time (B, G, I, M).

(18) Herds of zebras break up during the breeding season and reform afterwards (H).

(19) A chameleon changes color in response to sunlight (G, M).

(20) A cat produces insulin because of excess sugar in her blood (B, G, I, M).

To assess views of behavioural biologists on the meaning of the word behaviour, we invited members of three scientific societies producing behavioural biology journals (Animal Behavior Society, ABS, International Society for Applied Ethology, ISAE, and Society for Plant Neurobiology, SPNB) to participate in a survey (see Supplementary Material). Invitations were sent to directors or newsletter editors of each society, with an html link to an online survey hosted by zoomerang.com (Market Tools, Inc., San Francisco, CA, U.S.A.). A distinct link to an identical survey was sent to each society, so that we would be able to tell from which society a participant had heard about our survey. Participants were asked to self-report their own level of expertise in behavioural biology by choosing one of the following statements.

(1) 'I am a professional in behavioral biology.'

(2) 'I am knowledgeable about behavioral biology. (Have taken a course on behavioral biology, or gained equivalent knowledge.)'

(3) 'I have little specialized knowledge regarding behavioral biology.'

Participants were then asked to state, by clicking in boxes, whether, for each phenomenon listed above (1–20), they considered it to be an example of behaviour, were not sure whether it was a behaviour, or considered it not to be a behaviour. Next, participants were asked to state whether they agreed with, were unsure about, or disagreed with each statement about behaviour listed above (A–M). Finally, participants were invited to submit their answers, and if they desired, send us additional comments or questions. Each survey was left active for 3 months, and anonymous individual data from all respondents were downloaded. Participants answering fewer than 10 questions were excluded from the analysis.

We calculated a percentage approval of each statement or phenomenon by counting an agreement as a 1, an answer of 'unsure' as 0.5, and a disagreement as 0, and calculating a mean for each question. An overall mean approval rating of 44% was found for all of the potential behavioural examples and definitional statements. Questions receiving 24% or less approval were deemed to be strongly disapproved, while questions receiving 64% or more were considered to be strongly approved. These boundaries were 20 percentage points on either side of the overall mean.

We scored each participant on internal consistency by looking for specific contradictions between their answers as to whether

certain phenomena were behaviours, and whether or not they agreed to the various statements about what is behaviour. Instances of stating that a phenomenon was a behaviour and then agreeing with a statement that disqualified that phenomenon from the definition of behaviour were counted as inconsistencies. Participants were coded as having committed no inconsistencies, one inconsistency, or multiple (2 or more) inconsistencies. We generated summary tables and calculated the effects of society membership, level of expertise and the interaction between the two on all other answers using stepwise logistic regression in the 'Build Model' script of JMP7 (SAS Institute, Cary, NC, U.S.A.).

We extracted a list of elements to include in a proposed definition by listing the definitional elements (A–M) and examples (1–20) that were strongly approved and those that were strongly disapproved. We composed a definition that, as much as possible, incorporated the conclusions embodied in this list.

RESULTS

Definitions Gathered

We found in excess of 25 operationally distinct definitions of the word 'behaviour' (or 'behavior') in the context of behavioural biology, as well as over 100 sources that we thought should have such a definition, but did not. In the interests of brevity, we here offer eight published definitions that we think are representative of much of the variation we found.

(1) Tinbergen (1955 page 2): 'The total movements made by the intact animal'.

(2) Beck et al. (1991, Glossary): 'Externally visible activity of an animal, in which a coordinated pattern of sensory, motor and associated neural activity responds to changing external or internal conditions'.

(3) Starr & Taggart (1992, Glossary): 'A response to external and internal stimuli, following integration of sensory, neural, endocrine, and effector components. Behavior has a genetic basis, hence is subject to natural selection, and it commonly can be modified through experience'.

(4) Wallace et al. (1991, Glossary): 'Observable activity of an organism; anything an organism does that involves action and/or response to stimulation'.

(5) Raven & Johnson (1989, page 1119): 'Behavior can be defined as the way an organism responds to stimulation'.

(6) Davis (1966, page 2): 'What an animal does'. (Note that the same text includes a section on behaviour of plants; see below.)

(7) Davis (1966, pp. 2, 4–5): What an animal (or plant) does.

(8) Grier & Burk (1992, page 4): 'All observable or otherwise measurable muscular and secretory responses (or lack thereof in some cases) and related phenomena such as changes in blood flow and surface pigments in response to changes in an animal's internal and external environment'.

Survey Participation

We received 181 responses to our survey, but seven of these responses were disqualified for being incomplete, yielding a total sample of 174 respondents. Table 1 gives sample sizes of included respondents by society and self-reported level of knowledge about behaviour. The Society for Plant Neurobiology is a significantly newer and smaller society than ABS or ISAE, and is less strictly focused on behaviour, which together may explain the smaller number of respondents and lower self-reported level of expertise in our sample from SPNB.

Table 1
Sample sizes of survey responses by society affiliation and level of knowledge

Society	Level of knowledge				
	Professional	Knowledgeable	Little knowledge	No response	Total
ABS	78	14	4	1	97
ISAE	44	14	5	0	63
SPNB	2	4	7	1	14
Total	124	32	16	2	**174**

ABS = Animal Behavior Society; ISAE = International Society for Applied Ethology; SPNB = Society for Plant Neurobiology. Self-reported level of knowledge: professional: a professional in behavioural biology; knowledgeable: knowledgeable about behavioural biology (have taken a course on behavioural biology, or gained equivalent knowledge); little knowledge: little specialized knowledge regarding behavioural biology. We excluded seven respondents who answered only one question.

Summary of Survey Responses

Approval as legitimate examples of behaviour ranged from 4.6% for 'a beetle is swept away by a strong current' to 99.1% for 'flocks of geese fly in V formations'. Approval of statements relating to necessary components of behaviour ranged from 7.6% for 'behavior always involves movement' to 87.1% for 'a behaviour is always in response to a stimulus or set of stimuli, but the stimulus can be either internal or external'. No potential behavioural example or component received 100% for any one answer; all were contested. See Appendix for full results of approval ratings for each survey question by society and level of expertise.

Survey Answers

Four statements about behaviour were generally agreed with ($\geq$64% agreement): (A): 'a developmental change is usually not a behaviour'; (F): 'behavior is always influenced by the internal processes of the individual'; (I): 'behavior is something whole individuals do, not organs or parts that make up individuals'; (J): 'a behavior is always in response to a stimulus or set of stimuli, but the stimulus can be either internal or external'.

Seven statements produced general disapproval ($\leq$24% agreement): (B): 'behavior is always in response to the external environment'; (C): 'a behavior is always an action, rather than a lack of action'; (E): 'people can all tell what is and is not behavior, just by looking at it'; (G) 'behavior always involves movement'; (H): 'behaviors are always the actions of individuals, not groups'; (L): 'in humans, anything that is not under conscious control is not behaviour'; (M): 'behavior is always executed through muscular activity'. The remaining two items (D, K) were neither strongly approved nor strongly disapproved.

The following seven phenomena met our criterion for approval as behaviours based on our survey results: (2): a sponge pumps water to gather food; (3): a spider builds a web; (11): a person decides not to do anything tomorrow if it rains; (14): a group of unicellular algae swims towards water with a higher concentration of nutrients; (16): flocks of geese fly in V formations; (17): a dog salivates in anticipation of feeding time; (18): herds of zebras break up during the breeding season and reform afterwards.

And the following seven items met our criterion for rejection as behaviours: (4): a rabbit grows thicker fur in the winter; (8): a person sweats in response to hot air; (9): a beetle is swept away by a strong current; (12): a horse becomes arthritic with age; (13): a mouse floats in zero gravity in outer space; (15): a frog orbits the Sun along with the rest of the Earth; (20): a cat produces insulin because of excess sugar in her blood.

Results for the remaining six phenomena (1, 5, 6, 7, 10, 19) indicated major divergences among respondents as to whether the phenomena were behaviours.

We found numerous statistically significant effects on responses based on both the professional society affiliation and level of expertise of respondents, as well as interaction effects. Responses to 12 of our 33 questions showed significant ($P < 0.05$) effects of organization, knowledge level and their interactions. These 12 are presented in Table 2.

To examine these results further, we sorted each of our respondents into one of seven subgroups, defined as affiliates of a single society with a single level of expertise, except that all of SPNB responses were pooled because of small sample sizes (2 societies with 3 knowledge levels and 1 society with knowledge levels combined, $N = 7$). We then examined for each of the 12 above questions, whether the conclusion of each subgroup differed from the overall survey consensus using our above-stated criteria of $\geq$64% and $\leq$24% for acceptance and rejection, respectively. With seven subgroups and 12 questions per subgroup, this yielded 84 opportunities for subgroup dissent.

Of these 84 opportunities for dissent, we found 24 instances in which a subgroup's responses would lead us to a different conclusion than the consensus result. This represents 28.6% of all possible responses to these 12 items. These deviations were sorted among societies as follows: ABS = 10, ISAE = 7, SPNB = 7. Before concluding that ABS supported the most deviants, note that 8 of the 10 deviations from ABS were made by the little knowledge cohort, which was also relatively small. The deviations assorted by knowledge level were as follows: professional = 1; knowledgeable = 3; little knowledge (including pooled SPNB) = 20. Thus, 83.3% of the deviations came from contributors with little knowledge. We lumped the SPNB subgroup into the little knowledge category because 7 of the 13 respondents from this society that answered the question about knowledge reported little knowledge.

Our data on internal consistency by individuals were most revealing. Fifty two per cent of respondents, including 51% of those self-identifying as professional behavioural biologists, contradicted themselves in their survey responses, including 26% who contradicted themselves multiple times. For example, 23 respondents that agreed with the idea that organisms other than animals do not behave also agreed that algae (non-animals) swimming up a nutrient gradient was an example of behaviour. Similarly, of the 24 people that agreed that behaviour is always executed through muscular activity, 18 (75%) agreed that sponges (which have no muscles) are behaving when they pump water to collect food, and 17 (71%) agreed that a person is behaving simply by deciding to do nothing if it rains tomorrow.

The percentage of respondents that we counted as having contradicted themselves (52%) does not include those committing inconsistencies that are more debatable. For example agreeing that 'a behavior is always in response to a stimulus or set of stimuli, but the stimulus can be either internal or external' and also agreeing that 'a rat has a dislike for salty food' is an example of behaviour was classified as consistent. While the rat's predisposition to dislike salty food will influence its response to salty food, and can only be measured through this response, the predisposition is not in and of itself a response. As this example and several similar ones are arguably subject simply to careless reading, we did not score these as inconsistencies. Had we done so, close to 90% of respondents would have committed inconsistencies.

Table 2
Questions to which responses varied significantly ($P < 0.05$) based on the self-reported level of knowledge, societal affiliations of respondents, or the interactions of these factors

Item ID	*P* value	Significant variables
18	0.0002	Organization, knowledge and interaction
B	0.0009	Organization and interaction
3	0.0029	Knowledge
I	0.0029	Organization and interaction
13	0.0083	Interaction
9	0.0089	Knowledge
K	0.0127	Organization
14	0.0140	Organization and knowledge
L	0.0242	Interaction
2	0.0270	Knowledge
G	0.0306	Organization
4	0.0316	Organization and interaction

Given the number of tests (33), one would expect approximately 1.65 spurious false positives at this alpha level, so a portion of these results may be misleading. The 12 questions are arranged in order of increasing *P* value.

DISCUSSION

Our results show that existing definitions of behaviour do not generally agree on what is or is not behaviour, and generally do not meet the requirements of our rules for definitions. Behavioural biologists in our survey also showed a corresponding confusion over the meaning of 'behaviour'. More than half of respondents at all levels of expertise gave contradictory answers. This high level of self-contradiction suggests that novices and experts alike rely on an inferential, rather than definitional, sense of what the word 'behaviour' means. Indeed, one behavioural biology professor commented, 'I know it when I see it, hear it, smell it, feel it or electrically sense it'. Yet only 13 (7%) of respondents agreed that, 'people can all tell what is and isn't behavior, just by looking at it'. Also, as mentioned, there was not a single question in our survey that produced a unanimous consensus. In fact, for 13 of 33 questions, no particular response achieved even 75% agreement by respondents. We can conclude that in addition to having no consensus as to a definition of behaviour, we have little operational inferential consensus. Contradictory and inferential understandings of the meaning of behaviour help explain why so few definitions seem designed to be operational and essential. Operational definitions set logical bounds between those items qualifying and those not qualifying, but our inferential understanding is varied and self-contradictory, defying any strict logical bounds. Moreover, it is apparent that the reported level of behavioural expertise can significantly influence one's views. Society affiliation can also contribute to heterogeneity of response, although it is perhaps surprising that only one item (statement K) produced a statistically significant heterogeneity based on organization alone (Table 2). In this case, the statement that behaviour is only for animals received no consensus for approval or rejection while the 'little knowledge' respondents from ISAE approved the contention and SPNB members strongly disapproved it.

In spite of this heterogeneity of views, however, we feel that it is important to have a working definition of behaviour that will be as operational and as essential as possible, thereby providing conceptual guidance as to where the boundaries are. We therefore offer a new definition, which we believe to be (1) operational, because it allows the inclusion or exclusion of all (except one, see below) of the boundary phenomena suggested by our survey, (2) essential, in that it is based on our survey of what practitioners in the field intuit the word to mean, and is therefore a formalization of their views of what the word means, (3) widely applicable, in that it avoids taxonomic bias and could be applied to any living organism

Table 3
Treatment of potential behaviours by eight published definitions, survey results and our definition

	Definition number from text	(1) Ants not breeding	(2) Sponge pumps	(3) Spider builds web	(4) Rabbit grows fur	(5) Stomata close	(6) Plant moves leaves	(7) Heart beats after nightmare	(8) Sweat in hot air	(9) Beetle in current	(10) Rat dislikes salt	(11) Decide to do nothing	(12) Horse grows arthritic	(13) Mouse in space	(14) Algae swim	(15) Frog orbits sun	(16) Geese fly in V formation	(17) Dog salivates	(18) Zebra herds fluctuate	(19) Chameleon changes colour	(20) Cat produces insulin
The total movements made by the intact animal	1	−	+	+	−	−	−	−	−	+	−	−	−	−	−	+	?	−	?	−	−
Visible activity of animal in response to external/internal conditions	2	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	?	+	?	+	−
Response to external/internal stimuli, genetic basis and subject to natural selection	3	?	−	+	+	−	−	−	+	−	−	?	−	−	−	−	+	+	+	+	+
Anything observable an organism does in response to stimuli	4	?	+	+	+	+	+	+	+	+	−	−	−	?	+	+	?	+	?	+	?
Responses to stimuli	5	?	+	+	+	+	+	+	+	+	−	+	+	−	+	+	?	+	?	+	+
What an animal does	6	?	+	+	+	−	−	+	+	+	+	+	+	+	−	+	?	+	?	+	+
What an animal/plant does	7	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	?	+	+
Measurable responses by the animal	8	?	+	+	?	−	−	+	+	−	−	?	−	−	−	−	?	+	?	+	+
Survey results		64	74	97	13	38	48	34	24	05	66	81	06	11	78	10	99	75	96	57	14
Our definition		+	+	+	−	−	+	?	−	−	−	−	−	−	+	−	+	+	+	+	−

The symbols '+', '−' and '?' signify acceptance, rejection and uncertainty, respectively, regarding these examples. The survey approval ratings (%) are from the questionnaire responses received from 174 behavioural biologists (Table 1). See the text for a full description of potential behavioural phenomena, and for full definitions and sources. The final row gives the treatment of each phenomenon by our proposed new definition.

and (4) succinct, in that each word is necessary to the proper functioning of the definition.

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. These 27 words succinctly define the biological phenomena that are the subject matter of behavioural biology. They are based, to the degree that coherence and consistency allow, on the consensus of views expressed by 174 behavioural biologists. Most importantly, the definition is consistent with current biological practise and its conceptual framework. To illustrate the applicability of the definition, Table 3 compares the treatment of each of our 20 potential examples of behaviour according to eight previously published definitions and our new definition.

Developmental processes are largely excluded from the definition, as they are generally much slower than phenomena considered as behaviour, and are primarily based on ontogenetic programmes specified by the individual's genetic makeup. Of course these programmes of ontogenetic change can be influenced by proximate environmental and internal circumstances, but generally such modifications are relatively slow. The above definition asks the investigator to consider whether or not borderline cases can most usefully be viewed as development. Thus, operationally, if the phenomenon is arguably development, it is best viewed in that domain.

While behaviours necessarily rely upon internal information processing by the individual (e.g. cognition and endocrine signalling), we do not consider the processing alone to be a response, and therefore do not include it as behaviour. Shettleworth (1998, page 5) defines cognition as 'the mechanisms by which animals acquire, process, store and act on information from the environment'. In behaviour, we include the action, but deem the processing as necessary but not sufficient. While this runs counter to the views of 80% of our respondents, we think it is illogical to include cognitive processing while excluding other forms of internal information processing such as genetic expression cascades or endocrine feedback. Information processing may be a necessary substrate for behaviour, but we do not consider it a behaviour by itself.

One of the important aspects of a good definition is, as we have emphasized, that it be operational in the sense that a given phenomenon can be tested against the definition for correspondence. Perhaps the most difficult boundary between behaviour and non-behaviour is the distinction between strictly physiological activities and functions that require coordinated responses of the whole organism. The problem is that all physiological functions occur in the context of the whole organism, and it is this context that constrains and even directs the physiological activities. So, how do we define boundary criteria? If the response can most simply and usefully be explained by cellular-, tissue- or organ-level processes alone, it would fall outside our definition of behaviour. For example, the secretion of digestive enzymes by the stomach in response to the presence of ingested food, sweating in response to increasing blood temperature and increased hunger in response to low blood sugar levels are not behaviours. On the other hand, if sweating causes the individual to move into the shade, or if hunger leads to food searching activities, these responses are clearly behavioural. In more complex animals, whole organism responses are generally mediated through the central nervous system, and this is often how a strictly physiological process can be transformed into some behaviour. In single celled organisms or others without a nervous system (such as plants or sponges), one has to look for analogous electron transfer mechanisms that serve as rapid coordinating mechanistic substrates. Also note that wholeness in this

context does not preclude behaviour by organisms that have suffered amputations, but rather indicates that a multiplicity of organ systems are involved.

Often organismal movements and other positive responses are clues that whole body coordination has occurred. However, inactions can also be considered behaviours in some situations. In such cases, this inaction must still be coordinated on the level of the organism. To take the famous example of a guard dog, which in recognizing its owner, does not bark (Conan Doyle 1903), such a dog must not only take in and process sensory information, and thereby recognize its owner, it must respond to this recognition by restraining itself from barking. By coordinating several body systems to generate this stimulus-dependent negative response, the dog is behaving.

By including coordinated inaction, but excluding both information processing and physiology from our interpretation of 'responses… of whole living organisms' we emphasize the distinction in levels of organization. The term 'response' should be viewed, in the context of our definition, as referring to events occurring at the level of organization of the whole individual or above, and should exclude the internal mechanisms (information processing and physiology). It is clear that this distinction, between mechanisms and behaviour, is not going to be easy to make in many instances. In Table 3 we acknowledge that despite our best efforts at forming an operational definition, the behaviour/physiology/information processing boundary is still not operational in every case. The statement 'a person's heart beats harder after a nightmare' may or may not be a result of coordinated actions within the individual as a 'whole'. Therefore, this example of information processing and physiology may or may not also be a behaviour. While in this instance this wholeness criterion fails, at least in principle, it provides a useful guideline.

In our treatment of development, information processing and physiology, we follow Tinbergen (1955) in distinguishing behaviours from these mechanistic substrates, while recognizing the importance of understanding those underlying causes. His definition, 'the total movements made by the intact animal', clearly excludes the underpinnings of behaviour from qualification as behaviours. While we think his focus on movement and on animals no longer encompasses the range of what we mean by behaviour, we follow his example and the majority of our respondents by disqualifying ontogeny and mechanism.

Tinbergen's specification of the 'animal' also implies that behaviours are phenomena of the singular (rather than plural) organism. But individuals operate in the contexts of populations and communities, and therefore individual behaviours also require knowledge of these levels of organization to be fully understood. Many of the definitions we cite are silent on the question of whether group actions can be behaviours, and therefore are nonoperational when discussing group actions. While 31% of our respondents stated that only individuals, not groups, can behave, 99% indicated that the characteristic V formations of flocks of geese were examples of behaviour. As the V formation is an emergent property of the simultaneous interactions of multiple individuals, it cannot be expressed by a single individual. Is it still behaviour? The existence of the vibrant subdiscipline of social behaviour attests to the existence of behaviours above the level of individuals. Examples would include mating behaviours, herding, flocking and schooling, a game of chess, giving and receiving alarm signals, a predator pursuing prey, duet singing, friendship bonds, pack hunting and many others.

Definitions are in a sense arbitrary and dynamic. They reflect the consensus wisdom of the moment. As such they are important as expressions of current conceptual perspectives, and are useful if they provide guidance for students and practitioners in a discipline. It is in this spirit that we suggest the approach outlined here. Our definition with its focus on the importance of levels of organization, will not meet with approval by every practitioner of behavioural biology, and we do not aim to end the debate. Rather, it is our hope to stimulate increased awareness of the difficulty of mapping the many conceptual boundaries we have considered, and thereby to spark discussion of what is meant by this term, 'behaviour'.

Acknowledgments

This paper would not have been possible without the input, aid and consultation of members of the Behavior Lunch group at UC Berkeley and the participation of members of the Animal Behavior Society, the International Society for Applied Ethology and the Society for Plant Neurobiology. We thank James Ha, Derek Haley and Elizabeth Van Volkenburgh for forwarding our survey to their societies, and numerous anonymous students and their professors for helping us refine our methodology. Previous drafts of this manuscript benefited greatly from suggestions made by Eileen Lacey, Lauryn Benedict and Walter Koenig and his Advanced Behavioral Ecology course at Cornell University as well as Michael Breed and two anonymous referees. D.L. was supported by the Ruth L. Kirschstein National Research Service Award (NIA grant T32-AG000246). This research was granted exempt status by the University of California at Berkeley Committee for the Protection of Human Subjects (CPHS Protocol No. 2007-10-45).

Supplementary Material

The survey described in this article is provided as supplementary material. It can be found, in the online version, at doi:10.1016/j.anbehav.2009.03.018.

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APPENDIX

Approval ratings for 20 potential examples of behaviour (1–20) and 13 postulated features of behaviour (A–M)

Organization	ABS	ABS	ABS	ISAE	ISAE	ISAE	SPNB*	All	All
Level of knowledge	1	2	3	1	2	3	All	1	All
Sample size	78	14	4	44	14	5	14	92	174
	Approval rating								
Examples of behaviour									
(1) Worker ants not breeding	0.67	0.75	0.38	0.52	0.68	0.80	0.75	0.61	0.64
(2) Sponge pumps water	0.83	0.71	0.88	0.75	0.57	0.50	0.50	0.82	0.74
(3) Spider spins web	1.00	1.00	0.75	1.00	0.93	0.60	0.89	1.00	0.97
(4) Rabbit grows fur	0.14	0.07	0.25	0.05	0.23	0.00	0.29	0.14	0.13
(5) Stomata open	0.37	0.39	0.63	0.28	0.31	0.10	0.71	0.37	0.38
(6) Leaves bend to light	0.49	0.57	0.38	0.35	0.43	0.30	0.79	0.49	0.48
(7) Heart beat after nightmare	0.37	0.36	0.25	0.26	0.25	0.30	0.54	0.36	0.34
(8) Person sweats	0.24	0.36	0.38	0.14	0.31	0.10	0.42	0.23	0.24
(9) Beetle swept by current	0.03	0.04	0.25	0.00	0.04	0.10	0.21	0.03	0.05
(10) Rat dislikes salt	0.71	0.57	0.38	0.59	0.75	0.80	0.61	0.70	0.66
(11) Person makes plans	0.80	0.75	0.25	0.82	0.86	1.00	0.86	0.80	0.80
(12) Horse becomes arthritic	0.06	0.04	0.13	0.05	0.04	0.00	0.14	0.06	0.06
(13) Mouse floats in space	0.10	0.00	0.38	0.13	0.04	0.00	0.32	0.10	0.11
(14) Algae swim towards food	0.87	0.86	0.63	0.69	0.68	0.50	0.79	0.86	0.78
(15) Frog orbits sun	0.05	0.07	0.63	0.10	0.14	0.10	0.14	0.05	0.09
(16) Geese in V formation	1.00	1.00	0.75	1.00	0.96	1.00	1.00	1.00	0.99
(17) Dog salivates	0.83	0.73	0.50	0.64	0.82	0.70	0.68	0.82	0.75
(18) Zebra herds form	1.00	1.00	0.50	0.92	1.00	0.90	0.92	1.00	0.96
(19) Chameleon changes colour	0.59	0.71	0.50	0.47	0.61	0.50	0.57	0.59	0.57
(20) Cat produces insulin	0.17	0.14	0.25	0.03	0.11	0.10	0.25	0.17	0.14
Features of behaviour									
(A) Developmental changes	0.65	0.73	1.00	0.66	0.71	0.70	0.79	0.65	0.69
(B) Response to external stimuli	0.17	0.00	0.50	0.06	0.14	0.00	0.61	0.16	0.16
(C) Action, not inaction	0.17	0.14	0.25	0.11	0.07	0.00	0.21	0.16	0.14
(D) Observable, measurable	0.38	0.27	0.50	0.56	0.54	0.40	0.69	0.39	0.46
(E) Intuitively identifiable	0.14	0.07	0.13	0.13	0.23	0.10	0.18	0.14	0.14
(F) Always internally controlled	0.81	0.82	0.63	0.79	0.64	0.30	0.89	0.80	0.78
(G) Always involves movement	0.08	0.04	0.50	0.00	0.07	0.00	0.21	0.08	0.08
(H) Individuals, not groups	0.35	0.29	0.50	0.29	0.07	0.20	0.32	0.34	0.31
(I) Individuals, not parts	0.75	0.58	0.38	0.78	0.71	0.70	0.43	0.75	0.70
(J) External/internal stimuli	0.81	0.89	0.88	0.94	0.93	1.00	0.85	0.82	0.87
(K) Animals only	0.29	0.25	0.25	0.54	0.46	0.70	0.14	0.30	0.36
(L) Human conscience control	0.09	0.00	0.25	0.09	0.15	0.00	0.25	0.09	0.10
(M) Muscular action	0.19	0.25	0.25	0.18	0.14	0.20	0.11	0.19	0.18

ABS = Animal Behavior Society; ISAE = International Society for Applied Ethology; SPNB = Society for Plant Neurobiology. Level of knowledge: 1 = professional; 2 = knowledgeable; 3 = little knowledge. Approval ratings are arranged by professional affiliation of respondents and by self-reported level of knowledge of behavioural biology. Approval ratings were calculated as number of respondents agreeing, plus 0.5 times the number of respondents that were unsure, divided by the total number of respondents to that question in that subgroup. See text for details of survey questions.

* Too few responses were received from SPNB to treat levels of knowledge separately for this society.