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## How Human Are Insects, and Does it Matter? 【Review article】

### 一定要把昆蟲想成人類那樣嗎？【綜合論述】

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### Abstract

Over the past two decades, a wealth of information on cognitive function in insects has been generated and this work has been tremendously useful in pinpointing just how much can be done with how little neural circuitry in miniature brains. However, other recent claims on the occurrence of 'teaching', 'culture', 'consciousness', or 'personality' in the insects seem to apply a relatively restrictive top-down approach, where researchers set out to discover human-like behaviours in animals. This approach is prone to terminological ambiguities, because terms taken from the domain of human experience often invoke more complex connotations than the restricted criteria used to test the phenomena in the animal world would permit. It also bears the risk of circularities as a consequence of selecting and shaping definitions and test criteria. Finally, the hypothesis-driven approach may be vulnerable to research biases, such as to predominantly report positive results or to mainly investigate "clever" animals. We suggest that the current approach needs to be supplemented by a complementary *modus operandi*. In a more exploratory, bottom-up 'ethomics' approach, psychological constructs would only emerge after multivariate data analysis of a broader range of animal behaviours. It is also necessary to consider the process of how we arrive at definitions as part of the research methods.

### 摘要

過去二十年來已有大量的資料在探討昆蟲的認知功能，即使昆蟲腦中的神經迴路是如此之小，也已有相當令人滿意的成果。然而近年的一些研究聲稱昆蟲存在「教導」、「文化」、「意識」或「性格」，科學家們開始著手探索動物的擬人行為，似乎涉及了相對限制性由上而下的方法。此方法容易導致術語的歧義性，由於這些術語出自人們的經驗，往往產生了比在動物世界中有限制條件試驗下可被允許的現象更複雜的含義。此結果也將承擔因主觀選擇或重新塑造了定義與測試標準所造成的後果之風險。最後，假說驅動的方法容易導致研究偏差被忽略，例如報告主要著重於正面的結果或以「聰明」的動物為主要研究對象。我們建議現行的方法需要加入互補性作法加以補充，以自動化程序進行行為的分類，透過由下而上的方法做更進一步的探索，在更廣範的動物行為多元數據分析後，也將揭露動物的心理構念，當然在研究方法中我們也必須注意我們是如何得到定義的。

**Key words:** ambiguity, arbitrariness, behaviour, cognition, methods, terminology

**關鍵詞:** 歧義、獨斷、行為、認知、方法、術語。

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# How Human Are Insects, and Does it Matter?

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## ABSTRACT

Over the past two decades, a wealth of information on cognitive function in insects has been generated and this work has been tremendously useful in pinpointing just how much can be done with how little neural circuitry in miniature brains. However, other recent claims on the occurrence of ‘teaching’, ‘culture’, ‘consciousness’, or ‘personality’ in the insects seem to apply a relatively restrictive top-down approach, where researchers set out to discover human-like behaviours in animals. This approach is prone to terminological ambiguities, because terms taken from the domain of human experience often invoke more complex connotations than the restricted criteria used to test the phenomena in the animal world would permit. It also bears the risk of circularities as a consequence of selecting and shaping definitions and test criteria. Finally, the hypothesis-driven approach may be vulnerable to research biases, such as to predominantly report positive results or to mainly investigate “clever” animals. We suggest that the current approach needs to be supplemented by a complementary *modus operandi*. In a more exploratory, bottom-up ‘ethomics’ approach, psychological constructs would only emerge after multivariate data analysis of a broader range of animal behaviours. It is also necessary to consider the process of how we arrive at definitions as part of the research methods.

**Key words:** ambiguity, arbitrariness, behaviour, cognition, methods, terminology

## Introduction

Some of the attraction for scientists to the insects, especially the social ones, is undoubtedly that they have evolved a number of feats that, to a non-biologist,

might be considered uniquely human domains: agriculture, slavery, territorial wars, castes, division of labour, consensus building, a symbolic language, and teeming cities with fantastic architecture (Lindauer, 1955; Frisch, 1967; Hölldobler and Wilson,

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1990). However, there is perhaps little scholarly information to be gleaned from such similarities: insects and humans are too distantly related for such comparisons to reveal anything but evolutionary convergence. The terms that label these features are merely metaphors, and they should not mislead us to construe that insects ‘think’ like humans. However, in recent work on insect cognition, the boundaries between human and insect performances have often been blurred, sometimes in ways that are not just innocent metaphors. There is no question that some insects perform impressive cognitive feats; recent discoveries include attention-like processes (Spaethe *et al.*, 2006; Van Swinderen and Andretic, 2011), categorization of visual stimuli (Zhang *et al.*, 2004), rule learning in delayed matching to sample tasks (Avarguès-Weber *et al.*, 2011), context learning (Collett *et al.*, 1997), sequence learning (Chittka *et al.*, 1995), various types of social learning (Leadbeater and Chittka, 2007), interval timing (Boisvert and Sherry, 2006), associative recall (Reinhard *et al.*, 2004) and sensitivity to number (Chittka and Geiger, 1995). However, other recent claims on the occurrence of ‘teaching’, ‘culture’, ‘consciousness’, or ‘personality’ in the insects seem to apply a relatively restrictive top-down approach, where researchers set out to discover human-like behaviours in animals. This approach is prone to terminological ambiguities, because terms taken from the domain of human experience often invoke more complex connotations than the restricted criteria used to test the phenomena in the animal world would permit.

Bordering on psychology, philosophy, physiology and ecology, the science of animal cognition attracts interest from many sides. Since all bring in their terminological traditions, cross-discipline communication can be difficult. However, this is not the only, and possibly not the most serious source of conceptual confusion. In this paper we argue that one of the most

fundamental conceptual problems in animal cognition science could be seen in the predominant approach of reducing complex behavioural or psychological constructs into small sets of experimental test criteria. We will explore the consequences of this top-down approach and compare it to an alternative, bottom-up approach, thereby touching on questions of terminological ambiguities, the arbitrariness of definitions, and problems of undetected circular reasoning.

## **The top-down approach in animal cognition**

Current work on animal cognition, where it is dealing with psychological constructs, typically follows a type of hypothesis-driven approach that is ‘top-down’ in more than one way. First, concepts and terms are mainly anchored in human psychology, and then superimposed on animals. Second, the hypotheses are often not strictly deductive, as good hypothesis-testing might be; instead the hypothesis is often that animals exhibit behaviour that is human-like, and researchers are content with confirming this hypothesis, and indeed with adjusting both procedures and definitions to see it confirmed.

The top-down approach in animal cognition relies on taking interesting psychological constructs that are rooted in the human domain, and translating these into experimental paradigms for animals. The constructs have acquired their names in the human world, not in the zoological sciences, and an almost inevitable consequence of this is terminological confusion, i.e. the chosen terms are ambiguous. Certainly, this hypothesis-driven way of conducting research on animal cognition is very powerful and has fuelled massive progress in the understanding of animal behaviour and animal cognition over the last few decades (Bekoff *et al.*, 2002). Nothing can beat the excitement accompanying the successful completion of a rigorously designed experiment that proves the

existence of a cognitive ability in an animal species for the first time. Pointing out problems in this approach, therefore, may carry the risk being regarded as a spoilsport activity (Shettleworth, 2010). However, we believe that it is worth taking this risk for the potential reward of new insights into the world of animal (and specifically insect) cognition.

### ***Terminology: the problem of ambiguity and content erosion***

Some terminological inaccuracies are innocent. When the words ‘queen’, or ‘honeybee dance’, or indeed ‘dance language’ are used in studies of social insects it is clear that the double meaning of the words will not endanger the conceptual clarity of entomological studies. The semantic distance of the word ‘queen’ between the worlds of insect and human societies is too large to lead to any misunderstandings. Thus, the metaphorical use of these anthropomorphisms is safe. Just using the word ‘queen’ in the title of a bee study does not offer any increased attention from readers.

In contrast, consider the question whether the individuals of certain animal species can be said to have ‘personality’. This term, *without* inverted commas, is now commonly used among vertebrate behavioural ecologists (Bell and Sih, 2007; Frost *et al.*, 2007), and this has recently expanded into the insect literature (Wray *et al.*, 2011), with the curious implication that insects have person-like qualities. Although the term may be defined concisely in an animal study, its grandeur, which has been acquired in psychology, may spill over into the world of insects – at the considerable risk that meanings are confounded. How is ‘personality’ defined in a psychology textbook? *“The term personality has many different meanings. To some, it refers to a mysterious charisma possessed by Hollywood actors and other popular, influential people, but not by everyone. To others, personality is the same as temperament, a natural, genetically based*

*predisposition to think, feel, and act in a particular way. To still others, personality consists of a person’s unique mixture of emotional, intellectual, and character traits (honesty, courage, etc.). To more behaviorally oriented psychologists, personality is not something internal, but rather an externally observable pattern of organized behavior typical of a person. Perhaps an acceptable compromise is to define human personality as a composite of cognitive abilities, interests, attitudes, temperaments, and other individual differences in thoughts, feelings, and behavior. This definition emphasizes the fact that personality is a unique combination of cognitive and affective characteristics describable in terms of a typical, fairly consistent pattern of individual behavior. From the last definition, it follows that methods of assessing personality should include a broad spectrum of cognitive and affective variables.”* (Aiken, 2000)

In humans, personality is now often quantified in terms of the ‘big five’ dimensions openness, conscientiousness, extraversion, agreeableness, and neuroticism (Goldberg, 1993), where each of these is explored using a multitude of questionnaires or tests. Contrast this complex picture of personality, emphasizing the plurality of approaches, with the approach to measure the correlation between just two behavioural variables in ‘personality’ studies in animals (Bell and Sih, 2007), or indeed just a basic level of consistency in a single behavioural trait (see e.g., references in Muller *et al.*, 2010). To add to the confusion, some authors use the terms “personality” and “behavioural syndrome” interchangeably, whereas others make a distinction (Dall *et al.*, 2004; Sih *et al.*, 2004; Quinn and Cresswell, 2005).

Terms like ‘personality’ have a very broad meaning in colloquial language, and many people might have a different understanding of the term. The technical meanings of the same words, developed over long periods of time in various disciplines like philosophy, psychology and

sociology, may just be as broad and diverse as in everyday language, but they are documented and are certainly (if only subtly) different from the colloquial meanings (e.g., Aiken, 2000, p. 262).

When using a term that has both technical and colloquial meanings, it is quite inevitable to invoke the broad meanings associated with the *non-technical* term, at least in cursory or non-specialist readers, and especially when it is placed in a prominent place like the title or abstract. Although this certainly increases the potential impact of the study by capturing the attention of a wider audience, many readers might feel slightly disappointed as soon as they arrive at the rather narrow and restricted technical definition. In this case, it is obvious that concepts are narrowed down for the operational purposes of the study, while the impression of a very complex concept is maintained.

We may indeed (by definition) call a behaviour that has been observed in an animal species 'personality', but this is only a short form of saying that a defined set of criteria has been met. This does not necessarily mean that the psychological processes in humans and animals that are described with the same term are equivalent or even comparable. However, by calling the observed behaviours in animals by the *same terms* used to describe human behaviour we risk invoking very colourful but – in some cases – relatively unsubstantiated associations in the interpretation of animal behaviour.

Therefore, as the attention that animal cognition studies are able to attract appears to depend at least partly on the unintentional or deliberate use of terminological ambiguity, perhaps the most acute danger to conceptual clarity in animal cognition may lie in the pressure to transform scientific results into sensational stories. As an example for the need to glamorise science to attract continued funding, see Pielke and Glantz (1995). Indeed, in some case such glamorization may detract from more

important scientific issues. There is no question that the study of interindividual behavioural variation is important from an evolutionary point of view (e.g., Thomson and Chittka, 2001; Raine *et al.*, 2006; Raine and Chittka, 2008) as well as for understanding the organisation of work in social insect colonies (Gordon, 1996; Chittka and Muller, 2009) – but this is quite independent of whether the term 'personality' applies to any of such variation. Insect researchers have been aware of consistent behavioural differences between individuals for decades (see Thomson and Chittka, 2001, and references therein; for an early example of between-individual differences in insects' 'intellect', see Christy, 1884). There is no scholarly information to be gained by giving a well established phenomenon a new label. This also applies to recent claims of teaching and culture in ants (Franks and Richardson, 2006; Reznikova and Panteleeva, 2008) or consciousness in bees (Griffin and Speck, 2004). There are many examples where definitions of cognitively loaded terminology have been broadened in the process of removing them from their (human-related) origins and applying them to animals across taxa (Leadbeater *et al.*, 2006; Penn *et al.*, 2008). Such inflationary usage of terminology is also unhelpful for the goals of comparative cognition i.e., to decipher the evolutionary paths to traits related to learning and memory. Giving two phenomena the same label does not turn them into the same biological trait (Chittka and Jensen, 2011).

The remedies against terminological ambiguity are obvious. Possible misunderstandings caused by double or multiple meanings in colloquial and technical language must be anticipated and definitions clarified by appropriate discriminants. Anthropomorphisms should be avoided when it is not clear that they are purely metaphorical. Where multiple technical definitions are available it should be justified and discussed why a particular

definition was chosen.

### ***Problems with using humans as a reference point***

Early researchers working on learning and memory, e.g., Pavlov and Skinner used various animal models to discover general principles, and (perhaps sometimes too liberally) applied them to other animals, including humans. However, more recent work on animal cognition almost universally uses human psychology as a point of reference. This might be in part because many of the processes investigated (e.g., consciousness, episodic memories, planning, theory of mind etc.) are, first and foremost, accessible by introspection. In applying these concepts to animals, we typically ask how they might manifest themselves in observable behaviour, establish a set of criteria that might be underpinned by similar processes as those accessible to us by introspection, and see whether they are met by our study animal. As a consequence of the necessarily human anchor in this form of the top down approach, it has an inbuilt tendency towards anthropomorphism. The problem with this form of the hypothesis-driven approach is that one can never discover anything genuinely novel, even though journal editors and the press love demonstrations that animals are clever and 'human-like'. The best outcome one could hope for is that the observed behaviour meets some criteria that have been derived from research on human cognition.

A more meaningful way of the top-down approach is to explore hypotheses grounded in the animals' natural environment. For example, von Frisch's exploration of colour vision in bees, was based on the observation that flowers are colourful; therefore, he argued, bees should be able to perceive the colour signals that are clearly addressed to them (Frisch, 1914).

### ***Problems with Circularity, Experimenter Biases and 'Clever Hans' Effects***

Any decision whether or not to include criteria for psychological constructs that is based on expected outcomes in animals denies us the possibility of a meaningful test of the construct in these animals. A revealing example is the discussion on definitions of animal intelligence in a textbook on animal cognition (Pearce, 2008). In this source (p. 13-14), the speed of learning is discarded as a suitable measure for intelligence, *because* bees perform better than rabbits or indeed human children on a colour learning task. Following this, any meaningful decision on whether bees or rabbits are more intelligent has become logically impossible. There may be good reasons to be uncomfortable with equating learning speed with intelligence, but the observation that humans do not top the chart should not be one of them. Such circular reasoning is probably often hidden, because how authors arrive at their chosen definition (set of criteria) for psychological constructs is not a feature described in the methods of animal cognition studies.

Recent controversies surrounding the possibility of misconduct in various studies related to animal behaviour and cognition (Abbott, 2004; Ledford, 2010) quite possibly miss the point: incidences of academics deliberately fabricating data are probably quite rare. However, experimenter biases, where observers inadvertently read their preconceived notions into what they see, are an integral part of human psychology (Rosenthal and Lawson, 1964). This might be an uncomfortable notion for many, and it might appear attractive to find scapegoats and accuse them of all-out fraud, rather than addressing subconscious biases that quite possibly affect the majority of us. Researchers need to immunise themselves against such biases, ideally by fully automated recordings of animal behaviour. Curiously however, methods such as those used in our laboratory, using electronic

flowers with infrared light barriers (Chittka, 1998), 3D video recordings of bee flight trajectories (Ings and Chittka, 2008) or radio frequency identification (RFID) (Stelzer and Chittka, 2010) often meet with resistance in certain quarters of the animal behaviour community who perceive such methods as unnecessarily technological, or too far removed from natural settings. They aren't – automated procedures should be standard in all recordings of animal behaviour. At the very least, observers entrusted with the test should be un-informed about what the experiment coordinator expects, as in double blind studies now standard in e.g. drug testing. Where these standards are not observed, researchers, editors and readers should be aware of the preliminary nature of the work.

An added complication of the experimenter knowing what he or she expects from his animal subject is the Clever Hans effect, named after a horse with a seemingly prodigious gift for numeracy in the early 1900s. However, a careful investigation revealed that Hans, instead of being able to count, paid attention to subtle cues from his trainer to respond in the correct manner (Pearce, 2008, p. 243). Such effects are probably especially common with domestic or experimental animals that interact with humans on a daily basis, but might also occur in insect studies. A possible example is a study by Gould (1984), where bees apparently learnt to anticipate the next location of a feeder that was being moved in regular steps. A conceivable interpretation is that bees learned to use the appearance of the experimenter himself as a landmark indicating the food, and if that experimenter inspected a previously unrewarded location, or indeed moved the feeder to a new location, the bees would simply follow him and search in the vicinity. Such complications may be pervasive in studies where informed experimenters interact directly with animals, again emphasising the need for automated data recording and/or

double blind studies.

The conclusion is that a one-dimensional search for human-ness in the animal kingdom, when paired with unchecked experimenter biases and more or less explicit encouragement from journal editors and the press, will generate somewhat predictable outcomes, but perhaps without making significant contributions to the advancement of scientific knowledge.

## **Bottom up-approaches to animal behaviour and cognition**

We are so frequently told that scientific discovery must be based on hypothesis testing that it's easy to forget that many major scientific breakthroughs were entirely data driven (see e.g., Langley *et al.*, 1987 for examples). These authors caution that the “very strength of the methods available in theory-driven discovery sometimes produce the danger that theories will be created that rationalize rather than explain the empirical data”. As we have seen, there are other dangers, i.e., to subconsciously adjust terminology, procedures or interpretations so that they support a particular idea. This risk is very low if large quantities of data are collected first, and rules or patterns extracted by automated procedures. New technologies and computational ‘high-throughput’ approaches to behaviour analysis, as well as new neurobiological tools make this increasingly feasible in studies of animal behaviour.

### ***Observations of behaviour***

Many luminaries in insect behaviour (for example Jean-Henri Fabre and Karl von Frisch) have started with careful observations of their animals in their natural environments. Fabre made discovery after discovery about the remarkable diversity of ‘instinctual’ behaviour in his study organisms, precisely because he did not observe them with preconceived notions of what he might find. (That said, he was also a careful experimenter – his

explorations of homing in parasitoid wasps, and the question of how they identify nest locations, were early masterpieces in behavioural ecology.)

A bottom-up 'inductive' approach also laid the foundations for von Frisch's work, and that of many of his disciples who started an investigation by carefully observing their study organisms in their natural settings, taking everything in, and getting to know the study organism thoroughly from many angles; this often resulted in the discovery of unexpected or inexplicable phenomena. Only then were testable hypotheses developed and rigorous experiments set up to zero in on how particular processes might be explained. One might argue that this approach is not entirely hypothesis-free either – that it is only possibly to discover the unexpected if there are certain expectations. But the point here is that the bottom-up approach to animal behaviour is open-ended: it does not start with a predefined goal that it seeks to reach, or an idea it wants to confirm.

For example, von Frisch would certainly never have discovered the bee 'dance language' if he had deliberately set out to find a form of symbolic communication in the animal kingdom (following a top down-approach). Or would Lubbock have discovered UV sensitivity in ants if he had looked for a colour vision system exactly like humans? Probably not – and indeed, these would have been rather misguided endeavours. J. Gould wrote about von Frisch: "*His pioneering work inspired the discovery of several otherwise unimaginable sensory systems in animals: infrared detectors in night-hunting snakes, ultrasonic sonar in dolphins and bats, infrasonic hearing in birds, and magnetic field sensitivity in a variety of animals. Doubtless, other systems are still to be discovered. The lesson is a melancholy one: We are blind to our own blindness, and must try not to read our own disabilities into the rest of the animal kingdom.*" (Gould, 1980). Note the awe

and excitement about diversity in animal information processing, the promise of alien perceptual worlds – how sad, in comparison is the one-dimensional search for human-like qualities in the animal kingdom! The take-home message is, quite simply, to keep your eyes open for the unexpected.

### ***Ethomics – automated behaviour classification***

Behaviour is essentially a coordinated series of precisely timed muscle contractions from simple ones such as leg extension to extended behavioural sequences, such as the waggle dance of honeybees. However, a complication is that the classification of behaviour typically follows entirely subjective criteria and is therefore difficult to compare across animals: for example 'leg extension', 'bee waggle dance' and 'consensus building in bee swarms' are not equivalent behavioural classifications, and are to some extent nested within one another. It is therefore desirable to classify behaviour by automated procedures so they can be objectively measured and compared using what Branson *et al.* (2009) have called an 'ethomics' approach.

New technologies in motion capture and video analyses make an entirely hypotheses free approach to the analysis of behaviour feasible. The complete classification of behavioural repertoires by automated procedures might soon be within reach; see for example Branson *et al.* (2009), Braun *et al.* (2010), Benjamini *et al.* (2011), for promising developments. For the future, it will be necessary to develop large-scale automated analytical tools to effectively mine the data collected with the aim of finding prototypical and atypical behaviours. To discover prototypical activity models a useful approach is to implement procedures for clustering accumulated trajectory data into representative patterns (Braun *et al.*, 2010).

We will ultimately have to break down behavioural sequences into their smallest



identifiable units, and quantify them in terms of trajectories of body parts, their speed, distance, acceleration, deceleration etc., thereby identifying behavioural prototypes (Braun *et al.*, 2010) that can subsequently be strung together into various sequences to reconstruct meaningful natural behaviour. To encode the variability of the behavioural repertoires, it will be necessary to develop a dedicated alphabet and syntax of movements that can be effectively compared between individuals and species. An automated 'data mining' approach will also facilitate the discovery of new behaviour patterns that have so far escaped the attention of human observers.

In this bottom-up approach, we are, at the early stages, less focussed on one particular concept, but we are also much freer to observe the peculiarities of the animals' behaviours. Insect behaviour, in all its diversity, is unlikely to be wholly describable by the concepts that are derived from just one, very unusual species, *Homo sapiens*. By looking at many more animal species, under more test conditions, and by testing many, and smaller, i.e. more basic criteria (cognitive or behavioural units), we probably could build psychological constructs that are more independent from the human world and therefore, ultimately, more meaningful.

It is clear that such an approach cannot stand on its own, and needs to be coupled with experimental manipulation which in turn needs to be hypothesis driven. Learnt behaviours can only be tested in meaningful ways by exposing animals to controlled stimuli, and these cannot be generated in a hypothesis free manner. Additionally, learning may generate a practically infinite number of behavioural routines, which might be difficult to pick up in clustering algorithms – consider, for example, that the diversity of flower handling procedures required of a generalist pollinator to extract nectar or pollen is presumably as great as the number of floral morphologies. Nonetheless

these might consist of small-scale hardwired motor routines strung together in flexible ways (Gould and Marler, 1984). Again, we would only pick this up by breaking down behaviour into small components, using methods as described above.

### ***Bottom-up approaches to cognition from neuroscience***

While the fully automated, bias-free analysis of behaviour is now becoming increasingly feasible, this is less straightforward with cognitive processes that might or might not have observable outcomes. There is no question that hypothesis driven behavioural experiments are a necessary ingredient of studying animal cognition (although the hypotheses might more suitably be driven by the motivation for scientific enquiry rather than for confirming that animals are clever). Nonetheless there is plenty of room for more bias-free approaches in the study of cognitive approaches as well. We need to understand the neural circuitry that underpins cognitive processes in more detail, not just because we really still do not understand how the brain works, but also to understand the evolution of cognitive capacity. 'Intelligence' is not a biological trait that can be mapped onto an evolutionary tree in any meaningful way. We need to know how many neurons (and with which connections) are engaged in any defined cognitive feat and how many sequential stages of information processing there are. Insects' small nervous systems should make it feasible to explore these questions at a very fine-grained level.

The quest for understanding the precise neuron-to-neuron connectivity underlying cognitive processes can be addressed both from an empirical angle, as well as from a modelling perspective. Multi-electrode recordings provided profound insights into how the brain stores and organises memories in the rodent hippocampus in the 1990s (Wilson and McNaughton, 1993; McNaughton *et al.*, 1996) and the number of cells recorded from simultaneously (>

100 in some cases) is impressive, and contributed substantially to the understanding of the neural ensemble code of the mammalian hippocampus. Although the settings in which the data are recorded are of course hypothesis driven, their subsequent analysis is largely data-driven, in that information contained about individual neuronal firing patterns, and their propagation and intergration needs to be extracted from the raw data by data mining processes. The adaptation of such techniques for insects could generate a much more comprehensive picture of ensemble neural code of any one brain area in insects than in mammals. A recent neuroanatomical study, for example, succeeded in identifying and mapping 16% of the ~100,000 neurons of the *Drosophila* brain (Chiang *et al.*, 2010), illustrating just how far we have progressed in understanding the full circuitry of insects' brains. Technology for multielectrode recording has already been adapted for use in insects (Du *et al.*, 2009; Bender *et al.*, 2010) but has yet to be tested on problems related to cognition. Other recent developments make the imaging of entire neural circuits, and possibly whole brains at micron resolution, increasingly feasible (Dodt *et al.*, 2007; Jahrling *et al.*, 2010). It is quite conceivable that, as such technologies develop, we will discover neural-computational solutions to cognitive tasks in insects (and other animals) quite unlike those in primates (even where the behavioural outcomes might be similar).

Neural network modelling can provide useful pointers for neuroscientists to concentrate their efforts on what to explore, and here, too, a more open-ended approach is needed. Often, modellers search for a single computational solution that best explains an empirically determined phenomenon. An alternative approach would be an emphasis on diversity – for example, for a given cognitive problem, how many neural solutions might be generated, and how does this depend on

the number of available neurons (and their connections)? Circuit functionality can be assessed by varying all parameters in discrete steps, and keeping a complete record of simulation results, including the output for each varied parameter value under all combinations of parameter settings, as has been done in simulations to derive optimal colour coding systems (e.g., Chittka, 1996) where thousands of systems were analysed. In conclusion, because the bottom-up approach reduces the importance of introspection for the “verification” of psychological constructs, it could contribute to create a more objective, more independent, and less arbitrary methodology.

### ***Bottom-up approaches in terminology***

At present, the plurality of definitions of psychological constructs seems to make positive results relatively easy to obtain when looking for human-like behavioural complexes in animals. However, as demonstrated above, this situation creates both confusion and room for exaggerated conclusions. As a first measure for more clarity we therefore suggest to increase the *diversity of terms* (each with a precise meaning), rather than a multitude of meanings attached to each of a few grand words. If findings do not fit under the umbrella of a particular and established cognitive construct they may still be close by and deserve a novel term. This is certainly better than repeatedly (and more or less forcefully) adjusting the size of the umbrella.

Consider, for example, Franks and Richardson's (2006) claim to have found an instance of ‘teaching’ in ants, explaining (correctly) that the behaviour they observed met or indeed exceeded the criteria for teaching as defined for other animals. However, the behaviour had already been described 30 years earlier (Hölldobler *et al.*, 1974; Möglich *et al.*, 1974), and its function had been (at least in part) revealed. Indeed the behaviour

had been given a name, ‘tandem running’, that emerged directly from what the authors observed, and which appropriately described the activity without making inferences about its function. The main advance by Franks and Richardson (2006) is in discovering that the behaviour fulfils the criteria for teaching as defined by Caro and Hauser (1992), although it is evident that these criteria have been adjusted to allow the term teaching to be expanded to animals and fall far short of how one would define teaching in the human realm (Leadbeater *et al.*, 2006). The scientists who originally discovered the behaviour labelled it exactly as we advocate here: they gave it a ‘bottom-up’ term, whereas (Caro and Hauser, 1992) started in a typical top-down fashion – adapt the definition of an established behaviour in humans so that it includes animals, then find animals that match the definition.

There are more risks here than just those related to sensationalism of inappropriate terminology. In some cases, permissive terms are misconstrued as being biological traits that one might map onto phylogeny. Following on from the (clearly rather inclusive) definition of teaching by Caro and Hauser, (1992), Hoppitt *et al.*, (2008) set out to investigate the taxonomic distribution of the phenomenon. They write: “Teaching was regarded as a uniquely human faculty. However, recent studies suggest that teaching might be more common in animals than previously thought.” – well, yes, but that is a result of broadening the meaning of the term so as to include many forms of animal signalling. The authors then note the “bizarre taxonomic distribution” of teaching, but the problem is that a colloquial term like teaching (like ‘intelligence’, or ‘speed’) is, quite simply, not a biological character that can be studied in evolutionary terms. Conversely, bottom-up terms, such as ‘tandem running’ or ‘bee dance’ that are designed to describe specific behaviour patterns, are accessible

to phylogenetic analysis. Words from the human cognitive world are unlikely to be sufficient for analysing all animal cognition and behaviour, and sticking to the human world terms will most likely impede progress, because it will just not leave enough freedom to capture novel processes. The recommendation would be to let terms emerge from patterns observed in the data themselves. In short: first the data, then the words.

### ***Consideration for Reporting Hypothesis Building and Validation***

In the task to avoid over-restriction or narrowness of psychological constructs (such as ‘personality’) that seem to limit the potential achievements of the current top-down approach, much can be learnt from the psychological sciences. The first thing to acknowledge is that the construction of the concept – the definition, as it were – is part of the *methods*, rather than an issue that can be safely put away into the *introduction* as something given. The bottom-up approach in animal cognition would need more effort invested in the development of such methods. But also within the top-down approach, a critical consideration of its methods could be possible (Hare, 2001; Sarter, 2004). The essential methodological tool that would be useful in both domains is a *validity* test.

*“The construct validity of a psychological assessment instrument refers to the extent to which the instrument measures a particular construct, or psychological concept, such as anxiety ...or intelligence. [...] it involves a network of investigations [...] designed to determine whether an assessment instrument that purportedly measures a certain psychological variable is actually doing so.”* (Aiken, 2000, p. 95)

Investigating the validity of a test for a cognitive construct is not an easy task, especially when dealing with animals,

because one of the most targeted tools for determining validity is barred from zoology, the in-detail and direct questioning of examinees “*about their responses to a test in order to reveal the specific mental processes involved in responding to the items...*” (Aiken, 2000, p. 95). However, there are other approaches to test the validity of an instrument that claims to reveal a cognitive construct. These include the (documented) judgement of experts about the relationship between the contents of the test instrument and the construct, as well as experimental studies that link the construct test instrument to external variables. One particularly interesting tool in the validity test tool box is *discriminant validation*, which compares how the same instruments (methods) measure different psychological constructs. It can be expected that tests of psychological constructs in animal cognition science would greatly benefit even from “quick and dirty” validity tests and that such tests might form an important tool to detect over-restriction in psychological constructs.

## Conclusion

Currently, many studies seem to ask to what degree animals (including insects) have cognitive properties that can be likened to human cognition. We suggest that the question, at present, is as difficult to answer as it is unimportant, at least in the insects. Looking for cognitive homologies between humans and their closest relatives is useful to understand the evolution of cognitive traits, although unless we know the underlying circuitry, and have good estimates about how quickly cognitive traits might evolve, the possibility of convergence needs to be considered even in such comparisons between close relatives.

More broadly, we will not be able to answer the question of how cognitive abilities are distributed in the animal kingdom, and how they evolved, if we

allow too many or too strong research biases, or terminological inaccuracies. These biases rest on the current scientific reward system that strongly favours studies with a sensational slant that can bring animal behaviour closer to human experience. Such a system invites usage of grand words with narrow definitions, to concentrate on the smart animals, and to report only positive results. The proposed approach for animal cognition and behaviour science would solve the problems of the positive results bias and the smart-animal bias, because it does not create failures in the results, as all possible results are equally positive. Clearly, an approach that is *only* bottom-up would not lead us very far, but a careful combination of both approaches could be very powerful indeed. As Francis Bacon points out in the *Novum Organum* (1620), the bee combines the best of both worlds: “*Empiricists, like ants, merely collect things and use them. The Rationalists, like spiders, spin webs out of themselves. The middle way is that of the bee, which gathers its materials from the flowers ... but then transforms and digests it by a power of its own.*”

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# 一定要把昆蟲想成人類那樣嗎？

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## 摘 要

過去二十年來已有大量的資料在探討昆蟲的認知功能，即使昆蟲腦中的神經迴路是如此之小，也已有相當令人滿意的成果。然而近年的一些研究聲稱昆蟲存在「教導」、「文化」、「意識」或「性格」，科學家們開始著手探索動物的擬人行為，似乎涉及了相對限制性由上而下的方法。此方法容易導致術語的歧義性，由於這些術語出自人們的經驗，往往產生了比在動物世界中有限制條件試驗下可被允許的現象更複雜的含義。此結果也將承擔因主觀選擇或重新塑造了定義與測試標準所造成的後果之風險。最後，假說驅動的方法容易導致研究偏差被忽略，例如報告主要著重於正面的結果或以「聰明」的動物為主要研究對象。我們建議現行的方法需要加入互補性作法加以補充，以自動化程序進行行為的分類，透過由下而上的方法做更進一步的探索，在更廣範的動物行為多元數據分析後，也將揭露動物的心理構念，當然在研究方法中我們也必須注意我們是如何得到定義的。

**關鍵詞：**歧義、獨斷、行為、認知、方法、術語。

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