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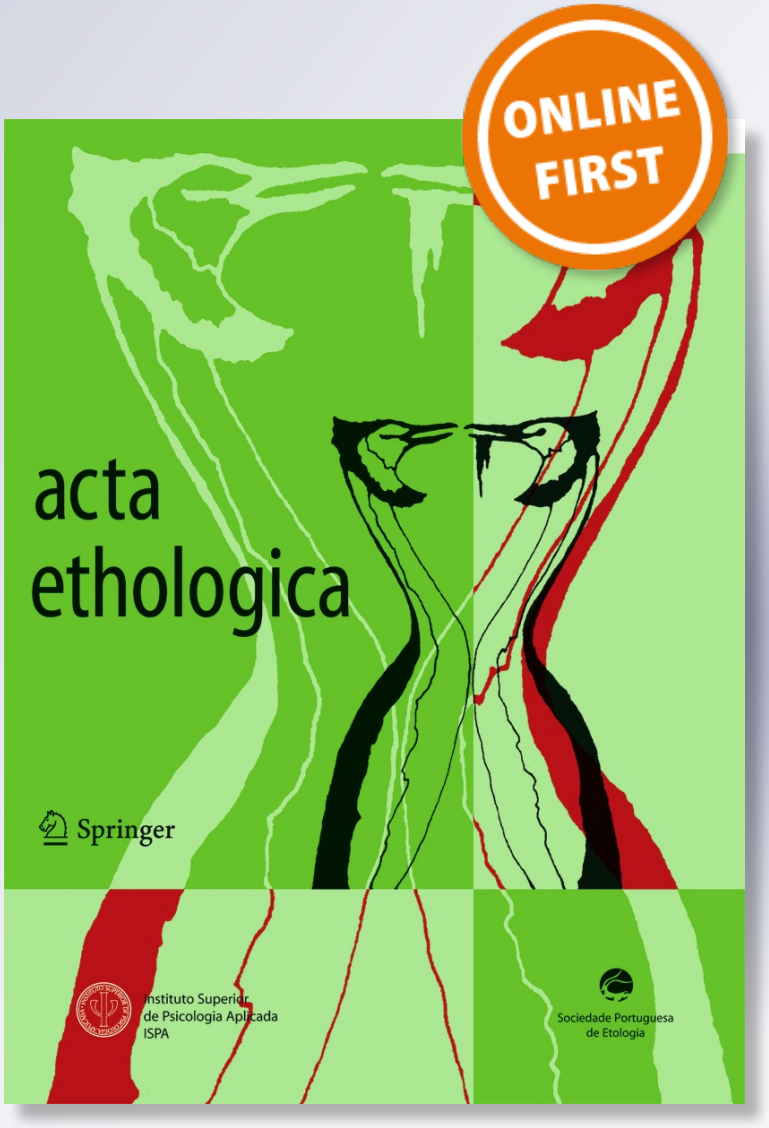

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COMMENTARY

Complexity in animal behaviour: towards common ground

Hélène Cochet · Richard W. Byrne

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Abstract The ambiguity of the term 'complex' in studies of animal behaviour and cognition can lead to theoretical and methodological disputes, as there seems to be little common ground regarding the features thought to introduce complexity. Based on examples not only in human and nonhuman primates but also in some species of birds, we explore three dimensions of complexity: motor precision, coordination, and anticipatory planning. We argue that it is necessary to identify which dimensions are present in each study to formulate and explore relevant questions in behavioural sciences, especially with an evolutionary perspective.

Keywords Complexity · Animal behaviour · Cognition · Evolution

The use of the adjective *complex* is increasingly common in the literature on animal behaviour and seems to cover a wide range of meanings in different species. Consider, for example, whether the 'complexity' cited by the original researchers was in any way the same thing in these three cases: vocal learning in some species of birds (e.g. Jarvis et al. 2000), following pointing signals (e.g. in crows, Taylor et al. 2010; in dogs, Elgier et al. 2012), and symbolic conceptual reasoning (e.g. Seed and Tomasello 2010). These few examples show that there is little common ground to understand the term *complexity* in the field of animal behaviour and cognition. Most of the time, ill-defined claims of complexity are made, more or less consciously, to champion the cognitive abilities of one's particular species. This becomes particularly problematic when researchers wish to use the comparative method to deduce evolutionary history and need to compare disparate sorts of animals: for instance, making comparisons between corvids, apes, and cetaceans (e.g. Emery and Clayton 2004; Marino 2002; Marino et al. 2007; Van Horik et al. 2012). There have been previous attempts to measure complexity on a single scale, for instance, by counting components (Sambrook and Whiten 1997) but here we argue that it may be necessary to describe complexity along several different dimensions. Identifying explicitly which dimensions are examined in each study should allow researchers to go beyond the often fruitless opposition of simple vs. complex mechanisms, which seems to have replaced the opposition of lower vs. higher cognition current in the mid-19th to the mid/late-20th century.

Too often, *complex cognition* is treated as an 'explanation' of behaviour that can apparently not be explained by associative processes; this categorization, generally implicit, tends to result in a heterogeneous category in which the complexity is of many different sorts. Moreover, it is difficult to disentangle the cognitive nature of these mechanisms since they are not directly palpable, especially in species that do not use language. Incomplete knowledge of animal behaviour and cognition may lead scientists to accept hypotheses because they are simpler to comprehend than alternative accounts (e.g. Heyes 1998), and sometimes, the possibility cannot be excluded that tasks characterized as complex are solved by taking advantage of a given species' gene pool or by learning task-specific responses in a situation rather than by applying general cognitive principles (see Byrne et al. 2013).

Focusing mainly on data in primates and birds, we describe here three key dimensions of complexity (which are not

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necessarily exhaustive), namely complexity in *motor precision*, complexity in *coordinating* activities or information, and complexity in *planning*. We review several studies in the recent literature, illustrating both individual and social activities and show that behaviour sometimes involves several dimensions of complexity.

Complexity in motor precision

The difficulty of any motor behaviour is tightly linked to the degree of accuracy required for a specific activity and the speed with which it can be done (Fitts 1954) but there is no clear consensus on the characteristics that define motor skills as complex. For example, complexity has been claimed to lie in 'exceptionally precise and rapid control of musculature' (birdsong, Tumer and Brainard 2007), in fine control of hand and finger movements in humans (and more specifically in using fingers in 'a nonconsecutive and non-repetitive order', Gerloff et al. 1998), and motor skills have also been characterized as complex, without any explicit definition, in invertebrates (Sanes and Donoghue 2000).

However, what makes a task difficult is likely to vary with the species under study and the activity considered. Motor skills are generally measured through the capacity to perform a specific task, in terms of efficiency (e.g. success rate across trials) or speed of movements. Complex motor actions mainly involve fine motor abilities, in particular, manual dexterity. Dexterity is usually assessed in a laboratory, for example, in peg-moving tasks (Annett 1970) or dot-tapping tasks (Tapley and Bryden 1985). The motor skills required to move dowel pegs quickly from one row of holes to another row are also primarily governed by genetic factors (the rate of learning being also significantly heritable, e.g. Fox et al. 1996), which emphasizes the relatively automatic level of variation at which behaviour is sometimes referred to as complex. This adjective thus does not seem very enlightening when it describes motor behaviour and should be used, if ever, with some caution.

Complexity in motor precision can also be highlighted at a social level, i.e. when more than one individual is involved. Adjusting to another person's body or hands may necessitate fine motor precision (see Table 1), although little research has been conducted on this question.

In addition to the ability vs. inability to perform motor tasks and the speed of performing them, considering a specific example reveals another dimension of complexity: the degree of precision needed to hold and manipulate small objects requires the ability to coordinate the thumb and the index finger to form a *precision grip* (Napier 1956), an ability that develops in human infants at the end of the first year. A key aspect of complexity may thus be based on the notion of coordination, which we consider next.

Complexity in coordination

Manual skills may involve being able to integrate and coordinate several elements together; for many complex actions, coordination may represent a key feature of skill. For instance, activities requiring the coordination of the two hands, especially when the latter plays highly differentiated roles (e.g. striking a match with one hand while holding the box with the other hand), have been characterized as complex in human and nonhuman primates (e.g. natural foraging, Byrne and Byrne 1993; the tube task, Fagard and Marks 2000; Hopkins et al. 2005).

Complexity in coordinated actions has been indicated in tool manufacture and tool use, in great apes (e.g. in chimpanzees, 'design complexity in termite-fishing tools', Sanz et al. 2009) and also in several species of birds (e.g. in cockatoos, 'complex tool innovations', Auersperg et al. 2012; in crows, 'complex behaviour such as tool manufacture' Kenward et al. 2005). Here, complexity has been defined as 'the degree of transformation necessary to produce a functional tool from the raw material' (Kacelnik et al. 2006, p. 7); different degrees of complexity can thus be distinguished, starting from the use of unmodified objects. Multistep tool-making most likely involves the highest level of coordination: adding, combining, or restructuring material to act on a specific target may even require some causal understanding of the relationships between different objects (e.g. Vaesen 2012). Moreover, the emergence of coordination skills in tool use and tool manufacture has long been hypothesized to play a key role in human evolution, in particular during the Paleolithic lithic revolution (e.g. Steele 1999).

In addition, chimpanzees have been reported to use several different tools successively: each tool specialized for a specific purpose. The use of such 'complex tool sets' (Boesch et al. 2009) may reflect *sequential coordination*: where the necessary starting conditions for applying one tool must first be realized by applying another different tool. Coordination here extends over time rather than space. Sequential coordination is also involved in other activities, such as choosing one's route to go from one place to another, when several route segments—each learned separately through experience—are coordinated into a novel route.

Social interactions may also require coordination. In numerous animal species, individuals adjust their own behaviour to others' actions. Interindividual coordination may reach a higher degree of complexity when intentional and referential signals are directly addressed to specific individuals who can interpret these signals and respond by moderating their behaviour accordingly. Joint attention skills are a typical example of such coordination, whether they involve body-orienting, eye-gazing, pointing, or verbal indications. Joint attention has mainly been reported in the human species (e.g. in young children, Liszkowski et al. 2004), but not

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Table 1 Illustration of the three dimensions of complexity expressed from individual and social perspectives

	Individual	Social
1. Motor precision	Accuracy and speed in positioning hand(s) with fixed environment (e.g. Peg-moving task in humans: Holper et al. 2009)	Accuracy and speed in positioning hand(s) with other person's body or hands (e.g. playing skipping rope: one person turns the rope, which is anchored at the other end, while another jumps)
2. Coordination	Coordination of the two hands (e.g. gorilla nettle-leaf folding, Byrne and Byrne 1993; the tube task in primates, Vauclair et al. 2005) Coordination of two fingers (e.g. transferring item to lower fingers to enable precision grip to be used between index finger and thumb while still holding items, Connolly and Dalgleish 1989 in human infants; Byrne et al. 2001 in gorillas) Coordination over time (sequential coordination): performing a sequence of action to reach a specific goal (e.g. cooking in humans, honey extraction from bee nests in chimpanzees, Boesch et al. 2009)	Adjusting to others' behaviour (e.g. playing tennis, playing skipping rope: two people turn the rope while one or more persons jump; collaborative interactions in social games in gorillas, Tanner and Byrne 2010)
3. Anticipatory planning	Mentally reviewing an intended action sequence to anticipate a future need (e.g. shopping without a list in humans to cook a specific dish, making termite-fishing tools in advance of need, Goodall 1986; Byrne et al. 2013)	Intention-reading abilities, rational imitation, pedagogical teaching (in human infants, Bellagamba et al. 2006; Gergely et al. 2002)

exclusively (e.g. in magpies, Kaplan 2011; in gorillas, Tanner and Byrne 2010).

However, as we mentioned in the introduction, we still need to determine to what extent the complexity of coordination, both at the individual and social levels, lies in cognitive processes yet to be deciphered. For example, nest building has been argued to require complex cognition (in birds, Healy et al. 2008) and engineering skills (in orang-utans, Van Casteren et al. 2012) but complexity of manufacture does not always imply complexity of cognition, and it is actually challenging to demonstrate the cognitive aspects of these behaviours. Similarly, the ability to integrate and adjust to others' actions does not necessarily require any understanding of others' knowledge or intentions. In those cases where tool-use activities *do* require anticipation of causal consequences or social coordination requires taking account of other's mental states, we must consider another dimension of complexity altogether, which we consider below.

Complexity in planning

With many activities, even those involving tool-use or tool-making, it is a moot point whether they can be fully explained as being driven by individuals' current perceptual assessment of a particular context or require postulation of the ability to represent the relationship between a sequence of actions and a specific goal (e.g. Wimpenny et al. 2009). But in some cases, it is clear that representation is involved when there is evidence of some assessment of the whole problem in advance of action, such as making or selecting an appropriate tool well before the place and time of use. This requires another dimension of complexity: *anticipatory planning capacity*. Future-oriented behaviours have long been considered to be uniquely human (and they have been widely studied in our species, e.g. Friedman et al. 1987) but nonhuman primates (e.g. Byrne 1998; Byrne et al. 2013; Mulcahy and Call 2006; Osvath 2009) and several species of birds have been reported to anticipate future need states by shaping and selecting tools (in rooks, Bird and Emery 2009; in New Caledonian crows, Kacelnik et al. 2006) or making food provision (in jays, Raby et al. 2007) depending on their future needs and purposes. The manufacture of different tools in goal-directed activities may reveal knowledge about these situations and planning abilities and have been argued to demonstrate 'high intelligence' (in wild chimpanzees, Sugiyama 1997). The fact that tool selection is influenced by environmental factors such as nut resistance (e.g. Luncz et al. 2012; and see Walsh et al. 2010 for a similar argument for bird nest building) has also been used as an argument supporting the complexity of this behaviour.

When we consider interindividual interactions, anticipatory planning skills imply the ability to predict another person's behaviour, potentially underwritten by the ability to discern and represent that person's knowledge and intentions. Mentalizing skills have been argued to characterize the human species, developing from the second and third years of life (e.g. Bellagamba et al. 2006; Kawakami et al. 2011). Although nonhuman primates are able to cooperate in experimental situations involving food competition, they do not seem to use cues that would reveal mutual understanding of

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each other's intentions (e.g. Bullinger et al. 2011). Other researchers have reported planning abilities in a tool-use task but not in an exchange task in chimpanzees (Dufour and Sterck 2008), suggesting that the capacity to mentally represent a situation sufficiently to allow anticipatory planning may be limited to nonsocial contexts.

However, the interpretations associated with the question of goal-directed behaviours and mental representations vary widely depending on the authors: results may be explained in reference to socio-cognitive skills, even 'rudimentary mind-reading' (in corvids, Seed et al. 2009), while less cognitively complex strategies may be invoked by other researchers (Vasconcelos et al. 2012). Conventional learning, which can rely on social learning in addition to the possibility of training in captive subjects, has been repeatedly opposed to more abstract forms of reasoning like anticipatory planning, in particular for nonhuman animals (e.g. Raby and Clayton 2009; Tebbich and Bshary 2004), and these learning processes do not necessarily imply a plan computed beforehand via a mental representation of a given situation. We clearly see here the need for explicit definitions of core concepts related to cognition. The strict distinction between goal-directed behaviour and future planning, along with the investigation of several plausible accounts of the latter behaviour (see Dickinson 2011, for a description of mnemonic-associative theory and mental time travel account), may be important directions to consider.

Conclusion

The term *complex* is misleadingly ambiguous, used to describe sequences of actions (e.g. tool manufacture), communicative signals (e.g. Ord and Martins 2006), and specific behaviours likely to involve mental processes (e.g. joint attention). We argue that this ambiguity can be greatly reduced by teasing out three dimensions: motor precision, coordination, and planning, each of which may involve individual and/or social activities (see Table 1). The complexity of a given mechanism/behaviour can be assessed by distinguishing which of these three dimensions are involved and to what degree. Moreover, although the distinction of several dimensions of complexity can clarify our understanding of animal behaviour and cognition, it is important to keep in mind that some activities involve more than one dimension. These independent aspects of complexity being potentially additive, social activities which involve motor precision, coordination, and anticipatory planning would thus represent greater complexity. For example, nut-cracking in chimpanzees necessitates not only manual precision in aiming and the coordination of the two hands (see Sections 1 and 2) but also the anticipation of a sequence of actions to feed from the nut, therefore, combining several dimensions of complexity. Several animal species show complex behaviour measured in this way, with perhaps the greatest cognitive challenge arising from interactions, including those between predator and prey but particularly those conspecific interactions requiring the ability to reason cooperatively with others (e.g. Byrne and Bates 2010). However, the planning abilities that characterize human cognition, reflected in particular in intentional communication and cultural learning, may represent an even more challenging form of complexity (Seed and Tomasello 2010).

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