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Essay

Transforming the body-only system into the body-plus-tool system

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The traditional definitions of tool use typically operationalize the functionality of an object and the effect of its use on the environment and, typically, do not account for the dynamic relation among the body, task and environment that result in actions with a tool. This omission severely restricts the utility of these definitions for comparisons of tool use behaviour across individuals, populations and species. To address this issue, we propose an embodied theory of tool use based on the premise that a tool transforms the body-only system into the body-plus-tool system. It (1) explains the development of a tool use behaviour in terms of constraints on the development of tool use movements imposed by different features of the body, task and environment, (2) measures the dexterity of an actor in terms of the spatiotemporal organization of tool use movements that optimize at least one composite performance outcome variable and (3) measures the complexity in the use of a tool in terms of the control of the biomechanical degrees of freedom of the body-plus-tool system. Such an embodied theory of tool use is applicable across species, tasks and environments.

The use of tools is the foundation of human technology; humans use tools in diverse contexts to modify their environment and expand their niche (Gibson & Ingold, 1993). Tool use is not a uniquely human trait, as many nonhuman animals also use tools (reviewed in: Beck, 1980; Sanz, Call, & Boesch, 2013; Shumaker, Walkup, & Beck, 2011). The long-standing interest of ethologists towards studying the use of tools by nonhuman animals has been fuelled mostly by the enduring question about its evolutionary origins. The understanding of tool use behaviour in nonhuman animals is shaped by concepts addressing what constitutes a tool use behaviour; until now, all judgments have been based on the use of an object aimed at altering the environment. Below is a list of a few definitions that have framed studies on animal tool use in the ethological literature over the past four decades.

Definitions of Tool Use

(1) The 'use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal' (van Lawick-Goodall, 1970, page 195).

(2) The 'manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object' (Alcock, 1972, page 264).

(3) The 'external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool' (Beck, 1980, page 10).

(4) The 'exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment' (St Amant & Horton, 2008, page 1203).

(5) The 'external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool' (Shumaker et al., 2011, page 10).

All these definitions assess whether the use of an object constitutes tool use behaviour based on the functionality of that object and how its use affects the environment. Most descriptions of tool use or tool-use-like behaviour in nonhuman animals framed on these definitions are of a limited value, as (1) they provide a teleological (teleological because they explain a behaviour based on its

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outcome) account of what constitutes a tool and what constitutes tool use behaviour, (2) they do not analyse the movements constituting tool use behaviour, nor do they elucidate which morphological and anatomical features of the body aid in executing these movements and (3) they do not consider different features of the environment that influence the use of tools. Consequently, identifying common elements in the use of tools among individuals, populations and species has remained difficult, limiting their value for understanding the developmental and evolutionary origins of tool use as well as the phylogenetic distribution of different forms of tool use.

Integrating Concepts from Embodied Cognition, Biomechanics and Development to Advance Research on Tool Use

Scientists have increasingly incorporated into models of cognition the notion that organisms have a body and that they inhabit an environment and, thus, that their behaviour is ecological, that is, that their behaviour emerges from the interaction between their body and the environment (Barrett, 2010; Chemero, 2009; Clark, 1997, 1999, 2008; Shapiro, 2010). Gibson's (1979) conception of the cyclic integration of perception and action laid the foundation for an ecological approach to studying behaviour; according to this approach, the body of an individual (beyond the brain), the environment and the complex interplay between the body and environment strongly influence the cognition of that individual, implying that cognition is embodied. It follows from the embodiment of cognition that tool use is embodied, with actions grounded in the musculoskeletal system and perception–action routines, and not anticipatory, with actions divorced from the task and environment.

Human movement science exploits the fact that physical laws and different features of the body, task and environment collectively impose constraints on movements in action. Physical laws impose mechanical and biomechanical constraints; the body imposes morphological, anatomical and physiological constraints. The task imposes ergonomic and goal-related constraints. The environment imposes universal constraints, such as gravity, and local constraints, such as the availability of specific raw materials usable as tools, both of which affect task performance. Finally, the (speed–accuracy–precision) demands of the task dictate how movements in action respond to constraints imposed by physical laws and different features of the body and environment (Newell, 1986). This constraint-based approach to movements in action complements Lockman's (2000) view: a tool use behaviour entails a gradual process of exploration and discovery that leads to perceptual learning, exploits the relations among objects and surfaces in the environment and encompasses only species-typical movements. Eventually, an individual develops ‘dexterity’ when it becomes sensitive to the outcome of its actions; dexterous movements exploit the affordances of a situation in an optimal manner. Thus the optimization of resources (e.g. space–time and energy) acts as an index of dexterity, and the dynamics of the optimization process reflects the learning process itself (Bernstein, 1967).

Biomechanics is the study of movements based on the fact that each vertebrate body is a complex system of segments linked by joints, with each joint having one to six degrees of freedom (henceforth, DoF; Bernstein, 1967). Each DoF allows translational movement along a plane or rotational movement about an axis (e.g. the elbow joint in humans allows two DoFs, and the shoulder joint allows three DoFs). A tool alters the boundary between the body and environment by transforming the body-only system into the body-plus-tool system; it adds at least one external DoF to the system along with reducing and redistributing the existing DoFs (e.g. holding a screwdriver in the hand adds one DoF between the hand and the screwdriver and redistributes the DoFs of the hand-only system by coupling the palm and digits into a rigid structure that supinates and pronates as a unit). In this way, using a tool poses the challenge of perceiving and responding to changes in the DoFs of the body-only system by identifying the relations among the DoFs of the body-plus-tool system and then monitoring and responding to these relations (Smitsman, 1997, 2005; Smitsman & Cox, 2008). It follows that the use of an object qualifies as tool use behaviour from a biomechanical standpoint only if its user controls the DoFs of the body-plus-object system differently compared to the body-only system.

A BIOMECHANICAL ANALYSIS OF TOOL USE BEHAVIOUR IN NONHUMAN ANIMALS

If the uniqueness of a tool use behaviour is contingent upon how individuals control the DoFs of the body-plus-tool system differently compared to the body-only system, an analysis of a behaviour of interest constituting the use of an object must account for the dynamics of the movements of the body-plus-object system. Furthermore, identifying how different features of the body, task and environment impose constraints on the dynamics of tool use movements can potentially lead to testable predictions about which features of a tool use behaviour should be species-specific and which features should be common across species based on commonalities in their body and environment. In the following section, we analyse behaviour of nonhuman animals that scientists commonly identify as tool use behaviour based on the functionality of an object and the effect of its use on the environment, as reviewed by Shumaker et al. (2011). For each behaviour, we analyse whether individuals control the DoFs of the body-plus-object system differently compared to the body-only system and explain how constraints imposed by different features of the body, task and environment on the dynamics of the movements of the body-plus-object system may shape that behaviour. Subsequently, we identify the elements common to these behaviours to sketch the outlines of an embodied theory of tool use.

Probing by New Caledonian Crows

New Caledonian (henceforth, NC) crows, *Corvus moneduloides*, manufacture and use probes to extract wood-boring beetle larvae from crevices in branches (Bluff, Troscianko, Weir, Kacelnik, & Rutz, 2010; Hunt, 1996; Hunt & Gray, 2004). Likewise, capuchin monkeys, *Sapajus* spp. (Mannu & Ottoni, 2009; Souto et al., 2011) and chimpanzees, *Pan troglodytes* (Boesch, Head, & Robbins, 2009; Sanz & Morgan, 2007; Suzuki, Kuroda, & Nishihara, 1995), manufacture and use probes to capture termites and other insects and to extract honey. We focus the following discussion on NC crows as data on several aspects of the probing behaviour, such as the manufacture of hooked probes (Hunt & Gray, 2004) and the effective use of hooked probes (Holzhaider, Hunt, Campbell, & Gray, 2008; St Clair & Rutz, 2013), is available only for NC crows.

NC crows may control the DoFs of the beak-plus-probe system differently than the beak-only system. Alternatively, the probe may not affect the number and organization of the DoFs of the beak-only system. Based on the DoF framework, we reason that probing is a tool use behaviour. Our reasoning is as follows: holding a probe in the beak adds one or more DoFs between the beak and the probe and redistributes the DoFs of the beak-only system by coupling the lower and upper jaws into a rigid structure that moves as a unit. Hence, the probe is a tool.

Wild NC crows manufacture hooked probes from twigs and stepped-cut (barbed) probes from the leaves of screw pines, *Pandanus amaryllifolius*, to extract wood-boring beetle larvae from