University of Groningen

On the psychological origins of tool use

Mangalam, Madhur; Fragaszy, Dorothy M; Wagman, Jeffrey B; Day, Brian M; Kelty-Stephen, Damian G; Bongers, Raoul M; Stout, Dietrich W; Osiurak, François

Published in:
Neuroscience and Biobehavioral Reviews

DOI:
10.1016/j.neubiorev.2022.104521

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2022

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Mangalam, M., Fragaszy, D. M., Wagman, J. B., Day, B. M., Kelty-Stephen, D. G., Bongers, R. M., Stout, D. W., & Osiurak, F. (2022). On the psychological origins of tool use. *Neuroscience and Biobehavioral Reviews*, *134*, Article 104521. https://doi.org/10.1016/j.neubiorev.2022.104521

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment.

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Download date: 20-09-2023

Neuroscience and Biobehavioral Reviews 134 (2022) 104521

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

On the psychological origins of tool use

Madhur Mangalam [a,*], Dorothy M. Fragaszy [b], Jeffrey B. Wagman [c], Brian M. Day [d], Damian G. Kelty-Stephen [e], Raoul M. Bongers [f], Dietrich W. Stout [g], François Osiurak [h,i]

[a] *Department of Physical Therapy, Movement and Rehabilitation Science, Northeastern University, Boston, MA 02115, USA*
[b] *Department of Psychology, University of Georgia, Athens, GA 30602, USA*
[c] *Department of Psychology, Illinois State University, Normal, IL 61761, USA*
[d] *Department of Psychology, Butler University, Indianapolis, IN 46208, USA*
[e] *Department of Psychology, State University of New York-New Paltz, New Paltz, NY 12561, USA*
[f] *Department of Human Movement Sciences, University Medical Center Groningen, University of Groningen, 9713 GZ Groningen, Netherlands*
[g] *Department of Anthropology, Emory University, Atlanta, GA 30322, USA*
[h] *Laboratoire d'Etude des Mécanismes Cognitifs, Université de Lyon, Lyon 69361, France*
[i] *Institut Universitaire de France, Paris 75231, France*

ARTICLE INFO

Keywords:
Affordance
Dexterity
Perception
Technical reasoning
Tooling

ABSTRACT

The ubiquity of tool use in human life has generated multiple lines of scientific and philosophical investigation to understand the development and expression of humans' engagement with tools and its relation to other dimensions of human experience. However, existing literature on tool use faces several epistemological challenges in which the same set of questions generate many different answers. At least four critical questions can be identified, which are intimately intertwined—(1) What constitutes tool use? (2) What psychological processes underlie tool use in humans and nonhuman animals? (3) Which of these psychological processes are exclusive to tool use? (4) Which psychological processes involved in tool use are exclusive to *Homo sapiens*? To help advance a multidisciplinary scientific understanding of tool use, six author groups representing different academic disciplines (e.g., anthropology, psychology, neuroscience) and different theoretical perspectives respond to each of these questions, and then point to the direction of future work on tool use. We find that while there are marked differences among the responses of the respective author groups to each question, there is a surprising degree of agreement about many essential concepts and questions. We believe that this interdisciplinary and intertheoretical discussion will foster a more comprehensive understanding of tool use than any one of these perspectives (or any one of these author groups) would (or could) on their own.

1. Introduction

The ubiquity of tools in human cultures since the origin of the genus *Homo* has provoked enduring philosophical inquiries into humans' engagement with tools (Gibson and Ingold, 1994), in part because tool use is often considered to reflect a unique dimension of technical intelligence (Preston, 2012). Aristotle wrote more than 2000 years ago, "The hand can become a claw, a fist, a horn or spear or sword or any other weapon or tool. It can be everything because it can grasp anything or hold anything" (Aristotle, The Animal Parts (IV, 10)). Today, anthropologists, ethologists, psychologists, and neuroscientists investigate the development and expression of humans' engagement with tools in relation to other dimensions of human experience, and the increased efficiency and complexity of tool use in human populations over generations (Boyd and Richerson, 1996; Osiurak and Reynaud, 2020a; Tomasello et al., 1993). The origin of this phenomenon, called cumulative technological culture, was judged in 2005 by the journal Science as one of the 125 big scientific questions of the millennium. It appears that deepening our understanding of the psychological bases of tool use is fundamental to understanding the origins of tool technological culture. One might conjecture at first glance that the answers would be within easy reach. After all, they only require conceiving experiments in which individuals use tools, with researchers manipulating different variables to reveal the underlying psychological processes. However, behind this apparent simplicity, research on tool use faces several epistemological challenges in which the same set of questions generate

---

* Corresponding author.
E-mail address: m.mangalam@northeastern.edu (M. Mangalam).

https://doi.org/10.1016/j.neubiorev.2022.104521
Received 17 July 2021; Received in revised form 1 December 2021; Accepted 1 January 2022

many different answers. In the present target article, six research groups answer four critical questions about tool use, which are intimately intertwined, and suggest what should be the direction of future research on tool use. We provide a brief overview of the four questions and introduce how each author group approaches tool use before presenting each group's answers.

What constitutes tool use? This question may appear trivial yet it is not. The process of defining any psychological concept is neither neutral nor viewpoint-free—any definition is necessarily limited and oriented toward the theoretical solutions provided to account for the phenomenon studied (Osiurak and Heinke, 2018). We have often posed this question to our academic friends, and responses have been quite varied. Those initiated in biomechanics, human movement science, or even neuroscience, such as Mangalam, Fragaszy, and Bongers, exclusively reserve the term 'tool use' for using objects to solve a mechanical problem (e.g., a hammer to drive in a nail). Cognitive archaeologists such as Stout and cognitive psychologists such as Osiurak classify any implement (e.g., a calculator and a smartphone) under the umbrella term of tool use or an even broader term of technology. Ecological psychologists such as Wagman and Day consider any use of an object as tool use, irrespective of its use so long as that object changes the perceptual or behavioral capabilities of the user. Complexity scientists like Kelty-Stephen consider any behavior that changes the boundary between the organism as its environment as tool use and hence thus highly divergent. The same difficulties arise in the scientific study of tool use because there is no consensus on what tool use is (Fragaszy and Mangalam, 2018; Osiurak et al., 2010). The definitions given by Beck (1980), and updated by Shumaker et al. (2011; see Table 1) are perhaps the most thoroughgoing and influential attempt to define tool use (at least in the comparative literature), although Beck (1980; also see Hansell and Ruxton, 2008) warned that his definition only reflects a behavioral description and does not imply any biological or psychological distinction. Beck's and Shumaker et al.'s definitions have two significant merits. The first feature is that these authors did not merely define 'tool use', but also concepts that are related to tool use, such as tool making and construction (Table 1). Thus, their definition of tool use is also a definition by exclusion (e.g., excluding tool making and construction). The second merit is that their definition is derived from the animal behavior literature, which facilitates discussions of the specificity of tool use to particular species.

What psychological processes underlie tool use in humans and nonhuman animals? The emphasis placed by Beck (1980) and Shumaker et al. (2011) on object manipulation is consistent with the literature on tool use that has repeatedly stressed the critical role of manipulation-related psychological processes or, more generally, of embodied cognitive processes. However, the embodied cognition approach is not unitary—there are several different versions. The first version is in direct line with the ecological approach to perception and action initially developed by Gibson (Gibson, 1966, 1979), in assuming that tool use can be fully understood as perception-action processes required for effective execution (Biryukova and Bril, 2012; Bril et al., 2009, 2012; Fragaszy and Mangalam, 2018; Kahrs and Lockman, 2014; Lockman, 2005; Mangalam, 2016; Mangalam and Fragaszy, 2016; Pagano and Day, 2020; Smitsman, 1997; Smitsman et al., 2005; Wagman and Carello, 2003). In this perspective, the emphasis is on the lawfully structured patterns of energy in the environment available to the perceiver as information. Tool users exploit this information when manipulating a tool. For instance, as mass increases and the center of mass is located farther from the point of rotation, objects are perceived to be more appropriate for power tasks (e.g., striking a nail or throwing for distance), and as mass decreases and the center of mass is located closer to the point of rotation, objects are perceived to be more appropriate for precision tasks (e.g., striking a small nail or throwing for precision) (Michaels et al., 2007; Wagman et al., 2016; Wagman and Carello, 2001). For example,

Table 1
Definitions of tool use, tool making and construction, according to Shumaker et al. (2011).

Label	Definition
Tool use	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 (p. 5).
Tool making	Structural modification of an object or an existing tool by the user or a conspecific so that the object/tool serves, or serves more effectively, as a tool (p. 11).
Construction	Two or more tools or objects physically linked to make a functional, semipermanent thing that, once completed, is not held or directly manipulated in its entirety. A construction itself is therefore *not* a tool. Nor is it tool manufacture, because the product is not a tool (p. 19).

Another version of embodied approaches to tool use has been developed in parallel, mainly from the neuropsychological literature (Buxbaum, 2001; Heilman et al., 1982; Rothi et al., 1991; van Elk et al., 2014). Contrary to the aforementioned (ecological) perceptuomotor approach, this version assumes that conceptual knowledge is directly extracted from the sensorimotor experience with familiar tools (e.g., hammer, knife). This knowledge about manipulation offers an advantage in any required information processing by avoiding the reconstruction de novo of each step of the process. A third approach has been formulated mainly from the idea that tools help modify the physical environment. Here, the emphasis is on the physical (or technical) reasoning involved to understand and perform these modifications (Goldenberg and Spatt, 2009; Johnson-Frey, 2004, 2003; Osiurak et al., 2020b; Vaesen, 2012). This approach can be viewed as 'disembodied,' considering that manipulative aspects are secondary and not the critical component of tool use.

Which of these psychological processes are exclusive to tool use? As defined by Beck (1980; see Fragaszy and Mangalam, 2018; Shumaker et al., 2011), tool use is notably characterized by the fact that it implies manipulating an external object to modify the state of the physical environment. Humans and a number of nonhuman species manipulate objects. Tool use concerns not just manipulating the tool but also acting with the tool on something in the environment – another object or a surface. This supposes the existence of an attentional shift from the effector on the body (e.g., hand, beak) to that on the tool (e.g., hammer's head, screwdriver's tip) (Fragaszy and Mangalam, 2018; Mangalam and Fragaszy, 2016; Osiurak and Federico, 2020), a phenomenon called "distalization of the end effector" (Arbib et al., 2009). A critical question is whether distalization of the end effector is exclusive to tool use. Construction behavior, like tool use, also results of modification in the physical environment, raising the question whether the same psychological processes underlie tool use and construction behavior (Arbib, 2012; Walsh et al., 2011). The question of the exclusivity of psychological processes to tool-use behavior can be extended to other aspects of tool use, such as the ability to combine several tool-use actions in sequence (meta-tool-use, such as using a tool to acquire another one or to use one tool to create another one).

Which psychological processes involved in tool use are exclusive to *Homo sapiens*? Humans, we now know, are not the only species that use tools. Thus, our fascination with human tool use behavior extends to other tool-using species in which tool use takes on a different character (Fragaszy and Mangalam, 2018; Mangalam and Fragaszy, 2016). Often observation of a member of nonhuman species using a tool prompts discussions about the potential advanced technical intelligence in that species compared to other, non-tool-using species (Chevalier-Skolnikoff, 1989; Huber and Gajdon, 2006; Mather, 1994; Matsuzawa, 2001; Osiurak and Reynaud, 2020a; Parker and Gibson, 1977; Seed et al., 2009; Vaesen, 2012; van Schaik and Burkart, 2011). This perspective has been criticized (Emery and Clayton, 2009; Haslam, 2013; Wagman et al., 2019). Thus, an outstanding question is whether at least some psychological processes involved in tool use are unique to the human lineage.

Mangalam and Fragaszy integrate concepts from ecological psychology and movement science to formulate an embodied theory of tooling. They specifically use ‘tool’ as a verb, meaning to act with an object to achieve a mechanical goal in the service of a functional goal, and ‘tooling’ as a noun to label these actions. Mangalam and Fragaszy’s embodied theory makes testable predictions about the development, form, or effectiveness of tool use in humans and nonhuman animals, many of which have been confirmed by neurocognitive findings (Colbourne et al., 2021).

Wagman and Day, who also approach tool use from the perspective of ecological psychology, emphasize that tool use is associated with changes in lawfully structured patterned energy arrays that provide information about the animal-environment relationship. Therefore, using a tool is the detection (and exploitation) of information about this changed relationship. Thus, any species capable of detecting and exploiting such information is capable of tool use.

Kelty-Stephen views tool use from Mandelbrot’s multifractal-geometrical lens and explains how tool use rests on nonlinear interactions across nested scales of activity that support scale-free flexibility in behavior. Tool use, in this view, occurs in an organism with porous and blurry boundaries between organism and environment. Kelty-Stephen deems tool use just another factor contributing to the intermittency (discontinuities) in behavior that characterizes the apaptability of organisms, as tools blink in and out of existence as a separate entity from the body. He cites many of his own studies to make a case that the multifractal structure inherent to fluctuations in movements is a meaningful way to understand and model the perceptual control of tools.

Bongers takes a more functional approach grounded in the control of the body-plus-tool system. Much of his arguments stem from findings that a tool is integrated in movement synergies. Properties of the body-plus-tool system thus affect how the user perceives objects and surfaces in their surroundings.

Stout takes an evolutionary anthropological perspective on tool use. He discusses tool use in the context of the broader realm of technology, highlighting interactions among technological production, collaboration, and reproduction. Further, he emphasizes the key role played by internal models for action prediction and synchronization of movements of the user.

Osiurak focuses on the cognitive aspects of tool use. He specifically talks about the neural substrates of causal and analogical reasoning about physical principles of mechanical actions (e.g., force and leverage), which together constitute technical reasoning. Osiurak posits that technical reasoning is involved in all manifestations of human materiality.

In this way, this review exemplifies the richness of psychological research on tool use. Considering diverse investigative approaches is critical to identify productive ways forward to investigate this phenomenon. The present review aims to fill this gap. Its originality lies in presenting under the same umbrella responses to standardized questions concerning tool use from practicing scientists following different psychological approaches. In closing, we offer suggestions to help orient future work on this fascinating topic, which may afford synthesis of different approaches.

Our unconventional format for this article is intended to provide the reader in just a glance an overview of several different psychological approaches to tool use, the kinds of questions they ask, and how they contribute to understanding tool use. The psychological processes that each of these approaches posits to be involved in tool use influence the study design and analytical methods used (e.g., Kelty-Stephen may use nonlinear analytical methods to examine the role of movement fluctuations in the perception of tool properties; Bongers may use cross-correlation analysis to study joint-angle coordination; Osiurak may use double dissociation to study the neurocognitive mechanisms specifying tool-related technical knowledge in the brain). If one approach posits that no psychological process is exclusive to tool use, then it would also reject the idea of specific brain regions dedicated to tool use. If another approach posits that a given psychological process is exclusive to humans, it will immediately point towards some uniquely human neuronal correlates. The reader can contrast these approaches and decide what kinds of questions about tool use can be satisfactorily answered. Of course, none of these approaches can explain empirical results to life scientists at all levels of interest: development, phylogeny, function, and mechanism, such as neurocognitive processes. But, at the very least, they may shed light on some aspect of tool use that other approaches take for granted. The idea is not to settle a debate for now or forever but rather to showcase the epistemological diversity of the scientific study of tool use to readers unfamiliar with these approaches.

2. Embodied tooling — Madhur Mangalam & Dorothy M. Fragaszy

We approach the topic of engagement with tools (henceforth, tooling) from a comparative, evolutionary perspective to explain phylogenetic and developmental origins of these behaviors in diverse species. Unfortunately, in our field, nearly all published works describe observations of nonhuman animals using objects to achieve a goal as ‘tool use,’ but rarely do they use these observations to test theoretical predictions relevant to the development, form, or effectiveness of the behavior because there has been no theory generating testable hypotheses regarding this behavior.

A theory that supports prospective experimental work is essential for progress in this field. We have been developing an embodied theory of tooling (Fragaszy and Mangalam, 2018) that integrates concepts from ecological psychology and movement science. Ecological psychology provides the concept of affordances (Fig. 1), enabled by the perception of object properties and surface layouts (including spatial relations among objects and orientation of body segments and objects attached to the body as a unit to objects in the environment) through the use of proprioceptive information (Gibson, 1966; Shaw, 2001). In other words, ecological psychology is primarily concerned with perception-action coupling (e.g., what perceptual information an individual uses to a specific end and how). Movement science provides the concept of controlling the bodily degrees of freedom for functional coordination of movements (Bernstein, 1967; Bernstein et al., 1996) and the concept of situating an activity within the organism-task-environment system

Fig. 1. Affordances. The surface of a loamy soil affords tunneling to a mole, probing in search of prey to a bird, and walking to a fox. Drawing courtesy of A. Osuna-Mascaró.

(Newell, 1986; Newell and Jordan, 2007). In other words, movement science is concerned with the kinetics and kinematics of movements and the constraints that influence the two (e.g., what biomechanical constraints limit the range of movements of an individual). This embodied theory of tooling is equally applicable to humans and other animal species. We use 'to tool' as a verb, meaning to act with an object to achieve a mechanical goal in the service of a functional goal (e.g., hit a nail to drive it into adjoining planks—the mechanical goal—to join the two planks into a rigid unit—the functional goal) and 'tooling' as a noun label for these actions. This wording privileges actions rather than an object, although an object is intrinsic to the activity, just as when we speak of 'eating' rather than 'ingesting food' as the general phenomenon.

What constitutes tool use? We propose the following definition derived from our embodied theory that integrates concepts from **ecological psychology** and **movement science**: "Tooling is deliberately producing a mechanical effect upon a target object or surface by first grasping an object, thus transforming the body into the body-object system, and then using the body-object system to manage (at least one) spatial relation(s) between a grasped object and a target object or surface, creating a mechanical **interface** between the two" (Fragaszy and Mangalam, 2018, p. 194). Here, 'deliberately' implies that tooling is goal-directed. This definition necessitates that the actor, the grasped or attached-to-the-body object, and the target come in contact with each other during the activity. That is, tooling begins with the act of establishing a spatial relation between an object attached to the body and the target, and lasts as long as this relation is maintained. For example, when hammering a nail into adjoining planks to make a rigid structure, tooling begins when the actor places the nail against the surface of one plank, continues as the actor strikes the nail with the hammer, and ends when the actor stops striking the nail and switches to some other activity.

This narrow definition of tooling differs from prevalent definitions of tool use widely adopted in the ethological literature (e.g., Shumaker et al., 2011; see Table 1) according to which tool use is the use of an external object to achieve a goal, with diverse additional conditions appended by various authors (Crain et al., 2013). In our view, many behaviors that have been traditionally described as tool use in nonhuman animals are properly categorized as instrumental problem-solving (acting on or with an object in some way to solve a problem, such as opening a door to pass through a wall), but not as tooling, which is a particular subset of this large class of behaviors (Table 2). A definition of tool use primarily couched in the goal-directed nature of action with an object, which may be adequate when applied to humans because tooling is so pervasive in our behavior, is so ambiguous when applied to nonhuman animals that the topic of tooling in nonhuman animals largely remains a scientific curiosity, outside of theoretically-motivated biological or psychological inquiry. A narrower definition drawn from a particular theory affords analytical clarity and could support productive engagement of scientists across disciplines. Note that whether a behavior with an object qualifies as tooling or rather as some other form of instrumental problem-solving has no bearing on a judgment about the user's 'intellect' or the complexity of its behavioral, cognitive, and neural processes. In fact, all forms of instrumental problem-solving merit investigation of their distinctive characteristics. A classification of action as tooling or not determines the analytical strategy one takes to examine the action; that is all.

Table 2
Example behaviors identified in the literature as tool use, categorized as 'Instrumental problem solving' or 'Tooling' according to Fragaszy and Mangalam's (2018) definition of tool use. Adapted from Fragaszy and Mangalam (2018).

Taxon	Instrumental problem solving	Source
Ants, *Aphaenogaster* spp.	Carry soft foods on or in pieces of leaf, mud, and sand grains	Fellers and Fellers (1976)
Collector urchins, *Tripneustes gratilla**	Camouflage by draping own body with objects	Ziegenhorn (2016)
Octopuses, *Octopus vulgaris**	Cover the entrance to their den with rocks	Mather (1994)
Octopuses, *Amphioctopus marginatus*	Obtain shelter in coconut shell halves	Finn et al. (2009)
Archerfish, *Toxotes jaculatrix*	Catch flying insects by spitting water droplets on them	Gerullis and Schuster (2014)
Crocodiles, *Crocodylus porosus**	Lure birds with twigs and sticks placed on body	Dinets et al. (2015)
Egyptian vultures, *Neophron percnopterus**	Break open eggs by throwing and dropping stones on them	Lawick-Goodall (1971)
Northwestern crows, *Corvus caurinus*	Break open whelks by dropping them on rock outcroppings	Zach (1978)
Rooks, *Corvus frugilegus**	Raise water level in a container to reach floating worms by dropping pebbles	Bird and Emery (2017)
North American badgers, *Taxidea taxus*	Block the entrance of the burrows of ground squirrels to assist in capturing them	Michener (2004)
Baboons, *Papio* spp.*	Threaten humans by throwing stones	Hamilton et al. (1975)
Bornean orangutans, *Pongo pygmaeus*	Modulate the frequency of their vocalizations with leaves	Hardus et al. (2009)
Bonobos, *Pan paniscus**	Reach a distant branch by climbing on conspecifics	Ingmanson (1996)
Chimpanzees, *Pan troglodytes*	Reach for a hanging banana by stepping on wooden boxes	Köhler (1925)
Chimpanzees, *Pan troglodytes**	Drink water from tree hollows using leaves to sponge up the water	Tonooka (2001)
	Tooling	
New Caledonian crows, *Corvus moneduloides**	Extract insect larvae from cavities in branches with probes	Hunt (1996)
Hyacinth macaws, *Anodorhynchus hyacinthinus*	Stabilize a nut in the beak with wood wedges	Borsari and Ottoni (2005)
Lion, *Panthera leo*	Rub a sore area of its paw using a thorn held in the mouth	Bauer (2001)
Elephants, *Elephus maximus*	Brush flies off their body with branches held in the trunk	Hart et al. (2001)
Bearded capuchin monkeys, *Sapajus libidinosus* *	Dig soil with stones to excavate tubers	Falótico and Ottoni (2016)
Long-tailed macaques, *Macaca fascicularis*	Floss their teeth with hair	Watanabe et al. (2007)
Sumatran orangutans, *Pongo abelii**	Wipe body with leaves to remove substance	Fox et al. (1999)
Chimpanzees, *Pan troglodytes**	Flush or disable vertebrate prey in tree hollow with stick	Pruetz and Bertolani (2007)
Chimpanzees, *Pan troglodytes*	Puncture soil with stick to reach underground termite nests	Sanz and Morgan (2007)
Golden lion tamarin, *Leontopithecus rosalia**	Groom conspecific with stick	Stoinski and Beck (2001)

[*] Additional taxa have been reported to behave in similar ways.

What psychological processes underlie tool use in humans and nonhuman animals? Our theory addresses tooling at the behavioral level. It draws attention to functional task demands (to create a particular form of mechanical interface—e.g., striking a nail at a particular angle with enough force to drive it into the plank), and to movement coordination in meeting these demands (Fragaszy and Mangalam, 2018). It further draws our attention to the **perceptuomotor** processes supporting relational actions (moving a grasped object in relation to another object or surface) necessary to meet functional task demands. In accord with our ecological stance (Gibson, 1966; Harrison and Stergiou, 2015; Wagman and Miller, 2003), we do not distinguish between perception and cognition. Perceptuomotor processes relating to (i) perceiving spatial relations among objects and surfaces, (ii) developing agency over objects attached to the body (the distalization of the end effector), and (iii) controlling the bodily degrees of freedom to meet functional task demands characterize tooling. These processes occur in the unified body-object-task-environment system; that is, tooling is an action of a given individual with specific materials to accomplish a particular task in a particular setting (Bril et al., 2012; Mangalam and Fragaszy, 2016; Smitsman, 1997).

We suggest joint deployment of these three perceptuomotor processes distinguishes tooling from other instrumental problem-solving. Particular experiences accompany these processes in humans. We do not know if nonhuman animals experience tooling as humans do, but these same perceptuomotor processes must occur in some form.

- **Establishing and managing spatial relation(s) between an object attached to the body and a target object or surface.** Tooling requires establishing and managing at least one spatial relation between an object attached to the body and a target object or surface (see Fragaszy and Mangalam, 2018, for detailed explanation). Spatial relations in a tooling activity can vary in several dimensions. First, the number of relations can vary; tooling can involve managing more than one spatial relation between the body, the tool, and the target object or surface, sequentially, or concurrently. For instance, to join two planks, an individual might align the planks in a certain way (first spatial relation), then place a nail at a particular point on the top blank (second spatial relation), then strike the nail with the hammer (third spatial relation) to drive it through the planks. Spatial relations can differ in their specificity: placement, orientation, and geometric alignment. Consider, for example, using a screwdriver to drive in a screw. The screwdriver's distal end must be placed quite precisely on the screw's head, and the screwdriver's shaft must be oriented parallel to the screw's long axis to enable the screwdriver's head to fit into the screw's head. Spatial relations can also vary in temporal dynamics, from static to dynamic. The relation between the two planks in the previous example is static because once they are placed in position, they are not moved relative to each other. Similarly, the nail is placed in a fixed location on the top plank. The relation between the hammer and the nail is dynamic because the hammer is moved relative to the nail.
- **Distalization of the end-effector.** Tooling requires the distalization of the end-effector—the locus of perceptuomotor control—from the body to the part on the tool that acts upon the target object or surface (Arbib et al., 2009). Studies have shown that in monkeys using pliers to grasp a food item, the grasp-related cortical regions encode for movements of the pliers' jaws rather than movements of the fingers (Umiltà et al., 2008). A specific grip configuration may be imposed by the mass, shape, and size of the pliers, and movements are adapted to the pliers' jointed feature (direct vs. reverse pliers). These findings have been replicated in humans (Gallivan et al., 2013). Tooling is also associated with remapping of somatic senses to perceive what is happening at the tool tip rather than at the fingertips (Miller et al., 2018; Takahashi and Watt, 2017). Some studies have also reported that the remapping of the space surrounding the body to perceive reaching **affordances** from the frame of reference of the handheld tool rather than the hand (Berti and Frassinetti, 2000; Farnè et al., 2005; Maravita and Iriki, 2004), but these reports have remained questionable because of the small overall effect size and low statistical power (Holmes, 2012). Indeed, it has been suggested that the effects observed in these studies might simply reflect a shift of spatial attention from the hands to the tooltips—a hypothesis that has remained untested (Holmes et al., 2007, 2004).
- **Coordinating the body-object system.** The body-object system is coordinated differently than the body-only system, as manifest in different movements and postures. A simple example makes this point: different postures and movements are used when gripping a nail with the hand than when gripping it with pliers. Even when the task demands do not manifestly require different postures and movements, moving with a grasped object alters movement coordination. For example, people move their arms differently to stabilize the end-point trajectory when using the arm and hand to point at a target than when pointing at the same target with a stick (Valk et al., 2016; van der Steen and Bongers, 2011).

Which of these psychological processes are exclusive to tool use? None of the above perceptuomotor processes is exclusive to tooling. The acts of establishing and managing spatial relation(s) between an object attached to the body and a target object or surface are part of several non-tooling activities and are observed in both humans and nonhuman species, such as chimpanzees and capuchin monkeys aligning a stick to a matching cut-out in an experimental task (Fragaszy et al., 2011, 2015; la Cour et al., 2014), or a weaver bird inserting grass or twigs into a partially completed nest (Walsh et al., 2011). The end-effector is distalized in many non-tooling contexts, such as when using a manipulandum to move a cursor on the screen, although this behavior has been classified by some as tool use (Heald et al., 2018; Ingram et al., 2010). (Using a manipulandum to move a cursor does not qualify as tooling according to our definition because the manipulandum does not directly and mechanically affect the screen.) We coordinate the body-object system all the time in non-tooling contexts, such as when passing through a doorway sideways when holding an object wider than the doorway (Higuchi et al., 2006), or when using assistive devices—from wheelchair to exoskeleton (Pazzaglia and Molinari, 2016). Transporting an object inevitably involves coordinating the body-object system, irrespective of the context. These examples clearly illustrate that each perceptuomotor process is involved in many activities beyond tooling.

Which psychological processes involved in tool use are exclusive to *Homo sapiens*? We do not suppose that tooling is exclusive to humans in a holistic way, although we have no doubt that there are large differences among species in the elaboration and efficiency of the perceptuomotor processes involved in tool use: (i) Establishing and managing spatial relation(s) between an object attached to the body and a target object or surface; (ii) distalization of the end-effector; and (iii) coordinating the body-object system. Unfortunately, few comparative studies isolate each one of the three processes. We have suggested differences across species in two of the three processes but some commonality between humans and other species in the third. With respect to perceiving and managing spatial relations between a grasped object and another object, by two years of age, humans readily align a straight stick to a matching cutout in a platform surface, whereas adult chimpanzees and capuchin monkeys do so imprecisely (Fig. 2) (Fragaszy et al., 2011, 2015; la Cour et al., 2014), suggesting a deep difference between humans and nonhuman primates in this domain. With respect to coordinating the body-object system when tooling, some evidence indicates that nonhuman species can do this modestly, but not as effectively as humans. For example, when cracking nuts using stone hammers,

Fig. 2. Drawing of bar, cross, tomahawk shapes, and the respective cut-outs presented to two-, three-, and four-year-old children, adult tufted capuchin monkeys (Sapajus spp.), and adult chimpanzees (Pan troglodytes). Two- and three-year-old children routinely aligned a bar-shaped stick and a cross-shaped stick to its matching cut-out, and four-year-old children can also align a tomahawk-shaped stick, which entails attending to multiple spatial features concurrently, but capuchin monkeys and chimpanzees faced severe difficulties in aligning even a simple bar-shaped stick to its matching cut-out. See Fragaszy et al. (2011), la Cour et al. (2014), and Fragaszy et al. (2015) for details. Drawing courtesy of D. Sharpe.

capuchin monkeys alter their strikes to strike a nut with less or more force based on the type and condition of the nut (Mangalam et al., 2016; Mangalam and Fragaszy, 2015); they do so by adjusting the amplitude and velocity of the strike but do not adjust the hammer's kinetic energy at impact (Fig. 3) (Mangalam et al., 2018a), as do humans (Mangalam et al., 2020d; also see Bril et al., 2012). Humans can control a larger number of functional parameters of the task when hammering with stones, as when manufacturing sharp flakes from stone cores, than nonhuman primates using stone hammers (Bril et al., 2015, 2012). With respect to distalization of the end-effector, Umiltà et al.'s (2008) work with macaques using pliers, mentioned above, stands as one example suggesting that nonhuman species, like humans, do distalize the end-effector when tooling to meet task demands.

What must be the direction for future work on tool use? We suggest that expanding our understanding of each of the three component perceptuomotor processes we have highlighted above, and our understanding of their integration in tooling and other instrumental actions with objects, will be particularly useful. Ethologists may most naturally consider these processes in diverse species and developmental, ecological, and evolutionary perspectives. Psychologists may most naturally consider them in relation to attentional and related cognitive demands, particularly affordance learning and skill learning. Neuroscientists may most naturally consider them in relation to the organization and function of the nervous system. Findings from studies on reach-to-grasp movements using the hand or using the hand with a tool (e.g., grasping with fingers or with a tong) suggest an effector-independent neural encoding of movements (Gallivan et al., 2013, 2011; Umiltà et al., 2008). The interpretational nuances added by comparing actions with different effectors to achieve the same goal would yield a more reliable neurophysiological understanding of tooling than the currently available explanations based on comparisons of actual tooling with gesturing with an object (Hermsdörfer et al., 2012, 2007).

Pantomimimg is the principal paradigm used to investigate the neural basis of tooling particularly in relation to cognitive and sensorimotor deficits in neurological patients (Buxbaum et al., 2005; Króliczak and Frey, 2009; Martin et al., 2016b). Several interesting findings of how brain-damaged individuals move objects gesturally paint an optimistic picture of what we understand about the neural correlates of tooling (Goldenberg and Spatt, 2009; Johnson-Frey, 2004; Renfrew et al., 2008). However, pantomiming with objects is not comparable to tooling in any biologically relevant way (a detailed discussion is beyond the scope of this essay; we hope to address this issue in greater detail in a future piece). Tooling could be investigated more productively by setting aside the notion that tooling is an index of 'complexity' to focus on the distinctive perceptuomotor processes of tooling noted above.

Bernstein (1967; et al., 1996) stressed the importance of the senses to the coordination of actions. From a different theoretical orientation, Gibson (Gibson, 1966) arrived at a convergent conclusion. There is an untapped opportunity to study how the **sensorimotor apparatus** of species and individuals constrains their engagement in specific forms of tooling (Martinho et al., 2014; Troscianko et al., 2012). Accounting for the anatomy, physiology, and sensory processes of the user is critical to situate 'tooling' within the realm of biological inquiry.

3. Tool use as detection and exploitation of information in an ecological niche — Jeffrey B. Wagman & Brian M. Day

In the ecological approach to perception-action, surrounding energy distributions such as reflected light are lawfully (unambiguously, uniquely, invariantly) structured by substance and surface properties of the surrounding environment. This lawful structuring creates a unique pattern of energy at each point of observation in that distribution. The point of observation at which a given animal actively encounters this structured energy distribution and how this point of observation changes over time is lawfully (unambiguously, uniquely, invariantly) determined by that animal's size, shape, mass, and how it moves through the world. Therefore, the structured energy patterns actively encountered by a given animal are lawfully determined by the relationship or fit between the animal's various action capabilities and the substance and surface properties. In other words, the structured energy patterns actively encountered at a point of observation are informative about the behaviors that the animal can perform with respect to these substances and surfaces—they are informative about affordances for that animal.

The inherent lawfulness of this process means that the (changing) patterns of structured energy encountered by a given animal do not need to be 'processed'. They need only be detected to be informative about affordances for that animal (Wagman, 2020). Thus, perceiving and actualizing affordances for a given behavior requires detecting and exploiting such information—no more and no less. The inherent lawfulness of this process also means that the same (or analogous) patterns are informative to a given animal about a given affordance regardless of (1) whether a tool alters the fit between animal and environment and (2) the sophistication of the brain and nervous system of that animal.

Therefore, **perceiving and actualizing affordances for performing a behavior with or by means of a tool requires detecting and exploiting such information—no more and no less.** Moreover, any animal species capable of detecting and exploiting such information is capable of tool use. And while tool use itself does not seem to depend on the sophistication of the brain and nervous system of a given species, the sophistication and proliferation of tool use may depend on the sophistication of the niche of a particular species. Consequently, investigating how to provide information about affordances by means of tools that are unique to the human niche (such as technological interfaces or virtual tools) is an important area for future research.

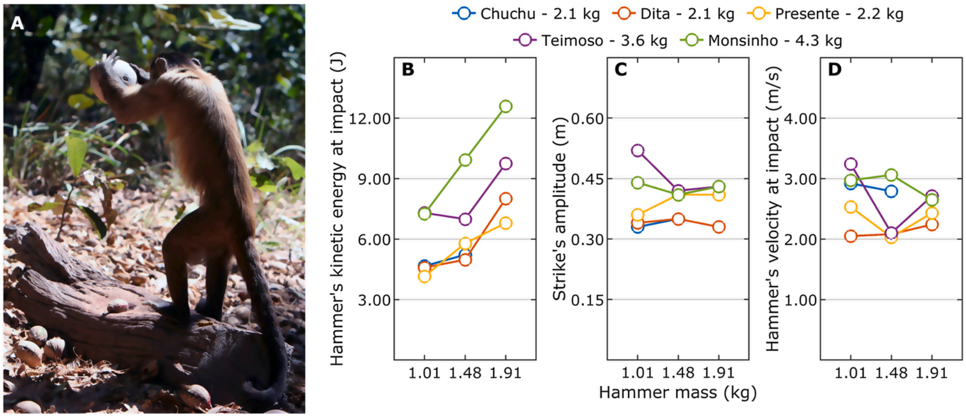

Fig. 3. When cracking nuts using stone hammers, wild bearded capuchin monkeys (Sapajus libidinosus) alter their strikes to strike a nut with less or more force based on the type and condition of the nut; they do so by adjusting the amplitude and velocity of the strike but do not adjust the hammer's kinetic energy at impact. (a) An adult monkey is striking an intact piaçava nut (inset)—placed in a pit on a log anvil—with a quartzite stone hammer. Photo courtesy of Barth A. Wright. (b) Hammer's kinetic energy at impact. (c) Strike's amplitude. (d) Hammer's velocity at impact. Adapted from Mangalam et al. (2018a).

What constitutes tool use? The ecological approach to perceiving and acting focuses on a scientific understanding of the lawful control of everyday goal-directed behavior. In this approach, the fundamental unit of analysis is the animal-environment system, not the animal or the environment in isolation (Gibson, 1979; Turvey, 2018). In the ecological approach, it is (only) at this level that all psychological processes—including tool use—occur. A key reason for this focus is that the relationship or the fit between the animal and environment determines what possibilities for behaviors—what *affordances*—are available to that animal (Wagman, 2020). It is *also* at this level that these possibilities become actualized in the performance of a given behavior.

A tool alters the fit between animal and environment by changing the ability of that animal to perceive or actualize affordances. Therefore, tool use is the exploitation of this altered animal-environment fit in the context of performing a given goal-directed behavior. By this definition, using a hammer to drive a nail qualifies as tool use. The hammer changes the ability to actualize many affordances, including the ability to forcefully strike another object. It is this change that is exploited in achieving the goal.

Alternatively, merely carrying a hammer *does not* qualify as tool use. This is *tool transport* rather than tool use. Stacking stones to build a barrier also *does not* qualify as tool use. This is *construction behavior* rather than tool use. In both cases, affordances are actualized in the context of a goal-directed behavior. However, in neither case does the object (the hammer or the stones) *change the animal's ability* to perceive or actualize affordances. Actualizing affordances is not the same as tool use. Bending a straight wire into a hook *also does not* qualify as tool use. Before and after it is bent, the wire alters the fit between animal and environment. Though bending the wire is likely to be goal-directed, doing so does not—in and of itself—exploit how it alters the fit between animal and environment. Changing the affordances of a given object is not the same as tool use. Instead, this is *tool making or tool modification*.

However, throwing stones at an aggressor, using a wheelbarrow to transport stones, and using a bent wire to retrieve a food item each qualify as tool use. Similarly, using a flashlight, a long cane, or a guide dog to safely navigate a cluttered environment *also* qualify as tool use. In each case, these objects change the ability to perceive and actualize affordances in ways that are exploited in achieving the goal.

What psychological processes underlie tool use in humans and nonhuman animals? In the ecological approach to perceiving and acting, the relationship between animal and environment lawfully structures **patterned energy distributions**. The structure actively encountered at a point of observation in such distributions provides information about this relationship (Fig. 4, bottom). That is, it provides information about affordances—whether, when, and how to move to achieve a given goal. Thus, perceiving and actualizing affordances for performing a goal-directed behavior requires the psychological processes of detecting and exploiting information—no more and no less (Wagman et al., 2019). These processes stand in contrast to more traditional psychological processes proposed to underlie perceiving and acting, such as remembering, computing, and inferring, among others.

When the fit between animal and environment is altered by means of a tool, the structure encountered at a point of observation provides *information about this altered relationship* (see Fig. 4, middle). That is, it provides *information about affordances for tool use*—whether, when, and how to use the tool to achieve a given goal. Consequently, **perceiving and actualizing affordances for performing a goal-directed behavior with or by means of a tool similarly requires the psychological processes of detecting and exploiting information—no more and no less.** These processes stand in contrast to the more traditional psychological processes proposed to underlie tool use, such as imagining, reasoning, and problem solving, among others.

The lawful structuring of energy distributions guarantees that the same (or analogous) patterns provide information about a given affordance regardless of details of the particular energy distribution being structured and the particular anatomical component(s) used to detect such structure. This is readily demonstrated in a context common to tool use—the hefting, wielding, or manipulating of objects by muscular effort (see Carello and Turvey, 2016). When wielding an occluded object, people can perceive many different affordances of that object, and they can perceive a given affordance of that object under many different wielding circumstances (Hajnal et al., 2007; Mangalam et al., 2017; Wagman et al., 2017). By the same token, when people probe a surface with an object, they can perceive many different affordances of that surface, and they can perceive a given affordance of that surface under many different probing circumstances (Wagman and Hajnal, 2016, 2014a,b).

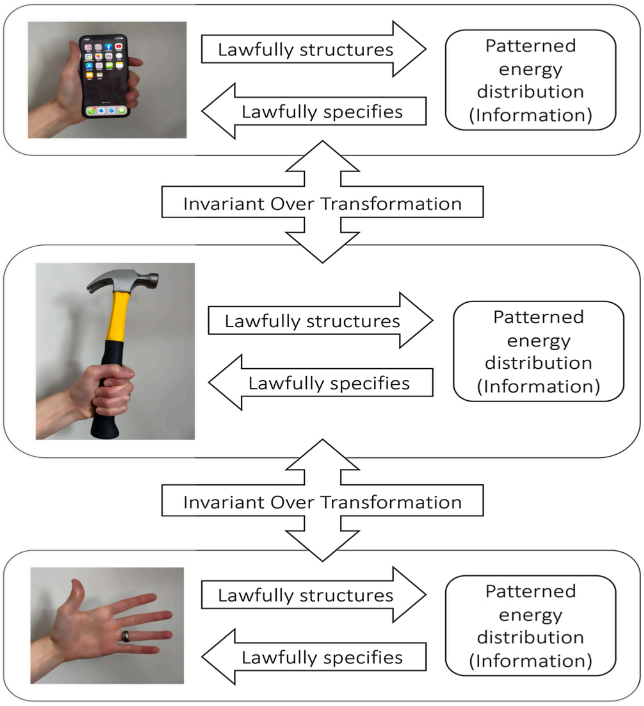

Fig. 4. The relationship between animal and environment lawfully structures patterned energy array so as to provide information about this relationship (bottom). Such lawfulness entails that information about a given affordance is invariant over transformations including whether or not a tool alters the fit between animal and environment (middle) and whether or not the tool is virtual (top).

Perceiving affordances of, and by means of, a tool requires spontaneously and temporarily assembling **task-specific detection units** from potentially independent components—across both body and tool. Actualizing affordances of a tool requires an analogous process of spontaneously and temporarily assembling **task-specific control units** from potentially independent components—again, across both body and tool. The detection and exploitation of lawfully structured energy distributions likely underwrites both phenomena (Carello and Wagman, 2009; Profeta et al., 2020).

Which of these psychological processes are exclusive to tool use? As described above, in the ecological approach, lawfully structured patterned energy distributions provide information about whether, when, and how to move to achieve a goal. The lawful structuring of energy distributions guarantees that the same (or analogous) patterns provide information about a given affordance across circumstances. This includes whether or not an animal exploits an altered animal-environment fit in the context of achieving a goal (i.e., whether or not an animal engages in tool use).

When an animal moves from place to place in a cluttered environment, it encounters a lawfully generated pattern of optical structure that is informative about the animal-environment relationship—specifically about how, when, and where it is moving. Moreover, such patterns are informative about whether, when, and how a person *must move to achieve a goal* (e.g., catching a ball, see Fink et al., 2009). Critically, such patterns are also informative as to whether, when, and how a person must *move a tool such as a vehicle* to achieve a goal (e.g., steering or stopping safely, Fajen, 2013, 2007; Fajen and Matthis, 2011; Kadar and Shaw, 2000).

Likewise, when an animal moves one of its limbs about a given joint, it encounters a lawfully generated pattern of resistance to rotational acceleration that is informative about the animal-environment relationship—specifically about how, when, and where the limb is moving. Moreover, such patterns are informative about whether, when, and how a person *must move that limb to achieve a goal* (e.g., pointing at a target, Pagano and Turvey, 1998). Critically, such patterns are *also* informative as to whether, when, and how a person should *move a hand-held tool* to achieve a goal (e.g., hammering or displacing another object (Wagman et al., 2016; Wagman and Carello, 2001).

In both cases, it is irrelevant whether achieving the goal requires controlling the person's movements or the person-plus-tool system. The lawful structuring of patterned energy distributions by the relationship between animal and environment entails that the information about how, where, and when to move to achieve the goal is the same (or analogous) across this transformation (see Fig. 3, middle). This likely explains why tools, be they vehicles or hand-held objects, are often 'functionally transparent' to skilled users. In both cases, tools are perceived as part of the body because they are perceived *the same way* as the body (Pagano and Turvey, 1998). In other words, perceiving the body and an object attached to it require identical psychological processes.

Which psychological processes involved in tool use are exclusive to *Homo sapiens*? The lawful structuring of energy distributions by the relationship between animal and environment guarantees that the same (or analogous) patterns provide information about a given affordance regardless of the specifics of the **sensory apparatus**, nervous system, and brain of the animal doing the perceiving. Such details are irrelevant so long as that animal can detect the structured energy patterns that are informative about whether, when, and how to move to achieve a given goal. Incontrovertibly, animals across all phyla perceive and actualize affordances. According to the ecological approach, these abilities result from the same lawful processes—psychological and otherwise—across species (Turvey, 2018; Wagman et al., 2019). Moreover, **the abilities of animals to exploit how a tool alters the ability to perceive and actualize affordances *are also* the result of *the same* lawful processes—psychological or otherwise—across species.**

Tool transport, construction behavior, and tool modification are widespread across the animal kingdom – even in so-called 'lower animals' such as crustaceans, insects, worms, and amoeba (Turvey, 2018; Wagman et al., 2019). Instances of *tool use* (as defined above in section 1), however, are less common—occurring mostly (but not exclusively) in birds and primates (Hunt et al., 2013). This observation begs the question as to why instances of tool use proper are not more common across the animal kingdom—especially, if as we suggest, the information about a given affordance is the same (or analogous) regardless of differences in sensory apparatus, nervous system, and brain across species.

We propose that this disparity is not due to differences in brain, nervous system, or intelligence across species. Rather, we propose that it is due to differences in the **ecological niche** occupied by those species. A niche is how a particular species lives, given the fit between animal and environment particular to that species. A niche is a way of life—it is a set of affordances for a particular species (Gibson, 1979; Turvey, 2018). Species occupying different niches necessarily encounter (and perceive and exploit) different affordances. The more complex the niche of a given species, the more diverse and complex the set of affordances available to that species' members, and the more likely those members will (learn to) perceive and exploit affordances for tool use.

Accordingly, species other than primates and birds engage in tool use when their niche is modified to include the opportunity (to learn) to perceive and exploit these affordances. For example, rats perceive and exploit affordances for driving a vehicle when their niche is modified to include opportunities to (learn to) do so (Crawford et al., 2020). Moreover, the driving skills of rats raised in an enriched environment (i.e., an enriched niche) are superior to those raised in a standard environment.

What must be the direction for future work on tool use? Affordances for tool use are relative to the niche that an animal species occupies. Humans occupy a unique niche that includes a vast array of technological, communication, and representation systems. In this niche, affordances for tool use include teleoperation of search and rescue robots, the Mars rover, or surveillance drones; the manipulation and repair of internal bodily organs and tissue by means of laparoscopic surgical instruments; and even the (un)locking of the door to one's home using a smart phone app. In all such cases, these devices change the ability to perceive and actualize affordances in ways that are exploited in achieving the goal.

In the general case, information about affordances for tool use is available in the structure in patterned energy encountered at a point of observation. However, in the situations described above occurring in the human socio-technological niche, information about affordances is available only by means of an interface (e.g., a computer-mediated visual display). This requires designing to preserve, enhance, or (in some cases) even generate the lawfully structured energy patterns that provide information about affordances (Pagano and Day, 2020; Fig. 3, top). Therefore, an important direction for future research is to determine precisely how to do so. In other words, **future research should be directed at designing the interface that allows for perceiving and actualizing affordances of virtual tools to be the detection (and exploitation) of relevant information—no more and no less.**

For example, researchers developed a laparoscopic surgery simulator interface that could provide haptic feedback to the user about how far simulated bodily tissue could be manipulated until it was accidentally torn (Altenhoff et al., 2017; Hartman et al., 2016; Long et al., 2016). The researchers based the haptic information about 'distance to break' on optical information about 'time to contact' with a surface (see above, Fink et al., 2009). They found that novice participants and experienced surgeons who used the device improved their performance in a simulated laparoscopic surgery task after only minimal practice. This suggests that only minimal practice using a tool may be required for that tool to become functionally transparent. However, it is unknown exactly what kind and how much tool use experience is necessary and sufficient for this to occur. Therefore, **future research should also be directed at determining those experiences that are necessary and sufficient to facilitate the functional transparency of a virtual tool or a user-tool interface (**Day et al., 2019, 2017**).**

4. Tools as intermittent properties of the fractal coastlines between organism and environment — Damian G. Kelty-Stephen

Tool use rests on the cascades underwriting organism-environment relationships. Cascade dynamics comprise nonlinear interactions across nested scales of activity that support scale-free flexibility resulting in an organism with porous and blurry boundaries. Organisms spread fluidly over contextual constraints, contacting the environment along intermittent coastlines where behavior ebbs and flows against the more stable land. The tool-using organism can be more adaptive as it is intermittent, avoiding lock-in, extending and retracting, wandering, and hovering. Tool use is just another intermittent function in the daily work of an organism. However, the more startling possibility is that tools are themselves intermittent participants in the organism-environment exchanges.

Tools are necessarily tuned to the scale of a task. So, the associated intermittency may require viewing Gibsonian ecological psychology through Mandelbrot's multifractal-geometrical lens. For Gibson (1979), organisms and the environment entail one another, and any coastline between them is porous and blurry. When studying the coastlines bounding Britain, Mandelbrot (1967) realized that such boundaries embody fractional (or 'fractal' for short) dimensions. Off-putting at first glance, fractal dimensionality aims to do the critical job of quantifying structure that fails to be integer-dimensional (e.g., zero-, one-, two-, or three-dimensional points, lines, surfaces, or Euclidean solids). Coastlines with varying fractionality can crucially originate from nonlinear interactions across scales. Indeed, the nonlinear interactions across scales—that is, the cascades—entail variation in these fractal dimensions. That is, they entail 'multifractal' dimensionality (Mandelbrot, 2013).

The multifractal structure is thus a meaningful way to understand and model tool use. Organisms' exploration of tools and task context depends on multifractal fluctuations in organisms' movement (Doyon et al., 2019; Hajnal et al., 2018; Kelty-Stephen and Dixon, 2014; Mangalam et al., 2019a,b,c; Mangalam et al., 2020a,b,c; Mangalam and Kelty-Stephen, 2020; Stephen et al., 2009, 2010; Stephen and Hajnal, 2011). This insight may lead to the startling idea that tools could be intermittent, blinking in and out of existence as a separate entity from the body. In this sense, the muddiness of 'tool' concepts noted by Fragaszy and Mangalam (2018) may be a defining feature rather than muddiness in the scholarship.

What constitutes tool use? Tools enact a subtle balance at the boundary between organism and environment. The boundary between organism and environment is a dynamic, sometimes blurry distinction, and tools themselves may appear or disappear **intermittently**. An organism uses a tool to take an object to engage in direct mechanical interaction with a target surface (Fragaszy and Mangalam, 2018). As such, tools are necessarily tuned to the scale of a task. The key for our front door only works because it has the specific shape and size that moves the tumblers of a lock just so. However, tool use does not live at any specific scale, and tool use relies on an organism's ability to slip up and down a hierarchy of scales. In this sense, the muddiness of 'tool' concepts noted by Fragaszy and Mangalam (2018) may be a defining feature rather than muddiness in the scholarship.

The blurriness of the boundary between organism and environment is not a denial of scientific inquiry. On the contrary, it is just such a blurriness that demands a specific class of scientific mechanism, namely the interaction across scales in a **cascade**. Tool use rests on the cascades underwriting organism-and-environment relationships. By 'cascades,' I only mean the nonlinear interactions across nested scales of activity. The cascades offer a theoretical modeling framework that has been embraced in geophysical domains (Lovejoy and Schertzer, 2018) and psychological domains (e.g., Oakes and Rakison, 2019). This modeling framework entails the use of specific kinds of hypotheses and specific kinds of data analysis. However, before introducing the further entailment of the cascades modeling framework, we first elaborate on cascades.

We can see the cascades implicated in using the tool of a key. Intentional tool-use events like "unlocking the door with a key" rest within a larger context like "arriving at the front door after an evening out." Nested within the intentional tool use are smaller movements and submovements, such as rifling through pockets and purses, looking for the key, curling fingers about this way, and that to leaf through coins and receipts. Nested again within those events are yet smaller movements. For example, neurons fire and tendons gradually stretch. Events at all these scales gradually percolate up across scales, from neurons to hand postures and so forth, and gradually they amount to the dawning understanding that the key is not in these pants pockets, not in this purse. The curl of the fingers and brush of the cloth weave against the skin, cueing memory of feeling the key in another pants pocket. These diffuse submovements and movements spill over into a new strategy altogether: we reach out back into the largest scales of the context, and we use the fact that the vast expanse of front-door-and-house contains a landscape of flower pots and garden stones. Under at least one of these landmarks, we have a spare key. So, then we cast about in among the flora of our front yard, and soon we have descended again into smaller scales of movements, submovements, fingers gripping and tapping against ceramics and stone in the dark.

The ability to slip from one scale to another and blend information at different scales is because organisms have porous and blurry boundaries. Organisms spread fluidly over contextual constraints, contacting the environment along intermittent coastlines where behavior ebbs and flows against the more stable land. The tool-using organism can be more adaptive as it is intermittent, avoiding lock-in, extending and retracting, wandering, and hovering. Tool use is just another intermittent function in the daily work of an organism. However, the more startling possibility is that tools are themselves intermittent participants in the organism-environment exchanges.

Tool use involves a mutual contingency between tool and user. Fragaszy and Mangalam (2018) acknowledge this mutuality as a 'body-plus-object' system, but they may have underspecified the issue by suggesting the mutuality is an addition. For Gibson (1979), organisms and environments entail one another. Though he saw the relationship so constructive as generative of perceptual experience, the relationship between organism and environment is not some polite addition of parallel and mutually well-wishing processes. On the contrary, organisms constantly exert their goals upon the environment, exploring, reshaping, and usually leaving environmental resources irretrievably disturbed. Furthermore, environments press their constraints upon the goalful organisms.

Organisms and environments branch outwards and into one another—this is no less a tenet of ecological psychology than it is a tenet of ecologically-focused developmental systems theories that seek to anchor intelligent behavior in the contextual structure at many scales beyond the cells of the organism (Griffiths and Gray, 2001; Japyassú and Laland, 2017; Lewontin, 1982). Ecological approaches to intelligent behavior like tool use thus focus on the coastlines between organism and environment. Organisms and environments are colliding and invading one another at very many scales: ambient energy deforms the extended tissues of the organism, and organisms chisel and carve into the ambient array for newer and deeper meanings (Gibson, 1979). Such coastlines are built according to cascades, with the small-scale roll of pebbles up and down the shore, the medium-scale pressure like tides and currents, and the long-scale pressures like the plate tectonics shifting the earth's surface.

The ecological psychology of Gibson and its insights into tool use may thus benefit from the geophysical research that has sought to make sense of the cascades in actual coastlines. When studying the coastlines bounding Britain, Mandelbrot (1967) realized that such boundaries embody fractional (or '**fractal**' for short) dimensions. Off-putting at first glance, fractal dimensionality aims to do the critical job of quantifying structure that fails to be integer-dimensional (e.g., zero-, one-, two-, or three-dimensional points, lines, surfaces, or Euclidean solids). Coastlines with varying fractionality can crucially originate from nonlinear interactions across scales. The nonlinear interactions across the scale—the cascade that blends information from multiple scales to generate dynamic, distributed, flexible behavior—entail variation in these fractal dimensions. That is, they entail '**multifractal**' dimensionality (Mandelbrot, 2013). Abstract and upsetting as the notion of fractional dimensions may be, multifractal geometry affords us with a quantitative toolset that converts the notion of a cascade from a lyrical example into a falsifiable model. A given measurement (e.g., of organism tool use) offers a clear testbed within which to test how strong or weak the interactions are across the scale.

Because the organism-environment relationship is never adrift from long-scale contingencies, it is not crucial that the tool and skin remain in constant immediate contact (cf. Fragaszy and Mangalam, 2018). The tool may drift from the immediate grasp, but the multi-scaled organization of the organism-environment relationship leaves no gap where the tool is 'gone.' Rather than an empty expanse, environmental space is full of clutter whose integral flow supports organisms via contact through distributed-but-rarely-distinct modalities (e.g., optical, acoustic, and haptic; Gibson (1979); Stoffregen and Pittenger (1995), and Harrison et al. (2021), respectively). The specificity of localized sensor cells is physiologically real, but it distracts from the non-exclusivity and often mutuality of manipulation and, say, observation when mechanical contact is lost (Stoffregen et al., 2017). Cascades span cross-scale interactions through these ecological flows like a spiderweb of contingency that the organism then manipulates to extend its reach.

We can revisit our considerations of using a key to open the door. The seemingly obvious 'tool' is the key. However, according to Fragaszy and Mangalam's (2018) definition, the narrowly defined 'tool' actually slips in and out of existence, and other tools flicker into existence to make up the difference. The key that we thought was in our pocket or pursued turns out only to be a tool in potential, not a tool on hand in direct contact with the skin. At a longer time scale, the key has been cast out into the hiding spaces in the front yard, much like a projectile that we have thrown away from ourselves only to catch it later. In the meantime, we have been clawing through the detritus of a purse or a pocket for a key that is not there, with curled and jabbing fingers that act just as a trowel or shovel might. The key under the flower pot has not been in hand and is not a tool until we ferret it out. By their narrow definition from Mangalam and Fragaszy (2018), the tool is here one minute and gone the next only to appear later. The hidden key is not a tool until we actualize its potential, that is, as we retrieve it from its status as just another projectile left out in the front yard.

The exploratory behaviors that allow us to dig for and then try to grasp tools are hazy, blurry structures. We thrive on this blurriness and would not want it another way—indeed, we might find ourselves locked out of our house if we did not have this fluid capacity to strategically launch tools far from our grasp and find them again later improvising tools of our bodily parts. As organism searches the environment, fashions tools out of their resources, copies and hide those tools at various locations, the coastline between organism and environment becomes very fluid and hazy indeed. Science need not shrug at this haziness and surrender to ignorance—instead, we might just as soon use the same multifractal geometry to probe this fluid coastline for the layout of cross-scale interactions (e.g., from movement to submovement so forth). Indeed, when we measure these behaviors, the multifractal geometry of these exploratory behaviors interacting with tools is predictive of what an organism comes to know about what the tool can do (Doyon et al., 2019; Hajnal et al., 2018; Kelty-Stephen and Dixon, 2014; Mangalam et al., 2020a,b,c; Mangalam and Kelty-Stephen, 2020; Stephen et al., 2010; Stephen and Hajnal, 2011).

What psychological processes underlie tool use in humans and nonhuman animals? Tools rest on the boundary between organism and environment, and the fate of the tool—its bobbling, its workings, and its flickering in and out of distinct existence—is bound up entirely in how this organism-environment coastline develops as a cascade. The term 'cascade' refers to any physical processes that branch, fracture, avalanche, diffuse, or otherwise spread apart across multiple scales across space or time. Blending information from events at multiple scales is centrally how biological systems of all types operate—another way to say this point is that any given event in a biological system only takes its meaning from smaller events composing it and from the larger events contextualizing it. Organism physiology exhibits cascades spatially (e.g., hierarchical branching of neural dendrites, cardiovascular vessels, and capillaries (Goldberger et al., 1990), actin-myosin architectures (Fernandez-Gonzalez and Zallen, 2011), DNA supporting cells (Dragovich and Mišić, 2019), collagen composing bones, (Fratzl, 2008), and tensegrity-like networks of connective tissue that span the entire organism, wrapped tautly across the muscles and bones (Turvey and Fonseca, 2014) as well as through a correspondingly hierarchical temporal structure whenever these multifractally-shaped parts operate (e.g., neuronal avalanches (Zorick et al., 2020). The spreading interactions across multiple scales of this hierarchy (e.g., Ingber, 2006) entail a multifractal structure (Turvey and Fonseca, 2014).

These physiological hierarchies work hand-in-glove with the psychological hierarchies, for example, looking for a key, fidgeting about for it, remembering a prior plan to hide a key, and then planning a new strategy of fidgeting for the hidden key. Furthermore, the multifractal geometries of exploratory behaviors will predict verbal, psychological reports of what a tool can do (Mangalam et al., 2020a,b,c; Mangalam and Kelty-Stephen, 2020). The knotting and curdling of the organism-environment coastline call for such startling mathematical constructs as fractional dimensions—let alone multiple fractional dimensions—to model this coastline on which tools bobble, work, and blink in and out of existence. Multifractal geometry is the primary mode of understanding how events coordinate across multiple scales—-whether within a single organism (Carver and Kelty-Stephen, 2017; Mangalam, Carver, et al., 2020b), between organisms (Carver and Kelty-Stephen, 2017), or between organism and environment (Stephen and Dixon, 2011; Teng et al., 2016)—no matter whether the coordination is visual or mechanical.

Which of these psychological processes are exclusive to tool use? These processes are not exclusive to tool use because tools are not specifically different. Tools are most valuable because they are not a closed set; they are craftable and fleeting structures that appear, disappear, come to hand and drop from grasp as needed. Tools are helpful because they are artifacts that grow, decay, and wander towards and away from the organism-environment coastline. Cascades and multifractal processes are the specific modeling framework that explains intermittent structures like tools. Tools themselves are happenstance structures that grow to mediate the organism-environment relationship. They are not a firm set of objects with a firm set of always-true conditions. My point here is that the muddiness of definitions of the toolset is less a problem for psychological research than it is a sign that tool use might benefit from not carving out an insulated niche for itself that keeps tools as solid rigidly defined structures. We need the muddiness of tool definitions because muddiness is what makes tools useful. The happenstance intermittency of tools is not a reason to shrug at tools but rather to take better stock of the reality of the muddiness. My concern is that over-formal distinctions between tool and not-tool could risk pricing this literature out of the chance to explain the critical issue of how an organism can use a tool to mediate its experiences of the environment.

Which psychological processes involved in tool use are exclusive to *Homo sapiens*? As I had discussed in the example of fishing for keys in pockets or under flower pots, humans exploit the intermittency of tools across their own organism-environment coastline. Nothing about this capacity to exploit a murky organism-environment coastline is unique to humans, and even the simplest species have the wondrous capacity to make a tool appear and disappear, to blend it in or distill it from either body or environment.

For instance, an amoeboid slime mold (Dictyostelium discoideum) uses the molecule cyclic adenosine monophosphate (**cAMP**) to navigate a ground surface find and coordinate other conspecific amoebae. D. discodeum spend the earlier, better-fed days as an amoeba, and it is only as food becomes more scarce that the amoebae coalesce into a multicellular body—either a fruiting body or a slug for locomotion to a niche with better nutrient stores (e.g., Schaap, 2021). This drama has all of the necessary features of tool use, but it also shows how the distinctions between tool and user may blur.

In the traditional sense, cAMP fits all the needs of a mechanical tool. The amoebae are manipulating cAMP, grasping molecules with its cell-membrane receptors, using the molecules to orient their own cytoskeletal posture towards and to inch up the cAMP gradient to the source (Chisholm and Firtel, 2004). Eventually, individual amoebae on the move will use cAMP to attract each other along the way, using a cAMP relay to latch on to slow amoeba behind them (Bagorda et al., 2006). Hence, at all points, the amoeba grasps cAMP and manipulates it to operate on the ground surface as well as the on the surface of other cell membranes.

However, the same intermittency of the tool that supports their adaptive use in humans gives us just the same intermittency in tools that amoebae use. Amoebae do the same not-quite-magic trick of making things tools or unmaking those tools that give the humans such flexibility in their tool use. The organismic coastlines of this example blur in three major respects. First, the tool is sometimes but not always clearly separate from the body. The relay use of cAMP involves the amoeba producing its own new cAMP under food scarcity (Chisholm and Firtel, 2004). Second, this tool use essentially invents a new body, a multi-cellular aggregate, effectively redrawing the organism-environment coastline (Bagorda et al., 2006). The third sense in which the organism-tool coastline blurs is that the body can fashion tools from itself. The slug tip's external curvature focuses visible and infrared light just like a lens, focusing light towards the rear the slug or fruiting body and thus Interrupting rearward cAMP production, leaving the cAMP-ful tip to drag it forward (Schaap, 2021). And although the tip touches no surface, light remains no less patterned by the ambient surfaces than in Gibson's (1979). So, there is no lack of contact—there is in fact, no empty room in which the slime mold can fail to respond to the constraints shaping and stimulating its body.

it is a clever thing that humans can make a thing a tool that did not meet the criteria for 'tool' before and then also break down or send elsewhere a tool into something that again no longer meets the criteria for 'tool.' And it is no less clever and remarkable when non-human species can engage in the same pragmatic use of resources to make and break tools as needed. The intermittency of the tool is of the same benefit to all species, which is all the more reason to care about tool use—even if the intermittency is also a stumbling block to scientists aiming at concise and closed definition of tools.

What must be the direction for future work on tool use? The intermittency of tools points immediately to the question of agency and its bounds. How do organisms extend or retract their scope of influence? How do they push their coastline outwards? Or give ground back to the environment? As the tool shimmers in and out of existence, the organism concedes and engulfs more of its surroundings, respectively. This intermittency of tools is nothing but the negative image of intermittency of control. An important focus for future study is whether the multifractal geometry of tool use can formalize a cascade-driven notion of agency or control.

5. A tool in use is incorporated into synergies — Raoul M. Bongers

The current contribution presents an ecological-dynamical approach to tool use. It is argued that tools are integrated in synergies and that these tooling synergies determine the possibilities for action (i.e., affordances) in the environment. In line with an ecological-dynamical account these processes are not specific for tool use nor for any given species. Some future routes are presented to expand this approach to account for more aspects of tool use than just perception-action.

What constitutes tool use? During our daily life activities, we often grasp an object in the environment to use that object as a tool to reach our goal. For instance, we use a knife to cut bread and a spoon to stir our coffee. Hence, a tool can be casually defined as an object in the environment that is temporarily attached to the body to act on other objects in the environment to reach a goal (cf. Beck, 1980; Fragaszy and Mangalam, 2018). Most of the time objects are used as tools when our own action system falls short or when action goals can be achieved more conveniently with a tool, that is, tools alter our capacity for action. Therefore, we take a perception-action perspective on tool use, one of the main lines of research on tool use that are outlined by Fragaszy and Mangalam (2018). We rigorously apply the ecological-dynamical approach (cf. Profeta and Turvey, 2018) to tool use within this perspective.

What psychological processes underlie tool use in humans and nonhuman animals? In the ecological approach to perception-action, control of an action does not come from an internal structure (such as a part of the central nervous system), but coordination of action and perception takes place in an organism-environment system (Gibson, 1979; see Michaels and Carello, 2000; Richardson et al., 2008; Warren, 2005 for overview papers of this approach). Properties of the organism as well as properties of the environment, which shape the organism-environment system, determine behavior. For instance, arm length (organism property) as well as the property of the object determine trunk-leaning during object grasping. An organism moving through an environment creates perceptual flow fields and these flow fields contain invariants that specify properties of an environmental feature or the relation between the organism and the environment (i.e., the focus of expansion in an optical flow field is informative about heading direction). That is, the **perceptual flow fields** specify functional relations between an organism and its environment that have meaning for an organism and this meaning is perceived directly (see the contribution of Wagman & Day). Therefore, organisms directly perceive affordances, the possibilities for action in the environment. For instance, someone can perceive whether the size of a handle affords a tool to be graspable with one hand.

Important for understanding tool use is that affordances have their counterparts in the organism, which are dubbed **effectivities** (cf. Michaels and Carello, 2000; Shaw et al., 1995). For instance, in his seminal paper on affordance perception, Warren (1984) demonstrated that the climbability of a stairs (i.e., its affordance) is perceived in terms of the riser height of the perceiver. Hence, properties of the environment (i.e., affordances) are perceived in terms of the properties of the organism (i.e., effectivities).

Effectivities are determined by the **synergies** that can emerge in the action system. From a dynamical systems perspective to movement coordination, synergies emerge from task, organism and environmental constraints in a self-organizing manner. Synergies are defined as the temporary functional units in which the abundant degrees of freedom are organized (Kelso, 2009; Turvey, 1990, 2007). Synergies maintain a functional organization through covariation of the degrees of freedom that make up the synergy (Kelso et al., 1984; Latash et al., 2007; Riley et al., 2011; Schöner, 1995). For instance, when pistol shooting the joint angles in the arm covary such that the aiming at the target is stabilized (Scholz et al., 2000). In sum, combining the principles presented in the foregoing gives an account of perception-action in which perceptual invariants act specify affordances that are linked to the effectivities that determine the synergies that should be formed.

An object in the environment that is attached to the body to function as a tool changes the geometry of the action system. For instance, a tool is often held in the hand and thereby the tool changes the shape (i.e., length) of the action system. Equally important, a handheld tool produces forces and torques in the muscles and joints that affect the constraints on the basis of which synergies in the action system emerge. For instance, a tool has a certain weight, and this weight changes the interactions between task, organism and environmental constraints on the basis of which synergies emerge. Hence, a tool in use affects the geometry of the action system as well as the available synergies (Fig. 5). Both these changes affect the effectivities that function as a scale to which the properties of the environment are perceived. That is, a tool in use becomes a part of the action system that establishes the effectivities and therefore the affordances (Bongers, 2001; Bongers et al., 2003).

The incorporation of the tool in the action system has been suggested in different studies examining the kinematic characteristics of the tooling end-effector. When learning to use a complex tool, kinematic characteristics that normally show up in hand movements can also be observed in movements of the tool tip (Heuer and Sülzenbrück, 2009). In examining the mechanisms underlying these phenomena we analyzed the synergy in the arm during pointing with a rod to a target. Using an **Uncontrolled Manifold (UCM) analysis** (Scholz and Schöner, 1999; Schöner, 1995), we showed that there is more covariation in joint angles stabilizing the position of the rod's tip in space than that there is other variability in the joint angles de-stabilizing the rod's tip position (Valk

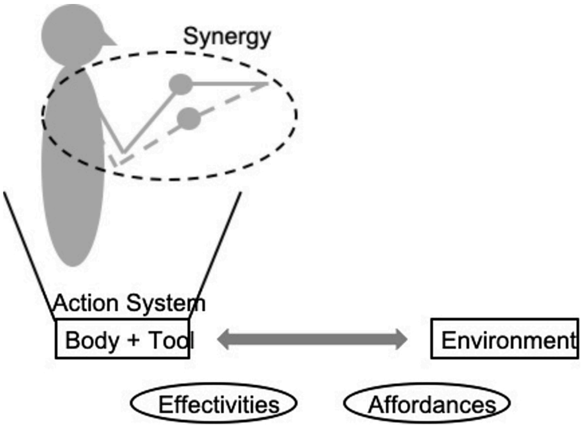

Fig. 5. The tool in the hand of the use is schematically depicted. Two arm postures are shown in which joint angles covary to stabilize the position of the tip of the tool in the environment, indicating that the tool is integrated in the synergy. The tool affects the synergies in the action system, and therefore the effectivities and the affordances.

et al., 2016; van der Steen and Bongers, 2011). Moreover, this effect did not depend on the length of the rod (10−40 cm) used to reach to a target. In a similar vein, Rein et al. (2013) showed that stone-knappers had more covariation in their joint angles than variation affecting the position of the hand and Mangalam et al. (2018a,b) showed that bearded capuchin monkeys stabilize the path of the hammer when cracking nuts. Therefore, several studies showed that joint angles covary to stabilize the end-effector at the tool, indicating that a tooling synergy is formed that incorporates the tool.

The incorporation of the tool in the synergy in the arm implies that constraints of the tool interact with constraints of the task, organism and environment to determine the effectivities. A change in effectivities as a function of the properties of the tool in use does also result in a change in affordances (Fig. 5). That is, the environment is perceived with reference to the properties of the action system that consists of the body and the tool. To examine this, several experiments were conducted in which participants had to select a distance from which to displace an object with the tip of a handheld rod (Bongers et al., 2004, 2003). Importantly, the to-be-displaced object was placed at hip-height and it was approached, and the distance had to be selected, with the tip of the rod pointing upwards so that the perceived affordance could be studied. Findings demonstrated that the selected distance was a function of the length of the rod and of the dynamic forces and torques created by the rod. Importantly, these effects interacted with properties of the to be displaced object (Bongers et al., 2004) emphasizing that tooling affordances refer to the relation between the properties of the action system, including the tool, and properties of the environment. The idea that tools affect the affordances and that the specifics of the tooling affordances are perceived by the organism is supported by studies of Wagman and colleagues. For instance, Wagman and Taylor (2005) showed that affordances can be perceived for the tool and for the body + tool system. Moreover, Wagman et al. (2016) showed that affordances of tools are perceived that are assembled out of other objects while also the affordances of the individual objects making up the tool can be perceived.

From the perspective outlined here we define a tool as an object from the environment that is incorporated in the emergent synergies in the action system to perform a goal-directed action. Based on this integration of the tool in the action system the end-effector displaces from the body to the tool and affects the effectivities and thus the affordances. Therefore, tools allow for actions that are not possible without the tool, while the performing of goal-directed actions with a tool emerge from similar principles as any other action. Hence, from this perspective tool use is a behavior as all other behaviors and does not require a specific label nor invoking specific psychological processes for its understanding.

Which of these psychological processes are exclusive to tool use? Which psychological processes involved in tool use are exclusive to *Homo sapiens*? From the ecological-dynamical approach it is straightforward to see that processes underlying tool use are not species specific. This is supported by the notion that affordances can be perceived by animals, as is specifically shown by Wagman et al. (Wagman et al., 2018, 2017). Moreover, self-organization is omnipresent as an organizing principle in the animate and the in-animate world. However, this does not mean that the same tooling behavior will be observed among species. That is, Mangalam et al. (2020d) showed differences in striking behavior in nut-cracking for bearded capuchin monkeys, expert humans and novice humans. Since these three groups have different organismic constraints, it is to be expected that their effectivities differ, their affordances differ and that the actualization of the affordances by the synergies differ. In sum, two basic notions of the ecological-dynamical approach, affordances and self-organization, play an essential role in tooling and non-tooling behavior among different species. Therefore, there is no principle reason why tool use cannot be understood with similar mechanisms as non-tooling behavior and over different species.

What must be the direction for future work on tool use? The approach presented in this contribution needs to be expanded to a broader range of behaviors and tools to be able to give a full-blown account of tool use. Here we present three possible routes in which the approach could be further expanded in the future. First, our earlier studies regarding synergies in rod reaching (Valk et al., 2016; van der Steen and Bongers, 2011) can be taken one step further. A defining characteristic of a synergy is not just covariation of joint angles, but also the actual location in joint space where the synergy emerges (Tuitert et al., 2020; Wissing et al., 2020). Studying whether, and if so how, the location in joint space where the synergy emerges depends on the tool's properties could further our understanding of the roles of tool constraints in the emergence of synergies.

Second, a topic that is relevant to understand tool use is the ability of organisms to construct tools (see contributions by Wagman & Day, Stout, Osiurak). Tool construction has been studied in the ecological-dynamical framework by Van Dijk and Bongers (2014), who examined the emergence of an action system when participants constructed new tools from available objects. Since affordances are prospective, they should be particularly apt to explain tool construction. A future line of research could focus on framing the problem of tool construction in terms of perceiving and actualizing affordances.

Third, tool use has often been approached as problem-solving behavior. Several approaches of tool use therefore incorporated cognitive mechanisms related to reasoning to give a full account of tool use (cf. Osiurak et al., 2010, 2017). Recently attempts have been made to broaden the ecological-dynamical approach to higher cognitive behaviors, such as action selection (Cox and Smitsman, 2019; Dineva and Schöner, 2018), representation-hungry behaviors (Golonka and Wilson, 2019), and language (Rączaszek-Leonardi et al., 2018; van den Herik, 2021). These expansions of an ecological-dynamical approach should in the future make it possible to explain aspects of tool use that are currently explained using cognitive mechanisms.

Together these developments should enable us to advance a full-blown account of tool use starting from the principles of an ecological-dynamical perspective. We believe that the starting point of such an account should lie in that tools are incorporated in synergies, and as such determine effectivities and affordances.

6. More than just tool use — Dietrich Stout

Humans have been described as tool-making animals but what is really distinctive is the broader realm of human technology. Technology is a broad and variable behavioral domain spanning a spatiotemporal range from neurons to institutions. Understanding its cognitive foundations will require comparative research across diverse technologies unified by an overarching evolutionary-developmental theoretical framework. This perspective highlights interactions between technological production, collaboration, and reproduction and the key role played by internal models for action prediction and synchronization.

What constitutes tool use (and is that the right question)? Many animals make and use tools, but humans are distinctive in the complexity, diversity, sophistication, omnipresence, and obligatory nature of our reliance on tools. Simply put, other animals use tools but only humans have technology. Indeed, humans inhabit a uniquely technological niche that we ourselves have constructed (Stout and Hecht, 2017), and which continues to shape our biology, behavior, and cognition. Attention to this broader technological sphere is clearly warranted. For example, Osiurak and colleagues (Osiurak and Heinke, 2018; Osiurak and Reynaud, 2020a) have argued that the prevailing conception of tool-use as object manipulation is too narrow because it excludes 'tools' such as machines, computers, containers, and structures. Thus, they suggest that it fails to emphasize a uniquely human capacity for 'technical reasoning.' Osiurak et al. propose neologisms like intoolligence (Osiurak and Heinke, 2018) to describe this broader sphere of investigation but the existing term technology might prove more apt if its meaning can be suitably constrained.

One approach is to ground the concept in an evolutionary perspective. Humans have evolved a tightly integrated adaptive strategy (Kaplan et al., 2010) in which a focus on high-value, difficult-to-acquire food resources provides the surplus nutrition needed to fund growth, survival, and reproduction, and is in turn enabled by the increased longevity and brain size that allow teaching, learning, and the cultural evolution of increasingly effective skills, knowledge, and equipment. This human-constructed niche is thereby populated by increasingly complex technological systems focused on material production. This evolutionary perspective converges with the 'technological systems' approach in the social sciences, which identifies a technology as an integrated system of hardware, people, skills, knowledge, social relations, and institutions (Dusek, 2006; Hughes, 1987).

On this view, technology comprises socially reproduced activities involving the manipulation or modification of objects to enact changes in the physical environment (Stout, 2013). This extends beyond simple tool use to encompass longer causal chains involving: 1) the coordinated activity of many individuals, 2) use of objects and materials in a wide range of roles other than as hand-held instruments, and 3) processes of social reproduction that sustain and elaborate technological systems. Communication is thus essential to technological systems but is not their ultimate goal. Technologies primarily pursue materially instrumental tasks to achieve physical changes in the world and only incidentally involve communicative tasks that seek to alter thoughts, behaviors, or experiences (cf. Legare and Nielsen, 2015). We could thus speak of technologies for the production of communications tools such as books or musical instruments but not for practices of teaching, storytelling, or musical composition. Systematic approaches to communications might then be termed 'arts' or 'sciences' rather than technologies. This semantic distinction is important because materially instrumental goals are shaped by relatively invariant physical constraints whereas the communicative goals must adapt to human psychology in the context of specific cultural systems of meaning. They will thus tend to implicate different cognitive processes (Finkel et al., 2018; Fischer et al., 2016; Tylén et al., 2016), learning strategies (Heyes, 2016; Kendal et al., 2018; Legare and Nielsen, 2015), and cultural evolutionary dynamics (Derex and Mesoudi, 2020).

What psychological processes underlie technology in humans and nonhuman animals? Attempts to specify a critical 'essence' of technology have invoked everything from skilled prehension (Buxbaum, 2017), to **causal reasoning** (Osiurak and Reynaud, 2020a), mental time travel (Suddendorf et al., 2018), **imitation** (Derex et al., 2019), and **mentalizing** (Tomasello et al., 1993). The technological niche perspective developed in the previous section recognizes all these as relevant and interacting. For example, the sophistication of human technology is often attributed to a process of incremental improvement termed as cumulative cultural evolution (CCE) (Mesoudi and Thornton, 2021). CCE is widely believed to require 'high fidelity' social reproduction dependent on mentalizing or imitation to enable the lossless accumulation of innovations (Derex et al., 2019; Tomasello et al., 1993). In the case of technology, however, capacities for causal and analogical reasoning (Gentner and Hoyos, 2017; Osiurak and Reynaud, 2020a), cognitive control (Gönül et al., 2018; McDougle et al., 2016; Stout et al., 2015), memory (Gruber and Ranganath, 2019), and perceptual-motor control (Sánchez et al., 2017) will often be implicated in the generation, identification, and retention of beneficial innovations (Legare and Nielsen, 2015; Miu et al., 2020). Insofar as innovation requires expertise, processes of knowledge reproduction (Gentner and Hoyos, 2017; Pan et al., 2020), skill acquisition (Gowlland, 2019), and innovation (Legare and Nielsen, 2015) will be thoroughly intertwined (Osiurak and Reynaud, 2020a; Stout and Hecht, 2017). Finally, the same capacities for **intersubjectivity** (Tomasello et al., 1993) and interactive synchrony (Pagnotta et al., 2020; Pan et al., 2020) that support the social reproduction of technology also underpin cooperation and coordination (Hill et al., 2009; Powers et al., 2016) that enable the complexity of collective human technologies to so far exceed that of individual animal tool-use. These complex interactions are organized around three key features of technology: production, collaboration, and reproduction.

Production. The materiality of technological production allows the open-ended accumulation of components and procedures (Derex and Mesoudi, 2020; Stout, 2013) and provides a durable medium for collaboration across time and space. Objects and infrastructure embody information and persist across generations, constituting a novel channel of cultural transmission and evolutionary inheritance (Laland et al., 2015). Technological artifacts and situations also scaffold cognition by externalizing information representation and manipulation and cuing the retrieval of appropriate event schemas (Barbey et al., 2009; Newen et al., 2018; Stout and Hecht, 2017).

Neuroscientific studies have largely focused on simple, hand-held tool use, leading to the identification of a dorsal occipital-parietal-frontal pathway instantiating spatial and kinematic object + body (Martel et al., 2016) models for action planning and perception and a ventral occipital-temporal pathway representing semantic information about properties and dynamics (Orban and Caruana, 2014; Stout and Hecht, 2017). This has now been extended to a broader account of object-driven cortex (Yildirim et al., 2019) including object and scene perception in ventral temporal cortex and intuitive physical reasoning about object dynamics (motion, support, collision) in frontoparietal cortex (Fischer et al., 2016). This "physics engine in the brain" is an assembly of regions involved in generating **internal models** for action planning (McNamee and Wolpert, 2019) and in cognitive control more generally (cf. frontoparietal control network; Dixon et al., 2018; Ptak et al., 2017).

Implicit technical reasoning supported by frontoparietal cortex may be sufficient for everyday tool use (Osiurak and Heinke, 2018), but more complex activities like the tool making and design impose additional demands (Ball and Christensen, 2019; Stout et al., 2015). These include **prospection** for future planning (Suddendorf et al., 2018), analogy and relational reasoning to find novel solutions (Ball and Christensen, 2019; Vendetti and Bunge, 2014), and metacognitive monitoring of strategic suitability and progress (Ball and Christensen, 2019) all of which involve a shift in attention from external stimuli to internal cognition that is thought to be supported by dynamic interactions between frontoparietal control and the default mode networks (Dixon et al., 2018).

Collaboration. Technology is most clearly distinguished from simple tool-use by its coordination of multiple individuals over extended periods of time and space. Small scale coordination between individuals relies on reciprocal prediction achieved by interpersonal coupling of internal forward models for anticipatory motor control (Curioni et al., 2019). This coupling can occur at multiple levels of abstraction (Hasson and Frith, 2016) and provides a key mechanism supporting the implicit mentalizing, empathy, communication, learning, and social affiliation (Alcalá-López et al., 2019; Hasson and Frith, 2016; Pan et al., 2020; Shamay-Tsoory et al., 2019) that in turn support larger scale collaboration. In addition to implicit processes of social alignment (Shamay-Tsoory et al., 2019) collaboration may require explicit negotiation to allocate responsibilities and agree on plans of action (Bang et al., 2017; Mathieu et al., 2017). This may involve metacognitive strategies such as confidence matching, deference to status or experience, and open discussion (Bang et al., 2017; Bang and Frith, 2021; Miu et al., 2020; Shea et al., 2014). Finally, collaboration may be enforced (Bang et al., 2017; Hughes, 1987) by explicit institutional rules and authority, which are in turn the emergent product of interactions between and within smaller groups (Powers et al., 2016; Pryor et al., 2019).

Reproduction. Technological learning is a protracted, collaborative process (Gobet, 2015; Gowlland, 2019; Pargeter et al., 2019; Suddendorf et al., 2016) reflective of demands for precise control of physical contingencies during material production. This problematizes dichotomies of social vs. asocial learning (Galef, 2013; Heyes, 2018), product vs. process copying (e.g., Tennie et al., 2009), and 'blind' vs. guided innovation (Mesoudi, 2021) that have been prevalent in culture evolution research. This is exemplified in technological apprenticeship (Gowlland, 2019; Sterelny, 2012), in which an extended program of alternating social learning and individual practice (Stout, 2013; Whiten, 2015) enables the reproduction of increasingly sophisticated skills. Such learning is scaffolded by everything from the exemplar artifacts, available tools, recurring situations, and observable behaviors of culturally constructed 'learning niches' (Flynn et al., 2013; Fragaszy et al., 2013; Stout and Hecht, 2017) to intentional demonstration, explicit instruction, and affective feedback from teachers (Kline, 2015) guides learners to re-create increasingly sophisticated skills though **deliberate practice** over extended periods, with each round of individual practice allowing deeper appreciation of the available social information.

The resulting expertise combines internal models for efficient action perception, control, and prediction (McNamee and Wolpert, 2019; Sokolov et al., 2017) with flexible task-related, hierarchical knowledge structures of increasing depth and complexity (Gobet, 2015; Stout, 2013). The relevance of each to particular technologies will help determine the efficacy of different learning strategies such as trial-and-error experimentation (Truskanov and Prat, 2018), end-product **emulation** (Reindl et al., 2017), body movement mimicry (Heyes, 2018; Tennie et al., 2009), intention sharing (Tomasello et al., 1993), and various forms of social scaffolding and teaching (Kline, 2015). Rather than one key reproductive mechanism we should thus expect context-dependent diversity (Caldwell, 2020).

Which of these psychological processes are exclusive to technology? By the definition proposed here, technology is an evolutionarily relevant domain of human activity rather than a discrete process or capacity. As such, technological cognition is 'soft-assembled' from neurocognitive mechanisms and systems as they become behaviorally relevant, rather than hard wired as a dedicated system. Thus, there would be no particular processes exclusive only to technology although the functional networks recruited by various technologies might be expected show a family resemblance distinct from other behavioral domains. On the other hand, the definition proposed here is motivated by specific evolutionary hypotheses positing that key processes supporting modern technology are elaborated in humans specifically due to selection on technological capacity and aptitude (Stout and Hecht, 2017). In this evolutionary sense, processes such as intuitive physical reasoning, kinematic monitoring of self and other, and even interactional synchrony would be specifically 'for' technology. Similar logic would apply to answering the original question of psychological processes exclusive to tool use, which is also a highly diverse behavioral domain that has proved surprisingly difficult to define (Crain et al., 2013; Fragaszy and Mangalam, 2018).

Which psychological processes involved in technology are exclusive to *Homo sapiens*? It is not clear that any of the processes involved in supporting technology are qualitatively unique to humans. Perhaps the strongest case could be made for cognitive mechanisms like explicit theory of mind, metacognitive strategies, or analogical reasoning that may themselves be products of cultural evolution in a fully linguistic species (Heyes, 2018). It has, however, been said (although it is unclear by whom) that "Quantity has a quality all its own." Humans may not be qualitatively unique on any one dimension of technology but we are quantitatively exceptional on so many different dimensions at the same time that piecemeal adaptive accounts seem to miss a bigger picture.

As reviewed above, exceptional human capacities for skilled interaction with the physical world appear central to the evolution and development of many key aspects technological cognition. Stout and Hecht (2017) thus suggest a Perceptual Motor Hypothesis (PMH) for the evolutionary-developmental-cultural construction of human cognition from ancient primate systems for body awareness and sensorimotor engagement with the world. These systems are early-developing (Baum et al., 2020) and directly engaged with the (internal and external) sensory periphery (Margulies et al., 2016), making them a nexus for interaction between externalizing processes of technological **niche construction** and internalizing processes of neurocognitive development (Byrge et al., 2014; Flynn et al., 2013; Heyes, 2018; Kennedy et al., 2017). According to the PMH, enhanced human sensorimotor acuity and the experiences this enables guide construction of the internal models and intuitive physics required for technological production. Sensory predictions by these models support the sense of agency and self-other discrimination (Haggard, 2017) that underpin human self-awareness, imitation, social cognition, and empathy (de Guzman et al., 2016) and ultimately the development of "Theory of Mind" capacities (Heyes, 2018), all of which support further technological collaboration, reproduction, and biocultural evolutionary feedback. According to this view, the proper study of technology must cross levels of analysis from neurophysiological dynamics to the cultural evolution of norms and institutions in order to seek unity in diversity by identifying the common processes underlying diverse outcomes across different real-world contexts.

What must be the direction for future work on tool use? Broadly speaking, a future "cognitive science of technology" would be a comparative science seeking to identify patterned relations between contexts, mechanisms, and functions across superficially diverse technologies. This means embracing the real-world complexity, variation, and contextual particularism (Matusz et al., 2019) of technological behaviors. Among the many challenges facing this endeavor are the large spatial and temporal scale of many technological phenomena, which may require long-term study and a combination of experiments (e.g., Pargeter et al., 2019), ethnographic case studies (e.g., Gowlland, 2019), and comparative analyses (e.g., Koster et al., 2020). One more specific direction could be to test the PMH. This would require expanding our surprisingly limited understanding of perceptual-motor variation across primates as well as the proposal that patterns of human technological diversity can be explained in relation to underlying variation in perceptual-motor processes, demands, and developmental interactions. One key prediction of the PMH is that learning and reasoning about even non-mechanical technological properties (e.g. chemical reactivity) should rely substantially on concrete perceptual-motor simulation (Barsalou, 1999) vs. abstract symbolic and analogical thinking (Brand et al., 2021). This prediction might be tested across various tasks and contexts using methods such as neuroimaging (cf. Fischer et al., 2016), behavioral studies of the impact of linguistic instruction on learning different skills both in the lab and "in the wild" (Brand et al., 2021), and the combination of the two to study the neurocognitive basis of individual differences in technological learning (Hecht et al., 2015; Prat et al., 2020).

Such ambitious aims are increasingly plausible with the development of new methods for the study of behavior and cognition in natural contexts. Techniques such as motion tracking and EEG are promising for the study of motor control (Haar et al., 2020) and attention (Ladouce et al., 2019) in real-life technological settings, while methods for the study of interactional synchrony (Pan et al., 2020; Schirmer et al., 2021) offer insight into mechanisms of small-scale collaboration and social reproduction. At a larger scale, smartphone-based digital phenotyping methods (Onnela, 2021) might be adapted to study individual experience of and engagement with real world technological situations and institutions. Finally, performance in unconstrained real-world situations can be related to individual differences or experience-related plasticity in neuroanatomical, cognitive, affective, and perceptual-motor traits assessed in the lab (e.g., Hecht et al., 2015; Prat et al., 2020). This will require novel methods for quantifying technological performance (e.g., Pargeter et al., 2019; Stout et al., 2018) but offers a critical links between structure, function, and behavior needed to place variation in a broader evolutionary and developmental frame (Stout and Hecht, 2017).

7. The technical-reasoning hypothesis — François Osiurak

The main tenets of the **technical-reasoning** hypothesis are as follows. Technical reasoning refers to the ability to reason implicitly about physical object properties (see Osiurak et al., 2010, Osiurak et al., 2020a,b; Osiurak and Badets, 2016). This reasoning is both causal (i.e., predicting the effects on the environment) and analogical (i.e., transferring what is understood from one situation to another). It is based on non-verbal knowledge, called **mechanical knowledge**, which contains information about physical principles about mechanical actions (i.e., actions that involve physical objects; leverage, cutting, percussion). Technical reasoning is much more than spatial reasoning, which can consist, for instance, in determining whether a car can pass between two trees or whether two puzzle pieces can be arranged together. Indeed, it involves the understanding of the material dimension of objects (e.g., hardness, sharpness), which is the basis for the emergence of mechanical actions. Technical reasoning is involved in any manifestation of human materiality such as the use of physical tools (e.g., stone tool, hammer), but also tool making or construction (e.g., building a shelter). It is also thought to be exclusive to the human lineage. Thus, because it allows humans to discover and master a great amount of technical content, its emergence over evolution might explain why **cumulative technological culture**, that is the increase in efficiency and complexity of tools and techniques over generations, has been observed only in human populations (Osiurak and Reynaud, 2020b). In the following lines, I present the technical-reasoning hypothesis in more detail[1] .

What constitutes tool use? The technical-reasoning hypothesis does not really confer any special status to tool use because it considers it as one of the manifestations of human materiality in the same ways as tool making or construction (or any technical devices that need the use of natural forces such as wind or fire). In this respect, as argued by Beck (1980) and Shumaker et al. (2011), any definition of tool use necessarily refers to a behavioral description, which does not imply any psychological or biological prerequisites. Thus, it is not because two species exhibit tool behavior that the same cognitive processes are at work in both species (Osiurak and Heinke, 2018). Note that the same is true for tool making or construction behavior. For these reasons, the technical-reasoning hypothesis is in line with the behavioral definitions of tool use, tool making, and construction proposed by Beck (1980) and more recently updated by Shumaker et al. (2011; Table 1). As explained, although the technical-reasoning hypothesis assumes that, in humans, technical reasoning is involved in any manifestation of human materiality (i.e., tool use, tool making, and construction), it nevertheless recognizes that tool use is characterized by an additional mechanism, that is, **distalization** (Osiurak and Federico, 2020). Distalization refers to the fact that, once a tool is grasped appropriately to be used, the natural effector (usually the hand) is no longer the end-effector. Instead, this end-effector becomes the active part of the tool, that is, the part of the tool that is used to act upon another object (e.g., the head of the hammer). Thus, there is an attentional shift, from the natural effector to the active part of the tool, while it is still the hand that needs to be controlled (for evidence for this distalization mechanism, see Cardinali et al., 2009; Iriki et al., 1996; Maravita et al., 2001; Maravita and Iriki, 2004; Miller et al., 2018; Osiurak et al., 2017; for an alternative explanation, see Holmes, 2012). This distalization mechanism also implies that the user needs to control the degrees of freedom of the body-tool system differently to the body-only system, a phenomenon called tooling (Fragaszy and Mangalam, 2018; Mangalam, 2016; Mangalam and Fragaszy, 2016). Importantly, this distalization mechanism is not unique to humans, which can explain why tool use can also be reported in nonhuman species. In broad terms, this distalization mechanism is orthogonal to technical reasoning in that it only allows a species to use tools, but it does not imply that this species possesses technical-reasoning skills.

What psychological processes underlie tool use in humans and nonhuman animals? Four cognitive functions are mainly involved in human tool use, each dedicated to a specific role: Technical reasoning, motor control, semantic memory, and planning[2] . The role of technical reasoning is to generate technical solutions to solve physical problems, which can be novel (e.g., to get a small ball that rolled under a couch) or familiar (e.g., to peel an apple). In this respect, the technical-reasoning hypothesis diverges from related proposals, which consider that technical-reasoning-like processes are primarily involved in novel situations and, at best, can be employed as an alternative strategy in familiar activities (e.g., Buxbaum, 2017; Caruana and Cuccio, 2017; Martin et al., 2016a,b; Norman, 2002). According to the technical-reasoning hypothesis, technical-reasoning skills support both familiar and novel tool use, even if the process can be faster for familiar activities than for novel situations. Technical reasoning is critical to determine the appropriate mechanical actions as well as to select the appropriate tools and objects to solve these problems. The outcome of technical reasoning is a mental simulation of the mechanical action to be performed (e.g., the motion of a knife on an apple). However, simulating a mechanical action is not sufficient to realize it in the physical environment. This realization needs the selection and on-line control of the most appropriate motor actions. This is the role of the motor-control system, which is unaware of the goal of the action (e.g., tool use, object transport). If someone intends to perform back-and-forth movements with a knife on an apple, this is the expected effect, which constrains the motor actions selected within the motor-control system. Likewise, if someone has the idea to move an object from one location to another, the expected effect is the motion of the object, which also constrains the motor actions selected. Said differently, the motor-control system is only concerned with the economy of motor actions performed. Because tools and objects are not always directly available, the user needs to get them from other places. The role of semantic memory is to organize the search in episodic

---

[1] I will limit the discussion on tool use to physical tool use (e.g., stone tool, hammer, fork; also called free tool use in Osiurak and Heinke, 2018). In other words, I will not discuss the use of arbitrary tools (i.e., interface-based technologies; e.g., washing machine, computer, smartphone) or assistive tools (i.e., “autonomous” technologies; e.g., heating system), that is, two phylogenetically recent categories of tools that need technical reasoning to be made but, at best, procedural or associative learning to be used (for more discussion on these tool categories; see (Osiurak, 2020; Osiurak and Heinke, 2018). In this way, they differ from physical tool use, which need technical reasoning to be made and used. The terms tool use and physical tool use will be employed here interchangeably.

[2] I am aware that motor control is not a cognitive function, strictly speaking. Nevertheless, for the sake of simplicity, I will consider it as one of the four main “cognitive” functions discussed in this section.

memory to know and, thus, to remember where to get the tools and objects appropriate for the ongoing activity (for discussion, see Osiurak, 2014, 2017). Indeed, knowledge about semantic categories (e.g., cooking, washing) is helpful to carry out an efficient search in episodic memory and to think of about tools and objects that are not here now (see Tulving, 1985). Finally, tool-use activities usually require a sequence of mechanical actions that can involve several tools and objects. An individual can generate these different mechanical actions in an unordered way. The role of planning skills is to rearrange this sequence in an ordered way so that to optimize time and to avoid potential fatal errors (i.e., the realization of a mechanical action that blocks the realization of another one). Thus, planning skills allow the individual to foresee future changes of the environment.

Evidence for the technical-reasoning hypothesis has come from the study of left brain-damaged patients, which has revealed a strong relationship between the ability to use and select familiar tools as well as to use, select and make novel tools to solve mechanical problems (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak et al., 2009; for a review, see Osiurak et al., 2020a,b). This behavioral association has also been confirmed by brain lesion studies, which have indicated that difficulties in using both familiar and novel tools are associated with damage to the brain area PF within the left inferior parietal lobe (Goldenberg and Spatt, 2009; Martin et al., 2016a; Mengotti et al., 2013; Salazar-López et al., 2016). Two recent neuroimaging meta-analyses have also revealed that the left area PF is preferentially and selectively activated when healthy participants focus on the mechanical actions between a tool and an object as well as when they observe others using tools (Reynaud et al., 2019, 2016). In other words, technical-reasoning skills could mainly be supported by the left area PF, allowing humans to generate and understand mechanical actions. By contrast, the ability to select the appropriate motor actions (to use tools or not) has been associated with more superior parietal structures and particularly the intraparietal sulci (e.g., Reynaud et al., 2016; Vingerhoets, 2014). Concerning semantic memory, a significant body of evidence has shown that semantic memory is neither necessary nor sufficient to actually use familiar or novel tools with objects (e.g., Buxbaum, 2017; Hodges et al., 2000; Lesourd et al., 2016; Silveri and Ciccarelli, 2009; for discussion, see Osiurak and Badets, 2016). In broad terms, this indicates that semantic memory is not useful to determine appropriate mechanical actions. However, the loss of semantic memory after temporal lobe lesions can impair the ability to use tools presented in isolation (Baumard et al., 2016; Hodges et al., 2000; Osiurak et al., 2008; Sirigu et al., 1991). thereby suggesting that semantic memory is first and foremost involved in the ability to link a tool with a specific usage (Osiurak, 2014). Finally, it has been found that patients with frontal lobe lesions or dysexecutive syndrome are impaired when they have to perform complex tool-use activities that require a sequence of mechanical actions and not when they have to solve less complex tool-use activities that require only one mechanical action (e.g., Goldenberg et al., 2007). To sum up, the four main cognitive functions that support human tool use are each dedicated to a specific role and associated with a specific neural basis (Technical reasoning: To solve physical problems/Mainly Left area PF; Motor control: To perform appropriate motor actions/Notably motor, premotor, and somatosensory cortices, along with the basal ganglia, thalamus, and cerebellum; Semantic memory: To get absent tools and objects/Mainly temporal lobes; Planning: To rearrange sequences of actions in an economical way/Mainly prefrontal cortex).

Which of these psychological processes are exclusive to tool use? None of the four aforementioned cognitive functions are considered as exclusive to tool use, except the distalization mechanism of the motor-control system, which could constitute the very essence of tool use (see above). Indeed, as explained, technical reasoning is also at work when humans make tools or build constructions. The motor-control system is unaware of the goal of the action. Semantic memory is involved more generally in our knowledge about the world and is not critical to actually use tools with objects. Finally, planning skills are in charge of optimizing time when a sequence of actions is performed, irrespective of whether this sequence is tool-centered or not (e.g., construction behavior, but also when people play chess or optimize their shopping trips).

Which psychological processes involved in tool use are exclusive to *Homo sapiens*? There is a tendency in the animal cognition literature to give to nonhuman tool-using species a special status, as if tool use reflected a specific sign of intelligence. As argued by Hansell and Ruxton (Hansell and Ruxton, 2008), this status might be exaggerated because it is based on a confusion or even a kind of bijection (i.e., strict correspondence) between tool use and specific physical-cognitive skills. As explained above, tool use could be observed in any species that possesses a distalization ability. However, this ability is orthogonal to the level of physical understanding that the species has. In this way, the technical-reasoning hypothesis obviously recognizes that tool use is not exclusive to humans. However, it also stresses that the study of tool use is not sufficient to understand how humans and nonhuman animals are able to understand their physical environment. As a matter of fact, the technical-reasoning hypothesis suggests that even if some animals could possess some of the components of technical reasoning (e.g., the causal component), technical reasoning in its entirety could be exclusive to humans. This claim is based on evidence from **micro-society paradigms**[3], which have shown that cumulative performance can emerge over generations even when individuals only transmit the product made (e.g., a tower or a basket; i.e., reverse engineering; (Caldwell and Millen, 2009; Derex et al., 2019; Osiurak et al., 2021b; Zwirner and Thornton, 2015). Technical-reasoning skills (assessed with psychotechnical tests; e.g., selecting among four pictures depicting four different nails the easiest one to hammer) have also been found to be the best predictor of cumulative performance in these micro-society experiments (De Oliveira et al., 2019; Osiurak et al., 2021a, 2020a, 2016). Conversely, cumulative performance observed in this kind of paradigm is also accompanied by an increase in understanding of the physical system (Osiurak et al., 2021b). Taken together, these results indicate that technical-reasoning skills could have played a key role in cumulative technological culture, namely, a phenomenon that is considered as unique to the human lineage[4]. In sum, although tool use is not unique to humans, it might be nevertheless exclusive in humans because of its 'recycling' by technical-reasoning skills.

What must be the direction for future work on tool use? There is a crucial need in the literature to draw a marked distinction between tool-use skills from technical-reasoning skills, because of their orthogonality at a cognitive level. It is one thing to be able to manipulate a tool to use it with an object and another to understand the physical effects of this interaction. In this respect, three distinct lines of research should be developed. The first line should consist in extending the question of physical understanding in human tool use to tool making and

---

[3] Micro-society paradigms aim to investigate cultural evolution in laboratory (e.g., Caldwell and Millen, 2009; Morgan et al., 2015). The most popular version is the transmission chain paradigm. The task can be to optimize the speed of a wheel that descends an inclined track by moving the four weights placed along each spoke of the wheel (Derex et al., 2019; Osiurak et al., 2021b). The first participant of the chain performs the task. The second participant can scrutinize the product of (i.e., reverse-engineering), observe the action made by, or communicate with the first participant before performing the task themselves. Then, the third participant does the same with the second one, and so on.

[4] Studies on New Caledonian crows indicate that some signs of cumulative technological culture have been observed in this species, which is for its elaborate causal-reasoning skills (Rutz and Hunt, 2020; Taylor and Jelbert, 2020). In other words, although the technical-reasoning hypothesis in its strong form posits that both cumulative technological culture and technical-reasoning skills might be unique to humans, much more evidence is needed to demonstrate it (or to invalidate this claim).

construction behavior. One of the goals of this extension can be to test whether technical-reasoning skills are really involved in any manifestation of human materiality. More generally, this could allow emergence of a specific field in cognitive sciences investigating cognitive skills needed to modify the physical environment, that is, technition (Osiurak et al., 2020b). The second line should consist in deepening our understanding of the cognitive mechanisms that are required to use tools (potentially the distalization mechanism). Taken together, these two lines of research can help us to specify the cognitive components associated with tool-use skills versus technical-reasoning skills. Finally, a third line of research could explore whether a certain link can exist between both. For instance, even if these two kinds of skills are orthogonal, it remains very plausible that the ability to manipulate tools can favor the exploration of the physical environment and can be an important prerequisite for the emergence of technical-reasoning skills in a given species. Thus, these three lines of research should be particularly useful to understand the specific trajectory of technological evolution in the human lineage on the basis of a plurality of methods and techniques from distinct but complementary disciplines, such as neuropsychology, cognitive neuroscience, developmental and comparative psychology, archaeological and anthropological sciences.

8. Discussion

Multiple lines of scientific and philosophical investigation are concerned with the development and expression of humans' engagement with tools and its relation to other dimensions of human experience. At first sight, these multiple lines of inquiry (including those described by the six author groups in this collection) may appear to be incongruent. However, as we shall discuss below, these seemingly divergent perspectives converge on some common themes and consequently foster a more comprehensive, interdisciplinary understanding of tool use than any of these perspectives would (or could) on their own. It is to these seeming consistencies and their integration that we turn now.

What constitutes tool use? So, what are the points of convergence across researchers in their ideas about what constitutes tool use. All authors noted that tool use is associated with transforming the body into the body-tool system (i.e., all incorporate the notion of distalization of the end-effector). Mangalam and Fragaszy, Wagman and Day, and Bongers each focus on tool use to detect and exploit lawfully structured patterns of energy that provide 'information about' affordances of tools. Mangalam and Fragaszy provide a definition in which tooling is a deliberate act in which the body-object system produces a mechanical effect on a target. This definition necessitates that the actor, tool, and target physically contact each other during the activity of tooling and that the act of tooling lasts only as long as this spatial relationship is maintained (Fragaszy and Mangalam, 2018; Mangalam and Fragaszy, 2016). The authors justify this narrow definition because it affords analytical clarity. Wagman and Day expand the scope of this definition by including any interaction with an intermediary object that changes the ability to perceive and actualize affordances in the context of performing a goal-directed behavior. Consequently, Wagman and Day classify behaviors as tool use that Mangalam and Fragaszy would not, such as throwing objects at a target and using a wheelbarrow to transport material. Except for this discrepancy, Wagman and Day's views are mostly compatible with those of Mangalam and Fragaszy—both rooted in the Gibsonian concepts of affordances and information detection. Bongers' perspective is rooted in these concepts as well: tool use occurs when an environmental object temporarily alters the capacity for action, requiring the new coordination patterns in the act of performing that action (cf. Profeta and Turvey, 2018).

Kelty-Stephen also grounds his analysis in lawful relations, but shifts focus away from psychological processes per se and toward generic processes of cascade dynamics. Kelty-Stephen emphasized that tool use is an intermittent cascade of contingencies across a permeable animal-environment boundary. This permeability allows tool movement to inherit the multifractal fluctuations inherent in limb movement and return new multifractal fluctuations to those limbs (see also Mangalam et al., 2020a,b). Fluctuations flow through a continuous medium spanning the organism, tool, and environment via informational contact (acoustic, mechanical, optical). So, for Kelty-Stephen (like Wagman & Day), tool use does not necessitate continual mechanical contact between the object and the body.

Stout and Osiurak, respectively, focus more on processing and cultural transmission of information. Stout finds no utility in defining tool use per se and instead chooses to subsume tool use under the broader umbrella of technology. For him, technology (but not tool use) is a uniquely human endeavor—tool use (considered on its own) fails to capture the uniquely human capacity for 'technical reasoning.' Stout's view is consistent with that of Osiurak for whom 'intelligence' is the intelligent use of technological innovations including, but not limited to, tools (Osiurak and Heinke, 2018; Osiurak and Reynaud, 2020a). Osiurak does not confer any special status to tool use because it is merely one of the ways in which technical reasoning is brought to bear in human materiality. However, Osiurak suggests that tool use requires an additional mechanism beyond technical reasoning: distalization (Osiurak and Federico, 2020).

What psychological processes underlie tool use in humans and nonhuman animals? A fundamental question in the study of tool use concerns the psychological processes that underlie this phenomenon, but the divergence among researchers about what constitutes tool use may hamper a coherent answer to this question. Some researchers have investigated the neurophysiological underpinnings of tool use by studying brain-damaged patients (Goldenberg and Spatt, 2009; Lewis, 2006; Wheaton and Hallett, 2007) or noninvasive functional neuroimaging in everyday settings (Bril et al., 2005; Krakauer et al., 2017). Others have done so by conducting comparative analyses of tool use across species (Bril et al., 2012; Mangalam et al., 2020d; Mangalam and Fragaszy, 2016). Unfortunately, any observed pattern of brain activation is mute on the psychological processes reflected by that activation pattern. A lack of a coherent theoretical framework makes it challenging to conduct studies across species that yield testable predictions about the psychological processes involved in tool use. So, we take this opportunity to suggest some degree of convergence on the psychological processes involved in tool use.

For Mangalam and Fragaszy, the psychological processes of interest in tool use are at the level of perception and action—in particular, the functional task demands establishing and maintaining a mechanical interface. In their embodied theory of tooling (Fragaszy and Mangalam, 2018), tool use depends on the perceptuomotor processes related to perceiving spatial relations among objects and surfaces, developing agency over objects attached to the body (the distalization of the end effector), and controlling the bodily degrees of freedom to meet functional task demands. Mangalam and Fragaszy emphasize that these processes occur in the body-object-task-environment system. Moreover, together, these processes distinguish tool use from other instrumental problem-solving.

Similarly, for Wagman and Day, the psychological processes of interest in tool use are at the level of perception and action. They focus their analysis on detecting and exploiting lawfully structured stimulation patterns ('information'). When the animal-environment fit is altered by a tool, the structure encountered at the point of observation provides information about affordances for tool use—whether, when, and how the tool can be used to achieve a goal. The lawfulness of this process entails that information about tool use is invariant over transformations (Hajnal et al., 2007; Mangalam et al., 2017; Wagman et al., 2017; Wagman and Hajnal, 2014a,b, 2016). Perceiving (and actualizing) such affordances requires spontaneously and temporarily assembling task-specific detection units (and task-specific control units) across body and tool capable of detecting (and exploiting) such information.

Kelty-Stephen takes the lawful grounding of tool use described by Wagman & Day one step further. The processes that underlie tool use are cascade dynamics—the same generic processes that underlie the behavior of all systems that branch, avalanche, diffuse, or spread apart across multiple temporal or spatial scales. Cascade dynamics are exhibited at all levels of the organization and all levels of scale both within an organism and across the animal-environment system (Fernandez-Gonzalez and Zallen, 2011; Fratzl, 2008; Goldberger et al., 1990). Moreover, the spreading of these interactions across levels and scales of the analysis entails a multifractal structure (e.g., Ingber, 2006; Turvey and Fonseca, 2014). The waxing and waning of multifractal fluctuations predict cascade-driven coordination of events during tool use (Mangalam et al., 2020a,b).

Bongers' analysis is also at the level of perception and action and has the same lawful grounding in specificity relations as Wagman and Day's analysis and Kelty-Stephen's analysis. Bongers' focus is on the control of coordinated action in actualizing affordances for tool use. Actualizing affordances (with or without a tool) requires establishing synergies—emergent coordinative patterns among numerous degrees of freedom spanning the task, organism, and environmental constraints. The synergies that can emerge under these circumstances determine an animal's capability for acting—its effectivities. An object attached to the body that functions as a tool affects the emergence of synergies, and hence, the effectivities of the action system. Therefore, tool use requires integrating the tool into the synergy emerging in the action system consisting of body-tool. This thesis is consistent with the analysis provided by Mangalam and Fragaszy.

Stout's emphasis on technology rather than tool use per se leads him to consider a broader range of psychological processes that are more intimately tied to traditional cognitive psychology than any of the preceding authors, especially so because of the relationship between technology and culture. At the technological level, these processes include causal and analogical reasoning, cognitive control, memory, and perceptual-motor control in behavioral exploration. At the level of a technological society, these processes are organized around production, collaboration, and reproduction.

Finally, Osiurak posits that tool use is supported by four cognitive functions: technical reasoning, motor control, semantic memory, and planning. Importantly, technical reasoning results in a simulation of the mechanical action performed but not the performance of those actions. Motor control is thus required to select and control the simulated actions. Semantic memory is required to think about tools appropriate for performing the simulated action and where such tools might be located. Planning is required to prospectively organize the actions involving tools in a way that is efficient and as error-free as possible.

So, what are the points of convergence across researchers in their ideas about the psychological processes involved in tool use? All author groups note that tool use is associated with transforming the body into the body-tool system (i.e., all incorporate the notion of distalization of the end-effector). Mangalam and Fragaszy, Wagman and Day, and Bongers each focus on tool use to detect and exploit lawfully structured patterns of energy that provide 'information about' affordances of tools. Kelty-Stephen also grounds his analysis in lawful relations, but shifts focus away from psychological processes per se and toward generic processes of cascade dynamics. Stout and Osiurak, respectively, focus more on processing and cultural transmission of information. Specifically, they identify technical reasoning, semantic memory, and planning as cognitive abilities fundamental to the production, collaboration in, and reproduction of novel tool-use behaviors.

Which of these psychological processes are exclusive to tool use? This question is important because if any psychological process is exclusive to tool use, it will imply that a particular developmental or evolutionary trajectory enables or facilitates tool use. Indeed, this trajectory is what Mangalam and Fragaszy's definition attempts to uncover. Their definition of tool use attempts to provide a theoretical foundation for making testable predictions about which individuals (and species) can use tools, to what extent they can do so, and under which conditions. For Mangalam and Fragaszy, the three processes that support tool use are: (1) establishing and managing spatial relation(s) between an object attached to the body and a target object; (2) distalization of the end-effector; (3) coordinating the body-object system. They propose that while none of these perceptuomotor processes are exclusive to tool use, the concurrent involvement all three is a distinctive feature of tool use.

Osiurak posits that four cognitive functions support tool use (technical reasoning, motor control, semantic memory, and planning). For Wagman & Day, the lawfully structured patterned energy arrays that provide information about whether, when, and how to move to achieve a goal are invariant across transformations—including whether (or not) a tool is used in the act. For example, invariant mechanical patterns are informative about controlling limb movement regardless of whether a person is using a hand-held object. Along similar (but perhaps not identical) lines, Bongers and Kelty-Stephen advocate that the processes underlying self-organization in complex tool-using systems are entirely generic, underlying self-organization in all complex systems—human and animal, living and non-living.

For all authors except Osiurak, there are no psychological processes that are exclusive to tool use. For Wagman & Day, the lawfully structured patterned energy arrays that provide information about whether, when, and how to move to achieve a goal are invariant across transformations—including whether (or not) a tool is used in the act of doing do (e.g., invariant mechanical patterns are informative about controlling limb movement regardless of whether a person is using a hand-held object). Along similar (but perhaps not identical lines), Bongers and Kelty-Stephen advocate that the processes underlying self-organization in complex tool-using systems are entirely generic, underlying self-organization in all complex systems—human and animal, living and non-living.

The distalization of the end-effector when using tools has received attention in various forms, such as the tooltip becoming the end-effector (Arbib et al., 2009; Takahashi and Watt, 2017; Umiltà et al., 2008), changes in the perception of space (Berti and Frassinetti, 2000; Canzoneri et al., 2013), and the extension of sensorimotor processing (Miller et al., 2018). Mangalam and Fragaszy (and to some extent Osiurak) argue that this condition is necessary but not sufficient for tool use. Yet Wagman and Day, Kelty-Stephen, and Bongers' argue that distalization (or any other psychological process) is neither sufficient nor necessary for tool use. How might this be resolved? For Mangalam and Fragaszy, the distalization of the end-effector is a behavioral description associated with the shift of the locus of perceptual and action control from the biological effector (e.g., hand, beak). Hence, any investigation must, at least, explain such patterns of variation in the perceptual and action outcomes of using a tool. For Wagman and Day, Bongers, and Kelty-Stephen, these processes are the same ones that enable perception and movement of the body without a tool (Harrison et al., 2011; Mangalam et al., 2019c; Pagano et al., 1993; Wagman et al., 2017). These two approaches address two distinct sets of questions—one associated with perception-action shift (Mangalam and Fragaszy, 2016), and the other associated with informational support for perception (Thomas et al., 2019).

Which psychological processes involved in tool use are exclusive to *Homo sapiens*? Any special association of tool use with humans depends on whether any psychological process involved in tool use is exclusive to humans. Otherwise, shared processes would suggest that human tool use differs from that observed in nonhuman species in the degree but not the type of psychological processes.

Mangalam and Fragaszy address tool use at the behavioral level, emphasizing perceptuomotor processes of perceiving spatial relations among objects and surfaces, developing agency over objects attached to the body (the distalization of the end effector), and controlling the bodily degrees of freedom to meet functional task demands. Importantly, Mangalam and Fragaszy suggest that none of these processes are unique to humans—nonhuman species show behaviors supported by each of these processes in isolation. However, they propose that what is unique to humans is the degree to which these processes can be regulated simultaneously and the number of functional parameters that can be controlled in a given tool use task, such as when manufacturing sharp flakes from stone cores (Bril et al., 2015, 2012).

Wagman and Day argue that lawful structuring of energy distributions by the animal-environment relationship entails that the information about a given affordance (for tool use) is invariant over the sensory apparatus, nervous system, and brain of the animal doing the perceiving. Therefore, any animal capable of detecting (and exploiting) such structure is capable of tool use. For them, any differences in the ability to use tools between humans and non-humans is due to the sophistication of the ecological niche occupied by that species (Gibson, 1979; Turvey, 2018). The more sophisticated the environment occupied by a given species, the more sophisticated the affordances available to that species. This argument explains why nonhuman primates that do not use tools in their natural habitat use tools more frequently when in captivity (Haslam, 2013). Hence, Wagman and Day's thesis is consistent with that of Stout who argues that humans inhabit a uniquely technological environment and (like many nonhuman animal species) participate in the construction of that environment.

Bongers offers a similar view, arguing that the lawfulness underlying (the self-organization of) perception-action entails that the processes underlying tool use are not (and cannot be) species-specific. Any differences between species in their capacity to use tools will be due (in part) to differences in emergent synergies given task, organism, and environmental constraints. Kelty-Stephen also relies on the lawful dynamics of self-organization by drawing an analogy between how an amoeboid slime mold fashions a tool from its bodily degrees of freedom and how a human fashions a tool from some external object. Stout emphasizes that none of the processes involved in supporting technology are qualitatively unique to humans. Finally, Osiurak argues that whereas tool use itself is not a uniquely human phenomenon, some of the psychological processes underlying it (technical reasoning skills) may be so. He argues that these technical reasoning skills have contributed to the cumulative technical culture that is exclusive to humans.

In summary, although the authors differ significantly in their views on whether any psychological process is exclusive to tool use, none identified even a single psychological process involved in tool use that is exclusive to humans. The emerging theme is that the psychological processes that underlie humans' unprecedented capability to use tools, make new tools, and recycle old tools for new purposes are shared in some manner with other species.

What must be the direction for future work on tool use? As noted above, how each author group defines tool use drives how that author group investigates tool use and hence envisions the direction for future work on tool use. Mangalam and Fragaszy suggest that future work must be concerned with the three-component perceptuomotor processes involved in tool use: (1) establishing and managing spatial relation(s) between an object attached to the body and a target object; (2) distalization of the end-effector; and (3) coordinating the body-object system during tool use. Kelty-Stephen suggests applying his perspectives on tool use to a broader set of questions related to whether and how the multifractal geometry of tool use can formalize agency as a cascade-driven process. Examples of such studies include the role of fluctuations within the body (Mangalam et al., 2019a,b), the role of fluctuations at the postural center of pressure (Mangalam et al., 2020c; Mangalam and Kelty-Stephen, 2020), and the flow of multifractal fluctuations to-and-fro between the body and the tool (Mangalam et al., 2020a,b). Bongers makes three specific suggestions about applying the ecological-dynamics approach to the emergence of synergies in tool use, tool construction, and higher cognitive behaviors such as action selection and language (Cox and Smitsman, 2006; Keen et al., 2014; Smitsman and Cox, 2008; Valk et al., 2016; van Dijk and Bongers, 2014). Osiurak and Stout, respectively, also suggest that future work must focus on the processes underlying tool (and technology) use; both suggest taking advantage of noninvasive brain imaging techniques to investigate the neurophysiological underpinnings of tool use (Baumard et al., 2016; Jarry et al., 2013; Osiurak et al., 2009; Reynaud et al., 2016; Stout et al., 2015, 2008; Stout and Chaminade, 2007). Specifically, Stout highlights that using multiple techniques simultaneously such as motion tracking and electroencephalography (EEG) (Haar et al., 2020) has enormous potential for the study of technological production.

Like Bongers, Osiurak suggests that future work must investigate tool making and tool construction, but for him, the goal of such investigations should be to uncover the technical reasoning skills as well as the cognitive mechanisms that underlie distalization of the end-effector (Osiurak et al., 2018; Pazen et al., 2020). Wagman and Day propose that future work on tool use focus on the technological, communication, and representation systems characteristic of tool use in the human niche. They propose the development of interfaces for teleoperation of devices such as laparoscopic surgical tools, surveillance drones, or phone apps that preserve, enhance, or generate lawful structuring of energy patterns at any point of observation, and how to best train users of such devices (cf. Pagano and Day, 2020). Similarly, Stout promotes 'real-world technological situations' to investigate relations among structure, function, and behavior. However, he focuses less on the development of technology itself and more on understanding relations between performance in tool-use tasks and individual differences or experience-related plasticity in neuroanatomical, cognitive, affective, and perceptuomotor traits assessed in the lab (Stout, 2021; Stout et al., 2008; Stout and Chaminade, 2012).

In summary, the six author groups with extensive research experience ($>$ 100 years in total) present quite distinct perspectives on the direction of future work on tool use. To a student just beginning his/her research career, or to a seasoned researcher, tool use might not appear as multifaceted a phenomenon with a wide scope for study as this review suggests. All eight authors hope that this review inspires both new and seasoned researchers alike to look again at tool use—a behavior that sparks the feeling of wow in a child successfully hammering a nail for the first time, and that is arguably a keystone of human existence.

Data availability

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

References

Alcalá-López, D., Vogeley, K., Binkofski, F., Bzdok, D., 2019. Building blocks of social cognition: Mirror, mentalize, share? Cortex 118, 4–18. https://doi.org/10.1016/j.cortex.2018.05.006.

Altenhoff, B.M., Pagano, C.C., Kil, I., Burg, T.C., 2017. Learning to perceive haptic distance-to-break in the presence of friction. J. Exp. Psychol. Hum. Percept. Perform. 43, 231–244. https://doi.org/10.1037/xhp0000298.

Arbib, M.A., 2012. Tool use and constructions. Behav. Brain Sci. 35, 218–219. https://doi.org/10.1017/S0140525X11002123.

Arbib, M.A., Bonaiuto, J.B., Jacobs, S., Frey, S.H., 2009. Tool use and the distalization of the end-effector. Psychol. Res. 73, 441–462. https://doi.org/10.1007/s00426-009-0242-2.

Bagorda, A., Mihaylov, V.A., Parent, C.A., 2006. Chemotaxis: moving forward and holding on to the past. Thromb. Haemost. 95, 12–21. https://doi.org/10.1160/TH05-07-0483.

Ball, L.J., Christensen, B.T., 2019. Advancing an understanding of design cognition and design metacognition: progress and prospects. Bull. Soc. Belg. Etud. Geogr. 65, 35–59. https://doi.org/10.1016/j.destud.2019.10.003.

Bang, D., Frith, C.D., 2021. Making better decisions in groups. R. Soc. Open Sci. 4, 170193 https://doi.org/10.1098/rsos.170193.

Bang, D., Aitchison, L., Moran, R., Herce Castanon, S., Rafiee, B., Mahmoodi, A., Lau, J.Y. F., Latham, P.E., Bahrami, B., Summerfield, C., 2017. Confidence matching in group decision-making. Nat. Hum. Behav. 1, 117. https://doi.org/10.1038/s41562-017-0117.

Barbey, A.K., Krueger, F., Grafman, J., 2009. Structured event complexes in the medial prefrontal cortex support counterfactual representations for future planning. Philos. Trans. R. Soc. B Biol. Sci. 364, 1291–1300. https://doi.org/10.1098/rstb.2008.0315.

Barsalou, L.W., 1999. Perceptual symbol systems. Behav. Brain Sci. 22, 577–660. https://doi.org/10.1017/S0140525X99002149.

Bauer, H., 2001. Use of tools by lions in Waza National Park. Cameroon. Afr. J. Ecol. 39, 317. https://doi.org/10.1046/j.1365-2028.2001.00311.x.

Baum, G.L., Cui, Z., Roalf, D.R., Ciric, R., Betzel, R.F., Larsen, B., Cieslak, M., Cook, P.A., Xia, C.H., Moore, T.M., Ruparel, K., Oathes, D.J., Alexander-Bloch, A.F., Shinohara, R.T., Raznahan, A., Gur, R.E., Gur, R.C., Bassett, D.S., Satterthwaite, T.D., 2020. Development of structure–function coupling in human brain networks during youth. Proc. Natl. Acad. Sci. 117, 771–778. https://doi.org/10.1073/pnas.1912034117.

Baumard, J., Lesourd, M., Jarry, C., Merck, C., Etcharry-Bouyx, F., Chauviré, V., Belliard, S., Moreaud, O., Croisile, B., Osiurak, F., Le Gall, D., 2016. Tool use disorders in neurodegenerative diseases: roles of semantic memory and technical reasoning. Cortex 82, 119–132. https://doi.org/10.1016/j.cortex.2016.06.007.

Beck, B.B., 1980. Animal Tool Behavior. Garland STPM Press, New York, NY.

Bernstein, N.A., 1967. The Co-ordination and Regulation of Movements. Pergamon Press, New York, NY.

Bernstein, N.A., Latash, M.L., Turvey, M.T., 1996. Dexterity and Its Development. Lawrence Erlbaum, Marwah, NJ.

Berti, A., Frassinetti, F., 2000. When far becomes near: remapping of space by tool use. J. Cogn. Neurosci. 12, 415–420. https://doi.org/10.1162/089892900562237.

Bird, C.D., Emery, N.J., 2017. Rooks use stones to raise the water level to reach a floating worm. Curr. Biol. 19, 1410–1414. https://doi.org/10.1016/j.cub.2009.07.033.

Biryukova, E., Bril, B., 2012. Biomechanical analysis of tool use: a return to Bernstein's tradition. Z. Psychol. 220, 53–54. https://doi.org/10.1027/2151-2604/a000092.

Bongers, R.M., 2001. An Action Perspective on Tool Use and Its Development. Printpartners Ipskamp BV, Enschede, Netherlands.

Bongers, R.M., Smitsman, A.W., Michaels, C.F., 2003. Geometries and dynamics of a rod determine how it is used for reaching. J. Mot. Behav. 35, 4–22. https://doi.org/10.1080/00222890309602117.

Bongers, R.M., Michaels, C.F., Smitsman, A.W., 2004. Variations of tool and task characteristics reveal that tool-use postures are anticipated. J. Mot. Behav. 36, 305–315. https://doi.org/10.3200/JMBR.36.3.305-315.

Borsari, A., Ottoni, E.B., 2005. Preliminary observations of tool use in captive hyacinth macaws (*Anodorhynchus hyacinthinus*). Anim. Cogn. 8, 48–52. https://doi.org/10.1007/s10071-004-0221-3.

Boyd, R., Richerson, P.J., 1996. Why culture is common, but cultural evolution is rare. In: Evolution of Social Behaviour Patterns in Primates and Man, Proceedings of The British Academy, Vol. 88. Oxford University Press, New York, NY, US, pp. 77–93.

Brand, C.O., Mesoudi, A., Smaldino, P.E., 2021. Analogy as a catalyst for cumulative cultural evolution. Trends Cogn. Sci. (Regul. Ed.) 25, 450–461. https://doi.org/10.1016/j.tics.2021.03.002.

Bril, B., Roux, V., Dietrich, G., 2005. Stone knapping: Khambat (India), a unique opportunity? In: Roux, V., Bril, B. (Eds.), Stone Knapping: The Necessary Conditions for a Uniquely Hominin Behaviour. McDonald Institute for Archaeological Research, Cambridge, UK, pp. 53–71.

Bril, B., Dietrich, G., Foucart, J., Fuwa, K., Hirata, S., 2009. Tool use as a way to assess cognition: how do captive chimpanzees handle the weight of the hammer when cracking a nut? Anim. Cogn. 12, 217–235. https://doi.org/10.1007/s10071-008-0184-x.

Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata, S., Roux, V., 2012. Functional mastery of percussive technology in nut-cracking and stone-flaking actions: experimental comparison and implications for the evolution of the human brain. Philos. Trans. R. Soc. B Biol. Sci. 367, 59–74. https://doi.org/10.1098/rstb.2011.0147.

Bril, B., Parry, R., Dietrich, G., 2015. How similar are nut-cracking and stone-flaking? A functional approach to percussive technology. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 370, 20140355 https://doi.org/10.1098/rstb.2014.0355.

Buxbaum, L.J., 2001. Ideomotor apraxia: a call to action. Neurocase 7, 445–458. https://doi.org/10.1093/neucas/7.6.445.

Buxbaum, L.J., 2017. Learning, remembering, and predicting how to use tools: distributed neurocognitive mechanisms: comment on Osiurak and Badets (2016). Psychol. Rev. 124, 346–360. https://doi.org/10.1037/rev0000051.

Buxbaum, L.J., Johnson-Frey, S.H., Bartlett-Williams, M., 2005. Deficient internal models for planning hand–object interactions in apraxia. Neuropsychologia 43, 917–929. https://doi.org/10.1016/j.neuropsychologia.2004.09.006.

Byrge, L., Sporns, O., Smith, L.B., 2014. Developmental process emerges from extended brain–body–behavior networks. Trends Cogn. Sci. (Regul. Ed.) 18, 395–403. https://doi.org/10.1016/j.tics.2014.04.010.

Caldwell, C.A., 2020. Using experimental research designs to explore the scope of cumulative culture in humans and other animals. Top. Cogn. Sci. 12, 673–689. https://doi.org/10.1111/tops.12391.

Caldwell, C.A., Millen, A.E., 2009. Social learning mechanisms and cumulative cultural evolution: is imitation necessary? Psychol. Sci. 20, 1478–1483. https://doi.org/10.1111/j.1467-9280.2009.02469.x.

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013. Tool-use reshapes the boundaries of body and peripersonal space representations. Exp. Brain Res. 228, 25–42. https://doi.org/10.1007/s00221-013-3532-2.

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., Farnè, A., 2009. Tool-use induces morphological updating of the body schema. Curr. Biol. 19, R478–R479. https://doi.org/10.1016/j.cub.2009.05.009.

Carello, C., Turvey, M., 2016. Dynamic (effortful) touch. In: Prescott, T., Ahissar, E., Izhikevich, E. (Eds.), Scholarpedia of Touch. Atlantis Press, Paris, pp. 227–240. https://doi.org/10.2991/978-94-6239-133-8_18.

Carello, C., Wagman, J.B., 2009. Mutuality in the perception of affordances and the control of movement. In: Sternad, D. (Ed.), Progress in Motor Control. Springer, Boston, MA, pp. 273–292. https://doi.org/10.1007/978-0-387-77064-2_14.

Caruana, F., Cuccio, V., 2017. Overcoming the acting/reasoning dualism in intelligent behavior. Phenomenol. Cogn. Sci. 16, 709–713. https://doi.org/10.1007/s11097-016-9471-1.

Carver, N.S., Kelty-Stephen, D.G., 2017. Multifractality in individual honeybee behavior hints at colony-specific social cascades: reanalysis of radio-frequency identification data from five different colonies. Phys. Rev. E 95, 22402. https://doi.org/10.1103/PhysRevE.95.022402.

Chevalier-Skolnikoff, S., 1989. Spontaneous tool use and sensorimotor intelligence in *Cebus* compared with other monkeys and apes. Behav. Brain Sci. 12, 561–588. https://doi.org/10.1017/S0140525X00057678.

Chisholm, R.L., Firtel, R.A., 2004. Insights into morphogenesis from a simple developmental system. Nat. Rev. Mol. Cell Biol. 5, 531–541. https://doi.org/10.1038/nrm1427.

Colbourne, J.A.D., Auersperg, A.M.I., Lambert, M.L., Huber, L., Völter, C.J., 2021. Extending the reach of tooling theory: a neurocognitive and phylogenetic perspective. Top. Cogn. Sci. n/a. https://doi.org/10.1111/tops.12554.

Cox, R.F.A., Smitsman, W., 2006. Action planning in young children's tool use. Dev. Sci. 9, 628–641. https://doi.org/10.1111/j.1467-7687.2006.00541.x.

Cox, R.F.A., Smitsman, A.W., 2019. Action-selection perseveration in young children: advances of a dynamic model. Dev. Psychobiol. 61, 43–55. https://doi.org/10.1002/dev.21776.

Crain, B.J., Giray, T., Abramson, C.I., 2013. A tool for every job: assessing the need for a universal definition of tool use. Int. J. Comp. Psychol. 26, 281–303.

Crawford, L.E., Knouse, L.E., Kent, M., Vavra, D., Harding, O., LeServe, D., Fox, N., Hu, X., Li, P., Glory, C., Lambert, K.G., 2020. Enriched environment exposure accelerates rodent driving skills. Behav. Brain Res. 378, 112309 https://doi.org/10.1016/j.bbr.2019.112309.

Curioni, A., Vesper, C., Knoblich, G., Sebanz, N., 2019. Reciprocal information flow and role distribution support joint action coordination. Cognition 187, 21–31. https://doi.org/10.1016/j.cognition.2019.02.006.

Day, B., Ebrahimi, E., Hartman, L.S., Pagano, C.C., Babu, S.V., 2017. Calibration to tool use during visually-guided reaching. Acta Psychol. (Amst). 181, 27–39. https://doi.org/10.1016/j.actpsy.2017.09.014.

Day, B., Ebrahimi, E., Hartman, L.S., Pagano, C.C., Robb, A.C., Babu, S.V., 2019. Examining the effects of altered avatars on perception-action in virtual reality. J. Exp. Psychol. Appl. 25, 1–24. https://doi.org/10.1037/xap0000192.

de Guzman, M., Bird, G., Banissy, M.J., Catmur, C., 2016. Self–other control processes in social cognition: from imitation to empathy. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150079 https://doi.org/10.1098/rstb.2015.0079.

De Oliveira, E., Reynaud, E., Osiurak, F., 2019. Roles of technical reasoning, theory of mind, creativity, and fluid cognition in cumulative technological culture. Hum. Nat. 30, 326–340. https://doi.org/10.1007/s12110-019-09349-1.

Derex, M., Mesoudi, A., 2020. Cumulative cultural evolution within evolving population structures. Trends Cogn. Sci. (Regul. Ed.) 24, 654–667. https://doi.org/10.1016/j.tics.2020.04.005.

Derex, M., Bonnefon, J.-F., Boyd, R., Mesoudi, A., 2019. Causal understanding is not necessary for the improvement of culturally evolving technology. Nat. Hum. Behav. 3, 446–452. https://doi.org/10.1038/s41562-019-0567-9.

Dinets, V., Brueggen, J.C., Brueggen, J.D., 2015. Crocodilians use tools for hunting. Ethol. Ecol. Evol. 27, 74–78. https://doi.org/10.1080/03949370.2013.858276.

Dineva, E., Schöner, G., 2018. How infants' reaches reveal principles of sensorimotor decision making. Conn. Sci. 30, 53–80. https://doi.org/10.1080/09540091.2017.1405382.

Dixon, M.L., De La Vega, A., Mills, C., Andrews-Hanna, J., Spreng, R.N., Cole, M.W., Christoff, K., 2018. Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks. Proc. Natl. Acad. Sci. 115, E1598–E1607. https://doi.org/10.1073/pnas.1715766115.

Doyon, J.K., Hajnal, A., Surber, T., Clark, J.D., Kelty-Stephen, D.G., 2019. Multifractality of posture modulates multisensory perception of stand-on-ability. PLoS One 14, e0212220. https://doi.org/10.1371/journal.pone.0212220.

Dragovich, B., Mišić, N.Ž., 2019. *p*-Adic hierarchical properties of the genetic code. Biosystems 185, 104017. https://doi.org/10.1016/j.biosystems.2019.104017.

Dusek, V., 2006. Philosophy of Technology: An Introduction. Blackwell, Malden, MA.

Emery, N.J., Clayton, N.S., 2009. Tool use and physical cognition in birds and mammals. Curr. Opin. Neurobiol. 19, 27–33. https://doi.org/10.1016/j.conb.2009.02.003.

Fajen, B.R., 2007. Affordance-based control of visually guided action. Ecol. Psychol. 19, 383–410. https://doi.org/10.1080/10407410701557877.

Fajen, B., 2013. Guiding locomotion in complex, dynamic environments. Front. Behav. Neurosci. 7, 85. https://doi.org/10.3389/fnbeh.2013.00085.

Fajen, B.R., Matthis, J.S., 2011. Direct perception of action-scaled affordances: the shrinking gap problem. J. Exp. Psychol. Hum. Percept. Perform. 37, 1442–1457. https://doi.org/10.1037/a0023510.

Falótico, T., Ottoni, E.B., 2016. The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. Behaviour 153, 421–442. https://doi.org/10.1163/1568539X-00003357.

Farnè, A., Iriki, A., Làdavas, E., 2005. Shaping multisensory action–space with tools: evidence from patients with cross-modal extinction. Neuropsychologia 43, 238–248. https://doi.org/10.1016/j.neuropsychologia.2004.11.010.

Fellers, J.H., Fellers, G.M., 1976. Tool use in a social insect and its implications for competitive interactions. Science (80-.) 192, 70–72. https://doi.org/10.1126/science.192.4234.70.

Fernandez-Gonzalez, R., Zallen, J.A., 2011. Oscillatory behaviors and hierarchical assembly of contractile structures in intercalating cells. Phys. Biol. 8, 45005. https://doi.org/10.1088/1478-3975/8/4/045005.

Fink, P.W., Foo, P.S., Warren, W.H., 2009. Catching fly balls in virtual reality: a critical test of the outfielder problem. J. Vis. 9, 14. https://doi.org/10.1167/9.13.14.

Finkel, L., Hogrefe, K., Frey, S.H., Goldenberg, G., Randerath, J., 2018. It takes two to pantomime: communication meets motor cognition. Neuroimage Clin. 19, 1008–1017. https://doi.org/10.1016/j.nicl.2018.06.019.

Finn, J.K., Tregenza, T., Norman, M.D., 2009. Defensive tool use in a coconut-carrying octopus. Curr. Biol. 19, R1069–R1070. https://doi.org/10.1016/j.cub.2009.10.052.

Fischer, J., Mikhael, J.G., Tenenbaum, J.B., Kanwisher, N., 2016. Functional neuroanatomy of intuitive physical inference. Proc. Natl. Acad. Sci. 113, E5072–E5081. https://doi.org/10.1073/pnas.1610344113.

Flynn, E.G., Laland, K.N., Kendal, R.L., Kendal, J.R., 2013. Target article with commentaries: developmental niche construction. Dev. Sci. 16, 296–313. https://doi.org/10.1111/desc.12030.

Fox, E.A., Sitampul, A.F., van Schaik, C.P., 1999. Intelligent tool use in wild Sumatran orangutans. In: Parke, S.T., Mitchell, R.W., Miles, L.H. (Eds.), The Mentality of Gorillas and Orangutans. Cambridge University Press, Cambridge, UK, pp. 99–116.

Fragaszy, D.M., Mangalam, M., 2018. Tooling. Adv. Study Behav. 50, 177–241. https://doi.org/10.1016/bs.asb.2018.01.001.

Fragaszy, D.M., Stone, B.W., Scott, N.M., Menzel, C., 2011. How tufted capuchin monkeys (*Cebus apella* spp) and common chimpanzees (*Pan troglodytes*) align objects to surfaces: insights into spatial reasoning and implications for tool use. Am. J. Primatol. 73, 1012–1030. https://doi.org/10.1002/ajp.20966.

Fragaszy, D.M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., Visalberghi, E., 2013. The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 368, 20120410 https://doi.org/10.1098/rstb.2012.0410.

Fragaszy, D.M., Kuroshima, H., Stone, B.W., 2015. "Vision for action" in young children aligning multi-featured objects: development and comparison with nonhuman primates. PLoS One 10, e0140033. https://doi.org/10.1371/journal.pone.0140033.

Fratzl, P., 2008. Collagen: structure and mechanics, an introduction. In: Fratzl, Peter (Ed.), Collagen. Springer US, Boston, MA, pp. 1–13. https://doi.org/10.1007/978-0-387-73906-9_1.

Galef, B.G., 2013. Imitation and local enhancement: detrimental effects of consensus definitions on analyses of social learning in animals. Behav. Processes 100, 123–130. https://doi.org/10.1016/j.beproc.2013.07.026.

Gallivan, J.P., McLean, A., Culham, J.C., 2011. Neuroimaging reveals enhanced activation in a reach-selective brain area for objects located within participants' typical hand workspaces. Neuropsychologia 49, 3710–3721. https://doi.org/10.1016/j.neuropsychologia.2011.09.027.

Gallivan, J.P., McLean, D.A., Valyear, K.F., Culham, J.C., 2013. Decoding the neural mechanisms of human tool use. Elife 2, e00425. https://doi.org/10.7554/eLife.00425.

Gentner, D., Hoyos, C., 2017. Analogy and abstraction. Top. Cogn. Sci. 9, 672–693. https://doi.org/10.1111/tops.12278.

Gerullis, P., Schuster, S., 2014. Archerfish actively control the hydrodynamics of their jets. Curr. Biol. 24, 2156–2160. https://doi.org/10.1016/j.cub.2014.07.059.

Gibson, J.J., 1966. The Senses Considered As Perceptual Systems. Houghton Mifflin, Boston, MA.

Gibson, J.J., 1979. The Ecological Approach to Visual Perception. Houghton Mifflin, Boston, MA.

Gibson, K.R., Ingold, T., 1994. Tools, Language and Cognition in Human Evolution. Cambridge University Press, Cambridge, UK.

Gobet, F., 2015. Understanding Expertise: A Multi-disciplinary Approach. Macmillan International Higher Education.

Goldberger, A.L., Rigney, D.R., West, B.J., 1990. Chaos and fractals in human physiology. Sci. Am. 262, 42–49.

Goldenberg, G., Hagmann, S., 1998. Tool use and mechanical problem solving in apraxia. Neuropsychologia 36, 581–589. https://doi.org/10.1016/S0028-3932(97)00165-6.

Goldenberg, G., Spatt, J., 2009. The neural basis of tool use. Brain 132, 1645–1655. https://doi.org/10.1093/brain/awp080.

Goldenberg, G., Hartmann-Schmid, K., Sürer, F., Daumüller, M., Hermsdölrfer, J., 2007. The impact of dysexecutive syndrome on use of tools and technical devices. Cortex 43, 424–435. https://doi.org/10.1016/S0010-9452(08)70467-2.

Golonka, S., Wilson, A.D., 2019. Ecological representations. Ecol. Psychol. 31, 235–253. https://doi.org/10.1080/10407413.2019.1615224.

Gönül, G., Takmaz, E.K., Hohenberger, A., Corballis, M., 2018. The cognitive ontogeny of tool making in children: the role of inhibition and hierarchical structuring. J. Exp. Child Psychol. 173, 222–238. https://doi.org/10.1016/j.jecp.2018.03.017.

Gowlland, G., 2019. The sociality of enskilment. Ethnos 84, 508–524. https://doi.org/10.1080/00141844.2018.1455726.

Griffiths, P., Gray, R., 2001. Darwinism and developmental systems. In: Oyama, S., Griffiths, P., Gray, R. (Eds.), Cycles of Contingency. MIT Press, Cambridge, MA, pp. 195–218.

Gruber, M.J., Ranganath, C., 2019. How curiosity enhances hippocampus-dependent memory: the prediction, appraisal, curiosity, and exploration (PACE) framework. Trends Cogn. Sci. (Regul. Ed.) 23, 1014–1025. https://doi.org/10.1016/j.tics.2019.10.003.

Haar, S., van Assel, C.M., Faisal, A.A., 2020. Motor learning in real-world pool billiards. Sci. Rep. 10, 20046. https://doi.org/10.1038/s41598-020-76805-9.

Haggard, P., 2017. Sense of agency in the human brain. Nat. Rev. Neurosci. 18, 196–207. https://doi.org/10.1038/nrn.2017.14.

Hajnal, A., Fonseca, S., Harrison, S., Kinsella-Shaw, J.M., Carello, C., 2007. Comparison of dynamic (effortful) touch by hand and foot. J. Mot. Behav. 39, 82–88. https://doi.org/10.3200/JMBR.39.2.82-88.

Hajnal, A., Clark, J.D., Doyon, J.K., Kelty-Stephen, D.G., 2018. Fractality of body movements predicts perception of affordances: evidence from stand-on-ability judgments about slopes. J. Exp. Psychol. Hum. Percept. Perform. 44, 836–841. https://doi.org/10.1037/xhp0000510.

Hamilton, W.J., Buskirk, R.E., Buskirk, W.H., 1975. Defensive stoning of baboons. Nature 256, 488–489. https://doi.org/10.1038/256488a0.

Hansell, M., Ruxton, G.D., 2008. Setting tool use within the context of animal construction behaviour. Trends Ecol. Evol. (Amst.) 23, 73–78. https://doi.org/10.1016/j.tree.2007.10.006.

Hardus, M.E., Lameira, A.R., van Schaik, C.P., Wich, S.A., 2009. Tool use in wild orangutans modifies sound production: a functionally deceptive innovation? Proc. R. Soc. London B Biol. Sci. 276, 3689–3694. https://doi.org/10.1098/rspb.2009.1027.

Harrison, S.J., Stergiou, N., 2015. Complex adaptive behavior and dexterous action. Nonlinear Dynamics Psychol. Life Sci. 19, 345–394.

Harrison, S.J., Hajnal, A., Lopresti-Goodman, S., Isenhower, R.W., Kinsella-Shaw, J.M., 2011. Perceiving action-relevant properties of tools through dynamic touch: effects of mass distribution, exploration style, and intention. J. Exp. Psychol. Hum. Percept. Perform. 37, 193–206. https://doi.org/10.1037/a0020407.

Harrison, S.J., Reynolds, N., Bishoff, B., Stergiou, N., 2021. Assessing the relative contribution of vision to odometry via manipulations of gait in an over-ground homing task. Exp. Brain Res. https://doi.org/10.1007/s00221-021-06066-z.

Hart, B.L., Hart, L.A., McCoy, M., Sarath, C.R., 2001. Cognitive behaviour in Asian elephants: use and modification of branches for fly switching. Anim. Behav. 62, 839–847. https://doi.org/10.1006/anbe.2001.1815.

Hartman, L.S., Kil, I., Pagano, C.C., Burg, T., 2016. Investigating haptic distance-to-break using linear and nonlinear materials in a simulated minimally invasive surgery task. Ergonomics 59, 1171–1181. https://doi.org/10.1080/00140139.2015.1127429.

Haslam, M., 2013. 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. Philos. Trans. R. Soc. B Biol. Sci. 368, 20120421 https://doi.org/10.1098/rstb.2012.0421.

Hasson, U., Frith, C.D., 2016. Mirroring and beyond: coupled dynamics as a generalized framework for modelling social interactions. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150366 https://doi.org/10.1098/rstb.2015.0366.

Heald, J.B., Ingram, J.N., Flanagan, J.R., Wolpert, D.M., 2018. Multiple motor memories are learned to control different points on a tool. Nat. Hum. Behav. 2, 300–311. https://doi.org/10.1038/s41562-018-0324-5.

Hecht, E.E., Gutman, D.A., Khreisheh, N., Taylor, S.V., Kilner, J., Faisal, A.A., Bradley, B. A., Chaminade, T., Stout, D., 2015. Acquisition of Paleolithic toolmaking abilities involves structural remodeling to inferior frontoparietal regions. Brain Struct. Funct. 220, 2315–2331. https://doi.org/10.1007/s00429-014-0789-6.

Heilman, K.M., Rothi, L.J., Valenstein, E., 1982. Two forms of ideomotor apraxia. Neurology 32. https://doi.org/10.1212/WNL.32.4.342, 342–342.

Hermsdörfer, J., Terlinden, G., Mühlau, M., Goldenberg, G., Wohlschläger, A.M., 2007. Neural representations of pantomimed and actual tool use: evidence from an event-related fMRI study. Neuroimage 36, T109–T118. https://doi.org/10.1016/j.neuroimage.2007.03.037.

Hermsdörfer, J., Li, Y., Randerath, J., Goldenberg, G., Johannsen, L., 2012. Tool use without a tool: kinematic characteristics of pantomiming as compared to actual use and the effect of brain damage. Exp. Brain Res. 218, 201–214. https://doi.org/10.1007/s00221-012-3021-z.

Heuer, H., Sülzenbrück, S., 2009. Trajectories in operating a handheld tool. J. Exp. Psychol. Hum. Percept. Perform. 35, 375–389. https://doi.org/10.1037/0096-1523.35.2.375.

Heyes, C., 2016. Imitation: not in our genes. Curr. Biol. 26, R412–R414. https://doi.org/10.1016/j.cub.2016.03.060.

Heyes, C.M., 2018. Cognitive Gadgets : The Cultural Evolution of Thinking. Cambridge University Press, Cambridge, MA.

Higuchi, T., Cinelli, M.E., Greig, M.A., Patla, A.E., 2006. Locomotion through apertures when wider space for locomotion is necessary: adaptation to artificially altered bodily states. Exp. Brain Res. 175, 50–59. https://doi.org/10.1007/s00221-006-0525-4.

Hill, K., Barton, M., Hurtado, A.M., 2009. The emergence of human uniqueness: characters underlying behavioral modernity. Evol. Anthropol. Issues, News, Rev. 18, 187–200. https://doi.org/10.1002/evan.20224.

Hodges, J.R., Bozeat, S., Ralph, M.A.L., Patterson, K., Spatt, J., 2000. The role of conceptual knowledge in object use Evidence from semantic dementia. Brain 123, 1913–1925. https://doi.org/10.1093/brain/123.9.1913.

Holmes, N.P., 2012. Does tool use extend peripersonal space? A review and re-analysis. Exp. Brain Res. 218, 273–282. https://doi.org/10.1007/s00221-012-3042-7.

Holmes, N.P., Calvert, G.A., Spence, C., 2004. Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. Neurosci. Lett. 372, 62–67. https://doi.org/10.1016/j.neulet.2004.09.024.

Holmes, N.P., Sanabria, D., Calvert, G.A., Spence, C., 2007. Tool-use: Capturing multisensory spatial attention or extending multisensory peripersonal space? Cortex 43, 469–489. https://doi.org/10.1016/S0010-9452(08)70471-4.

Huber, L., Gajdon, G.K., 2006. Technical intelligence in animals: the kea model. Anim. Cogn. 9, 295–305. https://doi.org/10.1007/s10071-006-0033-8.

Hughes, T.P., 1987. The evolution of large technological systems. The Social Construction of Technological Systems: New Directions in the Sociology and History of Technologyechnology. MIT Press, Cambridge, MA.

Hunt, G.R., 1996. Manufacture and use of hook-tools by New Caledonian crows. Nature 379, 249–251. https://doi.org/10.1038/379249a0.

Hunt, G.R., Gray, R.D., Taylor, A.H., 2013. Why is tool use rare in animals. In: Sanz, C., Call, J., Boesch, C. (Eds.), Tool Use in Animals: Cognition and Ecology. Cambridge University Press, Cambridge, UK, pp. 89–118.

Ingber, D.E., 2006. Cellular mechanotransduction: putting all the pieces together again. FASEB J. 20, 811–827. https://doi.org/10.1096/fj.05-5424rev.

Ingmanson, E.J., 1996. Tool-using behavior in wild Pan paniscus: social and ecological considerations. In: Russon, A.R., Bard, K.A., Parker, S.T. (Eds.), Reaching into Thought: The Minds of the Great Apes. Cambridge University Press, New York, NY, pp. 190–210.

Ingram, J.N., Howard, I.S., Flanagan, J.R., Wolpert, D.M., 2010. Multiple grasp-specific representations of tool dynamics mediate skillful manipulation. Curr. Biol. 20, 618–623. https://doi.org/10.1016/j.cub.2010.01.054.

Iriki, A., Tanaka, M., Iwamura, Y., 1996. Attention-induced neuronal activity in the monkey somatosensory cortex revealed by pupillometrics. Neurosci. Res. 25, 173–181. https://doi.org/10.1016/0168-0102(96)01043-7.

Japyassú, H.F., Laland, K.N., 2017. Extended spider cognition. Anim. Cogn. 20, 375–395. https://doi.org/10.1007/s10071-017-1069-7.

Jarry, C., Osiurak, F., Delafuys, D., Chauviré, V., Etcharry-Bouyx, F., Le Gall, D., 2013. Apraxia of tool use: more evidence for the technical reasoning hypothesis. Cortex 49, 2322–2333. https://doi.org/10.1016/j.cortex.2013.02.011.

Johnson-Frey, S.H., 2003. What's so special about human tool use? Neuron 39, 201–204. https://doi.org/10.1016/S0896-6273(03)00424-0.

Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. Trends Cogn. Sci. (Regul. Ed.) 8, 71–78. https://doi.org/10.1016/j.tics.2003.12.002.

Kadar, E.E., Shaw, R.E., 2000. Toward an ecological field theory of perceptual control of locomotion. Ecol. Psychol. 12, 141–180. https://doi.org/10.1207/S15326969ECO1202_02.

Kahrs, B.A., Lockman, J.J., 2014. Tool using. Child Dev. Perspect. 8, 231–236. https://doi.org/10.1111/cdep.12087.

Kaplan, H., Gurven, M., Winking, J., Hooper, P.L., Stieglitz, J., 2010. Learning, menopause, and the human adaptive complex. Ann. N. Y. Acad. Sci. 1204, 30–42. https://doi.org/10.1111/j.1749-6632.2010.05528.x.

Keen, R., Lee, M.-H., Adolph, K., 2014. Planning an action: a developmental progression in tool use. Ecol. Psychol. 26, 98–108. https://doi.org/10.1080/10407413.2014.874917.

Kelso, J.A.S., 2009. Synergies: atoms of brain and behavior. Prog. Mot. Control 83–91. https://doi.org/10.1007/978-0-387-77064-2_5.

Kelso, J.S., Tuller, B., Vatikiotis-Bateson, E., Fowler, C.A., 1984. Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. J. Exp. Psychol. Hum. Percept. Perform. 10, 812–832. https://doi.org/10.1037/0096-1523.10.6.812.

Kelty-Stephen, D.G., Dixon, J.A., 2014. Interwoven fluctuations during intermodal perception: fractality in head sway supports the use of visual feedback in haptic perceptual judgments by manual wielding. J. Exp. Psychol. Hum. Percept. Perform. 40, 2289–2309. https://doi.org/10.1037/a0038159.

Kendal, R.L., Boogert, N.J., Rendell, L., Laland, K.N., Webster, M., Jones, P.L., 2018. Social learning strategies: bridge-building between fields. Trends Cogn. Sci. (Regul. Ed.) 22, 651–665. https://doi.org/10.1016/j.tics.2018.04.003.

Kennedy, D.P., D'Onofrio, B.M., Quinn, P.D., Bölte, S., Lichtenstein, P., Falck-Ytter, T., 2017. Genetic influence on eye movements to complex scenes at short timescales. Curr. Biol. 27 https://doi.org/10.1016/j.cub.2017.10.007, 3554-3560.e3.

Kline, M.A., 2015. How to learn about teaching: an evolutionary framework for the study of teaching behavior in humans and other animals. Behav. Brain Sci. 38, e31. https://doi.org/10.1017/S0140525X14000090.

Köhler, W., 1925. The Mentality of Apes. Vintage Books, New York, NY.

Koster, J., McElreath, R., Hill, K., Yu, D., Shepard, G., et al., 2020. The life history of human foraging: cross-cultural and individual variation. Sci. Adv. 6 https://doi.org/10.1126/sciadv.aax9070 eaax9070.

Krakauer, J.W., Ghazanfar, A.A., Gomez-Marin, A., MacIver, M.A., Poeppel, D., 2017. Neuroscience needs behavior: correcting a reductionist bias. Neuron 93, 480–490. https://doi.org/10.1016/j.neuron.2016.12.041.

Króliczak, G., Frey, S.H., 2009. A common network in the left cerebral hemisphere represents planning of tool use pantomimes and familiar intransitive gestures at the hand-independent level. Cereb. Cortex 19, 2396–2410. https://doi.org/10.1093/cercor/bhn261.

la Cour, L.T., Stone, B.W., Hopkins, W., Menzel, C., Fragaszy, D.M., 2014. What limits tool use in nonhuman primates? Insights from tufted capuchin monkeys (*Sapajus* spp.) and chimpanzees (*Pan troglodytes*) aligning three-dimensional objects to a surface. Anim. Cogn. 17, 113–125. https://doi.org/10.1007/s10071-013-0643-x.

Ladouce, S., Donaldson, D.I., Dudchenko, P.A., Ietswaart, M., 2019. Mobile EEG identifies the re-allocation of attention during real-world activity. Sci. Rep. 9, 15851. https://doi.org/10.1038/s41598-019-51996-y.

Laland, K.N., Uller, T., Feldman, M.W., Sterelny, K., Müller, G.B., Moczek, A., Jablonka, E., Odling-Smee, J., 2015. The extended evolutionary synthesis: its structure, assumptions and predictions. Proc. R. Soc. B Biol. Sci. 282 https://doi.org/10.1098/rspb.2015.1019, 20151019.

Latash, M.L., Scholz, J.P., Schöner, G., 2007. Toward a new theory of motor synergies. Motor Control 11, 276–308. https://doi.org/10.1123/mcj.11.3.276.

Lawick-Goodall, J.Van, 1971. Tool-using in primates and other vertebrates. Adv. Study Behav. 3, 195–249. https://doi.org/10.1016/S0065-3454(08)60157-6.

Legare, C.H., Nielsen, M., 2015. Imitation and innovation: the dual engines of cultural learning. Trends Cogn. Sci. (Regul. Ed.) 19, 688–699. https://doi.org/10.1016/j.tics.2015.08.005.

Lesourd, M., Baumard, J., Jarry, C., Etcharry-Bouyx, F., Belliard, S., Moreaud, O., Croisile, B., Chauviré, V., Granjon, M., Le Gall, D., Osiurak, F., 2016. Mechanical problem-solving strategies in Alzheimer's disease and semantic dementia. Neuropsychology 30, 612–623. https://doi.org/10.1037/neu0000241.

Lewis, J.W., 2006. Cortical networks related to human use of tools. Neuroscience 12, 211–231. https://doi.org/10.1177/1073858406288327.

Lewontin, R.C., 1982. Organism and environment. In: Plotkin, H.C. (Ed.), Learning, Development, and Culture. Wiley, New York, NY, pp. 151–170.

Lockman, J.J., 2005. Tool use from a perception–action perspective: developmental and evolutionary considerations. In: Roux, V., Bril, B. (Eds.), Stone Knapping: The Necessary Conditions for a Uniquely Hominid Behaviour. McDonald Institute for Archaeological Research, Cambridge, UK, pp. 313–330.

Long, L.O., Pagano, C.C., Singapogu, R.B., Burg, T.C., 2016. Surgeon's perception of soft tissue constraints and distance-to-break in a simulated minimally invasive surgery task. Proc. Hum. Factors Ergon. Soc. Annu. Meet. 60, 1600–1604. https://doi.org/10.1177/1541931213601369.

Lovejoy, S., Schertzer, D., 2018. The Weather and Climate: Emergent Laws and Multifractal Cascades. Cambridge University Press, Cambridge, UK.

Mandelbrot, B., 1967. How long is the coast of britain? Statistical self-similarity and fractional dimension. Science (80-.) 156, 636–638. https://doi.org/10.1126/science.156.3775.636.

Mandelbrot, B.B., 2013. Multifractals and 1/f Noise; Wild Self-Affinity in Physics. Springer Verlag, New York, NY.

Mangalam, M., 2016. What makes a tool. In: Weekes-Shackelford, V., Shackelford, T.K., Weekes-Shackelford, V.A. (Eds.), Encyclopedia of Evolutionary Psychological Science. Springer, New York, NY, pp. 1–5. https://doi.org/10.1007/978-3-319-16999-6_3153-1.

Mangalam, M., Fragaszy, D.M., 2015. Wild bearded capuchin monkeys crack nuts dexterously. Curr. Biol. 25, 1334–1339. https://doi.org/10.1016/j.cub.2015.03.035.

Mangalam, M., Fragaszy, D.M., 2016. Transforming the body-only system into the body-plus-tool system. Anim. Behav. 117, 115–122. https://doi.org/10.1016/j.anbehav.2016.04.016.

Mangalam, M., Kelty-Stephen, D.G., 2020. Multiplicative-cascade dynamics supports whole-body coordination for perception via effortful touch. Hum. Mov. Sci. 70, 102595 https://doi.org/10.1016/j.humov.2020.102595.

Mangalam, M., Izar, P., Visalberghi, E., Fragaszy, D.M., 2016. Task-specific temporal organization of percussive movements in wild bearded capuchin monkeys. Anim. Behav. 114, 129–137. https://doi.org/10.1016/j.anbehav.2016.01.011.

Mangalam, M., Barton, S.A., Wagman, J.B., Fragaszy, D.M., Newell, K.M., 2017. Perception of the length of an object through dynamic touch is invariant across changes in the medium. Attention, Perception, Psychophys. 79, 2499–2509. https://doi.org/10.3758/s13414-017-1403-9.

Mangalam, M., Pacheco, M.M., Izar, P., Visalberghi, E., Fragaszy, D.M., 2018a. Unique perceptuomotor control of stone hammers in wild monkeys. Biol. Lett. 14, 20170587 https://doi.org/10.1098/rsbl.2017.0587.

Mangalam, M., Rein, R., Fragaszy, D.M., 2018b. Bearded capuchin monkeys use joint synergies to stabilize the hammer trajectory while cracking nuts in bipedal stance. Proc. R. Soc. B Biol. Sci. 285, 20181797 https://doi.org/10.1098/rspb.2018.1797.

Mangalam, M., Conners, J.D., Kelty-Stephen, D.G., Singh, T., 2019a. Fractal fluctuations in muscular activity contribute to judgments of length but not heaviness via dynamic touch. Exp. Brain Res. 237, 1213–1216. https://doi.org/10.1007/s00221-019-05505-2.

Mangalam, M., Conners, J.D., Singh, T., 2019b. Muscular effort differentially mediates perception of heaviness and length via dynamic touch. Exp. Brain Res. 237, 237–246. https://doi.org/10.1007/s00221-018-5421-1.

Mangalam, M., Pacheco, M.M., Fragaszy, D.M., Newell, K.M., 2019c. Perceptual learning of tooling affordances of a jointed object via dynamic touch. Ecol. Psychol. 31, 14–29. https://doi.org/10.1080/10407413.2018.1473714.

Mangalam, Madhur, Carver, N.S., Kelty-Stephen, D.G., 2020a. Multifractal signatures of perceptual processing on anatomical sleeves of the human body. J. R. Soc. Interface 17, 20200328. https://doi.org/10.1098/rsif.2020.0328.

Mangalam, Madhur, Carver, N.S., Kelty-Stephen, D.G., 2020b. Global broadcasting of local fractal fluctuations in a bodywide distributed system supports perception via effortful touch. Chaos Solitons Fractals 135, 109740. https://doi.org/10.1016/j.chaos.2020.109740.

Mangalam, Madhur, Chen, R., McHugh, T.R., Singh, T., Kelty-Stephen, D.G., 2020c. Bodywide fluctuations support manual exploration: Fractal fluctuations in posture predict perception of heaviness and length via effortful touch by the hand. Hum. Mov. Sci. 69, 102543 https://doi.org/10.1016/j.humov.2019.102543.

Mangalam, Madhur, Roles, L.K.R., Fragaszy, D.M., 2020d. Distinct perceptuomotor features of percussive tooling in humans (*Homo sapiens*) and wild bearded capuchin monkeys (*Sapajus libidinosus*). J. Comp. Psychol. 134, 84–97. https://doi.org/10.1037/com0000197.

Maravita, A., Iriki, A., 2004. Tools for the body (schema). Trends Cogn. Sci. (Regul. Ed.) 8, 79–86. https://doi.org/10.1016/j.tics.2003.12.008.

Maravita, A., Husain, M., Clarke, K., Driver, J., 2001. Reaching with a tool extends visual–tactile interactions into far space: evidence from cross-modal extinction. Neuropsychologia 39, 580–585. https://doi.org/10.1016/S0028-3932(00)00150-0.

Margulies, D.S., Ghosh, S.S., Goulas, A., Falkiewicz, M., Huntenburg, J.M., Langs, G., Bezgin, G., Eickhoff, S.B., Castellanos, F.X., Petrides, M., Jefferies, E., Smallwood, J., 2016. Situating the default-mode network along a principal gradient of macroscale cortical organization. Proc. Natl. Acad. Sci. 113, 12574–12579. https://doi.org/10.1073/pnas.1608282113.

Martel, M., Cardinali, L., Roy, A.C., Farnè, A., 2016. Tool-use: an open window into body representation and its plasticity. Cogn. Neuropsychol. 33, 82–101. https://doi.org/10.1080/02643294.2016.1167678.

Martin, M., Beume, L., Kümmerer, D., Schmidt, C.S.M., Bormann, T., Dressing, A., Ludwig, V.M., Umarova, R.M., Mader, I., Rijntjes, M., Kaller, C.P., Weiller, C., 2016a. Differential roles of ventral and dorsal streams for conceptual and production-related components of tool use in acute stroke patients. Cereb. Cortex 26, 3754–3771. https://doi.org/10.1093/cercor/bhv179.

Martin, M., Nitschke, K., Beume, L., Dressing, A., Bühler, L.E., Ludwig, V.M., Mader, I., Rijntjes, M., Kaller, C.P., Weiller, C., 2016b. Brain activity underlying tool-related and imitative skills after major left hemisphere stroke. Brain 139, 1497–1516. https://doi.org/10.1093/brain/aww035.

Martinho, A., Burns, Z.T., von Bayern, A.M.P., Kacelnik, A., 2014. Monocular tool control, eye dominance, and laterality in New Caledonian crows. Curr. Biol. 24, 2930–2934. https://doi.org/10.1016/j.cub.2014.10.035.

Mather, J.A., 1994. “Home” choice and modification by juvenile *Octopus vulgaris* (Mollusca: cephalopoda): specialized intelligence and tool use? J. Zool. 233, 359–368. https://doi.org/10.1111/j.1469-7998.1994.tb05270.x.

Mathieu, J.E., Hollenbeck, J.R., van Knippenberg, D., Ilgen, D.R., 2017. A century of work teams in the Journal of Applied Psychology. J. Appl. Psychol. 102, 452–467. https://doi.org/10.1037/apl0000128.

Matsuzawa, Tetsuro, 2001. Primate foundations of human intelligence: a view of tool use in nonhuman primates and fossil hominids. In: Matsuzawa, T. (Ed.), Primate Origins of Human Cognition and Behavior. Springer-Verlag, Tokyo, Japan, pp. 3–25.

Matusz, P.J., Dikker, S., Huth, A.G., Perrodin, C., 2019. Are we ready for real-world neuroscience? J. Cogn. Neurosci. 31, 327–338. https://doi.org/10.1162/jocn_e_01276.

McDougle, S.D., Ivry, R.B., Taylor, J.A., 2016. Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. Trends Cogn. Sci. (Regul. Ed.) 20, 535–544. https://doi.org/10.1016/j.tics.2016.05.002.

McNamee, D., Wolpert, D.M., 2019. Internal models in biological control. Annu. Rev. Control. Robot. Auton. Syst. 2, 339–364. https://doi.org/10.1146/annurev-control-060117-105206.

Mengotti, P., Corradi-Dell’Acqua, C., Negri, G.A.L., Ukmar, M., Pesavento, V., Rumiati, R.I., 2013. Selective imitation impairments differentially interact with language processing. Brain 136, 2602–2618. https://doi.org/10.1093/brain/awt194.

Mesoudi, A., 2021. Blind and incremental or directed and disruptive? On the nature of novel variation in human cultural evolution. Am. Philos. Q. 58, 7–20. https://doi.org/10.2307/48600682.

Mesoudi, A., Thornton, A., 2021. What is cumulative cultural evolution? Proc. R. Soc. B Biol. Sci. 285, 20180712 https://doi.org/10.1098/rspb.2018.0712.

Michaels, C., Carello, C., 2000. Direct Perception. Prentice-Hall, Englewood Cliffs, NJ.

Michaels, C.F., Weier, Z., Harrison, S.J., 2007. Using vision and dynamic touch to perceive the affordances of tools. Perception 36, 750–772. https://doi.org/10.1068/p5593.

Michener, G.R., 2004. Hunting techniques and tool use by North American badgers preying on Richardson’s ground squirrels. J. Mammal. 85, 1019–1027. https://doi.org/10.1644/BNS-102.

Miller, L.E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018. Sensing with tools extends somatosensory processing beyond the body. Nature 561, 239–242. https://doi.org/10.1038/s41586-018-0460-0.

Miu, E., Gulley, N., Laland, K.N., Rendell, L., 2020. Flexible learning, rather than inveterate innovation or copying, drives cumulative knowledge gain. Sci. Adv. 6 https://doi.org/10.1126/sciadv.aaz0286 eaaz0286.

Morgan, T.J.H., Uomini, N.T., Rendell, L.E., Chouinard-Thuly, L., Street, S.E., Lewis, H. M., Cross, C.P., Evans, C., Kearney, R., de la Torre, I., Whiten, A., Laland, K.N., 2015. Experimental evidence for the co-evolution of hominin tool-making teaching and language. Nat. Commun. 6, 6029. https://doi.org/10.1038/ncomms7029.

Newell, K.M., 1986. Constraints on the development of coordination. In: Wade, M.G., Whiting, H.T. (Eds.), Motor Development in Children: Aspects of Coordination and Control. Martinus Nijhoff, Dordrecht, Netherlands, pp. 341–360.

Newell, K.M., Jordan, K., 2007. Task constraints and movement organization: a common language. In: Broadhead, G.D., Davis, W.E. (Eds.), Ecological Task Analysis and Movement. Human Kinetics, Champaign, IL, pp. 5–23.

Newen, A., De Bruin, L., Gallagher, S., 2018. The Oxford Handbook of 4E Cognition. Oxford University Press, Oxford, UK.

Norman, J., 2002. Two visual systems and two theories of perception: an attempt to reconcile the constructivist and ecological approaches. Behav. Brain Sci. 25, 73–96. https://doi.org/10.1017/S0140525X0200002X.

Oakes, L.M., Rakison, D.H., 2019. Developmental Cascades: Building the Infant Mind. Oxford University Press, New York, NY.

Onnela, J.-P., 2021. Opportunities and challenges in the collection and analysis of digital phenotyping data. Neuropsychopharmacology 46, 45–54. https://doi.org/10.1038/s41386-020-0771-3.

Orban, G.A., Caruana, F., 2014. The neural basis of human tool use. Front. Psychol. 5, 310. https://doi.org/10.3389/fpsyg.2014.00310.

Osiurak, F., 2014. What neuropsychology tells us about human tool use? The four constraints theory (4CT): mechanics, space, time, and effort. Neuropsychol. Rev. 24, 88–115. https://doi.org/10.1007/s11065-014-9260-y.

Osiurak, F., 2017. Cognitive paleoanthropology and technology: toward a parsimonious theory (PATH). Rev. Gen. Psychol. 21, 292–307. https://doi.org/10.1037/gpr0000129.

Osiurak, F., 2020. The Tool Instinct. John Wiley & Sons.

Osiurak, F., Badets, A., 2016. Tool use and affordance: manipulation-based versus reasoning-based approaches. Psychol. Rev. 123, 534–568. https://doi.org/10.1037/rev0000027.

Osiurak, F., Federico, G., 2020. Four ways of (mis-)conceiving embodiment in tool use. Synthese. https://doi.org/10.1007/s11229-020-02960-1.

Osiurak, F., Heinke, D., 2018. Looking for intoolligence: a unified framework for the cognitive study of human tool use and technology. Am. Psychol. 73, 169–185. https://doi.org/10.1037/amp0000162.

Osiurak, F., Reynaud, E., 2020a. The elephant in the room: what matters cognitively in cumulative technological culture. Behav. Brain Sci. 43, e156. https://doi.org/10.1017/S0140525X19003236.

Osiurak, F., Reynaud, E., 2020b. The elephant in the China shop: when technical reasoning meets cumulative technological culture. Behav. Brain Sci. 43 https://doi.org/10.1017/S0140525X20000291.

Osiurak, F., Aubin, G., Allain, P., Jarry, C., Richard, I., Le Gall, D., 2008. Object utilization and object usage: a single-case study. Neurocase 14, 169–183. https://doi.org/10.1080/13554790802108372.

Osiurak, F., Jarry, C., Allain, P., Aubin, G., Etcharry-Bouyx, F., Richard, I., Bernard, I., Le Gall, D., 2009. Unusual use of objects after unilateral brain damage. The technical reasoning model. Cortex 45, 769–783. https://doi.org/10.1016/j.cortex.2008.06.013.

Osiurak, F., Jarry, C., Le Gall, D., 2010. Grasping the affordances, understanding the reasoning: toward a dialectical theory of human tool use. Psychol. Rev. 117, 517–540. https://doi.org/10.1037/a0019004.

Osiurak, F., De Oliveira, E., Navarro, J., Lesourd, M., Claidière, N., Reynaud, E., 2016. Physical intelligence does matter to cumulative technological culture. J. Exp. Psychol. Gen. 145, 941–948. https://doi.org/10.1037/xge0000189.

Osiurak, F., Rossetti, Y., Badets, A., 2017. What is an affordance? 40 years later. Neurosci. Biobehav. Rev. 77, 403–417. https://doi.org/10.1016/j.neubiorev.2017.04.014.

Osiurak, F., Lesourd, M., Delporte, L., Rossetti, Y., 2018. Tool use and generalized motor programs: we all are natural born poly-dexters. Sci. Rep. 8, 10429. https://doi.org/10.1038/s41598-018-28759-2.

Osiurak, F., De Oliveira, E., Navarro, J., Reynaud, E., 2020a. The castaway island: distinct roles of theory of mind and technical reasoning in cumulative technological culture. J. Exp. Psychol. Gen. 149, 58–66. https://doi.org/10.1037/xge0000614.

Osiurak, F., Lesourd, M., Navarro, J., Reynaud, E., 2020b. Technition: when tools come out of the closet. Perspect. Psychol. Sci. 15, 880–897. https://doi.org/10.1177/1745691620902145.

Osiurak, F., Cretel, C., Duhau-Marmon, N., Fournier, I., Marignier, L., De Oliveira, E., Navarro, J., Reynaud, E., 2021a. The pedagogue, the engineer, and the friend: from whom do we learn? Nat. Hum. Behav. In press.

Osiurak, F., Lasserre, S., Arbanti, J., Brogniart, J., Bluet, A., Navarro, J., Reynaud, E., 2021b. Technical reasoning is necessary not to reinvent the wheel. Nat. Hum. Behav. In press.

Pagano, C.C., Day, B., 2020. Ecological interface design inspired by ‘The meaningful environment. In: Wagman, J.B., Blau, J.J.C. (Eds.), Perception as Information Detection: Reflections on Gibson’S Ecological Approach to Visual Perception. Routledge, New York, NY, pp. 37–50.

Pagano, C.C., Turvey, M.T., 1998. Eigenvectors of the inertia tensor and perceiving the orientations of limbs and objects. J. Appl. Biomech. 14, 331–359. https://doi.org/10.1123/jab.14.4.331 10.1123/jab.14.4.331.

Pagano, C.C., Fitzpatrick, P., Turvey, M.T., 1993. Tensorial basis to the constancy of perceived object extent over variations of dynamic touch. Percept. Psychophys. 54, 43–54. https://doi.org/10.3758/BF03206936.

Pagnotta, M., Laland, K.N., Coco, M.I., 2020. Attentional coordination in demonstrator-observer dyads facilitates learning and predicts performance in a novel manual task. Cognition 201, 104314. https://doi.org/10.1016/j.cognition.2020.104314.

Pan, Y., Dikker, S., Goldstein, P., Zhu, Y., Yang, C., Hu, Y., 2020. Instructor-learner brain coupling discriminates between instructional approaches and predicts learning. Neuroimage 211, 116657. https://doi.org/10.1016/j.neuroimage.2020.116657.

Pargeter, J., Khreisheh, N., Stout, D., 2019. Understanding stone tool-making skill acquisition: experimental methods and evolutionary implications. J. Hum. Evol. 133, 146–166. https://doi.org/10.1016/j.jhevol.2019.05.010.

Parker, S.T., Gibson, K.R., 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. J. Hum. Evol. 6, 623–641. https://doi.org/10.1016/S0047-2484(77)80135-8.

Pazen, M., Uhlmann, L., van Kemenade, B.M., Steinsträter, O., Straube, B., Kircher, T., 2020. Predictive perception of self-generated movements: commonalities and differences in the neural processing of tool and hand actions. Neuroimage 206, 116309. https://doi.org/10.1016/j.neuroimage.2019.116309.

Pazzaglia, M., Molinari, M., 2016. The embodiment of assistive devices—from wheelchair to exoskeleton. Phys. Life Rev. 16, 163–175. https://doi.org/10.1016/j.plrev.2015.11.006.

Powers, S.T., van Schaik, C.P., Lehmann, L., 2016. How institutions shaped the last major evolutionary transition to large-scale human societies. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150098 https://doi.org/10.1098/rstb.2015.0098.

Prat, C.S., Madhyastha, T.M., Mottarella, M.J., Kuo, C.-H., 2020. Relating natural language aptitude to individual differences in learning programming languages. Sci. Rep. 10, 3817. https://doi.org/10.1038/s41598-020-60661-8.

Preston, B., 2012. A Philosophy of Material Culture: Action, Function, and Mind. Routledge, London, UK.

Profeta, V.L.S., Turvey, M.T., 2018. Bernstein’s levels of movement construction: a contemporary perspective. Hum. Mov. Sci. 57, 111–133. https://doi.org/10.1016/j.humov.2017.11.013.

Profeta, V.L.S., Turvey, M.T., Carello, C., 2020. Goal-directed action and the architecture of movement organization. In: Latash, M.L. (Ed.), Bernstein’s Construction of Movements. Routledge, New York, NY, pp. 308–319.

Pruetz, J.D., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes* verus, hunt with tools. Curr. Biol. 17, 412–417. https://doi.org/10.1016/j.cub.2006.12.042.

Pryor, C., Perfors, A., Howe, P.D.L., 2019. Even arbitrary norms influence moral decision-making. Nat. Hum. Behav. 3, 57–62. https://doi.org/10.1038/s41562-018-0489-y.

Ptak, R., Schnider, A., Fellrath, J., 2017. The dorsal frontoparietal network: a core system for emulated action. Trends Cogn. Sci. (Regul. Ed.) 21, 589–599. https://doi.org/10.1016/j.tics.2017.05.002.

Rączaszek-Leonardi, J., Nomikou, I., Rohlfing, K.J., Deacon, T.W., 2018. Language development from an ecological perspective: ecologically valid ways to abstract symbols. Ecol. Psychol. 30, 39–73. https://doi.org/10.1080/10407413.2017.1410387.

Rein, R., Bril, B., Nonaka, T., 2013. Coordination strategies used in stone knapping. Am. J. Phys. Anthropol. 150, 539–550. https://doi.org/10.1002/ajpa.22224.

Reindl, E., Apperly, I.A., Beck, S.R., Tennie, C., 2017. Young children copy cumulative technological design in the absence of action information. Sci. Rep. 7, 1788. https://doi.org/10.1038/s41598-017-01715-2.

Renfrew, C., Frith, C., Malafouris, L., Frey, S.H., 2008. Tool use, communicative gesture and cerebral asymmetries in the modern human brain. Philos. Trans. R. Soc. B Biol. Sci. 363, 1951–1957. https://doi.org/10.1098/rstb.2008.0008.

Reynaud, E., Lesourd, M., Navarro, J., Osiurak, F., 2016. On the neurocognitive origins of human tool use: a critical review of neuroimaging data. Neurosci. Biobehav. Rev. 64, 421–437. https://doi.org/10.1016/j.neubiorev.2016.03.009.

Reynaud, E., Navarro, J., Lesourd, M., Osiurak, F., 2019. To watch is to work: a review of neuroimaging data on tool use observation network. Neuropsychol. Rev. 29, 484–497. https://doi.org/10.1007/s11065-019-09418-3.

Richardson, M.J., Shockley, K., Fajen, B.R., Riley, M.A., Turvey, M.T., 2008. Ecological psychology: six principles for an embodied–embedded approach to behavior. In: Calvo, P., Gomila, A.B.T.-H., of, C.S. (Eds.), Perspectives on Cognitive Science. Elsevier, San Diego, pp. 159–187. https://doi.org/10.1016/B978-0-08-046616-3.00009-8.

Riley, M., Richardson, M., Shockley, K., Ramenzoni, V., 2011. Interpersonal synergies. Front. Psychol. 2, 38. https://doi.org/10.3389/fpsyg.2011.00038.

Rothi, L.J.G., Ochipa, C., Heilman, K.M., 1991. A Cognitive neuropsychological model of limb praxis. Cogn. Neuropsychol. 8, 443–458. https://doi.org/10.1080/02643299108253382.

Rutz, C., Hunt, G.R., 2020. New Caledonian crows afford invaluable comparative insights into human cumulative technological culture. Behav. Brain Sci. 43, e177. https://doi.org/10.1017/S0140525X20000187.

Salazar-López, E., Schwaiger, B.J., Hermsdörfer, J., 2016. Lesion correlates of impairments in actual tool use following unilateral brain damage. Neuropsychologia 84, 167–180. https://doi.org/10.1016/j.neuropsychologia.2016.02.007.

Sánchez, C.C., Moreno, F.J., Vaíllo, R.R., Romero, A.R., Coves, Á., Murillo, D.B., 2017. The role of motor variability in motor control and learning depends on the nature of the task and the individual's capabilities. Eur. J. Hum. Mov. 38, 12–26.

Sanz, C.M., Morgan, D.B., 2007. Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. J. Hum. Evol. 52, 420–433. https://doi.org/10.1016/j.jhevol.2006.11.001.

Schaap, P., 2021. From environmental sensing to developmental control: cognitive evolution in dictyostelid social amoebas. Philos. Trans. R. Soc. B Biol. Sci. 376, 20190756 https://doi.org/10.1098/rstb.2019.0756.

Schirmer, A., Fairhurst, M., Hoehl, S., 2021. Being 'in sync'—is interactional synchrony the key to understanding the social brain? Soc. Cogn. Affect. Neurosci. 16, 1–4. https://doi.org/10.1093/scan/nsaa148.

Scholz, J.P., Schöner, G., 1999. The uncontrolled manifold concept: identifying control variables for a functional task. Exp. Brain Res. 126, 289–306. https://doi.org/10.1007/s002210050738.

Scholz, J.P., Schöner, G., Latash, M.L., 2000. Identifying the control structure of multijoint coordination during pistol shooting. Exp. Brain Res. 135, 382–404. https://doi.org/10.1007/s002210000540.

Schöner, G., 1995. Recent developments and problems in human movement science and their conceptual implications. Ecol. Psychol. 7, 291–314. https://doi.org/10.1207/s15326969eco0704_5.

Seed, A., Emery, N., Clayton, N., 2009. Intelligence in corvids and apes: A case of convergent evolution? Ethology 115, 401–420. https://doi.org/10.1111/j.1439-0310.2009.01644.x.

Shamay-Tsoory, S.G., Saporta, N., Marton-Alper, I.Z., Gvirts, H.Z., 2019. Herding brains: a core neural mechanism for social alignment. Trends Cogn. Sci. (Regul. Ed.) 23, 174–186. https://doi.org/10.1016/j.tics.2019.01.002.

Shaw, R., 2001. Processes, acts, and experiences: three stances on the problem of intentionality. Ecol. Psychol. 13, 275–314. https://doi.org/10.1207/S15326969ECO1304_02.

Shaw, R.E., Flascher, O.M., Kadar, E.E., 1995. Dimensionless invariants for intentional systems: measuring the fit of vehicular activities to environmental layout. In: Flach, J.M., Hancock, P.A., Caird, J., Vicente, K.J. (Eds.), Global Perspectives on the Ecology of Human-Machine Systems. Lawrence Erlbaum, Hillsdale, NJ, pp. 293–357.

Shea, N., Boldt, A., Bang, D., Yeung, N., Heyes, C., Frith, C.D., 2014. Supra-personal cognitive control and metacognition. Trends Cogn. Sci. (Regul. Ed.) 18, 186–193. https://doi.org/10.1016/j.tics.2014.01.006.

Shumaker, R.W., Walkup, K.R., Beck, B., 2011. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. Johns Hopkins University Press, Baltimore, MD.

Silveri, M.C., Ciccarelli, N., 2009. Semantic memory in object use. Neuropsychologia 47, 2634–2641. https://doi.org/10.1016/j.neuropsychologia.2009.05.013.

Sirigu, A., Duhamel, J.-R., Poncet, M., 1991. The role of sensorimotor experience in object recognition: a case of multimodal agnosia. Brain 114, 2555–2573. https://doi.org/10.1093/brain/114.6.2555.

Smitsman, A.W., 1997. The development of tool use: changing boundaries between organism and environment. In: Dent-Read, C., Zukow-Goldring, P. (Eds.), Evolving Explanations of Development. American Psychological Association, Washington, DC, pp. 301–329.

Smitsman, A.W., Cox, R.F.A., 2008. Perseveration in tool use: a window for understanding the dynamics of the action-selection process. Infancy 13, 249–269. https://doi.org/10.1080/15250000802004379.

Smitsman, A.W., Cox, R.F.A., Bongers, R.M., 2005. Action dynamics in tool use. In: Roux, V., Bril, B. (Eds.), Stone Knapping: The Necessary Conditions for a Uniquely Hominid Behaviour. McDonald Institute for Archaeological Research, Cambridge, UK, pp. 129–144.

Sokolov, A.A., Miall, R.C., Ivry, R.B., 2017. The cerebellum: adaptive prediction for movement and cognition. Trends Cogn. Sci. (Regul. Ed.) 21, 313–332. https://doi.org/10.1016/j.tics.2017.02.005.

Stephen, D.G., Dixon, J.A., 2011. Strong anticipation: multifractal cascade dynamics modulate scaling in synchronization behaviors. Chaos Solitons Fractals 44, 160–168. https://doi.org/10.1016/j.chaos.2011.01.005.

Stephen, D.G., Hajnal, A., 2011. Transfer of calibration between hand and foot: functional equivalence and fractal fluctuations. Attention, Perception, Psychophys. 73, 1302–1328. https://doi.org/10.3758/s13414-011-0142-6.

Stephen, D.G., Boncoddo, R.A., Magnuson, J.S., Dixon, J.A., 2009. The dynamics of insight: mathematical discovery as a phase transition. Mem. Cognit. 37, 1132–1149. https://doi.org/10.3758/MC.37.8.1132.

Stephen, D.G., Arzamarski, R., Michaels, C.F., 2010. The role of fractality in perceptual learning: exploration in dynamic touch. J. Exp. Psychol. Hum. Percept. Perform. 36, 1161–1173. https://doi.org/10.1037/a0019219.

Sterelny, K., 2012. The Evolved Apprentice: How Evolution Made Humans Unique. MIT Press, Cambridge, MA.

Stoffregen, T.A., Pittenger, J.B., 1995. Human echolocation as a basic form of perception and action. Ecol. Psychol. 7, 181–216. https://doi.org/10.1207/s15326969eco0703_2.

Stoffregen, T.A., Mantel, B., Bardy, B.G., 2017. The senses considered as one perceptual system. Ecol. Psychol. 29, 165–197. https://doi.org/10.1080/10407413.2017.1331116.

Stoinski, T.S., Beck, B.B., 2001. Spontaneous tool use in captive, free-ranging golden lion tamarins (*Leontopithecus rosalia rosalia*). Primates 42, 319–326. https://doi.org/10.1007/BF02629623.

Stout, D., 2013. Neuroscience of technology. In: Richerson, P.J., Christiansen, M. (Eds.), Cultural Evolution: Society, Technology, Language, and Religion. MIT Press, Cambridge, MA, pp. 157–173.

Stout, D., 2021. The cognitive science of technology. Trends Cogn. Sci. (Regul. Ed.) 25, 964–977. https://doi.org/10.1016/j.tics.2021.07.005.

Stout, D., Chaminade, T., 2007. The evolutionary neuroscience of tool making. Neuropsychologia 45, 1091–1100. https://doi.org/10.1016/j.neuropsychologia.2006.09.014.

Stout, D., Chaminade, T., 2012. Stone tools, language and the brain in human evolution. Philos. Trans. R. Soc. B Biol. Sci. 367, 75–87. https://doi.org/10.1098/rstb.2011.0099.

Stout, D., Hecht, E.E., 2017. Evolutionary neuroscience of cumulative culture. Proc. Natl. Acad. Sci. 114, 7861–7868. https://doi.org/10.1073/pnas.1620738114.

Stout, D., Toth, N., Schick, K., Chaminade, T., 2008. Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. Philos. Trans. R. Soc. London B Biol. Sci. 363, 1939–1949. https://doi.org/10.1098/rstb.2008.0001.

Stout, D., Hecht, E., Khreisheh, N., Bradley, B., Chaminade, T., 2015. Cognitive demands of lower paleolithic toolmaking. PLoS One 10, e0121804.

Stout, D., Chaminade, T., Thomik, A., Apel, J., Faisal, A., 2018. Grammars of action in human behavior and evolution. bioRxiv. https://doi.org/10.1101/281543, 281543.

Suddendorf, T., Brinums, M., Imuta, K., 2016. Shaping one's future self–The development of deliberate practice. In: Michaelian, K., Klein, S.B., Szpunar, K.K. (Eds.), Seeing the Future: Theoretical Perspectives on Future-Oriented Mental Time Travel. Oxford Univeristy Press, pp. 343–366.

Suddendorf, T., Bulley, A., Miloyan, B., 2018. Prospection and natural selection. Curr. Opin. Behav. Sci. 24, 26–31. https://doi.org/10.1016/j.cobeha.2018.01.019.

Takahashi, C., Watt, S.J., 2017. Optimal visual–haptic integration with articulated tools. Exp. Brain Res. 235, 1361–1373. https://doi.org/10.1007/s00221-017-4896-5.

Taylor, A.H., Jelbert, S., 2020. The crow in the room: new Caledonian crows offer insight into the necessary and sufficient conditions for cumulative cultural evolution. Behav. Brain Sci. 43, e178. https://doi.org/10.1017/S0140525X20000102.

Teng, D.W., Eddy, C.L., Kelty-Stephen, D.G., 2016. Non-visually-guided distance perception depends on matching torso fluctuations between training and test. Attention, Perception, Psychophys. 78, 2320–2328. https://doi.org/10.3758/s13414-016-1213-5.

Tennie, C., Call, J., Tomasello, M., 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. B Biol. Sci. 364, 2405–2415. https://doi.org/10.1098/rstb.2009.0052.

Thomas, B.J., Riley, M.A., Wagman, J.B., 2019. Information and its detection: the consequences of Gibson's theory of information pickup. In: Wagman, J.B., Blau, J.J.C. (Eds.), Perception as Information Detection: Reflections on Gibson's Ecological Approach to Visual Perception. Routledge, New York, NY, pp. 237–252.

Tomasello, M., Kruger, A.C., Ratner, H.H., 1993. Cultural learning. Behav. Brain Sci. 16, 495–511. https://doi.org/10.1017/S0140525X0003123X.

Tonooka, R., 2001. Leaf-folding behavior for drinking water by wild chimpanzees (*Pan troglodytes verus*) at Bossou. Guinea. Anim. Cogn. 4, 325–334. https://doi.org/10.1007/s100710100110.

Troscianko, J., von Bayern, A.M.P., Chappell, J., Rutz, C., Martin, G.R., 2012. Extreme binocular vision and a straight bill facilitate tool use in New Caledonian crows. Nat. Commun. 3, 1110. https://doi.org/10.1038/ncomms2111.

Truskanov, N., Prat, Y., 2018. Cultural transmission in an ever-changing world: trial-and-error copying may be more robust than precise imitation. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170050 https://doi.org/10.1098/rstb.2017.0050.

Tuitert, I., Golenia, L., Otten, E., Bootsma, R.J., Bongers, R.M., 2020. Task constraints act at the level of synergies and at the level of end-effector kinematics in manual reaching and manual lateral interception. J. Exp. Psychol. Hum. Percept. Perform. 46, 1511–1526. https://doi.org/10.1037/xhp0000861.

Tulving, E., 1985. Memory and consciousness. Can. Psychol. 26, 1–12. https://doi.org/10.1037/h0080017.

Turvey, M.T., 1990. Coordination. Am. Psychol. 45, 938–953. https://doi.org/10.1037/0003-066X.45.8.938.

Turvey, M.T., 2007. Action and perception at the level of synergies. Hum. Mov. Sci. 26, 657–697. https://doi.org/10.1016/j.humov.2007.04.002.

Turvey, M.T., 2018. Lectures on Perception: An Ecological Perspective. Routledge, New York, NY.

Turvey, M.T., Fonseca, S.T., 2014. The medium of haptic perception: a tensegrity hypothesis. J. Mot. Behav. 46, 143–187. https://doi.org/10.1080/00222895.2013.798252.

Tylén, K., Philipsen, J.S., Roepstorff, A., Fusaroli, R., 2016. Trails of meaning construction: symbolic artifacts engage the social brain. Neuroimage 134, 105–112. https://doi.org/10.1016/j.neuroimage.2016.03.056.

Umiltà, M.A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V., Rizzolatti, G., 2008. When pliers become fingers in the monkey motor system. Proc. Natl. Acad. Sci. U.S.A. 105, 2209–2213. https://doi.org/10.1073/pnas.0705985105.

Vaesen, K., 2012. The cognitive bases of human tool use. Behav. Brain Sci. 35, 203–218. https://doi.org/10.1017/S0140525X11001452.

Valk, T.A., Mouton, L.J., Bongers, R.M., 2016. Joint-angle coordination patterns ensure stabilization of a body-plus-tool system in point-to-point movements with a rod. Front. Psychol. 7, 826. https://doi.org/10.3389/fpsyg.2016.00826.

van den Herik, J.C., 2021. Rules as resources: an ecological-enactive perspective on linguistic normativity. Phenomenol. Cogn. Sci. 20, 93–116. https://doi.org/10.1007/s11097-020-09676-0.

van der Steen, M.C., Bongers, R.M., 2011. Joint angle variability and co-variation in a reaching with a rod task. Exp. Brain Res. 208, 411–422. https://doi.org/10.1007/s00221-010-2493-y.

van Dijk, L., Bongers, R.M., 2014. The emergence of an action system: the organization of gaze in creating novel tools. Ecol. Psychol. 26, 177–197. https://doi.org/10.1080/10407413.2014.929476.

van Elk, M., van Schie, H., Bekkering, H., 2014. Action semantics: a unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. Phys. Life Rev. 11, 220–250. https://doi.org/10.1016/j.plrev.2013.11.005.

van Schaik, C.P., Burkart, J.M., 2011. Social learning and evolution: the cultural intelligence hypothesis. Philos. Trans. R. Soc. B Biol. Sci. 366, 1008–1016. https://doi.org/10.1098/rstb.2010.0304.

Vendetti, M.S., Bunge, S.A., 2014. Evolutionary and developmental changes in the lateral frontoparietal network: a little goes a long way for higher-level cognition. Neuron 84, 906–917. https://doi.org/10.1016/j.neuron.2014.09.035.

Vingerhoets, G., 2014. Contribution of the posterior parietal cortex in reaching, grasping, and using objects and tools. Front. Psychol. 5, 151. https://doi.org/10.3389/fpsyg.2014.00151.

Wagman, J.B., 2020. A guided tour of Gibson's theory of affordances. In: Wagman, J.B., Blau, J.J.C. (Eds.), Perception as Information Detection: Reflections on Gibson's Ecological Approach to Visual Perception. Routledge, New York, NY, pp. 130–148.

Wagman, J.B., Carello, C., 2001. Affordances and inertial constraints on tool use. Ecol. Psychol. 13, 173–195. https://doi.org/10.1207/S15326969ECO1303_1.

Wagman, J.B., Carello, C., 2003. Haptically creating affordances: the user-tool interface. J. Exp. Psychol. Appl. 9, 175–186. https://doi.org/10.1037/1076-898X.9.3.175.

Wagman, J.B., Hajnal, A., 2014a. Task specificity and anatomical independence in perception of properties by means of a wielded object. J. Exp. Psychol. Hum. Percept. Perform. 40, 2372–2391. https://doi.org/10.1037/xhp0000014.

Wagman, J.B., Hajnal, A., 2014b. Getting off on the right (or left) foot: perceiving by means of a rod attached to the preferred or non-preferred foot. Exp. Brain Res. 232, 3591–3599. https://doi.org/10.1007/s00221-014-4047-1.

Wagman, J.B., Hajnal, A., 2016. Use your head! Perception of action possibilities by means of an object attached to the head. Exp. Brain Res. 234, 829–836. https://doi.org/10.1007/s00221-015-4509-0.

Wagman, J.B., Miller, D.B., 2003. Nested reciprocities: the organism–environment system in perception–action and development. Dev. Psychobiol. 42, 317–334. https://doi.org/10.1002/dev.10114.

Wagman, J.B., Taylor, K.R., 2005. Perceiving affordances for aperture crossing for the person-plus-object system. Ecol. Psychol. 17, 105–130. https://doi.org/10.1207/s15326969eco1702_3.

Wagman, J.B., Caputo, S.E., Stoffregen, T.A., 2016. Hierarchical nesting of affordances in a tool use task. J. Exp. Psychol. Hum. Percept. Perform. 42, 1627–1642. https://doi.org/10.1037/xhp0000251.

Wagman, J.B., Langley, M.D., Higuchi, T., 2017. Turning perception on its head: cephalic perception of whole and partial length of a wielded object. Exp. Brain Res. 235, 153–167. https://doi.org/10.1007/s00221-016-4778-2.

Wagman, J.B., Langley, M.D., Farmer-Dougan, V., 2018. Carrying their own weight: dogs perceive changing affordances for reaching. Q. J. Exp. Psychol. 71, 1040–1044. https://doi.org/10.1080/17470218.2017.1322990.

Wagman, J.B., Lozano, S., Jiménez, A., Covarrubias, P., Cabrera, F., 2019. Perception of affordances in the animal kingdom and beyond. In: Zepeda, I., Camacho, J., Camacho, E. (Eds.), Aproximaciones Al Estudio Del Comportamiento y Sus Aplicaciones. Universidad de Guadalajara, Ocotlátan, Mexico, pp. 70–108.

Walsh, P.T., Hansell, M., Borello, W.D., Healy, S.D., 2011. Individuality in nest building: do Southern Masked weaver (*Ploceus velatus*) males vary in their nest-building behaviour? Behav. Processes 88, 1–6. https://doi.org/10.1016/j.beproc.2011.06.011.

Warren, W.H., 1984. Perceiving affordances: visual guidance of stair climbing. J. Exp. Psychol. Hum. Percept. Perform. 10, 683–703. https://doi.org/10.1037/0096-1523.10.5.683.

Warren, W.H., 2005. Direct perception: the view from here. Philos. Top. 33, 335–361.

Watanabe, K., Urasopon, N., Malaivijitnond, S., 2007. Long-tailed macaques use human hair as dental floss. Am. J. Primatol. 69, 940–944. https://doi.org/10.1002/ajp.20403.

Wheaton, L.A., Hallett, M., 2007. Ideomotor apraxia: a review. J. Neurol. Sci. 260, 1–10. https://doi.org/10.1016/j.jns.2007.04.014.

Whiten, A., 2015. Experimental studies illuminate the cultural transmission of percussive technologies in *Homo* and *Pan*. Philos. Trans. R. Soc. B Biol. Sci. 370, 20140359 https://doi.org/10.1098/rstb.2014.0359.

Wissing, M.B.G., Golenia, L., Smith, J., Bongers, R.M., 2020. Adjustments in end-effector trajectory and underlying joint angle synergies after a target switch: order of adjustment is flexible. PLoS One 15, e0238561. https://doi.org/10.1371/journal.pone.0238561.

Yildirim, I., Wu, J., Kanwisher, N., Tenenbaum, J., 2019. An integrative computational architecture for object-driven cortex. Curr. Opin. Neurobiol. 55, 73–81. https://doi.org/10.1016/j.conb.2019.01.010.

Zach, R., 1978. Selection and dropping of whelks by Northwestern crows. Behaviour 67, 134–147. https://doi.org/10.1163/156853978X00297.

Ziegenhorn, M.A., 2016. Best dressed test: a study of the covering behavior of the collector urchin, *Tripneustes gratilla*. PLoS One 11, e0153581. https://doi.org/10.1371/journal.pone.0153581.

Zorick, T., Landers, J., Leuchter, A., Mandelkern, M.A., 2020. EEG multifractal analysis correlates with cognitive testing scores and clinical staging in mild cognitive impairment. J. Clin. Neurosci. 76, 195–200. https://doi.org/10.1016/j.jocn.2020.04.003.

Zwirner, E., Thornton, A., 2015. Cognitive requirements of cumulative culture: teaching is useful but not essential. Sci. Rep. 5, 16781. https://doi.org/10.1038/srep16781.

Glossary

Embodied tooling

Ecological psychology: An approach to psychology developed by James Gibson that takes the animal-environment system to be the fundamental unit of analysis and that describes perception as a process of detecting energy patterns that are unambiguously (lawfully) related to the set of behaviors that are possible in the surroundings.

Movement science: A scientific discipline concerned with the study of movement in humans and nonhuman animals from various perspectives, including biomechanics, physiology, and motor control and development.

Interface: How a person monitors or controls the operation of a machine such as a computer. Examples include a keyboard, visual display, touchscreen, and computer mouse, among many others.

Perceptuomotor: Describing the movement of a limb in response to a perception.

Affordance: An affordance is what an organism can do with an object or a surface based on its capabilities.

Pantomiming: Gesturing movements without the object with which or the goal towards which that movement is typically performed.

Tool use as detection and exploitation of information in an ecological niche

Patterned energy distributions: Surrounding energy distributions such as reflected light, odor gradients, and patterns of deformation on bodily tissue that are lawfully structured by surface and substance properties.

Task-specific detection units: Independent anatomical (and sometimes inert) units that are coordinated to perceive a particular affordance. For example, the arm, hand, and probe can be coordinated in perceiving properties using the probe.

Task-specific control units: Independent anatomical (and sometimes inert) units that are coordinated to perform a particular behavior. For example, the legs, arm, hand, and crutch can be coordinated in moving from place to place.

Sensory apparatus: The various anatomical and physiological components (sense organ, associated receptors) used to perceive a given property.

Ecological niche: niche is how a species of animal lives in its environment determined by the fit between its Action capabilities and environmental properties. It can be contrasted with habitat, which is where an animal lives independent of its action capabilities.

Functional transparency: The phenomenal experience in which a tool no longer feels like a separate object and instead feels like part of the body.

Tools as intermittent properties of the fractal coastlines between organism and environment

Intermittency: An uneven distribution of events across time or space, characterized by the unpredictable, sudden appearance or disappearance of stability—or by the unpredictable, sudden transitions among stable states.

Cascade: A physical process characterized by a blending of information or structure built at multiple scales. For instance, when events spread from one scale to another, e.g., cellular to genetic, or cellular to whole-tissue, and then to organ- and to whole-organism scale, what we have is a cascade of effects.

Fractional dimension: A statistical index of complexity—which lies between 1 and 2—describing how detail in a fractal pattern changes with the scale at which it is measured.

Multifractality: A generalization of a fractal system in which one fractal dimension is not enough to describe its dynamics; instead, a continuous spectrum of exponents (the so-called singularity spectrum) is needed.

cAMP: Cyclic adenosine monophosphate is an organic molecule that participates in second-messenger signaling in a wide variety of organisms. Slime mold cells (Dictyostelium discoideum) secrete cAMP when their food sources dwindle, and cAMP released by starving slime mold cells becomes a cue for other slime mold cells to approach.

A tool in use is incorporated into synergies

Perceptual flow field: Lawful, patterned changes in perceptual stimulation—due to physical constraints on how the visual, auditory, and mechanical energy flow through a medium—revealing the information that it affords for controlling activity, about both the topography of the environment and the movement of the organism relative to the environment.

Effectivities: The properties of an animal that allow an action to place in a specific environment.

Synergies: Temporary functional units in which the degrees of freedom of the neuromotor system (e.g., joint angles, muscles) are organized. Task performance is maintained within a synergy through co-variation in degrees of freedom making up the synergies. These functional units emerge from interaction between organismic, environmental and task constraints.

Uncontrolled Manifold (UCM) analysis: An analytical technique used to evaluate the joint coordination by focusing on the trial-to-trial variance of angular motion about joints. The target UCM is a subspace of joint angles whose variability does not affect the end-effector's position (e.g., the tip of the hammer when using it to drive in a nail).

More than just tool use

Causal reasoning: Systematic thinking about the relation between events based on logical, statistical, or simulation-based mental models. Some recent literature efers to causal reasoning about physical object properties as technical reasoning.

Imitation: Behavior copying. This term has been used to mean everything from social learning to the reproduction of action intentions but is now most commonly used in the narrow sense of copying the form or topography of observed movements.

Mentalizing: The process of representing and reasoning about the mental states, thought, and feelings of the self and others. Also known as Theory of Mind.

Intersubjectivity: Sharing mental states through mutual attempts to understand or perceive a situation from the other's perspective.

Internal model: A simulation of a system's response to events or states. In motor control, forward models use motor commands to predict sensory consequences, whereas inverse models use intended sensory consequences to generate appropriate motor commands.

Prospection: The ability to represent, reason about, and evaluate possible future conditions and events.

Deliberate practice: Systematic practice deploying focused attention with the explicit goal of improving performance.

Emulation: Outcome copying. This term has been used to mean everything from object movement re-enactment to goal reproduction but is most commonly intended to mean using one's means to achieve observed action outcomes.

Niche construction: A form of ecological inheritance in which organisms alter the environment to affect the developmental context and selection pressures acting on subsequent generations.

The technical-reasoning hypothesis

Technical reasoning: Aility to solve physical problems by using abstract physical principles acquired through experience. This reasoning is both analogical and causal.

Mechanical knowledge: Non-declarative knowledge about physical principles, which is acquired through experience.

Cumulative technological culture: Accumulation of socially learned information over generations, allowing humans to develop tools and technologies that are too complex to have been invented by a single individual.

Distalization: Attentional shift from the effector to the active part of a tool, while it is still the effector that must be controlled.

Microsociety paradigms: Paradigms modeling cumulative technological culture in experimental conditions where participants can share information either via direct (i.e., observation, communication or indirect transmission (i.e., reverse engineering).