

Although Vaesen's nine capacities provide mechanisms for tool use transmission, maintenance, and improvement, thereby advancing technology, they are not preconditions for tool use as such. Therefore, although human technological achievements are unique, Vaesen's capacities and tool use itself may not be.

Studies of behavioral trait evolution demand an appropriate comparison group (i.e., all hominoidea, all anthropoidea, or all primates), but surveying analogous behaviors in distant taxa can elucidate the ecological and evolutionary contexts of these traits. Vaesen focuses on great ape studies that support his claims and ignores conflicting data. He extensively refers to the (phylogenetically distant) monkey literature that suits his argument (e.g., Cummins-Sebree & Frigaszy 2005; Hauser 1997) and ignores relevant monkey and even ape studies that do not (e.g., Hauser et al. 2002; Santos et al. 2003; Whiten et al. 2005; although Whiten et al. 2005 is mentioned later in a different context). In fact, Whiten et al.'s (2005) study and a new study (Hanus et al. 2011) may very well indicate functional fixedness in chimpanzees. The ape studies Vaesen does mention here are placed in Note 14, and one (Carvalho et al. 2009) provides a strong case of tool reuse.

Among more distant taxa, bottlenose dolphins in Shark Bay, Australia, reuse basket sponge tools for a little more than an hour, as presumably during that period the tool remains functional; but much beyond that, functionality is lost and the tool is discarded (Patterson & Mann 2011). Furthermore, functional fixedness is not necessarily a valuable cognitive trait and may even be inhibitory (e.g., Hanus et al. 2011). Flexibility, on the other hand, is a cognitive bonus, as with little to no modification a single tool becomes many (e.g., chimpanzees use sticks to fish for termites, honey [Fay & Carroll 1994], and ants [McGrew 1974] and even as hunting spears [Pruetz & Bertolani 2007]). When discussing executive control and forethought, Vaesen focuses on ape studies by Osvath and Osvath (2008) but fails to mention other ape research (e.g., Biro & Matsuzawa 1999; Boesch 1994; Boesch & Boesch 1989; Dufour & Sterck 2008; Noser & Byrne 2010; Osvath 2008). Vaesen does mention two additional studies, but again they are buried, in Note 20 rather than in the main body of his text. In fact, conflicting literature is repeatedly placed in notes (e.g., hand-eye coordination [5], functional representation [14], executive control and forethought [20], heuristics for selecting models for social learning [29], and food sharing [31]).

While not implicitly stating it, Vaesen strongly implies that human tool use and his nine capacities coevolved. If so, then Vaesen must address whether the phenotype was selected for and whether its current utility is the same as its historic use (Gould & Lewontin 1979). Human technology is obviously indicative of higher cognitive ability, but may be a product of our cognition rather than the selective force behind it. Two other well-established brain evolution theories deserve consideration: the social brain hypothesis (Byrne & Whiten 1988; Dunbar 1998) and the ecological complexity hypothesis (Reader & Laland 2002). Although tool use likely played a role in our cognitive evolution, either as a product or as a driving factor, it demands a systematic and comprehensive approach.

Finally, most of Vaesen's arguments rely on a lack of evidence, rather than evidence of absence (de Waal & Ferrari 2010). This amounts to trying to prove the null hypothesis, a nearly futile task when comparing across taxa because of (1) a lack of data for some species, (2) low ecological validity, (3) poor internal validity due to poorly designed tasks, (4) biases in research effort, and (5) the sheer difficulty of researching cognition in animals. Vaesen even admits, but is not deterred by the fact, that for 8 of the 16 traits he claims are decidedly more pronounced in humans than in chimpanzees, few data are available (Table 2).

Tool use should be studied with a comparative approach, including the examination of other taxa and analogous behaviors, and by maintaining an appreciation for the ecological and social contexts in which tool use arises (de Waal & Ferrari 2010). For

example, Povinelli's studies on captive chimpanzees using human behavioral models fail to show causal reasoning (but see Call 2010), whereas Cheney and Seyfarth's (1995) study with wild baboons, which uses more relevant tests, seems to demonstrate causal reasoning in natural social contexts. With more appropriate tests, apes may very well excel (albeit, not to the level of humans) in all of the nine capacities. Non-primates, such as rats, crows, and likely elephants, show causal reasoning (Blaisdell et al. 2006; Plotnik et al. 2011; Taylor et al. 2009a).

Other areas that could benefit from this comparative approach include, but are not limited to, imitation (e.g., dolphins; Herman 2002), social learning (e.g., woodpecker finches; Tebbich et al. 2001), social intelligence (e.g., dolphins; Connor 2007), insight learning (e.g., crows; Taylor et al. 2010), forethought (e.g., dolphins; McCowan et al. 2000), teaching (e.g., meerkats; Thornton & McAuliffe 2006), inhibition (e.g., rodents, birds, and marine invertebrates; Dally et al. 2010; Kim 2010; Vander Wall et al. 2009), food sharing (e.g., killer whales; Ford & Ellis 2006), and theory of mind (e.g., dolphins and elephants; Douglas-Hamilton et al. 2006; Plotnik et al. 2010; Xitco et al. 2004).

Surely those without hands deserve another look.

So, are we the massively lucky species?

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Derek C. Penn,^a Keith J. Holyoak,^a and Daniel J. Povinelli^b

^aDepartment of Psychology, University of California, Los Angeles, Los Angeles, CA 90095; ^bDepartment of Biology, University of Louisiana, Lafayette, LA 70560.

dcpenn@ucla.edu <http://reasoninglab.psych.ucla.edu/>
 holyoak@lifesci.ucla.edu <http://reasoninglab.psych.ucla.edu/>
 povinelli@louisiana.edu

Abstract: We are in vehement agreement with most of Vaesen's key claims. But Vaesen fails to consider or rebut the possibility that there are deep causal dependencies among the various cognitive traits he identifies as uniquely human. We argue that "higher-order relational reasoning" is one such linchpin trait in the evolution of human tool use, social intelligence, language, and culture.

We are in vehement agreement with most of Vaesen's key claims. We have long argued that sophisticated tool use and abstract causal reasoning reflect a fundamental cognitive discontinuity between humans and all other extant animals (Penn & Povinelli 2007a; Penn et al. 2008; Povinelli 2000). And we have previously proposed, in this very journal, an explanation for the discontinuity between human and non-human minds that overlaps with Vaesen's in many respects (Penn et al. 2008).

The remainder of this commentary, then, should be read as an intramural critique. We have a couple of small issues with Vaesen's argument and one big one.

Causal reasoning. Vaesen correctly points out that "causal understanding involves more than just noticing (e.g., through trial and error) the covariance between a cause ... and an effect" (sect. 4, para. 1). But then Vaesen goes on to claim, incorrectly in our view, that a cognizer must "infer a mechanism" in order to possess true causal understanding. To be sure, there are those who have advanced such a view (e.g., Ahn et al. 1995). However, the notion that prior knowledge of a mechanism is required for causal understanding offers no insight into how causal learning can get started: that is, how can a reasoner infer a *causal* mechanism from *noncausal* observations (Cheng 1993; 1997)? More recent theoretical work based on variants of causal Bayes nets has established that a cognizer can recognize a relation as specifically causal without necessarily understanding anything about unobservable

causal mechanisms (for reviews see Gopnik & Schulz 2007; Holyoak & Cheng 2011).

Because Vaesen overlooks the distinction between causal reasoning and the representation of unobservable causal mechanisms, he misconstrues the results of Povinelli's rake experiments as evidence that chimpanzees learn through "associative learning" (sect. 4, para. 3). We have argued that the chimpanzees in these experiments were perfectly capable of first-order causal understanding (Penn & Povinelli 2007a). It is the ability to reason about higher-order causal relationships that eludes them (Penn et al. 2008; Povinelli 2000).

Function representations. Vaesen is probably correct that chimpanzees do not form "functional representations" (sect. 5) of tools in the same manner as humans. But it seems implausible to us that chimpanzees do not form functional representations at all. They certainly perceive stick-like objects as able to "function" in a certain manner for achieving certain goals, and these representations generalize over a fairly wide variety of shapes, colors, and textures. In our view, chimpanzees are perfectly able to form functional representations of stick-like objects in terms of surface features of the objects – they just fail to represent "functions" in terms of the underlying causal mechanisms involved (Povinelli 2000).

Explaining the discontinuity. In summarizing his findings from the first half of the paper, Vaesen (sect. 11) argues that "no individual cognitive trait" can be singled out as the key trait differentiating humans from other animals, and then claims that his argument is an antidote to "single-trait explanations of 'humaniqueness'" (sect. 11, para. 3). This is our major point of contention with Vaesen.

To be sure, we know of no researcher who claims that there is one and only one trait that distinguishes human and nonhuman cognition. There are, indeed, a large number of cognitive traits that appear to be distinctively human – ranging from mental state attribution and language to causal reasoning and contingent cooperation. But Vaesen does not consider or rebut the possibility that there might be a deep dependency between many or even all of these disparate traits both at a cognitive/computational level of explanation and at an evolutionary/biological level of explanation.

It is possible, of course, that each of our uniquely human cognitive traits evolved independently of each other, and that each is embodied in a separate and independent "module" in the human brain. There are certainly researchers who defend such a "massively modular" explanation for human cognition (Carruthers 2005; Tetzlaff & Carruthers 2008). But to our eyes, it seems wildly implausible that one and only one species was lucky enough to have evolved separate and independent mechanisms for each of these uniquely human traits (in a few million years to boot), whereas no other species evolved any of them. It seems much more likely (not to mention parsimonious) that there are deeper dependencies among these disparate traits such that a species that evolved a few linchpin traits would be in a more propitious state, from an evolutionary point of view, to acquire the others.

We have argued that the ability to represent and reason about the relation among relations – that is, "high-order relational reasoning" – is a plausible candidate for one of these linchpin traits (Penn et al. 2008). It certainly seems noteworthy that many of the cognitive traits Vaesen identifies as instrumental in the evolution of human tool use – causal reasoning, functional representations, foresight, teaching, mental state attribution, contingent reciprocity, goal sharing – appear to depend upon a common set of higher-order relational competences.

Numerous researchers, for example, have demonstrated a strong empirical relationship between higher-order relational reasoning and theory-of-mind competence (e.g., Andrews et al. 2003; Zelazo et al. 2002). And almost all theoretical models of mental state attribution presume higher-order relational reasoning as an underlying mechanism (e.g., see the theories proposed

in Carruthers & Smith 1996). With respect to causal reasoning, most contemporary researchers agree that the ability to reason about a *network* of causal relations in a systematic and allocentric fashion is the bedrock of human causal cognition (e.g., Lagnado et al. 2005; Tenenbaum et al. 2006). Higher-order relations are also central to language (e.g., Gomez & Gerken 2000; Hauser et al. 2002; Pinker & Jackendoff 2005).

The cognitive traits Vaesen subsumes under the heading of "executive control" are a motley set. There is good evidence that some of these – e.g., inhibition, autocoing, and self-monitoring – are necessary components of the ability to reason about higher-order relations (Andrews et al. 2003; Cho et al. 2010; Halford et al. 1998; Robin & Holyoak 1995). Others – for example, foresight, hierarchical planning, and inferential coherence – are plausibly the *result* of being able to reason about higher-order relations.

Much work remains to be done to disentangle the necessary and sufficient components of higher-order relational reasoning in humans, and to understand how such a unique computational mechanism evolved in the brain of one particular species. However, there is already strong evidence, from a wide variety of domains and researchers, that this ability lies at the heart of "what makes us so smart" (Gentner 2003). Our principle difference with Vaesen is that he neither considers nor rebuts this possibility.

The key to cultural innovation lies in the group dynamic rather than in the individual mind

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Sonia Ragir and Patricia J. Brooks

College of Staten Island, City University of New York, Staten Island, NY 10314.

soniaragir@gmail.com patricia.brooks@csi.cuny.edu

http://www.csi.cuny.edu/faculty/BROOKS_PATRICIA.html

Abstract: Vaesen infers unique properties of mind from the appearance of specific cultural innovation – a correlation without causal direction. Shifts in habitat, population density, and group dynamics are the only independently verifiable incentives for changes in cultural practices. The transition from Acheulean to Late Stone Age technologies requires that we consider how population and social dynamics affect cultural innovation and mental function.

By focusing on human cognitive capabilities, Vaesen dismisses the function of the group dynamic in the emergence of complex social repertoires (Garrod & Doherty 1994; Steels 2006; Steels et al. 2002). Underlying biological capacities tend to be difficult to delineate; the same biology often displays considerable behavioral flexibility in response to shifts in social dynamics and environmental challenges. Vaesen's nine cognitive prerequisites are important for human cultural evolution, but one can make only educated guesses about how, why, or when these capabilities emerged. Evidence for cognitive capacities is inferred from the presence of the tool assemblages they purport to explain, without independent evidence for the direction of causation. Certainly, one can argue that many if not all of these capacities, including language, were present in *Homo erectus* toolmakers.

Three parameters are consistently associated with complex cultural adaptations to an environment: (1) relatively large brains and prolonged postnatal, activity-dependent maturation of the central nervous system, (2) environmental stress, and (3) increased population densities. Over hominin evolution, as a consequence of maturational delays and encephalization, human brains came to have remarkable developmental plasticity throughout the lifespan. Changes in life history created the potential for behavioral flexibility and altered social dynamics among mothers, infants, and others (Hrdy 2009; Kaplan et al. 2000; O'Connell et al. 2002; Ragir 1985). Evidence for

maturational changes is abundant in the fossil record beginning 3–4 mya and indicates a relatively modern profile of prolonged juvenile growth and encephalization beginning with *H. erectus* (Ragir 2000). The altered human life history is best explained through changes in habitat, diet, and locomotion (Aiello & Wells 2002; Cachel & Harris 1995; Laden & Wrangham 2005; Ragir et al. 2000). The transition from Acheulean to Middle Palaeolithic in Europe (Middle Stone Age in Africa) took place long after the appearance of a human-size brain and developmental profile. This leaves the interdependence between environmental stress and regional population growth as the incentive for the proliferation of human technologies in the Middle Pleistocene.

Improvements in diet supported increases in population densities by decreasing birth spacing (Aiello & Key 2002). Intensification of exploitation of local resources has been closely associated with a division of labor and the specialization of knowledge required for rapid technological advancement (Jochim 1981). Technological advancement progresses slowly where populations are small and widely dispersed, and where there is little external pressure for change, as in modern hunter-gatherer societies (Jochim 1976); indeed, technological advances may be lost between generations when there is a drop in population density (Boserup 1981).

Let us consider how changes in population density result in the specialization of labor and knowledge using cooking as an example. Within a community, cooking skills are typically widespread, but the quality of production is uneven. In small communities, foods are often limited to local produce and ethnic tradition, and equipment is general purpose. Among home cooks, some are especially talented and capable of producing high-quality meals, but their innovative recipes and techniques often disappear after a generation or two. As communities increase in size, functional institutions appear (e.g., courts, estates, the army) that use full-time cooks to prepare meals for dozens of people. Professionals design specific tools to take the guesswork out of combining ingredients and systematize the techniques and timing of food preparation. With specialization comes a formal transfer of skills in the form of recipes, apprenticeships, and schools that disseminate a standardized knowledge of cooking methods. Archaeologically, the simple artifacts of home cooking appear as early as sedentary villages; and these continue to be found even after the appearance of the specialized toolkits of professional chefs. One does not supersede the other – they continue, one changing slowly and the other proliferating innovations, spatially but not temporally distinct.

Studies of language formation offer further insights into the emergence of complex cultural repertoires. Among deaf individuals, the effect of community size on the emergence of communication systems from home sign to fully developed sign languages demonstrates the centrality of social dynamics. Isolated deaf children invariably use gestures to communicate with family members and achieve a perceptible degree of systematization in their gestural repertoires (Goldin-Meadow 2003). However, within a broader community, systemization creates stable, broadly shared system of signs (Kendon 1984). Given a community open to new learners, the informal syntax of a pidgin coalesces into a formal syntactic system within a few generations (Kegl et al. 1999). Whereas isolated deaf children create idiosyncratic conventions in interaction with their families, global conventions emerge only within communities of some critical size (Ragir 2002; Senghas et al. 2005).

Simulations and experimental studies further demonstrate the role of collaborative learning in the proliferation and maintenance of novel systems of information exchange. Fay, Garrod, and colleagues (e.g., Fay et al. 2010; Garrod et al. 2010) compared the emergent graphic communicative systems of those participants engaged in pair-wise interactions with different group members and those of isolated pairs over an equivalent number of communicative turns. Only in the case of

community-wide interactions did individuals converge on a global system. Furthermore, global signs were found to be more transparent with respect to meaning than were those produced by isolated pairs (Fay et al. 2008). These results suggest that system standardization and streamlining may require collaborative negotiations among members of groups larger than a family (Fay et al. 2000).

Group dynamics lead to the emergence of conventional procedures and global symbols, in such domains as ceramics, fashion, music, and the Internet, from cottage crafts to the assembly line. The resultant technologies alter the ontogeny of individual minds, in the form of activity-dependent changes in information processing (Bavelier et al. 2010; Donald 1991; Greenfield 1984; Tobach et al. 1997). Simple negotiations of information are capable of producing unexpectedly complex behavioral repertoires, such as seen among social insects, migratory birds, and animals engaged in cooperative parenting (Hrdy 2009). Social interactions that systematize activities and negotiate global conventions effect significant changes in neural connectivity and cognitive functions. Unique human faculties are likely to emerge as the result of, rather than as necessary conditions for, innovative cultural repertoires.

The limits of chimpanzee-human comparisons for understanding human cognition

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Simon M. Reader^{a,b} and Steven M. Hrotic^b

^aDepartment of Biology, McGill University, Montréal, Québec H3A 1B1, Canada; ^bBehavioural Biology, Department of Biology and Helmholtz Institute, Utrecht University, Utrecht 3508 TB, The Netherlands.

simon.reader@mcgill.ca <http://biology.mcgill.ca/faculty/reader/>
stevenhrotic@yahoo.co.uk

Abstract: Evolutionary questions require specialized approaches, part of which are comparisons between close relatives. However, to understand the origins of human tool behavior, comparisons with solely chimpanzees are insufficient, lacking the power to identify derived traits. Moreover, tool use is unlikely a unitary phenomenon. Large-scale comparative analyses provide an alternative and suggest that tool use co-evolves with a suite of cognitive traits.

We are sympathetic to Vaesen's view that no single cognitive trait differentiates human tool behavior from that of other animals, and we agree that comparative analysis has an important role in understanding the cognitive bases of human tool use. However, in our view, several vital issues are unaddressed. Have tool-using capacities driven human cognitive evolution, or is tool use the by-product of another ability? To what degree are the perceptual and cognitive traits underlying tool use and technological cultural evolution independent from each other and from morphological, societal, or ecological traits? What is the role of culture and development in shaping patterns of tool innovation and social learning? How much of cumulative cultural evolution rests on increases in causal understanding of tools, as Vaesen suggests, and how much on retention of "blind" variants (Simonton 2003)?

Here we focus on problems raised by the analysis of human tool behavior based on comparisons with one taxon, chimpanzees. Vaesen's aim is not to compare humans and chimpanzees, but to understand the cognitive bases of human tool use. As useful as comparisons with chimpanzees are, Vaesen's application of this tactic is critically flawed for at least four reasons. Although Vaesen admits his narrow focus on chimpanzees, the flaws are germane both to his conclusions and to other work in the field.

First, Vaesen's chimpanzee-human comparison assumes that shared ancestry explains similarities, whereas differences are explained by independent evolution of the trait in humans and not, for example, the loss of the trait in chimpanzees. However, the ancestral state must be established, which requires investigation of additional species (de Kort & Clayton 2006).

Second, tool use is unlikely a unitary phenomenon. A variety of neurocognitive and genetic mechanisms can underlie a behavioral outcome such as tool use (Shumaker et al. 2011). Hence, it is not a given that similarities and differences between species in tool-related behavior or test performance equate to similarities and differences in underlying cognition, potentially compromising the explanatory power of species comparisons. Independent evolution may have produced similar behavioral specializations with different underlying mechanisms (de Kort & Clayton 2006), or behavioral similarities may appear as a consequence of some third variable, such as enhanced social tolerance (van Schaik et al. 1999). Furthermore, tool-using capacities may be present but unexpressed. For example, expression of true and proto-tool use (Shumaker et al. 2011) appears sensitive to variation in social and ecological conditions. Finches turn to tools in arid conditions, rarely using tools to extract prey where food is abundantly accessible (Tebich et al. 2002); dolphins use sponges to locate prey that cannot be detected by other means (Patterson & Mann 2011); adult male capuchin monkeys are strong enough to bite open certain nuts, whereas females and juveniles require tools to open them (Fragaszy & Visalberghi 1989); and grackles use water to soften hard food when the risks of kleptoparasitism are low (Morand-Ferron et al. 2004). These observations suggest tool use may frequently be a costly option employed flexibly, taken when other options fail or are unavailable. Similarly, innovation in tool use can be employed flexibly; for example, driven by the social milieu (Reader & Laland 2003; Toelch et al. 2011). Hence, numerous variables could underlie species differences in tool-related behavior, and even apparent similarities may reflect different underlying mechanisms.

Third, chimpanzees may be well studied, and our close relatives, and provide much informative data (e.g., Hrubesch et al. 2009; Marshall-Pescini & Whiten 2008), but other animals provide relevant data and counterpoints to Vaesen's proposals. For example, work on finches and crows demonstrates that social learning is not essential for the acquisition of tool use (Kenward et al. 2005; Tebich et al. 2001); meanwhile macaque observational data suggest that social transmission of nonfunctional object manipulation occurs outside humans (Leca et al. 2007, who do not class nonfunctional behavior as tool use). Similarly, selective social learning may be rarely documented in apes but has been described in numerous other species, including monkeys, other mammals, fish, and birds (Laland 2004; Lindeyer & Reader 2010; Seppänen et al. 2011; van de Waal et al. 2010). Selective social learning may be necessary for cumulative cultural evolution, but is clearly not sufficient, unless cumulative cultural evolution occurs unobserved in these animals. Researchers have demonstrated several other behaviors in non-primates that Vaesen identifies as distinctively human: ants, pied babblers, and meerkats teach; fish punish and image-score; birds use baits to trap prey, forgoing immediate rewards in a manner not unlike the human traps that Vaesen argues require foresight and inhibition (Bshary & Grutter 2005; 2006; Shumaker et al. 2011; Thornton & Raihani 2011). We urge caution in interpreting even flexible and sophisticated tool use as necessarily the product of complex cognition.

Finally, any comparison based on an effective sample size of two is problematic. Humans and chimpanzees differ on numerous characteristics. In the absence of additional behavioral data on the role of underlying candidate mechanisms in tool use, any of these characteristics alone or in combination could account for differences in tool behavior. To robustly identify correlates of tool use with comparative data, repeated and

independent co-evolution must be observed, using modern techniques to focus on independent evolutionary events and to account for multiple confounding variables (Nunn & Barton 2001). Confidence in such results is strengthened further if the same patterns are observed in multiple taxa. Such correlational comparative analyses, incorporating large numbers of species, reveal that avian and primate tool use has co-evolved with several cognitive traits and with brain volume measures, and (in primates) with manual dexterity (Byrne 1997; Deaner et al. 2006; Lefebvre et al. 2002; 2004; Overington et al. 2009; Reader & Laland 2002; Reader et al. 2011; van Schaik et al. 1999). These data, supported by discoveries of tool use capabilities in species previously not noted tool users (Reader et al. 2011; Shumaker et al. 2011), are consistent with the idea that tool use can result from a generalized cognitive ability and that it forms part of a correlated suite of traits. However, such analyses would benefit from experimental data teasing apart the processes underlying tool behavior.

If human tool use really is unique, identification of its cognitive bases by comparison with any species will be problematic. We must unpack tool use, understand the underlying motivational and neurocognitive mechanisms in humans and other species, and study a range of species that both possess and lack these abilities in order to understand the consequences for tool behavior. Evolutionary approaches hence have an important role to play in investigations of cognition. Work with chimpanzees is but one part of solving this important issue.

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The dual nature of tools and their makeover

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Antonio Rizzo

Department of Communication Science, Università di Siena, Siena, 53100 Italy.

rizzo@unisi.it <http://rizzo.media.unisi.it>

Abstract: Vaesen argues that functional knowledge differentiates humans from non-human primates. However, the rationale he provides for this position is open to question – with respect to both the underlying theoretical assumptions and inferences drawn from certain empirical studies. Indeed, there is some recent empirical work that suggests that functional fixedness is not necessarily uniquely human. I also question the central role of stable function representations in Vaesen's account of tool production and use.

In his target article, Vaesen acknowledges the fundamental role of tools in characterizing uniquely human psychological skills, but he perseveres with a vision that distinguishes material tools from psychological (ideal) ones. The argument he develops in the article omits a long-standing and important conceptual tradition in psychology, namely the cultural-historical tradition (e.g., Cole 1996). In this approach, tools have a dual nature; they are at the same time both material and ideal. The dual nature of tools has implications for many of the nine cognitive capacities noted by Vaesen. I will focus on functional representation, as it has important implications for how we understand and develop novel forms of artifacts. Vaesen argues that functional knowledge differentiates humans from non-human primates, but his argumentation is problematic – with respect both to the *empirical evidence* and to certain of his *theoretical assumptions*, which I outline briefly below.

Problems concerning empirical evidence. There is some recent empirical evidence that seems to show that functional fixedness is *not* uniquely human. Hanus et al. (2011) have provided suggestive evidence for the hypothesis, put forward by Tennie et al. (2010), that the difference they observed between chimpanzees and orangutans in their ability to solve the Floating Peanuts task (Mendes et al. 2007) was due to the functional fixedness of the chimpanzees with respect to the water dispenser. In Experiment 3, Hanus and colleagues showed that simply adding a new water dispenser in the experimental settings led the chimpanzees to use water as a tool for recovering the peanuts – but by taking water from the new dispenser only, and not from the one from which they used to drink. This would seem to indicate that the chimps also show functional fixedness.

Theoretical assumptions. Stable function representations cannot account for the peculiar human ability to generate functions that go beyond what is physically feasible to perform with any material thing. The generation of such functions is the result of the dual nature of artifacts (material and ideal), as expressed in cultural-historical psychology (Ilyenkov 1977). Vaesen (2011) recognizes the dual nature of tools, but addresses the ideal side as representing the intentions of the designers embodied in the tool (i.e., functional aspects) as well as by other roles involved in the production of the material object (marketing, manufacturing). But the ideal component is not a matter of capturing the functional or pragmatic factors that in different moments inform the production of a material tool. It has to do rather with how people harness material things (natural and artificial, abiotic and biotic) for thought.

It has to do with two complementary sides of the same coin: on the one side, with the ability to perceive, understand, and use for their own goals the intentional relations that other persons have with an object or tool in their everyday practice – the intentional relations that other people have to the world through that object (i.e., intentional affordances; Tomasello 1999). This intentional relation may or may not be related to the intentions of the people involved in the original production of the artifacts (Rizzo 2000; 2006). Indeed, as observed by the Victorian writer Samuel Butler (1912/1951): “Strictly speaking, nothing is a tool except during use. The essence of a tool, therefore, lies in something outside the tool itself” (p. 121).

On the other side, the ideal component has to do with our capacity to go beyond what is physically feasible to perform with any material thing. This is an ability humans show very early in their development; for example, in pretend play. In pretend play, meaning is cast on objects in virtue of the actions the objects allow the children to perform, yet these actions are performed *away from* conventional use of the object. Pretend objects still need to support the pretend act, but a pretend horse does not need to afford riding or feeding; it only needs to afford pretend riding or feeding. Actually, the child can select very different objects as a pretend horse, insofar as the objects are good enough to support the specific enactment. *It’s the pattern of action that specifies the meaning, not the object* (Szolnoky 2006). Lev Vygotsky (1933/1967) gave a clear description of this phenomenon:

In play the child creates the structure meaning/object, in which the semantic aspect – the meaning of the thing – dominates and determines his behavior. To a certain extent meaning is freed from the object with which it was directly fused before. I would say that in play a child concentrates on meaning severed from objects. (p. 11)

And Vygotsky was quite explicit in stating that “a child does not symbolize in play”:

A symbol is a sign, but the stick is not the sign of a horse. Properties of things are retained, but their meaning is inverted, i.e., the idea becomes the central point. It can be said that in this structure things are moved from a dominating to a subordinate position. (p. 11)

Pretend play is most likely a uniquely human social activity (Rakoczy 2008); and, like speech, it has to do with the emancipation of situational constraints and with the creation of a new reality, which exists only in virtue of the human ability to share intentions. This allows the arbitrary creation of what Searle (1995) has named the *status function* of objects. For example, there is nothing in the physical constitution of a 10-euro note that makes it money, as even if I could clone a 10-euro note atom by atom, the result would not be money. It is the collective, yet subjective, intentionality that creates an objective and factual reality, which exists only for humans.

Therefore, specifically human functional knowledge would be better characterized not by stable function representation but by pretend play and drama inquiry. Indeed, these are just the key components of human innovative strategies such as generative scenarios (Rizzo & Bacigalupo 2004) and tinkering with things:

Tinkering is what happens when you try something you don’t quite know how to do, guided by whim, imagination, and curiosity. When you tinker, there are no instructions – but there are also no failures, no right or wrong ways of doing things. It’s about figuring out how things work and reworking them. Contraptions, machines, wildly mismatched objects working in harmony – this is the stuff of tinkering. Tinkering is, at its most basic, a process that marries play and inquiry. (Banzi 2008, vi–vii)

The role of executive control in tool use

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Gijsbert Stoet^a and Lawrence H. Snyder^b

^aInstitute of Psychological Sciences, University of Leeds, Leeds, LS2 9JT, United Kingdom; ^bDepartment of Anatomy and Neurobiology, Washington University School of Medicine, St. Louis, MO 63110.

g.stoet@leeds.ac.uk <http://volition.leeds.ac.uk/~stoet>
larry@eye-hand.wustl.edu <http://eye-hand.wustl.edu>

Abstract: Comparing cognitive functions between humans and nonhuman primates is helpful for understanding human tool use. We comment on the latest insights from comparative research on executive control functions. Based on our own work, we discuss how even a mental function in which non-human primates outperform humans might have played a key role in the development of tool use.

Research on executive control has rapidly grown over the last 15 years. There has been an increasing conjunction of psychology and neuroscience, not only in brain imaging, but also in single-neuron studies in monkeys (Stoet & Snyder 2004; 2009).

There is general agreement that the functions involved in executive control are used to coordinate and resolve conflicts between more basic processes. There are a number of different mechanisms that are part of the executive control family: (1) *flexibility* – the capacity to switch attention between different tasks; (2) *goal setting* – the capacity to set a goal; (3) *planning*, including initiation and sequencing – the capacity to determine a series of steps necessary to reach a goal; (4) *inhibitory control* – the capacity to suppress distracting or irrelevant information and thoughts; (5) *monitoring* – the capacity to monitor whether actions result in their intended outcome; (6) *adjustment* – the capacity to adjust a course of action even after it has been initiated; and (7) *maintenance* – short-term maintenance of information related to the above functions; for example, goal setting implies that the brain can maintain the goal representation for a certain time.

Vaesen lists only some of these executive functions, namely, inhibitory control, planning, and monitoring. Further, he lists *autocueing*; that is, the capacity to think about things other than those triggered by external stimuli. This use of autocueing

was introduced by Donald (1993; cited by Vaesen), who states that animals “are creatures of conditioning, and cannot ‘think’ except in terms of reacting to the present or immediately past environment” (p. 146). Donald continues: “Humans alone have self-initiated access to memory, or what may be called ‘autocueing’” (p. 146). The difficulty with the concept is that autocueing has not received much attention from other researchers; further, research in the past decade has unequivocally shown that animals actually use internal representations to guide the processing of external stimuli (often referred to as *endogenous control*). Such internal representations can, for example, encode which potential responses are relevant in a certain task context; and such internal representations enable animals to respond in ways that are quite different from the nature of the external stimuli. A number of laboratories have successfully recorded single neurons encoding endogenously activated action and task representations (for a review, see Stoet & Snyder 2009).

What is most important for this commentary, though, is that there is a difference in the abilities of humans and monkeys to switch between endogenously controlled task representations. Extensive research has demonstrated that monkeys are more flexible in rapidly switching between tasks than are humans, who even with long training can still not switch as rapidly as monkeys can (Caselli & Chelazzi 2011; Stoet & Snyder 2003; 2007).

Therefore, by some measures, monkeys outperform humans in mental flexibility. We hypothesize that although humans are at a disadvantage in laboratory task-switching experiments, this limited flexibility might come as an advantage for cognitive development associated with the construction and use of complex tools. (With “complex tools” we mean constructed tools.) Limited mental flexibility supports concentration. We know that humans are good at concentration. The human skill to concentrate develops mostly before the age of 10, although it seems to continue improving during adolescence. Concentration is a necessary component of long-lasting and complex tasks, some of which may have played an important survival role in prehistory, including keeping a fire burning, cooking, hunting a herd of animals for days, and designing and using complex tools. Our ability to concentrate is likely to have co-evolved with and may even have preceded our ability to use tools. Hence, a human’s limited mental flexibility in comparison with a monkey’s may actually be a key element in the causal chain that led to tool use.

Evidence from convergent evolution and causal reasoning suggests that conclusions on human uniqueness may be premature

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Alex H. Taylor^{a,b} and Nicola S. Clayton^a

^aDepartment of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, United Kingdom; ^bDepartment of Psychology, University of Auckland, Private Bag 92019, Auckland, New Zealand.
at564@cam.ac.uk nsc22@cam.ac.uk

Abstract: We agree with Vaesen that there is evidence for cognitive differences between humans and other primates. However, it is too early to draw firm conclusions about the uniqueness of the cognitive mechanisms underlying human tool use. Tests of causal understanding are in their infancy, as is the study of animals more distantly related to humans.

Imagine if we had attempted to define the uniqueness of human social cognition in the year 2000. Investigations examining primate theory of mind had started more than 30 years before.

Despite this, researchers had still not developed experimental paradigms with sufficient ecological validity to thoroughly test the cognitive abilities of primates. We would have concluded that there was a large gap between human and ape social cognition. Hare et al.’s seminal work (2001), where chimpanzees were put into competitive situations rather than cooperative ones, suggests that they can take the perspective of others, though as always, this conclusion is controversial (see Vonk & Povinelli 2006). This work has been built on in the past 10 years, with a number of novel paradigms being designed, where, for example, food must be stolen from others or an ape must infer which food item another individual has eaten (see Call and Tomasello 2008 for review). Because of the high level of behavioral sophistication uncovered by these recent findings, it is now possible to make a case for the gap between human and ape social cognition being far smaller than previously thought (Call and Tomasello 2008; Schmelz et al. 2011; but see Penn & Povinelli 2007b; Penn et al. 2008).

What research on social cognition teaches us is that we have to be careful that our paradigms are sufficiently fine tuned and ecologically valid before drawing strong conclusions.

Is the trap-tube, the current paradigm predominantly used in physical cognition tests (and discussed by Vaesen in the target article), sufficient for drawing conclusions about animals? We suggest not. The trap-tube problem requires an animal to extract food from an apparatus while avoiding a trap in its surface. Slight changes to this test, such as whether an animal is allowed to pull food out of the tube, leads to differences in performance at test, and consequently, the conclusions drawn about what the animal understands (Mulcahy & Call 2006a).

Furthermore, whereas great apes do fail to transfer information between the trap-tube and trap-table tasks while using tools, the same pattern is not seen when they do not need a tool and can instead use their own finger (Seed et al. 2009). It appears, then, that the tool-use aspect of the trap-tube problem creates an additional cognitive load that interferes with problem solving. Most important, adult humans fail to solve a control condition where the trap-tube is inverted (Silva et al. 2005). Given that objects only fall down and not up, an animal that understands why the trap works should treat an upside-down trap as non-functional. In contrast, an animal that has associatively learnt to avoid the trap should continue to avoid it, irrespective of its position in the tube. Adult humans, however, make the striking error, as some animals have done (e.g., Visalberghi & Limongelli 1994), of continuing to avoid the trap when it is in the upside-down position. In contrast, apes, woodpecker finches, and New Caledonian crows do not avoid the trap in an inverted tube (Mulcahy & Call 2006a; Taylor et al. 2009a; 2009b; Tebbich & Bshary 2004).

It seems premature to draw strong conclusions about the absence of inferential causal reasoning abilities from a test that seems to be confounded by tool use and solved incorrectly by adult humans.

Claims about human uniqueness also need to consider evidence from evolutionary convergence. There is no reason why distantly related species facing similar socio-ecological challenges as humans were could not have evolved cognitive mechanisms lacked by species more closely related to humans. Imagine if we had stopped the clock in 1995 and attempted then to draw a line between humans and animals. At that point in time we would have thought that wooden hook tools, experience projection, and planning for tomorrow were capacities exclusive to humans. The reason for this is that few scientists had investigated the possibility that convergent evolution may have led birds to have evolved complex behaviors and cognition.

Today, evidence from work on the *Corvidae* family has shown that New Caledonian crows can manufacture hook tools by sculpting wood (Hunt 1996; Hunt & Gray 2004) and can spontaneously solve multi-stage metatool problems (Taylor et al.

2010), while scrub-jays have been shown to recall the past (Clayton & Dickinson 1998) and plan for tomorrow (Raby et al. 2007). In the social sphere, ravens engage in play caching to identify thieves (Bugnyar et al. 2007), and only scrub-jays with experience of stealing food engage in sophisticated cache-protection strategies (Emery & Clayton 2001). The only non-human evidence for experience projection and hook tool manufacture in the wild comes from corvids, as does the strongest evidence for future planning. Finally, although apes cannot transfer knowledge between the trap-tube and trap-table while using tools, New Caledonian crows can (Taylor et al. 2009a).

Evidence from convergent evolution, therefore, needs to be considered if we are to draw the right conclusions about human uniqueness. As the results from the trap-tube exemplify, failure of the great apes on a cognitive task does not mean that no other animal will succeed. We simply do not yet know if, for example, New Caledonian crows have diagnostic learning. It may seem unlikely that a species with a brain the size of a walnut may be capable of such cognition, but then in 1995, who would have predicted that members of the crow family would manufacture wooden hook tools or plan for the future?

This is not to say that we disagree with attempts to draw conclusions about what cognition is used by humans during tool use, or with the highlighting of how weak the single-factor argument for human uniqueness is. In contrast, summarizing the field to date and suggesting the potential boundaries between humans and other animals in the tool domain will drive and focus research effort on understudied areas, such as diagnostic learning and functional representation. Our cherry-picking mental time travel is simply to highlight that much may change in the future. Who knows where the boundaries will lie in 10 years time.

Cultural intelligence is key to explaining human tool use

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Claudio Tennie and Harriet Over

Max Planck Institute for Evolutionary Anthropology, Leipzig 04013 Germany.
 tennie@eva.mpg.de www.claudiotennie.de
 harriet_over@eva.mpg.de http://www.eva.mpg.de/psycho/staff/over

Abstract: Contrary to Vaesen, we argue that a small number of key traits are sufficient to explain modern human tool use. Here we outline and defend the cultural intelligence (CI) hypothesis. In doing so, we critically re-examine the role of social transmission in explaining human tool use.

Vaesen presents a list of social and cognitive factors that he believes, in concert, explain the differences between human and chimpanzee tool use. We believe that Vaesen is too quick to reject explanations based on a smaller number of key traits; in particular, the traits outlined in the cultural intelligence hypothesis.

Cultural intelligence (CI) can come about in two (potentially complementary) ways. First, culture can enhance intelligence during an individual's lifetime ("ontogenetic" CI; Herrmann et al. 2007; Tomasello 1999). The ontogenetic CI hypothesis postulates that growing up in a culturally rich environment enables children to develop cognitive skills they would not otherwise have done (Moll & Tomasello 2007). According to this perspective, human-unique forms of social learning and teaching are responsible for qualitative changes in cognition – including changes in the ways in which we use tools. Therefore, at least some of the factors that Vaesen identifies as *causes* of human

tool use are, in fact, *effects* of growing up in rich cultural environments.

Second, culture can play a role in the evolution of cognition across generations ("phylogenetic" CI; see also van Schaik & Pradhan 2003). Much less is known about this form of cultural intelligence. However, van Schaik & Pradhan (2003) modeled the co-evolution of culture and innovations and found that "high intelligence will often be a by-product of selection on abilities for socially biased learning." In other words, selection pressure for better social learning leads *indirectly* to the evolution of individual learning (and not vice versa).

In defense of his claims, Vaesen argues that as culture became more complex, greater intelligence was needed in order to deal with increasingly sophisticated cultural artifacts. However, this neglects the possibility that culture positively impacts on intelligence – as posed by the two CI hypotheses. In support of this perspective, Enquist et al. (2008) modeled cultural accumulation and showed that culture would level off unless faithful forms of social transmission impact on innovation levels. As culture has increased exponentially in modern humans, the most plausible view is that culture and intelligence form a feed-forward loop.

So far we have suggested that cumulative culture explains human intelligence in general, and sophisticated forms of tool use in particular. What then explains the existence of cumulative culture? We believe that the answer lies in species-unique forms of social learning and teaching.

Vaesen identifies a number of potential differences between social learning in humans and in chimpanzees. Although these differences may be accurate, we believe that the most basic differences between human and chimpanzee social learning lie elsewhere. Below we outline our alternate account of social learning in chimpanzees and compare it with the case of human children.

After critically reviewing the available evidence on social learning in chimpanzees, Tennie et al. (2009) argued that chimpanzee cultures are best described as serial reinventions across multiple generations. Social learning can still play some role in explaining the distribution of behaviors over time and space (e.g., Whiten et al. 1999), as it can increase the chance of reinvention. Social learning could even be responsible for cases in which the best target for a particular behavior is found and maintained over time (e.g., the whereabouts of the most bountiful feeding place). But the form that chimpanzee behaviors (including these "cultures") take is most strongly determined by biological and ecological factors. This account is supported by evidence suggesting that if chimpanzees copy behavioral forms (i.e., imitate) in the absence of training, then they do so rarely and/or not very precisely (Tennie et al. 2009; Whiten et al. 2009). In addition to this, teaching is virtually absent in chimpanzees (although see Boesch 1991). Without teaching, and with imitation severely limited, chimpanzees lack the transmission fidelity necessary to sustain true cumulative culture (where the form of behavior is transmitted). In turn, ontogenetic CI in chimpanzees (at least in the wild) is probably severely limited.

In contrast to social learning in chimpanzees, human social learning is typified by faithful transmission. Human children often imitate the specific actions of a model. Indeed, they do so even when it results in less efficient performance on their part (Nagell et al. 1993) and when they have been explicitly instructed not to (Lyons et al. 2007). This faithful transmission is at least partially the result of the social motivations and pressure underlying imitation (Over & Carpenter 2011). In contrast to chimpanzees, human children experience a strong drive to be like their group members (Nielsen 2009; Nielsen et al. 2008; Over & Carpenter 2009). This motivation can lead children to produce faithful copies of modeled acts even when it appears irrational to do so. Furthermore, humans often experience social pressure to imitate in particular ways. One form of social pressure is teaching. Gergely and Csibra (2006) have shown that even infants are sensitive to teaching cues and that they copy actions more

precisely when teaching cues are present. Social pressure to imitate can also come from the group in general. Haun and Tomasello (2011) have recently demonstrated that preschool children conform to the behavior of their peers and that they do so more in public than in private. Evidence from Rakoczy et al. (2008) suggests that not only do children experience social pressure; they exert it on those around them by enforcing social norms.

Thus, in contrast to Vaesen, we emphasize that a small number of key factors (e.g., imitation and teaching) render human culture a more social enterprise than is chimpanzee culture. Over time, these factors have played a causal role in producing qualitative changes in human cognition, including in the ways we use tools.

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Neurocognitive anthropology: What are the options?

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Guy Vingerhoets

Laboratory for Neuropsychology, Ghent University, B-9000 Ghent, Belgium.
guy.vingerhoets@ugent.be

Abstract: Investigation of the cerebral organization of cognition in modern humans may serve as a tool for a better understanding of the evolutionary origins of our unique cognitive abilities. This commentary suggests three approaches that may serve this purpose: (1) cross-task neural overlap, referred to by Vaesen; but also (2) co-lateralization of asymmetric cognitive functions and (3) cross-functional (effective) connectivity.

On several occasions in his systematic comparison, Vaesen refers to neuroscientific data to make his argument. In some instances, he underlines the absence of certain functional regions in the brains of non-human primates that are relevant for tool manipulation and production (Orban et al. 2006). In other sections the author points to the human recruitment of the same specialized cortical regions during different tasks of complex motor behavior such as speech or tool manipulation (Higuchi et al. 2009; Stout et al. 2008). The latter neuroscientific findings are taken as evidence for a common origin of tool use and language.

The use of neuroimaging and neurobehavioral research to speculate on evolutionary theories of cognition maybe tempting, but for the moment the available information is limited. I suggest that there are three major observations that can be employed in the discussion of neurocognitive evolution in humans: (1) neural overlap, (2) co-lateralization, and (3) cross-functional (effective) connectivity.

Cross-task neural overlap, or *neurofunctional overlap*, refers to the observation that a single brain region is recruited by different cognitive tasks. In neuropsychological studies, neurofunctional overlap is hinted at by the frequent co-occurrence of cognitive deficits, such as aphasia with apraxia or finger agnosia with acalculia; but lesion research provides only limited spatial resolution. Neuroimaging sparked a much more detailed investigation of the brain's functional organization, including clear cross-task activation in brain regions that can be measured at the 2–4 mm scale. Increased spatial resolution also allowed for a more detailed description of the match of cross-task neural overlap (*overlap correspondence*), although I'm unaware of systematic studies using this approach. The detection of overlapping neurocognitive circuits in specific cortical locations has been interpreted in terms of a functional and even evolutionary link, for example, between spatial and numerical processing (Hubbard

et al. 2005; Walsh 2003) or between language and tool use (Arbib 2005; Higuchi et al. 2009).

The question remains whether overlapping neural responses reflect activation of the same or different neuronal populations. Separate neuronal populations may be interleaved in the same cortical area on a spatial scale below the resolution of conventional fMRI, in which case the corresponding neural circuits may function independently, yet show co-morbidity when this region gets damaged or disrupted. Despite this caveat, we may assume that the neural network activated by a given cognitive function is not randomly distributed over the cortex, but that it engages regions that are of strategic relevance for that function given its connections with other regions. Co-activation of the same region by different cognitive tasks therefore at least suggests a strategic similarity in the recruitment of a specific cortical area with its particular connections, that may or may not share neuronal resources. The shared neural localization of certain domain-general skills, such as hierarchical processing, also enticed scholars to theorize on the specificity and chronology of cognitive evolution (Arbib 2005). For the time being, these valuable hypotheses remain to be tested.

Co-lateralization is defined here as the covariance in the side and degree of hemispheric preference of two cognitive functions. Although many functions are asymmetrically represented in the brain, similarity in hemispheric preference as such is generally not considered to reflect a specific functional link, and there exists remarkably little research on the strength of lateralization within, let alone across, cognitively induced neural activation patterns (Pinel & Dehaene 2010). Significant correlations in the degree of asymmetric activation on sites of neural overlap would strengthen claims of biological association between cognitive functions.

A potentially very interesting source of information may be found in people with atypical language lateralization, such as in some extreme left-handers or in patients who suffered early brain damage. In these individuals it is possible to investigate how the atypical language dominance impacts on other lateralized cognitive abilities (Kroliczak et al. 2011). Recently, we compared a group of atypical language-dominant volunteers with a matched group showing typical language dominance on a tool-pantomiming paradigm while undergoing fMRI. In the group with atypical right language dominance, all individuals also demonstrated atypical right-hemispheric preference for praxis. Activation patterns for the language and praxis tasks revealed neural overlap in five cortical regions that showed highly correlated lateralization indices within and across tasks (Vingerhoets et al., in press).

So far, my arguments focus on the characteristics and interactions of the neural responses induced by different cognitive functions. Similarities in location and co-asymmetry should be supplemented by behavioral evidence of a link between cognitive traits. If two cognitive functions share an evolutionary origin, it is plausible to assume that they exhibit a functional bond over and above a common reliance on central resources such as attention and working memory. If, for example, tool use and linguistic tasks activate Broca's area (neural overlap) because they both require hierarchical structuring (underlying cognitive process), then we might expect behavioral interference between tool use and language tasks that manipulate hierarchical complexity.

Statistical dependencies in performance or neural activity only suggest a functional relation between cognitive traits or neural units, they do not entail causal information. Over the last years, several methods have been devised to investigate *effective (causal) brain connectivity* (Rubinov & Sporns 2010). In view of evolutionary queries, directional effects are of importance, as they may hint at the temporal order of cognitive evolution. Similarities in the directional interactions of networks of related cognitive functions and causal effects of cross-task interference may help elucidate the chronological sequence of

neurocognitive evolution, such as the link between gestures and speech to explain the evolution of language.

I conclude that neuroscientific research on the cerebral organization of cognitive function in modern humans may contribute to unraveling the evolutionary trace of unique abilities such as tool use, language, and numerical cognition. Available methods for this endeavor include (1) detailed analysis of the neural overlap of activity patterns elicited by allied cognitive functions, (2) investigation of the correlation of co-lateralization in direction and degree across cognitive abilities that have an asymmetric hemispheric representation, and (3) comparison of the causal interactions in the neural networks of related cognitive functions and their cross-functional interference.

Motor planning in primates

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Daniel J. Weiss,^a Kate M. Chapman,^b Jason D. Wark,^c and David A. Rosenbaum^d

^{a,b,d}Department of Psychology and ^aProgram in Linguistics, The Pennsylvania State University, University Park, PA 16802; ^cDepartment of Biology, Case Western Reserve University, Cleveland, OH 44106.

djw21@psu.edu kmc385@psu.edu

jason.wark@case.edu dar12@psu.edu

Abstract: Vaesen asks whether goal maintenance and planning ahead are critical for innovative tool use. We suggest that these aptitudes may have an evolutionary foundation in motor planning abilities that span all primate species. Anticipatory effects evidenced in the reaching behaviors of lemurs, tamarins, and rhesus monkeys similarly bear on the evolutionary origins of foresight as it pertains to tool use.

In discussing the impact of executive control on cumulative culture, Vaesen asks whether goal maintenance and planning are crucial for innovative acts – in particular, for innovative acts involving tool use. In this connection, we point to our work on goal maintenance and planning in two groups of nonhuman primates – cotton-top tamarin monkeys (Weiss & Wark 2009; Weiss et al. 2007) and lemurs (Chapman et al. 2010). The work we describe, as well as other research by us and others on anticipatory effects in reaching and grasping by humans (for reviews, see Rosenbaum 2010; Rosenbaum et al. 2006), may be unknown to Vaesen. Our aim in this commentary is to draw attention to this research, hoping that doing so will provide more tools with which Vaesen can evaluate and develop his hypothesis.

We have demonstrated that cotton-top tamarin monkeys (Fig. 1a) and lemurs (Fig. 1b) show a surprising level of goal maintenance and planning in a behavioral context. Our investigations reveal that these species spontaneously alter their object grasps depending on what they plan to do with the objects.

In these studies, the object to be moved was a cup with a piece of food stuck inside its bowl. The cup was positioned in a way that required manipulation of the cup to get the food out. The animals were allowed to interact with the cups as they pleased. Therefore, they could freely choose a canonical thumb-up initial posture followed by a non-canonical thumb-down posture, or they could freely choose a non-canonical thumb-down initial posture followed by a canonical thumb-up posture. These animals, like humans (Rosenbaum et al. 1990), chose the latter course of action. They adopted the non-canonical initial posture when grasping the cups to be inverted, thereby permitting the more canonical posture at the end of the cup rotation. The final thumb-up posture permitted greater control during the food extraction phase.

The pictures shown in Figure 1 are not rare instances of behavior, culled from video frames to finally find the poses we wanted. The pictures in Figure 1 illustrate behaviors that were reliably elicited whenever the cup needed to be turned to permit food

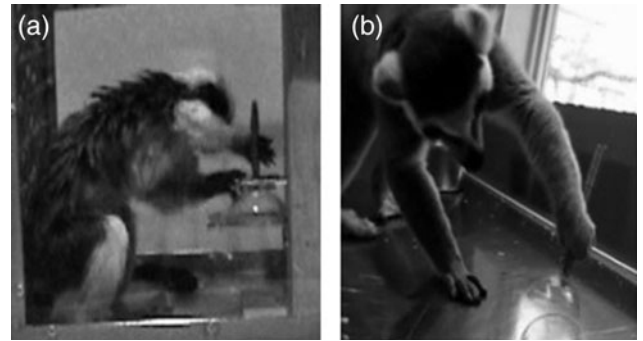


Figure 1 (Weiss). In (a), a cotton-top tamarin (*Saguinus oedipus*) grasps the stem of a cup (a plastic champagne glass with its base removed) to pull it from an apparatus and extract a marshmallow stuck in the cup's bottom. The tamarin uses a thumb-down grasp that permits a subsequent thumb-up grasp once the cup is pulled out and inverted (not shown). In (b), a ring-tailed lemur (*Lemur catta*) uses a thumb-down grasp to turn over a free-standing plastic champagne glass with a raisin affixed to the bottom of the bowl. Sources: (a) Weiss et al. 2007 (Courtesy of Sage Publications), (b) Chapman et al. 2010 (Courtesy of The American Psychological Association).

extraction. When the cup did not need to be turned, the animals adopted canonical thumb-up postures right from the start. The statistics from the carefully controlled studies we did to test the hypothesis that the animals plan ahead supported this claim. On this basis, we concluded that the evolutionary foundation of human motor planning abilities as they relate to tool use are likely shared across all primate species. The latter inference is further supported by similar research with Old World monkeys (Nelson et al. 2010).

Vaesen is interested in behaviors that take longer to complete than the ones we have described here, so he could say we are focusing on too narrow a slice of behavior. Still, it has been argued that short-span motor abilities provide a scaffold for the evolution of planning and goal maintenance over longer durations. One proposal is that the cognitive capacities underlying anticipatory motor planning in reaching and grasping provide a sufficient condition for the development of tool use (Johnson-Frey 2004). We believe, contrary to Johnson-Frey, that such cognitive capacities provide a necessary but not sufficient condition for tool use. Our reason for this alternative view is that tamarins and lemurs do not use tools in the wild or in captivity, at least as far as we know, yet they show the anticipatory motor planning abilities needed to turn cups in ways that afford maximal control during food extraction. The underlying cognitive abilities indexed by our tasks require an appreciation of means-end relationships as well as an ability to inhibit the deployment of canonical postures in the service of better later postures. Our appreciation of these facts leaves us skeptical of Vaesen's claim that humans possess unique abilities for inhibition and foresight.

A last thought: In his discussion of foresight in the context of prospective planning of action sequences (sect. 12.2), Vaesen differentiates between novel solutions and action routines. We question whether that distinction properly distinguishes humans from non-human animals. The nonhuman primates in our studies found novel solutions for the food extraction problems they faced. They had minimal experience with cups, yet they spontaneously adopted non-canonical grasps when presented with inverted cups, even in first trials. If foresight requires novel solutions to problems, as Vaesen asserts, then the behaviors we have described provide evidence for prospective planning and foresight in non-tool-using animals.

Author's Response

From individual cognition to populational culture

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Krist Vaesen

Philosophy & Ethics, School of Innovation Sciences, Eindhoven University of Technology, 5612 AZ Eindhoven, The Netherlands.

k.vaesen@tue.nl <http://home.ieis.tue.nl/kvaesen>

Abstract: In my response to the commentaries from a collection of esteemed researchers, I reassess and eventually find largely intact my claim that human tool use evidences higher social and non-social cognitive ability. Nonetheless, I concede that my examination of individual-level cognitive traits does not offer a full explanation of cumulative culture yet. For that, one needs to incorporate them into population-dynamic models of cultural evolution. I briefly describe my current and future work on this.

Let me start with a somewhat obvious caveat. Given the overwhelming amount of feedback I received, my response will miss out on numerous topics worthy of further discussion. I regret not being able to fully honor the careful thought and work put into each commentary, and I sincerely hope my response does not distort matters too much.

Below I do four things. First, I defend my methodology against three points of critique (sect. R1). Second, I reassess the nine cognitive capacities of the target article in light of the open peer commentary (sects. R2–R8). I conclude that my original conclusion stands firm: Human tool use still reflects a profound discontinuity between us and chimps in matters of social and non-social wit. Third, I briefly take up a topic underplayed in the target article, namely, the evolutionary history of the cognitive traits reviewed (sect. R9). Fourth, I reconsider a topic I found underplayed in the commentaries, namely, the question of technological accumulation (sect. R10). I sketch how I am currently incorporating the cognitive assumptions made explicit in the target article into existing population-dynamic models of human cultural evolution; I sketch, thus, how I am making the necessary move from the individual level to the level where cumulative culture must be studied eventually, namely, that of the population.

R1. Methodological notes

R1.1 Why chimpanzees?

In the target article, I justified my narrow focus on humans and chimpanzees primarily on pragmatic grounds (see target article Note 1): For reasons of space, and given the wealth of data on primate tool use, I used chimps, rather than crows, finches, dolphins, otters, or elephants, as a contrast class for humans. Obviously, albeit implicitly, my justification also assumed some argument by ancestry (as **Cachel** observes). In the absence of direct evidence of ancestral states, our closest relatives may serve as, be it imperfect, models for reconstructing human cognitive and technological evolution (McGrew 1993). Finally, my focus on chimpanzees was justified by the second part of the paper, where I attempted to explain the vast

Response/Vaesen: The cognitive bases of human tool use

discrepancy in technological accumulation between us and our closest relatives. The choice for the latter was not coincidental: Chimpanzees follow us on the technological accumulation list, so they offer a natural benchmark for examining which add-ons may account for the technological complexity observed in our lineage.

However, several commentators – most notably **Patterson & Mann**, **Reader & Hrotic**, and **Taylor & Clayton** – question my approach and stress the importance of including data on other (tool-using) animals. Such an extended comparative approach would allow me: (1) to see that none of the nine traits is *necessary* for tool use (Patterson & Mann); (2) to establish more realistic ancestral states (Reader & Hrotic); and (3) to determine the socioecological conditions under which tool use emerges (Patterson & Mann, Reader & Hrotic, Taylor & Clayton).

Although there is much to be said in favor of the two last points, let me first briefly dismiss point one. **Patterson & Mann** attribute to me the claim that I have identified a set of *necessary conditions for tool use*. As the title of the target article suggests, however, my actual concern was explaining *human* tool use (rather than tool use, full stop). Moreover, as stated in the abstract, my aim was to identify traits that *could help explain why technological accumulation evolved so markedly in humans, and so modestly in the great apes*. In sum, identifying necessary conditions for tool use was not one of the objectives of the target article.

Regarding the second point, **Reader & Hrotic** remark that contemporary chimpanzees likely misrepresent ancestral states. Differences between us and chimpanzees may be due to loss of traits in chimpanzees, rather than – as I assume – independent evolution of traits in us. Therefore, to decide which course evolution has taken (loss of the trait in chimps versus its acquisition by us) for any trait, the ancestral state must be established, which requires incorporating additional species. In this regard, Reader & Hrotic cite as a fruitful example a study by de Kort and Clayton (2006), who use phylogenetic analysis to reconstruct the ancestral state for caching behavior in corvids. de Kort & Clayton's methodology seems promising indeed. At this point, however, I have two worries. First, when it concerns a behavioral trait as cumulative culture, phylogenetic analyses will not be very helpful, given the apparent lack of the trait in other primate taxa – except perhaps in chimpanzees. Second, supposing one is interested in more basic traits (e.g., function representation, causal reasoning, theory of mind), phylogenetic analysis allows one to reconstruct ancestral states only on the condition that the trait in question has been properly diagnosed in all taxa under consideration. Reader & Hrotic's favored approach therefore still calls for carefully executed comparative work. The target article has done some of that necessary preparatory work, even if just for two species (i.e., humans and chimps).

Third, **Patterson & Mann**, **Reader & Hrotic**, and **Taylor & Clayton** correctly point out that the inclusion of other taxa may shed light on the socioecological conditions under which tool use emerges. For example, the fact that chimpanzees do not exhibit a certain trait may be due not so much to the absence of the trait as to its being unexpressed under current ecological conditions (for a similar point, see also **Nonaka**). Comparisons with

other taxa may prove valuable here – especially given the declining number of habitats occupied by wild chimpanzees. But unfortunately, inter-taxa comparisons will not suffice either. Much of what is said to be known about human cognition is based on studies of Westerners (see Note 44; see also Haun et al. 2006; Henrich et al. 2010). To rule out that their behavior was prompted by their specific ecological and/or cultural niche, many more cross-cultural studies have to be performed. In other words, in addition to inter-taxa comparisons, we also need *intra*-taxa comparisons, within our species in particular. Therefore I am even more skeptical than Taylor & Clayton are: I do not just believe that the conclusions of my paper may be premature, I am certain that they are. Still, they are as good as they can get given the present state of the field.

R1.2 Why not the environment?

Some commentators argue that the environment not just passively prompts certain behaviors, as just mentioned, but often plays a more active role. The environment, both natural and artificial, may scaffold cognition (**Jeffares** and **Blitzer & Huebner**). Instead of being localized exclusively in the head, cognition is an “intertwining of neural, bodily, and [external] material resources” (**Malafouris**). This kind of “ecological” approach to cognition is virtually absent in my story – much to the regret of Jeffares, Blitzer & Huebner, and Malafouris.

The reason for this omission has nothing to do with methodological prejudice, as I am very sympathetic to the movement set afoot by Andy Clark and others (see e.g., Clark et al., forthcoming). The omission is rather due to a lack of comparative evidence. To date, research on nonhuman species still works within an internalist mindset. Consequently, little to nothing is known about the scaffolds of the chimpanzee mind. Even our understanding of the importance of the external world in human cognitive processes is limited. Consider an example by **Jeffares**. He argues that the idea of a tool need not be internally represented, because existing tools can take over this role. The thought is that existing tools can be used as a template for the production of new ones; and this is presented as a clever strategy of using the environment to store ideas that we otherwise would need to store internally. However, before we accept that this form of scaffolding decreases rather than increases cognitive demands, Jeffares must show empirically that it does not depend on, for example: a capacity to conceptualize the existing tool as being for a particular purpose; a capacity for inferential reasoning to infer a production process from the tool’s functional properties; or a capacity for analogical reasoning to appreciate that the principles governing the template also (should) govern the copy. Relying on behavioral templates (also discussed by Jeffares) seems a more elegant strategy; but this was covered in the target article’s section on social learning.

R1.3 Why (only one sort of) neurology?

The claims of **Malafouris**, **Jeffares**, and **Blitzer & Huebner** raise another methodological issue. If the environment actively shapes cognition and, relatedly, brains are profoundly plastic, what should we make of

the neurological evidence in the target article? Am I not assuming too much that cognitive traits are “hardwired” (Jeffares’s word), each corresponding to a piece of “phylogenetically novel wetware” (Blitzer & Huebner’s words)?

I think I am not. The target article points to only one (!) suggestion of a humanique cortical specialization for a trait (my discussion of Orban et al. 2006; Stout & Chaminade 2007). Apart from a suggestion of neural overlap between language and tool use in human BA44 (my discussion of Higuchi et al. 2009), everywhere else neurological evidence concerns the recruitment of large brain structures: (pre)frontal cortex, (pre)motor cortex, parietal cortex, parietotemporal cortex, (non)lateralized distributed networks. Evidently, I do not believe, and did not suggest, that these large chunks of brain evolved specifically for the cognitive task in question. Finding out how cognitive labor is preferentially distributed across the brain does not entail a commitment to nativism nor blank-slateism.

I agree, however, with **Vingerhoets**’ methodological concerns. He remarks that I cover only one type of neuroscientific data used for speculating on the evolution of cognition, namely, data from cross-task neural overlap (in my discussion of Higuchi et al. 2009), thereby ignoring two alternatives, namely, co-lateralization and cross-functional connectivity analyses. His point is well taken that these may be or may become just as useful.

R2. Hand-eye coordination

In her commentary, **Dounskaia** conjectures that differences in human and nonhuman primate motor control may contribute substantially to the uniqueness of human tool use. She offers compelling evidence for the idea that some limb movements require much more cognitive effort than others do. The ability to perform accurately even these more effortful movements, Dounskaia suggests, may have enabled humans to deploy much more sophisticated tools.

At present, however, she lacks proper comparative evidence. Although it seems true that the repertoire of human motor actions greatly exceeds that of nonhuman primates, **Dounskaia** still needs to establish that this difference is attributable to a difference in the ability to perform more complex gestures. Chimpanzees may have such an ability but not, say, the creativity to exploit it. In this respect, Dounskaia’s argument may benefit from an observation made in the target article. Chimpanzees have less neural tissue devoted to their locomotor muscles (Walker 2009), so that they must recruit larger numbers of motor units at once. This limits their ability for fine motor control, and arguably, the level of movement complexity they can achieve. Regardless, I certainly find Dounskaia’s leading joint hypothesis promising enough to warrant further research, especially in a comparative setting.

Jacquet, Tessari, Binkofski, & Borghi (Jacquet et al.) argue that human tool use does not need to involve the high-level cognitive skills I discuss, as it may be based on much simpler detection systems. Their primary example is affordance perception: Humans are able to recognize manipulation opportunities, “matching the perceived physical features of objects and the agent’s

biomechanical architecture, *goals, plans, values, beliefs, and past experiences*" (italics added). The text in italics not only shows that Jacquet et al. deviate substantially from J. J. Gibson's original formulation of affordances, it threatens to undermine their argument.

J. J. Gibson (1979) indeed introduced affordance perception as a fairly low-level process. Affordance perception referred to an animal's unreflective capacity to discern in the environment possibilities for action, only constrained by its own physical constitution (e.g., that a rake can be grasped; that it *affords* grasping). As such, affordance perception was a capacity also exhibited by animals that did not have *goals, plans, values, or beliefs*. Goals, plans, values and beliefs were added as constraints only in the work of Norman (1988), whose research primarily concerned humans. Norman's reformulation (which **Jacquet et al.** adopt) is not merely terminological. It implies a shift of focus from direct, low-level perception to indirect perception; that is, perception dependent on interpretation and background knowledge. With an example of Norman's, a knob on a refrigerator may be directly perceived as turnable (per Gibson), but one needs a Normanian conceptual model to perceive it as "to-lower-the-temperature-with-able." Likewise, the "Delete" key on a keyboard may be directly perceived as pressable (per Gibson), but one needs a Normanian conceptual model to perceive it as "to-delete-a-character-with-able."

In sum, **Jacquet et al.** face a dilemma. They either endorse a Normanian notion of affordance, thereby making affordance perception a conceptually rich, and fairly demanding, enterprise (as the target article's section on function representation suggested). Or they pursue a Gibsonian account, at the cost of being unable to explain the humanlike ways in which humans navigate their humanly engineered environments.

R3. Body schema plasticity

Arbib and **Longo & Serino** find my conclusions regarding body schema plasticity unconvincing. According to these commentators, the question is not so much whether nonhuman primates *can* extend their body schema, but whether this happens as flexibly and rapidly as in humans. That question, **Arbib** and **Longo & Serino** believe, should be answered with a clear "no."

I remain unconvinced. Let me start with **Arbib**. **Arbib** refers to a study by **Arbib et al.** (2009) in support of his argument. Now, **Arbib** and colleagues observe the facility humans have in tool use, and infer from that fact that human body schema plasticity has unique properties (p. 458). But this does not follow. Tool use in nonhuman primates may be cumbersome due to numerous other reasons (limited grasp of causality, poor hand-eye coordination, and so forth). To be fair, this point is conceded a bit further in the text, when the authors suggest how *future* studies could establish the difference between humans and nonhuman primates as regards body schema plasticity. But in and of itself, the paper by **Arbib et al.** (2009) does not seem to provide the necessary evidence.

Longo & Serino's comparative evidence is wanting, too. They refer to a study by **Quallo et al.** (2009) in support of the idea that the body schema of monkeys is fairly rigid. **Quallo** and colleagues indeed demonstrate

fairly persistent increases of gray matter in, among other places, the intraparietal sulcus of macaques that were trained to use a tool. Still, what **Longo & Serino** do not mention is that similar increases were observed in human volunteers learning to juggle (reported by **Draganski & May** 2008, as cited by **Quallo et al.** 2009).

R4. Causal reasoning

By and large, commentators propose three useful extensions to the target article's section on causal reasoning.

First, that the section would have benefited from discussions of experimental paradigms other than trap-tube tasks (**Taylor & Clayton**) and of experimental paradigms other than those presented in the target article's Figure 1 (**Cachel**). In light of the study by **Seed et al.** (2009), **Taylor & Clayton** remark, for example (as I do), that the reason for the modest performance of chimpanzees in trap-tube tasks may be demands posed by the tool aspect of the task; that is, that the extra cognitive load may block the animals' ability to properly assess the task's causal set-up. Other changes, such as allowing animals to push rather than pull the food item in the tube, may also yield different results (**Mulcahy & Call** 2006a). In sum, one should not draw too strong conclusions about great ape causal cognition from only one, potentially confounded test. Perhaps **Taylor & Clayton** are right that trap-tubes received too much attention in my paper. On the other hand, I do shortly describe three other of **Povinelli's** (2000) seminal experiments (see also Fig. 1): the flimsy-tool problem, the inverted-rake problem, and the table-trap problem. Chimpanzees performed poorly on these tests too; and, as **Cachel** is right to point out, **Povinelli's** book describes even more experiments, which together are at the very least suggestive of the fact that chimpanzees' grasp of causality is rather modest. There is little follow-up research based on these other paradigms, which is rather unfortunate indeed.

Second, **Penn, Holyoak, & Povinelli (Penn et al.)** miss a treatment of non-mechanism approaches to causal understanding. Indeed, in the target article I suggested that causal understanding requires the cognizer to infer a mechanism that relates the cause to the effect. This mechanism account is associated most prominently with **Ahn** and colleagues (**Ahn & Kalish** 2000; **Ahn et al.** 1995) and is fairly intellectualist:

We suggest that people's beliefs about causal relations include (1) a notion of force or necessity, (2) a belief in a causal process that takes place between a cause and an effect, and (3) a set of more or less elaborated beliefs about the nature of that mechanism, described in theoretical terms. (**Ahn & Kalish** 2000, p. 302)

Penn et al. are right that there are other, less-demanding accounts of causal understanding. For example, **Waldmann** and **Holyoak** (1992; **Waldmann et al.** 1995) argue that human mental representations of cause-effect relations are organized into causal models. Basic causal models include representations of directionality (e.g., the causal arrow between A and B goes from A to B, not the reverse), strength (A impacts strongly/weakly on B), and polarity (A makes B happen versus A prevents B from happening); they typically do *not* refer to the mechanisms

responsible for the said cause-effect relation. A cognizer may know that there exists a strong causal arrow from eating rotten food to diarrhea without appreciating the unobservable underlying mechanisms – say, how bacterial toxins derange the normal bowel flora.

This position clearly conflicts with the view of Ahn & Kalish (2000; with their third point in the quote above in particular), but it can still be made to fit with the idea that chimpanzee causal understanding is limited. Using the terminology of **Penn et al.**, chimpanzees may be able to represent “first-order” causal models, but not “higher-order” ones. That is, whereas chimpanzees may be able to reason about the causal relationships between observable contingencies, they do not generalize these principles into higher-order “intuitive theories” (Penn et al. 2008), which typically refer to unobservable causal properties, such as gravity. Whereas for chimpanzees causal arrows between A and B remain on a perceptual level, no such limitations hold for the human case.

A third extension to my discussion of causal reasoning is offered by **Orban & Rizzolatti**, and it concerns a putative neuronal basis for the enhanced grasp of causality observed in humans. They refer to a study by Peeters et al. (2009), who found evidence that a specific sector of left inferior parietal lobule (i.e., anterior supramarginal gyrus, or aSMG) was activated in humans during the observation of tool use, but not in monkeys. Importantly, aSMG is not involved in understanding causal relationships in general; it codes tool actions in terms of the causal relationship between the intended use of the tool and the result obtained by using it. This study is interesting for at least two reasons. First, it may resolve some of the uncertainties regarding production-level representations of tool use skills (see Note 18). That is, aSMG may support larger motor repertoires, thereby supporting larger toolkits. Second, with the proviso that Peeters and colleagues studied rhesus monkeys and not chimpanzees, aSMG may perhaps explain why, as observed above, chimpanzees fail the trap-tube task when tools are implied. To wit, human aSMG would provide the computational power needed to overcome the additional demands posed by the tool aspect of the task.

R5. Function representation

Commentaries on the target article’s section on function representation reveal some confusion as regards the notion of function. Several authors (i.e., **Blitzer & Huebner**; **Osvath, Persson, & Gärdenfors** [**Osvath et al.**]; **Patterson & Mann**; **Penn et al.**) argue that monkeys and apes are able to form functional representations, because these animals are capable of distinguishing between “functional” and “non-functional” tools (see e.g., Osvath & Osvath 2008) and are able to distinguish between “functionally” relevant (e.g., the shape of a rake) and “functionally” irrelevant (e.g., the color of the rake) properties of a tool (see e.g., Santos et al. 2003). Where these authors refer to functionality, I would speak rather of causal efficacy: An ape may appreciate that a certain rake is causally efficacious for food retrieval, but this does not mean it attributes to the rake that function. For that to happen, the ape must somehow conceive the rake as being for the said purpose. To get a feeling for

the distinction: I may appreciate that a cup is causally efficacious to be used as a paperweight without attributing to it that particular function.

How could we know whether nonhuman primates form such permanent function representations? One way is to see whether they stick to a tool when functionally equivalent alternatives become available. The target article referred to a study by Cummins-Sebree and Frigaszy (2005) suggesting that they do not. **Patterson & Mann**, however, are right to point out that Whiten et al. (2005) may count as counter-evidence. In that study, chimpanzees continued to use a tool for its function even in the presence of functional equivalents.

Second, evidence of re-use of tools would support the idea of stable function attributions. I suggested that reports of tool re-use are scarce, with the exception of a study by Carvalho et al. (2009). Thanks to **Blitzer & Huebner**, I can here add a study by Sanz and Morgan (2010).

Finally, observations of functional fixedness would indicate that tools are conceptualized as being for one particular purpose rather than another. The target article suggested that functional fixedness was a humanique phenomenon. Yet, a study that was not available at the time of writing the paper – performed by Hanus et al. (2011) and pointed out to me by **Patterson & Mann** and **Rizzo** – may prove me wrong. Hanus and colleagues indeed provide suggestive evidence for functional fixedness in chimps. What remains to be seen, however, is whether chimpanzees’ fixedness attests to a conceptual system storing functional information (as in humans), rather than being the result of associative learning, where repeated exposure to a tool’s function blocks alternative, more creative uses.

For all three diagnostic features, it appears, commentators have raised quite forceful counter-arguments. Contrary to what I stated in the target article, it may therefore well be that nonhuman primates attach particular functions to particular objects. Whether they hereby rely on a conceptual system storing functional knowledge remains uncertain, as well as the question of what difference that would make.

Incidentally, **Gainotti** makes an intriguing remark about the conceptual system implied in human functional representation. He observes that tool concepts are typically represented unilaterally in a left-sided fronto-parietal network, because of their close link to actions, which are typically performed by the contra-lateral right hand. Living category concepts (e.g., about animals, plants), by contrast, rely more on visual data and are therefore stored in a bilateral network comprising rostral and ventral parts of the temporal lobes.

R6. Executive control

The target article subdivides executive control into mechanisms of monitoring online action, inhibition, foresight, and autocuing. Commentaries primarily take issue with my treatment of the latter two. **Weiss, Chapman, Wark, & Rosenbaum** (**Weiss et al.**) and **Osvath et al.** challenge my views concerning foresight; **Stoet & Snyder** add considerable refinement to my discussion of autocuing. Finally, the commentary by **Beck, Chappell**,

Apperly, & Cutting (Beck et al.) sheds new light on the role that executive control plays in tool innovation. Let me consider each commentary in turn.

Weiss et al. describe research evidencing anticipatory effects in the reaching behaviors of lemurs, tamarins, and rhesus monkeys. These monkeys were shown to prefer non-canonical hand postures in preparation of a subsequent grasping task. Such behavior, the authors point out, indicates some form of planning ahead. I agree. Still, the behavioral evidence does not meet the standards of foresight set in the target article; that is, it does not involve the formation of long-term goals, nor the prospection of needs other than those experienced in the immediate present. I certainly do not mean to downplay the significance of more basic forms of foresight, as those described by Weiss and colleagues. I believe indeed that these may increase our understanding of the evolution of planning and goal maintenance. To press the issue, however, the target article focused on those types of foresight where discrepancies between humans and nonhuman primates might be most apparent. In a search for discontinuities, I think, such an approach is justified. Nonetheless, I admit that to do right to the short-span motor-planning abilities discussed by Weiss et al., one would need to start with a much finer grained subdivision of executive control than the fourfold subdivision I deployed.

According to **Osvath et al.**, the target article misinterprets a study on great ape foresight by Osvath and Osvath (2008). They argue that I dismiss Osvath and Osvath's results too readily as a consequence of associative learning rather than as a consequence of foresight. In light of a paper by Osvath (2010) that Osvath et al. refer me to, I am willing to concede (again) that the experiments by Osvath and Osvath properly control for associative learning. Yet, my other observation still holds: The results of Osvath and Osvath (2008) may be due to inhibitory strength rather than to forethought – at least if we evaluate their experiments by the standards they set themselves:

[T]o ensure that the self-control setting offers competition between *different desires*, the stimuli in the choice situation must represent different kinds of rewards. The immediate reward must be qualitatively distinct from the future one; otherwise the outcome of the choice would only be an expression of inhibitory strength and not of the ability to distinguish the future oriented drive from the present oriented one. (p. 664, italics added)

The rewards that Osvath and Osvath believe to be tapping “different desires” are a grape and half a liter of rosehip berry soup. **Osvath et al.** agree, and they justify Osvath and Osvath's assumption based on the idea that “eating and drinking are dissimilar activities, with different physiological outcomes.” This may be a salient distinction when the comparison concerns, say, eating a grape and drinking water, but much less so when it concerns eating a grape and drinking rosehip berry soup. These latter activities have at least one target in common: a craving for fruity sugars. On this construal, subjects in the experiments of Osvath and Osvath may well have exercised inhibitory strength, but not have anticipated a drive different from the present one.

Stoet & Snyder refer to a set of recent and fascinating studies that demonstrate endogenous control – or as I called it, autocuing – in monkeys. These animals appear

capable of letting internal representations act as cues for their behavior, rather than merely reacting on external stimuli. The reason why I believe autocuing to be relevant for tool use differs from that of Stoet & Snyder. My thought, which does not conflict with the observations of Stoet & Snyder, is that it allows deliberate practice, needed to achieve skill in complex tool use. Stoet & Snyder also see a link with skill complexity, but spell this out in terms of enhanced concentration in humans. Humans appear less flexible to switch rapidly between endogenously controlled task representations. That, in turn, supports concentration, a necessary component of long-lasting and complex tasks, such as developing skill in complex tool use. Together, Stoet & Snyder's and my proposal make plausible why humans, compared with other primates, seem to be capable of learning so much more intricate tasks-sets.

Lastly, the commentary of **Beck et al.** targets one of the outstanding questions formulated at the end of the target article. There (sect. 12.2.1) I observed that executive control appears critical for innovative tasks, such as solving Tower of London problems, and I asked whether the same would hold for other innovative acts, especially those involving tools. Beck et al. report on evidence that tentatively supports my suggestion. The authors tested human children on a tool innovation task based on Weir et al.'s (2002) wire-bending problem. Children up to 5 years old had great difficulties fashioning a straight piece of wire to make a hook for retrieving a bucket from a vertical tube. Given that the children displayed a proper causal understanding of the task, Beck et al. suggest that the children's poor performance was due to the immaturity of their executive system. It is unclear, however, how much executive control is really needed for solving the wire-bending problem. Prototypical tests of executive function involve multi-step actions (e.g., the Tower of London task, the Six Element Test), where a solution must be planned ahead and kept in mind during each step of the task. No such goal maintenance is implied, it seems, in the single-step wire-bending problem, where the ultimate solution of the task and its execution can run almost in parallel. Future research on the performance of dysexecutive patients on similar single-step and open-ended tasks could perhaps corroborate the hypothesis of Beck et al.

R7. Social learning, teaching, social intelligence

Surprisingly few commentators seem to disagree with my presentation of primate social skills (social learning, teaching, and social intelligence). **Osvath et al.** find my treatment of theory of mind too short – I agree, but referred the reader to the much more detailed discussions by Penn and Povinelli (2007b) and Call and Tomasello (2008). **Moerman** points to the enormous impact of new kinds of social organization on recent technological developments – I fully agree, and consider this topic more fully in section R10. Finally, **Tennie & Over** believe that I too quickly reject explanations based on a small number of social traits. In particular, they make the following two claims: (1) Humanlike forms of social learning and teaching are sufficient to explain cumulative culture; and (2) cumulative culture positively impacts on cognition,

giving rise to many of the non-social cognitive skills discussed in the target article.

In the target article, I provided two arguments that undermine **Tennie & Over**'s first claim: the problem of the Acheulean, and the fact that non-social skills are part and parcel of sophisticated forms of social learning. This may not have convinced **Tennie & Over**. Therefore, let me provide an additional argument, which I draw, quite ironically, from a study referred to by **Tennie & Over** themselves, namely, **Enquist et al. (2008)**.

Tennie & Over invoke that paper in support of their second claim. Indeed, **Enquist** and colleagues show that exponential cultural accumulation requires feed-forward loops between culture and creativity (or "intelligence," as **Tennie & Over** call it). Whereas genetically evolved creativity may produce accumulation at a constant rate, only culturally evolved creativity has the power to yield accelerating accumulation. But what **Tennie & Over** omit to mention is that, according to the very same models of **Enquist** and colleagues, the process of accumulation can get started *only once genetically evolved creativity has evolved*. Genetically evolved creativity, *not* cultural transmission, is the primary genetic bottleneck for cumulative culture:

The evolution of cultural transmission is often considered the main genetic bottleneck for the origin of culture, because natural selection cannot favor cultural transmission without any culture to transmit. Our models suggest that an *increase in individual creativity may have been the first step toward human culture*, because in a population of creative individuals there may be enough non-genetic information to favor the evolution of cultural transmission. (**Enquist et al. 2008**, p. 46, italics added)

Put differently, for **Enquist** and colleagues, cultural transmission is insufficient for sustaining processes of cumulative culture – pace **Tennie & Over**. Incidentally, **Enquist** and colleagues black-box the cognitive skills that make up genetically evolved creativity. In the target article I discerned at least two contenders: a capacity for causal reasoning (sect. 12.1) and enhanced executive control (sect. 12.2; see also **Beck et al.**).

Let me turn to **Tennie & Over**'s second claim. Here the idea is that cultural environments are responsible for qualitative changes in cognitive skills. **Tennie & Over** write: "[A]t least some of the factors that Vaesen identifies as *causes* of human tool use are, in fact, *effects* of growing up in rich cultural environments." This may be right. To have bite, however, **Tennie & Over** need to specify which traits are implied. And evidently, they need to show for every single trait on the list that it is culturally acquired rather than innate. I am prepared to go for either option; but at present, especially in the face of a disheartening scarcity of cross-cultural data, I think it is more honest to admit that the science is not settled yet.

R8. Language

IJzerman & Foroni provide an argument that is structurally similar to the one of **Tennie & Over**. What social learning is for **Tennie & Over**, language is for **IJzerman & Foroni**. That is, **IJzerman & Foroni** argue that I underestimate the role of language in supersizing humans'

cognitive toolkit, and that I thereby overestimate the cognitive discontinuity between chimps and humans.

In response, let me repeat what I did and did not do in the target article. I compared humans and chimps with respect to nine tool-related cognitive skills (including linguistic ability, for that matter), and I found that humans excelled in almost all of them. Thereby, I deliberately bracketed questions of implementation. Our excellence may be hard-wired, culturally acquired (as **Tennie & Over** propose), a side effect of our linguistic ability (as **IJzerman & Foroni** propose), or a bit of all three (see also sections R1.2, R7, and R9). In my opinion, **IJzerman & Foroni** overestimate how much we know about the impact of language on our cognitive toolkit to be able to adjudicate among these four scenarios, but I do not want to press that point. Instead, let me formulate two further critical remarks.

First, to be able to make their argument, **IJzerman & Foroni** must rely on a comparative assessment of the sort that the target article gives. For example, **IJzerman & Foroni** believe that language supersedes human planning abilities and executive control (**Blitzer & Huebner**, by the way, make a similar observation in passing). Such a claim makes sense only if humans have superior planning ability and superior executive control to begin with – indeed, precisely what the target article attempted to show. More generally, one does not need to prove a trait's independence from linguistic ability to be able to judge whether humans have it and how good they are at it.

Second, there is something in **IJzerman & Foroni**'s charges that I cannot help but perceive as a plain inconsistency. The claim that language *supersedes* the human cognitive toolkit at the very least suggests a profound cognitive discontinuity between us and chimps; yet, **IJzerman & Foroni** charge *me* with overestimating the cognitive discontinuity between humans and chimps.

The second strand of comments concerning language comes from **Holloway, Arbib**, and **Barceló-Coblijn & Gomila**. These commentators point out, either implicitly or explicitly, that I have neglected the possibility that tool use and language co-evolved. And indeed, it is rather unfortunate that the target article examined only accounts according to which the evolution of tool use played a causal role in the subsequent evolution of language.

Holloway observes striking similarities between human language and toolmaking. He refers to his seminal paper "Culture: A Human Domain" (1969), where he described the similarities as follows:

[A]lmost any model which describes a language process can also be used to describe tool-making. . . . Both activities are concatenated, both have rigid rules about serialization of unit activities (the grammar, the syntax), both are hierarchical systems of activity (as is any motor activity), and both produce arbitrary configurations which thence become part of the environment, either temporarily or permanently. (p. 401)

Holloway's co-evolutionary thesis appears a bit further on: Tool-making and language are concordant. Selection favored the cognitive structures dependent on brain organization and social structure which resulted in both language and tool-making. (p. 404)

These early ideas clearly resonate in the more recent accounts of **Arbib** and **Barceló-Coblijn & Gomila**. According to **Arbib**, the evolution of complex forms of imitation underwrites the co-evolution of language and tool-making. Complex imitation, here, involves increased

capacities for recognizing and imitating hierarchically structured processes, needed for assembling both words (in the case of language) and actions (in the case of tool-making) into superordinate structures.

Also **Barceló-Coblijn & Gomila** are keen to point out the profound similarities between toolmaking and language. In knotting, in particular, they see a formal structure of similar complexity to a context-sensitive grammar. Tying knots in nets and basketry, for example, cannot be specified as an iterable sequence of steps at the service of a higher-level constructive plan, because “each single operation [e.g., tying one of the knots of the net] is conditional on the state of the rest of the fabric and the physical forces the knot is supposed to resist.”

There is much to be said in favor of the accounts of **Holloway**, **Arbib**, and **Barceló-Coblijn & Gomila**. Still, I have one worry, which is not sufficiently stressed in the target article. Attempts at determining structural commonalities between language and toolmaking are easy prey for charges of arbitrariness. Take **Barceló-Coblijn & Gomila**'s claim that context-sensitive procedures emerged very recently, only with the advent of knotting in *Homo sapiens*. Now, compare this with **Holloway**'s (1969) interpretation of Acheulean toolmaking:

Taking each motor event alone, no one action is complete; *each action depends on the prior one and requires a further one*, and each is dependent in another way on the original plan. In other words, at each point of the action except the last, the piece is not “satisfactory” in structure. Each unit action is meaningless by itself in the sense of the use of the tool; it is meaningful only in the context of the whole completed set of actions culminating in the final product. (p. 402, italics added)

As far as I can tell, **Holloway** here interprets Acheulean toolmaking as a context-sensitive procedure, in which each single blow is conditional on past and future blows. In the absence of a rigorous method for making similarity judgments, it is hard to decide whose interpretation is correct, **Holloway**'s or that of **Barceló-Coblijn & Gomila**. Even an analysis of hierarchical complexity in stone toolmaking as detailed and systematic as that of **Stout** (2011, referred to by **Arbib**) contains a fair amount of arbitrariness (as **Stout** himself admits, p. 1057); attempts to mirror his approach onto (proto)language would only add more of it. Presumably, similarity will keep residing in the eye of the beholder.

R9. Evolutionary issues

Even if one accepts my description of human tool-related cognitive abilities, how did all these abilities evolve? I am glad that so many commentators took up that pertinent question in my stead. Broadly speaking, their hypotheses fall into three groups.

First, **Crabb** endorses the view that human technological ingenuity emerged in response to a process of technological selection. He argues that hominids, unlike other tool-using species, depended on tools for their survival. The increasingly dry and open landscapes made our ancestors extremely vulnerable to attacks by predators; the use of weapons for protection would clearly confer fitness advantage. Subsequent elaborations on these early tools would have provided even more survival benefits, and as such, favor even more cognitive sophistication.

Crabb's hypothesis is reminiscent of, but interestingly different from, earlier technological intelligence hypotheses (for an elegant discussion, see **Byrne** 1997). According to these, tool use skills are favored whenever there is a premium on gains in efficiency with respect to (extractive) foraging; on **Crabb**'s account, in contrast, the premium would initially be on gains in efficiency with respect to protection. What puzzles me, however, is how **Crabb**'s account would accommodate the fact that the earliest known tools (i.e., Oldowan flakes) offer little protection against animal attacks. In this respect, earlier versions of the technological intelligence hypothesis seem to fare much better.

Second, several commentaries endorse some kind of cultural intelligence hypothesis. **Tennie & Over**, as discussed earlier, argue that the evolution of humanlike forms of social learning and teaching subsequently drove the cultural evolution of other tool-related cognitive skills. **Nielsen** expresses a similar view, but adds quite a forceful argument in its favor. He observes that humans are the only species to have a childhood as a life stage, which provides ample opportunities for the acquisition of complex skills – including cognitive skills related to tool use. Finally, the examples of niche construction given by **Blitzer & Huebner**, **Jeffares**, **Nonaka**, and **Arbib** seem consistent with a cultural intelligence hypothesis, although not necessarily of the ontogenetic kind (as the one of **Tennie & Over**).

Third, there is the view that technical and sociocultural cognitive traits co-evolved, in concert with increasing brain size and reflecting a *general* cognitive ability. On this account – endorsed by **Reader & Hrotic**, **Gibson**, and perhaps **Penn et al.** – neither social nor ecological challenges alone account for human cognitive and brain evolution. In support of this view, **Reader & Hrotic** point to a very recent study by **Reader et al.** (2011), which I find particularly compelling. **Reader** and colleagues compiled cognitive measures from multiple domains (social, technical, ecological), examined their interrelations (for 62 primate species), and found strong cross-species associations. Rather than that each trait evolved in response to species-specific social and ecological demands, it therefore seems more likely that social, technical, and ecological traits evolved in concert, as part of a highly correlated cognitive suite.

R10. From individual cognition to population-level culture

My primary reason for examining primate social and non-social wit was the belief that doing so would help us to explain why technological accumulation evolved so markedly in us, and so modestly in chimps. To be sure, I was fully aware that an examination of cognitive capabilities alone would offer only half an explanation; that for the other part, one would need to study how these abilities play out at the aggregate level.

Therefore, I am in agreement with **Ragir & Brooks** that human cultural evolution cannot be properly understood if population and group dynamics are ignored. But the reverse holds as well: One needs accurate micro-level data to be able to give meaningful descriptions at the macro level. Consider, for example, **Ragir & Brooks**' contention that “changes in population density result in

the specialization of labor and knowledge,” and that “as communities increase in size, functional institutions appear.” Without a proper micro-level foundation, these explanations are highly unsatisfactory. Increasing population densities will favor specialization and functional institutions only in animals that meet certain cognitive requirements; otherwise, the animal kingdom would have been replete with species as cooperative and institutionalized as humans are.

Moerman appreciates this complementarity well. He finds my characterization of human tool-related cognitive abilities exemplary but insufficient to account for such astonishing achievements as cathedrals, iPhones, and symphony orchestras. To explain these, Moerman argues, one also needs to consider the novel ways in which humans tend to organize themselves, acting collectively towards otherwise impossible outcomes. Although the target article described a set of micro-level mechanisms that enable these forms of cooperation (see e.g., sect. 12.3.1 and 12.3.2), I agree that their impact remained somewhat elusive.

Therefore, as a natural follow-up, I already started developing an agent-based model to assess the impact of collective learning on cumulative culture. Preliminary results indicate that at certain levels of technological complexity, default mechanisms of individual and social learning are unable to sustain further accumulation; and that at that point, only collective learning is able to reboot the cumulative process. The model is also used to examine the effects of certain population characteristics; for example, how isolation and interconnectedness of sub-populations play out at higher levels of aggregation.

In the present version of the model, complexity is defined just in terms of the number of components that a technology has. In a later stage, however, complexity will also be a measure of the number of interactions between components. Based on a paper by Rivkin (2000), the prediction now is that, even given collective learning, cumulation levels off at a critical level of complexity; and that the process can recover once the causal relationships between components are understood. Thereby, the macro-level impact of another favored micro-level trait, namely, causal reasoning, would have been addressed.

R11. Conclusion

Despite a set of methodological worries and worries about the details of my argument, the target article’s main contention, namely, that human tool use reflects higher cognitive ability, holds up pretty well. Only with respect to function representation may have my conclusions perhaps been too strong.

Evidently, there are plenty of topics worthy of further investigation, to begin with the outstanding questions formulated in section 12. Also, new experimental paradigms will undoubtedly force us to reformulate or refine our judgments about what humans and chimps can and cannot do. Furthermore, the methodological and evolutionary issues pointed out by the commentators are in need of clarification; and at various places I have said that I would welcome more comparative evidence. Finally, there is the question of how individual-level

cognitive processes scale up to population-level phenomena. As suggested above, that question will concern me most in the time to come. But whatever the results of that future work, I hope my current efforts have already contributed, even a little, to our understanding of our humanlike selves.

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[The letters “a” and “r” before author’s initials stand for target article and response references, respectively]

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