

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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**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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**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.