tool can use as a template other tools possessed by individuals in their community. Consequently, the "idea" of a tool need not be "in the head" of an individual, as tools possessed by other members of the group can play this role. There are any number of external resources that can assist individuals to stay "on track" in their manufacturing task.

This social world is crucial in learning to make tools. Other toolmakers are accessible behavioural templates of toolmaking activities. Tools, and other tool users, create an environment that can support the development of cognitive skills associated with tool manufacture. Tools are made in a world where there are other people making tools, and where there is close contact between toolmakers and their behavioural outputs. For a young hominin learning to make a tool, this environment provides a situation where the cost of learning a tool is relatively low. There are lots of behavioural templates around, some of whom may even have a genetic interest in ensuring the young hominin acquires the appropriate skills (Sterelny 2010b; 2012).

In his section on executive control (sect. 12.2), Vaesen notes that individuals with certain brain lesions can achieve complex sequences of tasks where there is clear "next steps" available in the form of environmental cues (the lunch box packing case; sect. 6) but cannot achieve tasks where purely mental planning is necessary (Tower of London tasks; sect. 6). For a social organism, tool manufacturing quite likely resembles the first task, with abundant physical props and a community of users and makers. Tools may scaffold executive control (Jeffares 2010b).

Therefore, we can resolve the apparent paradox of the Acheulean by understanding the environment that the tools are made in. Acheulean tools are made in a social context; and being members of a toolmaking community buffers the transmission of skills, reduces learning costs, and allows variation to develop. Nevertheless, the hominins that made these tools appear to not have the capacity to accumulate technological improvements in tool form. This suggests that suitable buffering effects were not present during deployment activities, or that different processes encouraged standardisation of tool form (Jeffares 2010a).

Regardless of the details of this case, what should be clear is that we have to acknowledge that cognitive skills do not straightforwardly facilitate technological accumulation. There is a cognitive ecology of co-evolutionary processes, external resources, scaffolds, and developmental influences that shape human cognition, both now and in the past. This matters to understanding human uniqueness and how it evolved.

Humans make tools because they live in a unique cultural environment that helps them learn, and fine-tune, the cognitive skills necessary for toolmaking. To understand cumulative culture, we must understand how culture scaffolds the learning of cognitive skills, and not presume the skills that underlie it. By not considering the historical environment and the external environment as part of that matrix of forces that shapes cognition, Vaesen potentially ignores the possibility that some of his package of cognitive skills are learnt.

Tool use induces complex and flexible plasticity of human body representations

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Abstract: Plasticity of body representation fundamentally underpins human tool use. Recent studies have demonstrated remarkably complex plasticity of body representation in humans, showing that such plasticity (1) occurs flexibly across multiple time scales and (2) involves multiple body representations responding differently to tool use. Such findings reveal remarkable sophistication of body plasticity in humans, suggesting that Vaesen may overestimate the similarity of such mechanisms in humans and non-human primates.

Vaesen presents a compelling and comprehensive overview of the cognitive abilities underpinning human tool use. Across diverse domains, Vaesen argues for important differences between humans and other primates in all but one. Here we focus on this last domain, body schema plasticity, which Vaesen suggests may not differ substantially between humans and apes. Although we agree that the fact of body schema plasticity characterises both human and non-human primate cognition, recent results have revealed a highly complex relation between plasticity of body representations and tool use in humans. We suggest that there are likely to be fundamental differences in such mechanisms between humans and other primates, with important implications for tool use and its relation to other cognitive abilities. In particular, we focus on two main issues: (1) the time course of plasticity in humans occurs flexibly across multiple time scales, and (2) multiple body representations coexist in the human brain, responding with differential plasticity in the context of tool use, and accounting for the different kinds of experience associated with different types of tools.

Apes and monkeys in the wild rarely use tools spontaneously, and they learn to do so only after long and laborious training (Iriki & Sakura 2008). In humans, however, tool use induces plasticity at multiple time scales, showing long-term learning in the case of specific expertise, but also flexibly changing over just a few seconds in experimental situations. For example, some studies have varied tool use on a trial-to-trial basis, finding clear modulation of peripersonal space representations depending on whether or not a tool is used (Holmes et al. 2007) or what length tool is used (Longo & Lourenco 2006), demonstrating that tool use induces nearly instantaneous plasticity. Other recent studies have demonstrated long-term plastic changes associated with expertise for specific tools. In blind cane users, for example, merely passively holding the cane extended auditory-tactile interactions along the length of the tool; in control participants, by contrast, active training with the cane was required to induce such extension (Serino et al. 2007). Analogous findings have been reported for everyday use of the computer mouse (Bassolino et al. 2010): Merely holding a mouse in the hand habitually used to control the mouse (the right) extended auditory-interactions to the space near the screen; whereas such effects were found only when the mouse was actively used, and not just passively held, in the hand *not* habitually used to control the mouse (the left). These results demonstrate that tool-induced plasticity is highly complex, occurring across multiple time scales and levels of abstraction.

Although the human brain certainly treats wielded tools at some level as if they were extensions of the body, distinctions between the body and tools must also be made, and at several levels. For example, Povinelli et al. (2010) rightly point out that one important function of tools is to allow actions that would otherwise be prohibitively dangerous, such as reaching into a fire or stirring a pot of boiling soup. In such cases, effective guidance of the tool may require it being treated as part of the body, even as safety considerations may necessitate it being strongly distinguished from the body. Such conflicting requirements highlight the need for multiple body representations, maintaining parallel, and potentially inconsistent, representations of the body with or without the tool.

This flexibility appears much less pronounced in non-humans primates: In monkeys, long-term tool use trainings induce structural changes in neural body representations, which are rigid and persist whether the animal is tested with the tool or without

(Quallo et al. 2009). In humans, conversely, long-term tool use expertise develops multiple body representations, which can be selectively activated depending on the presence/absence of the tool. In blind cane users, for example, peripersonal space representations were extended towards the far space, or limited around the hand (as in sighted subjects), depending on whether blind subjects held their cane during testing (Serino et al. 2007).

It is also interesting to note that in humans, the subjective experience of wielding a tool is strikingly different from that of illusions, such as the rubber hand illusion (Botvinick & Cohen 1998), in which external physical objects are treated as being part of the body. This dissociation suggests that the tool is "embodied" at a lower, more implicit level, what De Preester and Tsakiris (2009) refer to as "body-extension," distinguishing it from the higher-level, more conscious "body-incorporation" seen in the rubber hand and related illusions. An interesting, intermediate case is that of prosthesis implantation: A prosthesis is a tool, extending action potentialities of an accidentally limited body; but prostheses also replace the shape of the missing limb, hence restructuring the physical body. There seems to be wide variability in amputees' experiences of their prostheses, from those who experience the prosthesis as a corporeal structure to those who consider it an artificial device (Murray 2004). It is probable that both functional (level of motor control) and cosmetic (level of anthropomorphism) features of the prosthesis underlie such differences. Recent findings suggest that the sense of ownership over a prosthesis can be enhanced by illusory (Ehrsson et al. 2008) or physical (Marasco et al. 2011) sensory feedback to the stump. This level of abstraction in the experience of body incorporation of artificial objects cannot be investigated in non-human primates (Graziano 1999).

We suggest that different levels of body schema plasticity characterize human cognition and might account for the different experiences associated with the multiplicity of complex tools used by humans in everyday life. These and other recent findings have provided fundamental insight into the role of plasticity of body representations in human tool use. Together, they suggest that body schema plasticity is a highly complex, flexible, and task-dependent process, which should not be thought of as simple "present or absent" in an organism or species. Therefore, we believe Vaesen has too quickly excluded an important role for this factor as an important source of differences between human tool use and that of other primates.

Prosthetic gestures: How the tool shapes the mind

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Abstract: I agree with Vaesen that it is a mistake to discard tool use as a hallmark of human cognition. I contend, nonetheless, that tools are not simply external markers of a distinctive human mental architecture. Rather, they actively and meaningfully participate in the process by which hominin brains and bodies make up their sapient minds.

> If we could rid ourselves of all pride, if, to define our species, we kept strictly to what the historic and the prehistoric periods show us to be the constant characteristic of man and of intelligence, we should say not *Homo sapiens*, but *Homo faber.*
>
> — Henri-Louis Bergson, *Creative Evolution* (1911/1998, p. 139)

Despite the famous feats of termite-fishing chimpanzees and hook-crafting crows, Bergson's words from his *Creative Evolution* remain largely unchallenged (for a good review of the evidence, see Seed & Byrne 2010; Tomasello & Herrmann 2010). Even the most highly trained nut crackers could not manage to equal the abilities seen in the earliest hominin stone tool makers (Davidson & McGrew 2005; Iriki & Sakura 2008). There is more to the notion of *Homo faber*, however. For it is not the sheer variety and sophistication of human technologies, but rather the profound complexity of our engagement with tools and technologies that matters the most: We humans alone define and shape ourselves by the tools we make and use. Inspired from the work of Bernard Stiegler (1998) and André Leroi-Gourhan (1963/1993), I would like to describe human tool use as the *prosthetic gesture par excellence* (Malafouris 2010a). This is a species-unique and self-transforming human predisposition that leaves very little space for valid relational comparisons with other animals (or so I wish to suggest).

I understand that those committed to the long-held evolutionary ideal of a cognitive "continuum" between human and nonhuman animals would probably take my previous points as ill-conceived and anti-Darwinian: "The difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind" (Darwin 1871, p. 105). But I think that so far as the human entanglement with tools is concerned, Darwin's claim is rather misleading. What must have certainly started as a difference in *degree* soon became one of *kind* – that is, a difference that makes a difference. No doubt, the lack of conceptual clarity about the use and meaning of terms such as *degree, kind, mind*, and *tool* is a major contributing factor for our troubles with the question of "human cognitive autapomorphies" (Suddendorf 2008, p. 147), and I am afraid Vaesen's paper does very little to help us clear the ground.

In any case, the interesting question is not whether human and animal tool-using abilities are different, but rather, why they are, and how did they become so different. Where do we start, then? Mainstream approaches to the comparative study of cognition follow two main paths when it comes to answering those questions: The first seeks to explain apparent discontinuities in human mental function as the natural outcome of the human genome, that is, resulting directly from biological adaptations (e.g., the "supermodule" hypothesized by the relational reinterpretation [RR] hypothesis proposed in this journal by Penn et al. 2008). The second path seeks to account for the differences between human and nonhuman cognitive abilities by way of language, culture, learning, and the external symbolic representational means that these capacities afford (e.g., Tomasello et al. 2005; Tomasello & Herrmann 2010). The former path takes us into the realm of biology; the latter into the realm of culture.

Vaesen's approach combines both paths. His thesis is essentially that humans are born with better-equipped neural systems and cognitive machinery, which is sufficient to account for the discontinuity between human and nonhuman animal tool use capacity even in the absence of culture. He then shows how our superiority with respect to the nine cognitive capacities deemed crucial to tool use can also explain why technological accumulation evolved so markedly in humans. In other words, the aim of his study is not to question the barrier between "individual brain power" and "culture," (sect. 1) but instead to argue that human superiority is reflected at the former biological level as much as it is in the latter sociocultural level: "[h]uman tool use reflects higher social intelligence (indeed), but just as much greater non-social wit" (sect.1, para.2).

Here is, then, the nub of the problem – at least as I see it: Whilst Vaesen's comparative gaze seems squeezed *within* the artificial boundaries that separate the cultural from the biological realm, the sort of things we call tools stubbornly inhabit the hybrid realm *between* – that is, the realm where brain, body, and culture conflate, mutually catalyzing and constituting one another (Malafouris 2008; 2010b). As a result,