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Tool use induces complex and flexible plasticity of human body representations

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10. 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.

11. Main Text

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. While 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 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, while 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, Calvert, & Spence, 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, Bassolino, Farnè, & Làdavas, 2007). Analogous findings have been found for everyday use of the computer mouse (Bassolino, Serino, Ubaldi, & Làdavas, 2010): merely holding a mouse in the right hand (habitually used to control the mouse) extended auditory-interactions to the space near the screen, while such effects were found only when the mouse was actively used, and not just passively held, in the left hand (not habitually used to control the mouse). These results demonstrate that tool-induced plasticity is highly complex, occurring across multiple time scales and levels of abstraction.

While 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, Reaux, and Frey (2010) rightly point out that one important function of tools is to allow actions which 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, while 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 instance, 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 similarly treated as 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’, to distinguish 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: on the one hand, a prosthesis is a tool, extending action potentialities of an accidentally limited body; on the other hand, prostheses also replace the shape of the missing limb, thus re-structuring the physical body. There seems to be wide variability in amputees’ experiences of their prostheses, between who experience the prosthesis as a corporeal structure and who consider it as 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. Thus, 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.

12. References

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