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Imagined tool-use in near and far space modulates the extra-striate body area

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ABSTRACT

Active tool-use can result in the incorporation of the tool into the body schema, e.g., the representation of the arm is enlarged according to tool length. This modification even influences the processing of space: using a long tool leads to a remapping of far space as near space. We here further investigate the interaction of the neural representations of the human body, tool use, and spatial domain.

Functional magnetic resonance imaging (fMRI) was performed in twelve right-handed healthy individuals while they imagined moving a cylinder towards a target position in far or near space by mentally using either pliers or a joystick. The fMRI data revealed that already the imagined use of preferred tools in near and far space (i.e., pliers in far space, joystick in near space) modulated the neural activity in the extra-striate body area (EBA) located in the occipito-temporal cortex. Moreover, psycho-physical interaction analysis showed that during imagined tool-use the functional connectivity of left EBA to a network representing the near-personal space around the hand was strengthened. This increased functional connectivity is likely to reflect the neural processes underlying the incorporation of the tool into the body schema.

Thus, the current data suggest that simulating tool-use modulates the representation of the human body in extra-striate cortex.

1. Introduction

Understanding how the human body is represented in the human brain is an important prerequisite to elucidate the neural bases of body schema disorders observed in neurological patients suffering from neglect, apraxia, autotopagnosia or phantom limb experiences (Rumiati, Papeo, & Corradi-Dell'Acqua, 2010). Moreover, this understanding is likely to be essential for the development of efficient prosthesis and brain–computer-interfaces (Donoghue, 2008; Hochberg et al., 2006; Scott H.Frey, 2004, 2008; Velliste, Perel, Spalding, Whitford, & Schwartz, 2008). The body schema is a continuously updated map of body shape and posture (Maravita & Iriki, 2004). This map contains and combines sensory afferences and motor efferences. This central representation of the current position of body parts and the body's spatial properties (updated during body movement) is a prerequisite for the spatial organization of an action. Particularly relevant for our study, the notion of a body schema can be related to multisensory spatial integration within (peri-personal) space and its neural substrates (Maravita, Spence, & Driver, 2003).

One important feature of the body schema is that it is flexible and dynamic. Behavioral, electrophysiological, and imaging studies in non-human primates and humans showed that the use of tools modifies the neural representation of the body so that the tool is incorporated into the body schema (Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008; Holmes & Spence, 2004; Inoue et al., 2001; Iriki, Tanaka, & Iwamura, 1996; Obayashi et al., 2001). This modification of the neural representation of the human body even influences the processing of space: using a long tool leads to a remapping of far space as near space (Berti & Frassinetti, 2000). Repeatedly manipulating a tool to reach beyond body space establishes a strong association between the body part using the tool (hand/arm), the tool itself, and the spatial domain (i.e., far space), in which the tool is used. Thus, reaching for distant objects using a stick or a rake may alter the body-schema as if the hand was elongated to the tip of the tool (e.g., (Inoue et al., 2001; Iriki et al., 1996; Obayashi et al., 2001)). Electrophysiological studies in non-human primates revealed that polymodal cells responding to both tactile and visual information (with spatially congruent receptive fields in these modalities) constitute the neural basis for this phenomenon: when a monkey uses a rake to retrieve distant objects, visual receptive fields of visual-tactile cells are

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enlarged along the axis of the rake (Iriki et al., 1996). As a consequence, polymodal neurons which previously responded to stimuli around the hand, then also respond to visual stimuli at the far end of the rake. Consistent with these neurophysiological findings, imaging studies revealed corresponding changes in neural activity during actual tool-use in far space in both monkeys (Obayashi et al., 2001) and humans (Inoue et al., 2001).

However, the neural processes underlying the complex interaction of the neural representation of the human body, tool use, and spatial domain to date remain poorly understood (Scott H. Frey, 2004). Previous studies implicated the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001) in the representation of human body parts. Importantly, the EBA does not only seem to be involved in the visual processing of static body representations (Astafiev, Stanley, Shulman, & Corbetta, 2004; Downing et al., 2001; Peelen & Downing, 2005, 2007), but is also activated by many other body-part related processes including self generated (Astafiev et al., 2004) and goal directed (Takahashi et al., 2008) movements (even when the limb is not visible (Astafiev et al., 2004)), visual imagery of haptic exploration of body parts (Costantini, Urgesi, Galati, Romani, & Aglioti, 2011), as well as reaching to kinesthetically defined targets (Darling, Seitz, Peltier, Tellmann, & Butler, 2007). Thus, EBA represents the parts of the human body in a multisensory and dynamic manner (Astafiev et al., 2004; Costantini et al., 2011).

The current functional imaging study investigated whether EBA activity is already modulated by *simulating* tool-use actions without seeing or moving any body part. In particular, we hypothesized that imagining the use of an 'appropriate' tool for the respective spatial domain (defined by preference; here: pliers in far space and joystick in near space) would specifically alter neural activity in the EBA indicating an adaptation of the neural representation of the human body by motor simulation of tool use. Previous studies showed that situations in which there is an incongruency between body or action representations and movement-related visual signals activate EBA, thereby indicating that EBA represents the human body in a dynamic manner (David et al., 2007). By manipulating the visual feedback of the subjects' joystick-movement in half of the trials, EBA was more active when the visual feedback was incongruent to the subjects' own executed movements (David et al., 2007). Interestingly, in the same study EBA showed enhanced functional connectivity to posterior parietal cortex when visual feedback and joystick movements were congruent. In our study, participants imagined using one of two tools (joystick or long pliers) in order to virtually move objects around a circle at two displayed distances in near and far virtual space. Using simulated rather than actual tool-use movements reduced many confounding factors which would be triggered by overt actions or their perception. Any EBA activity observed during actual tool-use movements could be triggered by tool-induced body schema changes, but also by seeing/perceiving the moving body parts. Therefore, simulated tool-use actions are better suited to attribute changes of EBA activity either to the modulation of the body schema or to actually seeing/perceiving moving body parts. With respect to the current fMRI-investigation, actual tool-use would also have been prone to movement artefacts during scanning. Moreover, the visible moving pliers during actual tool-use would have led to strong visual differences of the stimuli compared to the joystick conditions. In contrast, relying on simulated tool-use allowed keeping the visual scene almost identical across conditions (only the little arrow pointing to either the pliers or the joystick changed location, see Fig. 1a). Given past evidence (Farnè & Làvadas, 2000; Inoue et al., 2001; Iriki et al., 1996; Maravita & Iriki, 2004; Obayashi et al., 2001) we expected that the pliers would be more effective at inducing plasticity in the representation of the upper limb when movements were simulated in far space, while the joystick (given its habitual use to move objects on a PC screen, i.e., usually located in near space) would rather induce such changes for movements being simulated in near space (Obayashi et al., 2002, 2004). It should be noted, that these two tools differ also in other ways. For instance, while joysticks are predominately used in near space (e.g., on one's desk), pliers can be used both in far, and, although uncomfortably, in near space. Pliers need to be lifted and are then manipulated with the opening and closing of the hand (i.e., more distal movements), while a joystick is stationary and (after grasping it with a whole hand grip) is usually operated by more proximal arm movements. Pliers and joystick also involve two qualitatively different movements and thus implied motion types. However, the current experimental design was factorial (factors tool and space). Therefore, both tools and thus both types of imagined tool-use movements (and hence implied motion types) were similarly present in the conditions involving near and far space. In the interaction term (space *x* tool), such 'confounding factors' (as different tool-related actions) are controlled for since the interaction term constitutes the difference of the differences ([F_P > F_J] > [N_P > N_J]). Thus, any differential activity we find for the interaction term cannot simply be explained by differences in simulating these two actions per se or by the implied motion that goes along with it.

Functional magnetic resonance imaging (fMRI) was performed in twelve right-handed healthy individuals while they imagined moving a red cylinder towards a target position in far or near space by mentally using either pliers or a joystick. They were asked to determine which of the two possible directions (clockwise or counter-clockwise) would provide the shortest path for transporting the cylinder. Whether tool-use induced modulations might occur also during motor imagery of tool-use, in absence of any overt movement and tactile feedback from the tool, is unknown. In light of the striking parallelism between motor imagery and motor execution (e.g., (Decety et al., 1994; Gerardin et al., 2000; Parsons et al., 1995; Stephan et al., 1995)), it could be predicted that already imagined tool-use may be sufficient to trigger specific changes of neural activity. While a dissociation between near and far *mental* space (in neglect) has been described (Ortigue et al., 2003), to date no study investigated yet the interaction of simulated tool-use with far and near (mental) space. Taking into account that Uddin and colleagues revealed a strong functional and structural connectivity between the parietal cortex and the lateral occipital cortex (containing putative EBA; (Uddin et al., 2010)), a modulation of these areas (or their connectivity) by simulating the use of a tool appropriate for the given spatial domain could be expected.

Based on our hypothesis that imagining the use of an appropriate tool for the respective spatial domain (here: pliers in far space and joystick in near space) would specifically draw on the body schema, the key analysis of the fMRI data relies on the interaction between spatial domain and tool. Furthermore, psycho-physical interaction (PPI) analyses were performed with bilateral EBA (as revealed by the interaction analysis) as seeds to assess the areas with increased connectivity with EBA during simulated tool-use.

2. Materials and methods

2.1. Subjects

Twelve (7 males) right-handed (Edinburgh Inventory, (Oldfield, 1971)) healthy subjects (age range 24–37 years, mean 30.5 years) with no past or present neurological or psychiatric disease gave informed consent to participate in the study. The study was approved by the local ethics committee.

2.2. Task, stimuli and experimental paradigm

2.2.1. Stimuli

Stimuli were created by using open source software (Blender, www.blender.org) with 3D-features to mimic far and near space (Fig. 1a) and depicted a chair and a green table with a size that would correspond to 100 × 200 cm. On the table, two circles of 70 cm diameter were marked, one in near space (at a distance of 65 cm from the centre of the circle to the chair in front of the subject) and the other in the