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Neural foundations of overt and covert actions

Panagiotis G. Simos[b], Eleftherios Kavroulakis[b], Thomas Maris[b], Efrosini Papadaki[b], Themistoklis Boursianis[b], Giorgos Kalaitzakis[b], Helen E. Savaki[a,b,*]

[a] *Institute of Applied and Computational Mathematics, Foundation for Research and Technology Hellas, Iraklion, Crete, Greece*
[b] *Faculty of Medicine, School of Health Sciences, University of Crete, Iraklion, Crete, Greece*

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ABSTRACT

We used fMRI to assess the human brain areas activated for execution, observation and 1st person motor imagery of a visually guided tracing task with the index finger. Voxel-level conjunction analysis revealed several cortical areas activated in common across all three motor conditions, namely, the upper limb representation of the primary motor and somatosensory cortices, the dorsal and ventral premotor, the superior and inferior parietal cortices as well as the posterior part of the superior and middle temporal gyrus including the temporo-parietal junction (TPj) and the extrastriate body area (EBA). Functional connectivity analyses corroborated the notion that a common sensory-motor fronto-parieto-temporal cortical network is engaged for execution, observation, and imagination of the very same action. Taken together these findings are consistent with the more parsimonious account of motor cognition provided by the mental simulation theory rather than the recently revised mirror neuron view Action imagination and observation were each associated with several additional functional connections, which may serve the distinction between overt action and its covert counterparts, and the attribution of action to the correct agent. For example, the central position of the right middle and inferior frontal gyrus in functional connectivity during motor imagery may reflect the suppression of movements during mere imagination of action, and may contribute to the distinction between 'imagined' and 'real' action. Also, the central role of the right EBA in observation, assessed by functional connectivity analysis, may be related to the attribution of action to the 'external agent' as opposed to the 'self'.

Introduction

A highly influential account of action recognition attributes a key role in a set of specialized neurons within the monkey ventral premotor area F5 (Gallese et al., 1996; Rizzolatti et al., 1996) and the inferior parietal area PF/PFG (Fogassi et al., 1998), comprising the monkey mirror neuron system (Rizzolatti and Craighero, 2004). More recent studies, however, have documented similar mirror neuron- like activity in several additional areas, including the primary motor (MI) and somatosensory (SI) cortices, the supplementary motor (SMA) and supplementary somatosensory (SSA) areas, the dorsal premotor cortex (PMd), and several parietal, parieto-occipital and temporal cortices (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Evangeliou et al., 2009; Kilintari et al., 2011, 2014; Raos et al., 2004, 2007; Tkach et al., 2007; Vigneswaran et al., 2013). These results raise doubt on the initial claim of the mirror neuron view, that areas F5 and PF/PFG are solely responsible for action recognition in monkeys (for critiques see Dinstein et al., 2008; Hickok, 2009; Savaki, 2010). Indeed, the mirror neuron account of action recognition was recently expanded to implicate a mirror mechanism implemented in a set of regions beyond F5 and PF/PFG (Gallese et al., 2004).

In humans, motor cognition can be studied within the framework of action representation, which is responsible for covert actions, such as action perception and motor imagery. Accordingly, the current study was designed to compare directly an overt action with its covert counterparts within the same experimental framework. The progressive expansions of the mirror neuron system, based on human neuroimaging data, have contributed little to ongoing discussions regarding the nature of the brain mechanism responsible for motor cognition. Furthermore, theoretical disputes were compounded by uncertainties regarding the correspondence of key regions between monkey and human brain. More explicitly, early human imaging studies on motor cognition (for a meta-analysis see Grezes and Decety, 2001) focused mainly on the inferior parietal lobule (IPL) including the angular and supramarginal gyri (BA39 and BA40) and on the inferior frontal gyrus (IFG) including the pars opercularis and pars triangularis (BA44 and BA45), which accorded with the assumption that they correspond to the monkey PF/PFG and F5, respectively

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[*] Correspondence to: Department of Basic Sciences, Faculty of Medicine, University of Crete, P.O. Box 2208, GR-71003 Iraklion, Crete, Greece.
E-mail address: savaki@uoc.gr (H.E. Savaki).

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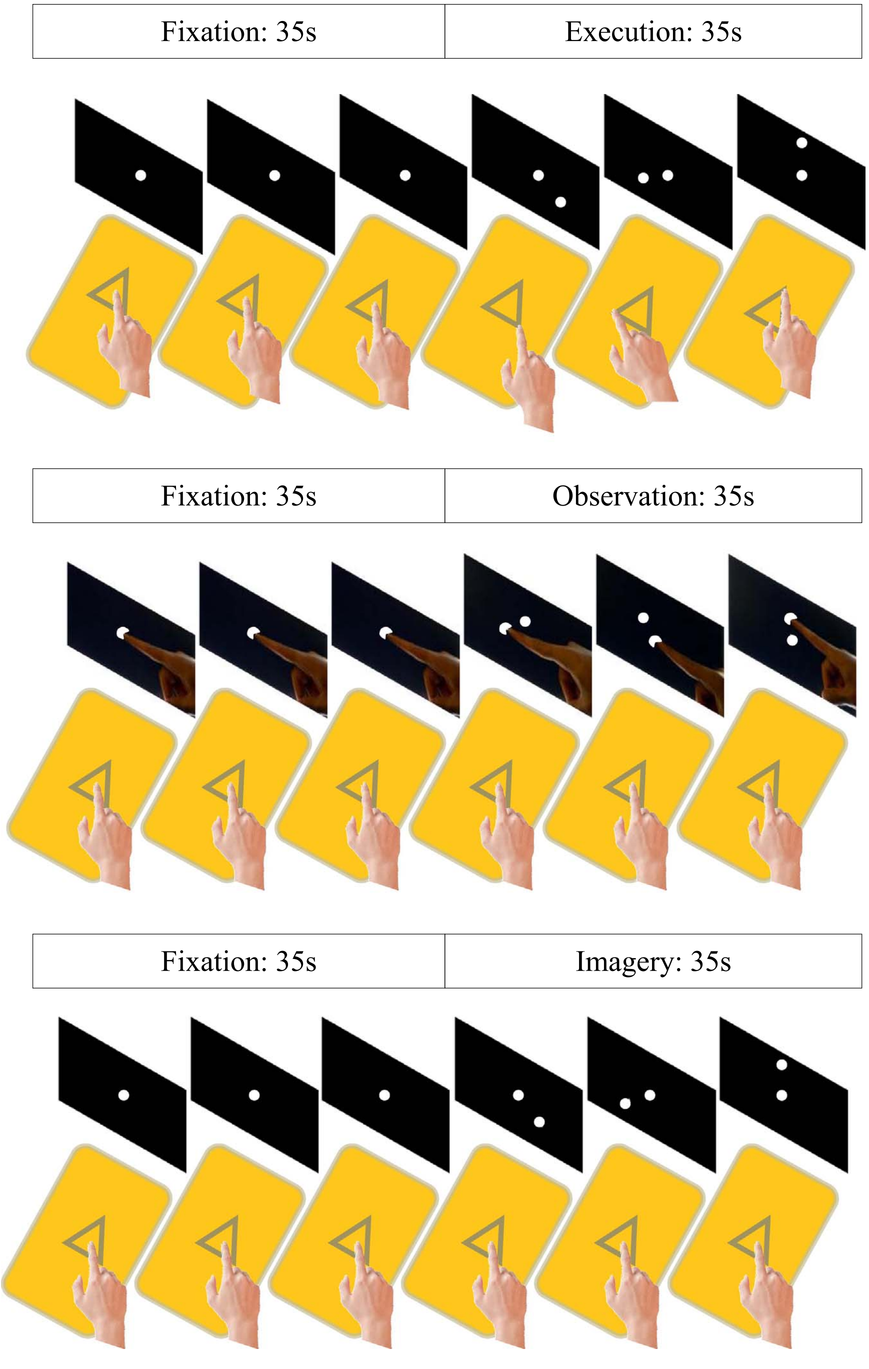

Fig. 1. Experimental Design. Schematic representation of the experimental design showing two data acquisition blocks (fixation and task performance) for each of the three experimental conditions: action execution, action observation and motor imagery. Single video frames used as stimuli are shown for each task: white spots flashing on a black screen for all tasks, and an additional tracing hand for the observation task. The corresponding hand position on the flat board with the engraved triangle, which was located on the participants' stomach, is illustrated under the video frames for each task.

(Rizzolatti et al., 1996). However, this assumption was challenged by neuroanatomical data demonstrating that the human equivalent of F5 comprises only the ventral aspect of BA6 and neither BA44 nor BA45 (Petrides, 2005; Petrides and Pandya, 2009; Tomaiuolo et al., 1999). Additionally, over the last two decades overt (execution) and covert (observation and motor imagery) actions were investigated in isolation from each other. Of the 335 papers cited by two recent meta-analyses of action observation (Caspers et al., 2010) and motor imagery (Hetu et al., 2013) only 18 are cited by both, demonstrating that these two topics have been largely considered separately (Vogt et al., 2013).

Bearing in mind that functional brain imaging data cannot provide information regarding the functional properties of distinct neuronal populations (such as mirror like properties), a systematic exploration of the functional anatomy and cortico-cortical functional interactions during execution, observation and imagination of the very same action in the entire human brain of the same subjects would be of great value. Surprisingly, this type of study is missing from the existing literature. Actually, the study of Filimon et al. examining execution, observation and imagery of reaching movements could have been an exception, had the authors studied the effects on core areas such as SI and MI and had they analyzed the functional interactions of all activated areas (Filimon et al., 2007; Filimon et al., 2015). Therefore, in the present fMRI study we examined the effects of execution, observation and imagination of the same action (visually guided tracing with the index finger of the