



Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution



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ABSTRACT

Several models propose Motor Imagery, Action Observation, and Movement Execution recruit the same brain regions. There is, however, no quantitative synthesis of the literature that directly compares their respective networks. Here we summarized data from neuroimaging experiments examining Motor Imagery (303 experiments, 4902 participants), Action Observation (595 experiments, 11,032 participants), and related control tasks involving Movement Execution (142 experiments, 2302 participants). Comparisons across these networks showed that Motor Imagery and Action Observation recruited similar premotor-parietal cortical networks. However, while Motor Imagery recruited a similar subcortical network to Movement Execution, Action Observation did not consistently recruit any subcortical areas. These data quantify and amend previous models of the similarities in the networks for Motor Imagery, Action Observation, and Movement Execution, while highlighting key differences in their recruitment of motor cortex, parietal cortex, and subcortical structures.

1. Introduction

Recent technological developments in the fields of brain computer interfaces, virtual/augmented reality, and neurofeedback have rekindled the longstanding scientific interest in the relationship between the simulation and physical execution of actions. Action simulation (i.e. the internal representation of motor programs without overt movement; Jeannerod, 2001) is typically examined through either Motor Imagery (i.e. imagining the execution of an action without physically performing it), or Action Observation (i.e. watching movements performed by others). In particular, Motor Imagery has received renewed interest following developments in brain computer interface and neurofeedback technology (Chaudhary et al., 2016; Liew et al., 2016). This research is supported by decades of work examining the use of Motor Imagery in elite athletic performance (Calmels et al., 2006; Cumming and Ramsey, 2009; Williams et al., 2015), skill acquisition (Lotze and Halsband, 2006; Pascual-Leone et al., 1995), and rehabilitation (Jackson et al., 2001; but see Ietswaart et al., 2011). Similarly, interest in Action Observation increased dramatically following the discovery of 'mirror-neurons' in non-human primates (di Pellegrino et al., 1992). Mirror neurons respond both when an action is physically performed,

and when the action is observed being performed by another actor. There has since been considerable investigation of the human Action Observation system (Grafton et al., 1996; Rizzolatti et al., 1996b). Action observation forms the basis of learning through imitation (Buccino et al., 2004), can induce the same changes in skills as seen in physical practice (Zhang et al., 2011), and is being increasingly examined as a tool for neurorehabilitation (Buccino, 2014; Ertelt et al., 2007; Chaudhary et al., 2016; Liew et al., 2016; Marchesotti et al., 2016). Studies have also begun to combine mental imagery and Action Observation (Vogt et al., 2013), allowing greater control over the content and vividness of action simulation (Holmes and Calmels, 2008). Improving our understanding of the brain networks involved in action simulation, and how they relate to the brain regions recruited during Movement Execution, is therefore of considerable interest to both basic scientific research and translational work across a diverse range of fields.

Several prominent models propose that Motor Imagery and/or Action Observation share neural substrates with Movement Execution (Crammond, 1997; Grèzes and Decety, 2001; Jeannerod, 2001). While early summaries of the literature examined the 'functional equivalence' between Motor Imagery, Action Observation, and Movement Execution,

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they identified consistent activations across studies in a subjective manner that did not include principled statistical tests (Grèzes and Decety, 2001; Jeannerod, 2001). Later meta-analyses have summarized the individual networks involved in Motor Imagery (Héту et al., 2013) and Action Observation, (Caspers et al., 2010), respectively, but provided no quantitative comparison between their respective networks, or how they compare to the network for Movement Execution. Such a comparison would address longstanding questions regarding which regions are consistently involved in action simulation, and whether a consistent network spans Motor Imagery, Action Observation, and Movement Execution. This could in turn provide critical information for translational studies aiming to use action simulation to engage brain networks involved in Movement Execution.

Coordinate-based meta-analysis allows the quantitative summary of the current neuroimaging literature. Pooling data increases statistical power, addressing the limited sample sizes in individual neuroimaging studies. Activation Likelihood Estimation (ALE) is an established technique for quantitative voxelwise random effects meta-analysis (Eickhoff et al., 2012, 2009; Laird et al., 2005; Turkeltaub et al., 2012, 2002). Consistently activated regions are determined based on spatial convergence of coordinates reported in previous studies. Statistical testing against a null distribution provides a quantitative summary of previous results.

In Summary, the question of whether Motor Imagery, Action Observation, and Movement Execution recruit shared brain networks has been of interest to the scientific community for several decades (Decety et al., 1994; Grafton et al., 1996; Gerardin et al., 2000; Jeannerod, 2001; Grèzes and Decety, 2001; Lotze and Halsband, 2006; Munzert et al., 2009; la Fougère et al., 2010; Sharma and Baron, 2013. Amemiya and Naito, 2016). Previous work has examined these questions in small-scale studies with limited sample sizes, or through reviews identifying common activations in a subjective manner without quantitative statistical comparisons. Here we address these limitations by conducting large-scale quantitative meta-analyses of Motor Imagery, Action Observation, and Movement Execution. Our results address this longstanding question by identifying a consistent network of premotor, parietal, and somatosensory brain areas that are consistently activated across Motor Imagery, Action Observation, and Movement Execution. Our analyses also identify novel differences between the recruitment of subcortical structures (the putamen and cerebellum) across the tasks.

2. Methods

2.1. Literature searches

Relevant neuroimaging papers were found through pubmed literature searches (as of June 2017). A search for papers on Motor Imagery was conducted using the search string "((fMRI) OR PET) AND Motor Imagery", and yielded 487 results. A similar search for papers on Action Observation was conducted using the search string "((fMRI) OR PET) AND (((Action Observation) OR mirror neurons) OR imitation)", providing 784 results. Reference sections of the reviewed articles were inspected to identify additional articles of interest. The term 'imitation' was included in order to identify contrasts in which participants observed actions prior to imitation. Papers identified in the literature searches were examined for control conditions involving Movement Execution, allowing us to identify a sample of Movement Execution tasks with properties similar to those used in the included Motor Imagery and Action Observation experiments. This approach reduced the likelihood that differences between the networks were due to inclusion of heterogeneous experimental tasks.

2.2. Inclusion/Exclusion criteria

Our literature survey identified 205 papers on Motor Imagery and 417 papers on Action Observation. Experiments contained in these

papers that used either Motor Imagery, Action Observation, or Movement Execution were assessed for eligibility to be included in the meta-analyses. Only experiments including coordinates from whole brain analyses in standard stereotaxic (MNI/Talairach) space were included in the analyses (to prevent biasing results based on the specific inclusion/exclusion of brain regions). Included experiments reported data from healthy adult participants (i.e. participants ≥ 18 years of age with no known neurological conditions). Data from healthy control groups in patient studies were included where provided. The meta-analyses examined within-subject contrasts (to prevent comparisons with patient groups, or comparisons across groups of unequal size). Finally, brain activations following neuromodulatory interventions (i.e. measuring the effects of non-invasive brain stimulation or pharmacological agents) were not included, though pre-intervention conditions/control groups were included as appropriate.

2.3. Data extraction and classification

Data extracted from each paper included the number of subjects participating in each experiment, and the coordinates of the reported activations in MNI or Talairach space. Coordinates reported in Talairach space were converted to MNI space using the Lancaster transform (Lancaster et al., 2007). Each task was categorized as involving Motor Imagery, Action Observation, and/or Movement Execution. In order to assess somatotopic activations, we recorded the effector(s) involved in the action, classifying them according to the use of the leg (foot inclusive), arm (hand inclusive), or face (including mouth movements, speech, and facial expressions). Where actions involved multiple effectors they were categorized as using the limbs (both arms and legs, or when contrasts involving the arms and legs were combined), upper body (i.e. movements involving both the face and arm, or contrasts in which face and arm movement were combined), or the whole body (e.g. tasks such as weight lifting or dancing, and conditions in which contrasts involving the leg, arm, and face were combined). Locomotor tasks (including stepping, walking, and running) were categorized as tasks performed with the legs (as the leg acts as the predominant effector). Where it was possible to determine, we also noted whether Motor Imagery or Action Observation was performed from a first person or third person perspective, and in the case of Action Observation, whether participants observed actions passively, or actively (i.e. with the intention to later perform the same action). These factors are further examined in sub-analyses (see supplementary materials). The data included in each meta-analysis and subanalysis are presented in Table 1. More detailed information on the individual experiments included in each meta-analysis is presented in Supplementary Table 1.

Table 1
Data included in the meta-analyses.

Analysis	Experiments	Participants	Foci
Motor Imagery	303	4902	3235
Somatotopy subanalyses:			
- Leg	65	916	801
- Arm	179	3041	1928
- Face ^a	6	111	57
Action Observation	595	11032	6561
Somatotopy Subanalyses:			
- Leg	34	453	297
- Arm	339	6494	3831
- Face	64	1103	761
Movement Execution	142	2302	1842
Somatotopy Subanalyses:			
- Leg	20	208	239
- Arm	107	1858	1324
- Face ^a	13	219	214

^a Analysis should be considered exploratory as it includes < 20 experiments (Eickhoff et al., 2016).

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