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# 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 (Hétu 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).

### 2.4. Data analyses

In a first step we conducted ALE meta-analyses to identify the individual task networks involved in Motor Imagery, Action Observation, and Movement Execution. Each task network was examined in greater detail using subanalyses including experiments using only the face, only the arm, and only the foot as an effector. We then assessed the convergence and divergence between the individual task networks. Networks were overlaid in a pairwise fashion, allowing us to identify the volume of each network that was specific to each individual task, and the volume that was activated across multiple tasks. We identified regions that were consistently engaged across different tasks by computing pairwise conjunction analyses, and in a final step a combined conjunction identified the regions consistently recruited across all three tasks.

### 2.5. Analysis procedure

All analyses were conducted using the revised version of the activation likelihood estimation (ALE) algorithm (Eickhoff et al., 2009; Turkeltaub et al., 2002). The ALE approach empirically determines whether converging activation coordinates (foci) across different experiments occurs at a level greater than expected by chance. Reported foci are modeled as the centers of 3D Gaussian probability distributions (Turkeltaub et al., 2002). The revised algorithm sets the width of these Gaussians using empirical between-subject and between-template comparisons, and models the increased spatial reliability of larger sample sizes by using smaller Gaussian distributions (Eickhoff et al., 2009). Comparisons between groups of different sizes are accounted for by computing a null-distribution using label-exchangeability (Eickhoff et al., 2012).

Foci for each experiment were combined across voxels to produce a modeled activation map (Turkeltaub et al., 2012). Combining modeled activation maps across experiments produced ALE scores, which described the convergence of coordinates for each location. ALE scores were compared to a non-linear histogram integration based on the frequency of distinct modeled activation maps (Eickhoff et al., 2012), determining areas where convergence is greater than expected by chance. ALE values were computed only for voxels with a $\geq 10\%$ probability of containing grey matter (Evans et al., 1994), as functional activations occur predominantly in grey matter areas. Results were thresholded at $p < 0.05$ (cluster-level FWE, corrected for multiple comparisons, cluster-forming threshold at voxel level $p < 0.001$) and provided at $2\text{mm}^3$ voxel resolution.

Contrasts between the resultant meta-analyses were conducted using random effects ALE subtraction analysis (Eickhoff et al., 2012). In a first step, voxel-wise differences between ALE maps were calculated for each pool of experiments. Experiments were then randomly shuffled into two samples of equal size to the compared analyses, and voxelwise differences between their ALE scores were recorded. This shuffling procedure was repeated 10,000 times to produce an empirical null distribution of ALE score differences between the compared conditions. The map of differences based on this procedure was thresholded at a posterior probability for true differences of $P > 0.95$, and inclusively masked by the respective main effect of the minuend (cf. Chase et al., 2011; Rottschy et al., 2012) with a minimum cluster volume of $100\,\text{mm}^3$ (Beissner et al., 2013; Erickson et al., 2014; Turkeltaub et al., 2012).

Volume comparisons were conducted by overlaying the networks and determining the number of voxels that were unique to each analysis, or co-recruited across analyses. As differences in the number of studies included in the meta-analyses could influence the size of the volume identified in each case, we also conducted 'volume matched analyses' (Hardwick et al., 2015). Each of these analyses compared two networks. In a first step the volumes (i.e. number of voxels) identified by each network were identified. The volume of the smaller network was set as the target size for the volume corrected analysis. We then took the larger network and iteratively increased the threshold applied to it (i.e. reduced its' volume) until we identified the threshold at which the difference in the volume of the two networks was minimized. This threshold value was then applied to the larger network, resulting in a volume corrected version of this network which contained a number of voxels closely matching that of the smaller network. This identified those regions most consistently implicated in a paradigm while controlling for differences in the resulting volumes.

Conjunction analyses were conducted to summarize the overlap between networks. These analyses used the conjunction null hypothesis and were calculated using the minimum statistic (Nichols et al., 2005), with a minimum cluster volume of $100\,\text{mm}^3$ (Beissner et al., 2013; Erickson et al., 2014; Turkeltaub et al., 2012). In a final step we conducted a conjunction across the analyses of Motor Imagery, Action Observation, and Movement Execution to identify neural substrates commonly recruited by all three tasks.

### 2.6. Labeling

Results were anatomically labeled according to their most probable macro-anatomical and cytoarchitectonic/tractographically assessed locations using the SPM Anatomy Toolbox 2 extension (Eickhoff et al., 2007, 2006, 2005). Additional functional labels for motor and premotor cortical regions were identified using the human motor area template (HMAT) as defined by Mayka et al. (2006). Coordinates were reported based on peak maxima in MNI space.

## 3. Results

Our literature searches identified over 1000 experiments suitable for inclusion in one of our three meta-analyses (see methods; breakdown of studies presented in Table 1, details of included studies are presented in supplementary tables 1–3).

### 3.1. Assessing the networks for motor imagery, action observation, and movement execution

In a first step we conducted quantitative meta-analyses of Motor Imagery, Action Observation, and Movement Execution (Fig. 1; see also Supplementary Tables 4–6).

Motor Imagery primarily recruited a network of bilateral premotor, rostral inferior and middle superior parietal, basal ganglia, and cerebellar regions, with left-lateralized recruitment of the dorsolateral prefrontal cortex. Two large bilateral premotor clusters spanned the SMA, extending to the dorsal and ventral premotor cortices. The left premotor cluster also extended to encompass areas of the cingulate and putamen (a separate smaller cluster included the right putamen). Two bilateral parietal clusters spanned the inferior and superior parietal lobules, with right lateralized activations in the inferior parietal sulcus. Further bilateral clusters were identified in the cerebellum (lobule VI).

Action Observation identified the network with the greatest overall volume of the three meta-analyses (a comparison of the volumes across networks is presented in Fig. 5). Similarly to Motor Imagery, Action Observation recruited a bilateral network of premotor and parietal regions; however, this also included large parietal-occipital volumes, and more bilateral recruitment. Two large bilateral clusters spanned the dorsal and ventral premotor cortices, while a third smaller premotor cluster was identified in the pre-SMA. A smaller cluster included the right superior occipital gyrus. The two largest clusters covered bilateral parietal-occipital regions, spanning from the superior to inferior parietal lobule, and portions of the occipital cortex. Notably, Action Observation did not consistently recruit subcortical regions; while the parieto-occipital clusters included small portions of the cerebellum, these areas did not include peak maxima.

Movement Execution identified the smallest in volume of the three

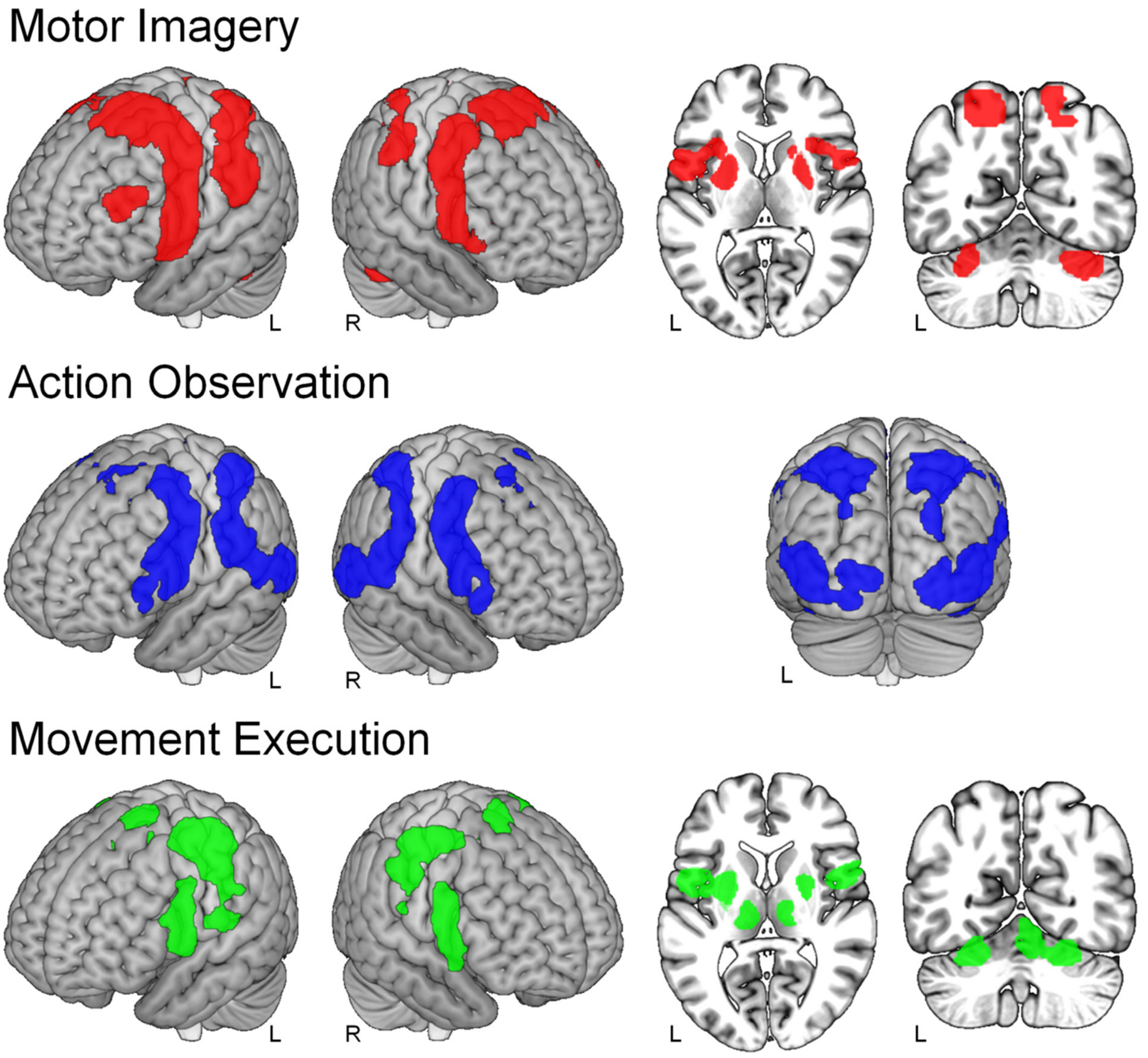

**Fig. 1.** Quantitative meta-analyses of the three tasks. Note that no slices are shown for Action Observation as no clusters were identified in subcortical areas.

meta-analyses. Cortical activations spanned the sensorimotor and premotor cortices, and included small regions of the inferior parietal lobule, while subcortical clusters were identified in the bilateral thalamus, putamen, and cerebellum. Though larger in the left hemisphere, two bilateral clusters spanned the primary motor and somatosensory cortex, with anterior regions reaching into the dorsal premotor cortex. Premotor convergence was identified in three clusters; one spanning the bilateral SMA that extended down to the cingulate cortex, and two bilateral clusters across the ventral premotor cortex. Consistent with the bilateral but primarily left-lateralized clusters in the sensorimotor cortex, subcortical activity included bilateral (primarily left lateralized) clusters in the thalamus, and bilateral (primarily right-lateralized) clusters in cerebellar lobule VI.

### 3.2. Somatotopy subanalyses

A series of subanalyses examined potential somatotopic organization for each task by separately analyzing data from experiments performed using the leg, arm, or face (Fig. 2; for coordinates see supplementary tables 7–9).

Subanalyses examining imagery tasks performed with either the leg or arm were broadly consistent with the main analysis of Motor Imagery (Fig. 2), though the network for the leg was more limited in volume Notably, tasks performed with the leg recruited the right dorsolateral prefrontal cortex, whereas in the main analysis only the left dorsolateral prefrontal cortex was recruited. Motor imagery with both the leg and arm recruited an overlapping volume in the right cerebellum; tasks performed with the leg also recruited clusters in the left cerebellum and cerebellar vermis, likely due to the bilateral nature of the included tasks. An exploratory analysis of six Motor Imagery experiments that used the face identified no converging activations.

Subanalyses of Action Observation tasks performed with the leg, arm, or face identified sub-networks relatively consistent with the main analysis (i.e. they recruited smaller volumes that mainly fell within that of the main analysis). There was limited evidence of somatotopic organization in the premotor and parietal lobes, with a greater likelihood of superior regions being recruited by observing the leg, and a greater likelihood for inferior regions being recruited when observing the face. The subanalyses also identified a region of the right extrastriate visual cortex responsive to actions performed with the leg, arm, or face, consistent with the extrastriate body area (Downing et al., 2001). Notably, contrary to the main analysis, the subanalysis of Action Observation tasks involving the face identified consistent recruitment of the left thalamus and bilateral amygdala.

Subanalyses of Movement Execution tasks performed with the leg and arm, and an exploratory subanalysis of 13 studies using the face,

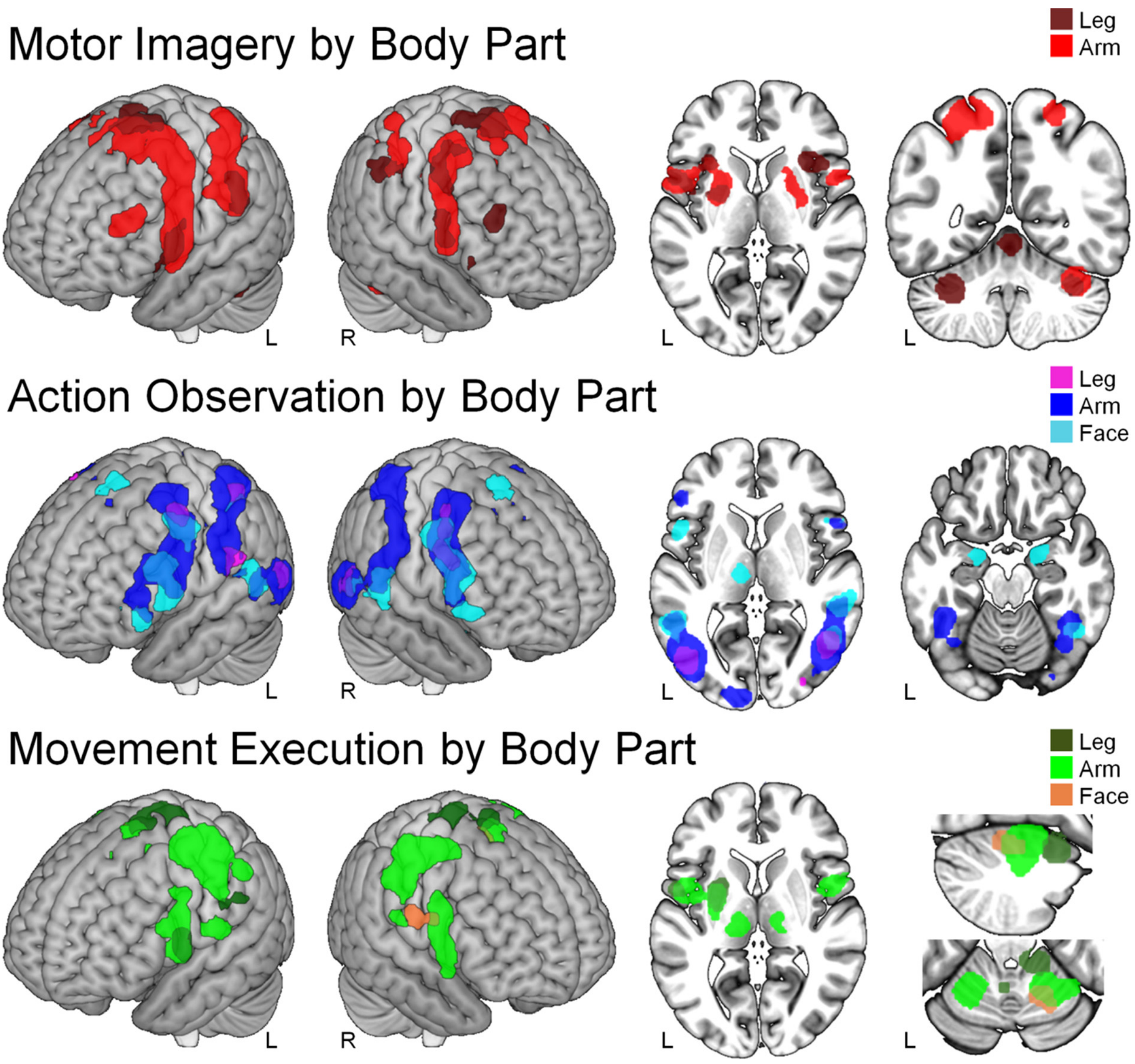

**Fig. 2.** Subanalyses for each task conducted according to the body part used.

identified a network similar to the main analysis of Movement Execution. Somatotopic recruitment occurred in cortical and subcortical areas. For the primary motor cortex, activity along the central sulcus was consistent with classic motor mappings, with relatively superior, central, and inferior regions being associated with the leg, arm, or face, respectively. The right cerebellum was also recruited in a somatotopic manner; relatively anterior, central, and posterior regions corresponded to tasks performed with the leg, arm, or face, respectively (Fig. 2, lower panel).

### 3.3. Contrast analyses

Contrast analyses identified regions more consistently implicated with one of the tasks when compared to another (Fig. 3).

Motor imagery, when compared to Action Observation, was more consistently associated with recruiting most premotor regions, including bilateral SMA, PMd, and PMv. Imagery was also more consistently linked with parietal regions, recruiting bilateral areas of the inferior parietal lobe, and regions of the (mainly left) superior parietal lobe. The left DLPFC was more closely linked with Motor Imagery. Subcortically, the bilateral putamen and cerebellum were both more consistently linked with Motor Imagery.

Relatively few clusters were identified as being more likely to be recruited during Action Observation compared to Motor Imagery. These areas included small bilateral regions of the inferior frontal gyrus and areas of the right inferior/superior parietal lobule. Notably, these regions correspond to the premotor and parietal regions in which mirror-neurons have been identified in non-human primates (see Fogassi et al., 2005; Gallese et al., 1996).

Motor Imagery, compared to Movement Execution, was more consistently associated with recruiting premotor regions, including the bilateral pre-SMA, PMd, and left PMv. A large volume spanning the left inferior and superior parietal cortex was also more consistently associated with Motor Imagery. No subcortical regions were more closely linked with Motor Imagery when compared to Movement Execution.

By contrast, Movement Execution was, in comparison to Motor Imagery, more consistently implicated with classic sensorimotor regions including the SMA-proper and cingulate motor areas, left primary motor and somatosensory cortex, and bilateral ventral premotor cortex. Subcortically, Movement Execution was associated with recruitment of the left putamen and lobule VI of the right cerebellum.

Action observation, in comparison to Movement Execution, recruited a mainly bilateral network of premotor, parietal, and occipital regions including the Pre-SMA, bilateral PMd and PMv, bilateral

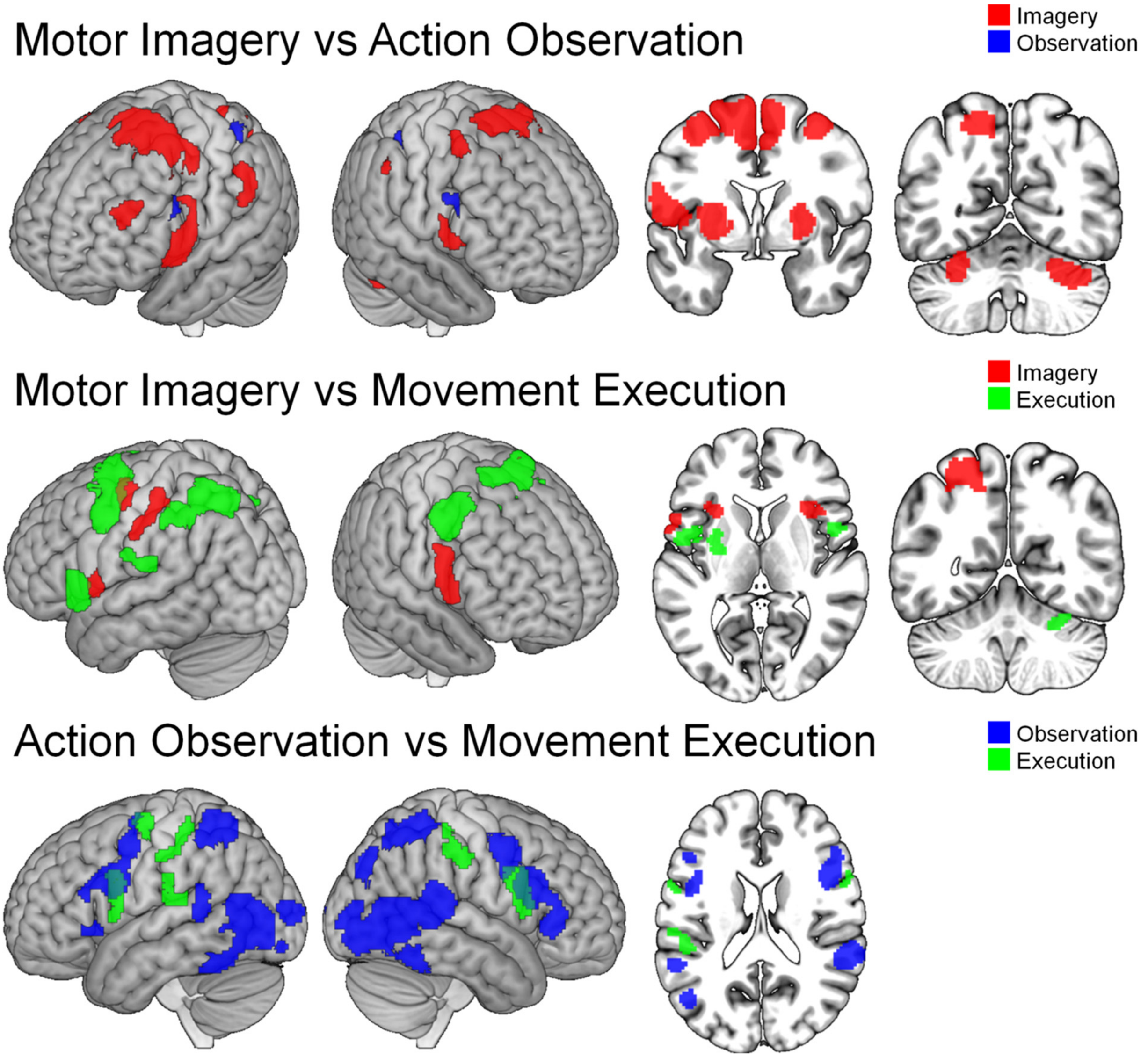

**Fig. 3.** Contrast analyses. Note that small regions of apparent 'overlap' present areas that are rendered on the cortical surface, but are present at different depths (slices show relative depths).

inferior and superior parietal lobe, and bilateral visual cortex. No subcortical regions were more closely associated with Action Observation when compared to Movement Execution.

Regions more consistently associated with Movement Execution than Action Observation spanned a mainly bilateral cortical sensorimotor network. This included the SMA proper, left primary motor cortex, bilateral somatosensory cortex, and bilateral ventral premotor cortex. No subcortical regions were more consistently implicated in Movement Execution than Action Observation.

### 3.4. Conjunction analyses

A series of conjunction analyses used the minimum statistic to identify regions consistently recruited across multiple tasks (Fig. 4; see also Supplementary Tables 10–13).

A conjunction between Motor Imagery and Action Observation identified areas consistently recruited during action simulation. This network included primarily bilateral premotor and rostral parietal regions, with greater cortical volumes in the left hemisphere (see Supplementary Table 10). A medial premotor cluster was identified within the pre-SMA, and further bilateral clusters spanned the dorsal and ventral premotor cortex for each hemisphere. Bilateral clusters were identified across the superior and inferior parietal lobules. Notably, a relatively small cluster was identified as having a peak maximum in the right cerebellar hemisphere. However, further inspection identified that the region from the Action Observation analysis that contributed to this cluster primarily corresponded to the extrastriate visual area, and included only small regions of the cerebellum without peak maxima. This indicates that the cerebellar cluster identified in the conjunction analysis may not have been driven by shared Cerebellar recruitment per-se, and could instead be attributed to mainly coincidental overlap between adjacent clusters.

A conjunction between Motor Imagery and Movement Execution identified a network including bilateral cortical sensorimotor and premotor clusters, with smaller subcortical clusters in the putamen and cerebellum. In premotor regions, one cluster included the bilateral pre-SMA and SMA proper, and another small cluster was identified in the right dorsal premotor cortex, while further bilateral clusters included the ventral premotor cortex. Posterior to these premotor clusters were two bilateral clusters that each included the primary somatosensory cortex. Subcortically, the bilateral putamen and cerebellum (lobule VI) were also identified as being consistently recruited across both constituent analyses.

Consistent activations across Action Observation and Movement

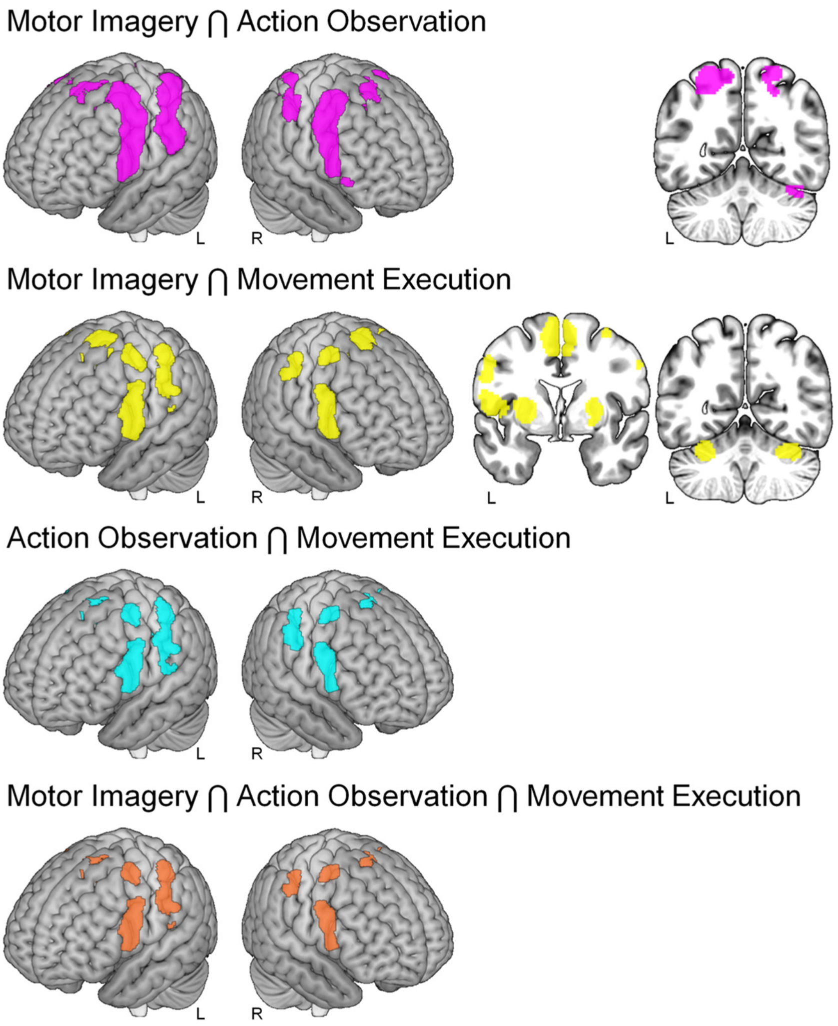

**Fig. 4.** Conjunction analyses conducted across combinations of the tasks. Note that slices are only shown in cases where analyses identified subcortical clusters. Fig. 5: Volume Comparisons. Bar chart illustrates the number of voxels contributing to the volume for each task. Pie charts illustrate the percentage of each volume that is unique to one task, or overlaps with other tasks. Note that as the volume of each network differs (see bar chart), the same absolute volume of overlap represents a different percentage of the corresponding individual networks.

Execution were identified in a bilateral premotor, parietal, and sensorimotor network. Premotor regions included the bilateral pre-SMA extending back into the left SMA-proper, separate clusters in the bilateral ventral premotor cortex, and a small cluster in the right dorsal premotor cortex. Parietal convergence spanned the inferior parietal lobule. A small cluster was identified in the right cerebellum; however, further inspection of the Action Observation meta-analysis indicated that the contributing cluster originated in the visual cortex. As in the conjunction between Motor Imagery and Action Observation, this is consistent with the cluster identified in the conjunction analysis not being a result of direct cerebellar recruitment in both constituent analyses; instead this may reflect coincidental overlap between these adjacent clusters.

A grand conjunction across Motor Imagery, Action Observation, and Movement Execution identified brain areas involved in both the simulation and performance of actions. This identified a bilateral network of premotor, parietal, and somatosensory regions. Separate premotor clusters spanned the pre-SMA and left SMA-proper, and the bilateral dorsal and ventral premotor cortices. More posterior clusters included bilateral regions of parietal and sensorimotor cortex.

### *3.5. Volume comparisons*

We examined the similarity and disparity between each network by quantifying the volume of grey matter within each network that overlapped with other analyses, and the volume of grey matter that was unique to each analysis (Fig. 5). Note that while the overall volume for each network differed, supplementary analyses using a previously established technique that matches the volumes of different networks (Hardwick et al., 2015) provided broadly consistent results (see supplementary materials).

## 4. Discussion

The question of whether Action Simulation (i.e. Motor Imagery and/or Action Observation) and Movement Execution recruit the same network of brain areas has been of longstanding interest to the scientific community (see 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 et al., 2013. Amemiya and Naito, 2016). Here for the first time we examined this question using large-scale meta-analysis techniques, overcoming the limited sample sizes of previous studies, and providing quantitative, statistically principled results. These analyses identified a consistent premotor, parietal, and somatosensory network of brain areas that were recruited across Motor Imagery, Action Observation, and Movement Execution. We also present novel differences relating to the involvement of subcortical structures (the putamen and cerebellum)

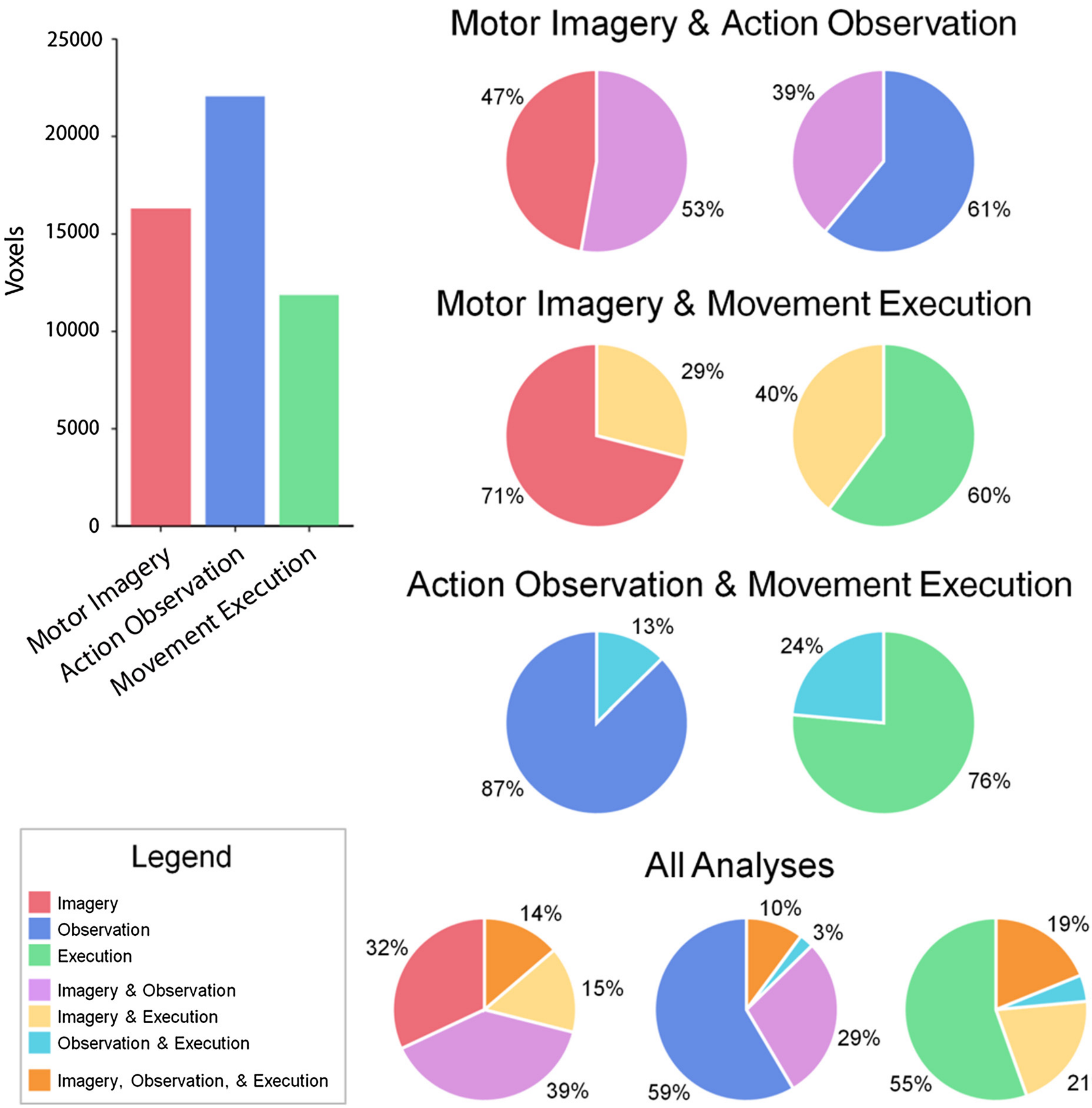

**Fig. 5.** Volume Comparisons. Bar chart illustrates the number of voxels contributing to the volume for each task. Pie charts illustrate the percentage of each volume that is unique to one task, or overlaps with other tasks. Note that as the volume of each network differs (see bar chart), the same absolute volume of overlap represents a different percentage of the corresponding individual networks.

across the tasks.

Our present results replicate, update, and extend previous meta-analyses of the individual networks for Motor Imagery (Hétu et al., 2013) and Action Observation (Caspers et al., 2010). As the results of these individual analyses are extremely similar to the previous meta-analyses, we direct the reader to the previous papers for discussion of these individual networks, and focus our discussion on the novel contributions provided by comparing results across these meta-analyses. This includes notable differences and similarities between their networks, and on how their networks relate to the network for Movement Execution.

### 4.1. Motor imagery

Notably, only Motor Imagery consistently recruited of the dorsolateral prefrontal cortex (DLPFC), and corresponding regions of the frontal thalamus. The DLPFC is implicated in frontal-executive functions related to action preparation (Mars and Grol, 2007), which is believed to have similar neural substrates to Motor Imagery. However, DLPFC was not consistently recruited during Action Observation or Movement Execution, possibly due to the relatively simple motor tasks used. DLPFC recruitment during Motor Imagery could be due to working memory demands, thought to be separate to frontal-executive DLPFC functions recruited during more complex movement tasks (Rottschy et al., 2012; Wollenweber et al., 2014). Alternatively, as DLPFC plays a role in movement inhibition (Blasi et al., 2006; Coxon et al., 2016; Nigel et al., 2015), it may prevent overt movement during Motor Imagery, which may have greater demands for inhibitory mechanisms than Action Observation due to the internal generation of movement sensations (Crammond et al., 1997).

The meta-analysis of Motor Imagery identified a predominantly premotor-parietal network, with subcortical recruitment of the putamen and cerebellum. While our volume comparison analysis identified the greatest overlap between Motor Imagery and Action Observation, this was mainly limited to premotor and parietal regions. In comparison, a more diverse range of regions was recruited during both Motor Imagery and Movement Execution, including the mid-cingulate cortex, putamen, and cerebellum.

Both Motor Imagery and Movement Execution recruited the mid-cingulate cortex. Motor Imagery recruited a relatively anterior region linked with more cognitive aspects of motor control (Hoffstaedter et al., 2013a). By contrast, Movement Execution recruited a relatively posterior region associated with more basic motor functions (Picard and Strick, 1996; Procyk et al., 2014). Conjunction identified a large cluster with peak maxima in the SMA that extended down into the mid-cingulate cortex, but had no peak maxima within the cingulate itself; the majority of this cingulate overlap was in relatively posterior regions, consistent with a role in movement production.

Motor Imagery and Movement Execution both recruited the bilateral putamen. A region of the basal ganglia that forms a critical node of the cortico-striatal sensorimotor circuit (Voon et al., 2015), the putamen is associated with automatic movement behaviors (Ashby and Crossley, 2012). Activity in the putamen correlates with the speed and extent of executed movements (Turner et al., 2003), and there is evidence that the basal ganglia are involved in assessing the energetic costs associated with movements (Shadmehr and Krakauer, 2008). This is notable as disorders of the basal ganglia related to Parkinson's disease lead to slowness of executed movements (Dickson, 2017). There is evidence that this slowing does not occur in order to preserve accuracy, but represents a shift in the cost/benefit ratio for moving at normal speed (Mazzola et al., 2003). Notably patients with Parkinson's disease also show increases in the duration of imagined movements (Helmich et al., 2007; Heremans et al., 2011), suggesting the same slowness of movement applies to their imagined actions. The putamen may therefore regulate the speed of self paced movements whether they are executed or imagined. This could also explain why the basal ganglia were not implicated in Action Observation; the viewer has no ability to regulate the speed of the observed movement.

The cerebellum was recruited during both Motor Imagery and Movement Execution; the right cerebellar lobule VI was consistently involved in both tasks as identified by a conjunction analysis. The cerebellum contains multiple representations of the body, and results from the meta-analysis of Movement Execution showed somatotopic effects in line with previous work (Buckner et al., 2011; Debaere et al., 2001). Cerebellar lobule VI contains body representations that are most prominent during Movement Execution (Schlerf et al., 2010). However, our Motor Imagery subanalysis identified little evidence of a corresponding somatotopic recruitment of the cerebellum. This suggests the cerebellum may have been recruited to perform differing functions in Motor Imagery and Movement Execution (discussed further below).

### 4.2. *Action observation*

The Action Observation meta-analysis identified a cortical network of mainly premotor-parietal and occipital regions. Occipital regions were uniquely associated with Action Observation, which was unsurprising given the extensive use of visual stimuli in the included contrasts. A subanalysis examining Action Observation studies according to the observed body part identified three notable features. First, we identified a right hemisphere extrastriate visual region that responded to the presentation of actions performed across the leg, arm, or face. This is consistent with the previously described 'Extrastriate Body Area' which is sensitive to the observation of parts of the body and movement (Downing et al., 2001; Ferri et al., 2013; Urgesi et al., 2007; for a review see Lingnau and Downing, 2015). Second, the subanalysis identified bilateral recruitment of the amygdala in response to observing faces, consistent with the emotional content of the facial stimuli presented in many of the included experiments. This is in line with work indicating that Action Observation can include processing of emotional components (Mazzola et al., 2003; Lagravinese et al., 2017). Finally, this analysis also provided limited evidence of somatotopic organization within the premotor and parietal cortex, in line with previous work (Buccino et al., 2001; Jastorff et al., 2010; Lorey et al., 2013).

The Action Observation meta-analysis did not identify consistent recruitment of any subcortical areas. While a cluster spanning parietal and extrastriate visual areas did include small areas of the cerebellum, no peak maxima were identified within the cerebellum itself. This result is consistent with a previous meta-analysis of Action Observation that found no evidence of consistent recruitment of the cerebellum or other subcortical regions (Caspers et al., 2010).

In a contrast analysis, Motor Imagery was more consistently associated with recruiting premotor and parietal regions than Action Observation. However, exceptions included small clusters in the inferior frontal gyrus (ventral premotor cortex) and inferior/superior parietal cortex that were more closely associated with Action Observation than Motor Imagery. This is notable as these regions are considered the human homologues of the areas in which mirror neurons have been identified in nonhuman primates. Mirror neurons were first discovered in macaque area F5 (di Pellegrino et al., 1992; Rizzolatti et al., 1996a), which is considered the putative equivalent of the human ventral premotor cortex. Later research found that the macaque rostral inferior parietal lobule, which in humans is believed to correspond to the rostral inferior parietal lobule or adjacent rostral intraparietal sulcus, also contained mirror neurons (Fogassi et al., 2005). As such, we propose that the specific sub-regions identified in these analyses may represent core regions in the Action Observation network (see also Caspers et al., 2010).

### 4.3. *Movement execution*

Movement execution recruited a cortical sensorimotor and premotor network, with further subcortical clusters in the putamen, thalamus, and cerebellum. These results were highly consistent with previously identified hallmarks of the motor system. Specifically, subanalyses identified somatotopic recruitment of the primary motor cortex and cerebellum, consistent with established motor maps within these structures (Buckner et al., 2011; Penfield and Rasmussen, 1950; Schlerf et al., 2010). The finding that this network also recruited the thalamus is consistent with the well established role of this structure as a cortico-subcortical relay (Sommer, 2003). Finally, we note that the network for Movement Execution identified here recruited a similar network to that identified in our previous meta-analysis of motor learning (Hardwick et al., 2013; see Supplementary Fig. 2 for a direct comparison). Notably, only the Movement Execution network was found to consistently recruit the primary motor cortex (see below for further discussion).

### 4.4. *Consistent sub-network for motor imagery, action observation, and movement execution*

A conjunction across all three tasks identified a network of premotor, rostral parietal, and somatosensory regions.

The bilateral ventral premotor cortex (PMv), dorsal premotor cortex (PMd), and pre-SMA were consistently recruited across all three tasks. These premotor regions are associated with action preparation (Hoshi and Tanji, 2007), which is believed to share similar neural substrates to Motor Imagery (Cunnington et al., 1996), and is proposed to be the mechanism by which several 'motor priming' effects of action observation occur (Edwards et al., 2003). PMv interacts with the primary motor cortex (M1) to play an important role in fine coordination of the hand during grasping (Davare et al., 2009; Rizzolatti et al., 1988). Work in primates indicates that the macaque homologue of PMv contains 'mirror neurons', sensitive to both the observation and execution of actions (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). Similarly, PMd has reciprocal connections with M1 and the spinal cord, but has limited ability to directly contribute to movement execution (Dum and Strick, 2005), and is associated more closely with action selection (Halsband et al., 1993; Rushworth et al., 1998). The firing patterns of PMd neurons change as primates learn arbitrary associations between stimuli and actions (Wise and Murray, 2000). These properties of the premotor cortex have been examined in studies that have established 'mirror' and 'counter-mirror' responses through training (Catmur et al., 2011, 2008). Similarly, SMA is associated with linking conditional rules to actions (Nachev et al., 2008), and is important to self-initiated actions (Debaere et al., 2003; Deecke and Kornhuber, 1978; Hoffstaedter et al., 2013b). Pre-SMA regions identified in the grand conjunction analysis are associated with both motor tasks and with non-motor cognitive processes (Leek and Johnston, 2009; Tanaka et al., 2005), consistent with the demands of Motor Imagery. These multimodal properties of the premotor cortex are therefore consistent with their recruitment across Motor Imagery, Action Observation, and Movement Execution.

Parietal region PFt was consistently activated across all analyses. The parietal cortex is typically involved in processing multisensory information (Block et al., 2013), and PFt is involved in motor behaviors and tactile processing (Klann et al., 2015), with a special role in tool use (Orban, 2016). Human area PFt has been proposed as the homologue of primate area PF (Caspers et al., 2010), which contains mirror neurons (Fogassi et al., 2005). Premotor-parietal co-recruitment as identified by the conjunction analyses is consistent with their interactions during visuomotor control of actions (Wise et al., 1997). Patients with damage to parietal regions also have impairments in using Mental Imagery to accurately predict the time required to perform motor tasks (Sirigu et al., 1996).

While large portions of the parietal cortex were involved in the networks for Motor Imagery and Action Observation, it was involved to a much lesser extent in Movement Execution. Notably, evidence from lesion studies indicates that parietal damage has more pronounced effects on complex actions (De Renzi et al., 1983; Weiss et al., 2008). The relative simplicity of the actions performed in Movement Execution conditions may therefore have contributed to this effect. We also note that the co-activation of the parietal cortex across Motor Imagery, Action Observation, and Movement Execution, could be explained by varying functions across these tasks. For example, PFt could play a role in timing performance during Motor Imagery, be recruited during Action Observation due to its' mirror properties, and be recruited during Movement Execution due to the processing of tactile information. The implications of such potential explanations for this 'consistent' co-activation is examined further below (see heading 4.6: "Is co-activation evidence of functional equivalence?").

Somatosensory recruitment is consistent with kinesthetic aspects of Motor Imagery (i.e. imagined sensations associated with performing actions). Models of Action Observation also propose that 'mirror' properties extend to tactile sensation (Keysers and Gazzola, 2009). The prominent 'threshold theory' of mirror-touch synesthesia (a condition in which observing another person being touched evokes the sensation of being touched) proposes that somatosensory 'mirror' activity occurs in all individuals, only becoming mirror-touch synesthesia once it passes the threshold for active perception (Ward and Banissy, 2015). In Movement Execution, sensory information provides critical feedback for the accuracy of movements, allowing comparison of the actual and predicted sensory consequences of actions (Hardwick et al., 2012; Muckli and Petro, 2017). This indicates that action simulation may lead to sensory efference in a similar manner as Movement Execution; this is consistent with the view of Crammond (1997), who proposed that motor imagery could be explained as the generation of sensory efference without accompanying movement execution (see also Kilteni et al., 2018).

### *4.5. Comparisons with previous models*

It has been noted that previous research on action simulation has placed a heavy emphasis on empirical research, and that comparatively little work has been directed toward the development of models and theoretical frameworks for action simulation (Guillot and Collet, 2005; Guillot et al., 2012; Moran et al., 2012; Glover and Baran, 2017). Theories relating to 'functional equivalence' (i.e. that action simulation engages the same network of brain regions as movement execution, but does so without overt movement) have been dominant in the field (Jeannerod 1996;2001, Decety 1994). Only recently has an alternative framework, the Motor-Cognitive model (which suggests action simulation - specifically motor imagery - depends more on brain regions involved in central executive functions) been introduced (Glover and Baran, 2017). Here we highlight how the results and analyses of the current meta-analyses relate to and inform these theories of action simulation.

Jeannerod's (2001) simulation theory proposed the same network of brain regions are recruited during Motor Imagery, Action Observation, and Movement Execution. The proposed simulation network included the prefrontal, primary motor, premotor, and parietal cortex, as well as the basal ganglia and cerebellum. Our conjunction analyses indicate that the majority of these areas were recruited across at least two tasks in our analyses; however, we only found consistent recruitment of the premotor and rostral parietal cortices across all three tasks, and in addition identified converging activity in the primary somatosensory cortex. The premotor-parietal network identified here is thus broadly consistent with earlier models proposing that Motor Imagery and Action Observation recruit the same neural structures involved in Movement Execution (Crammond, 1997; Grèzes and Decety, 2001; Jeannerod, 2001). However, our volume comparison analyses identified that less than half of the network for Movement Execution was also involved in Motor Imagery or Action Observation, suggesting previous models may have overestimated the similarity between these networks.

The recently proposed motor-cognitive model of motor imagery (Glover and Baran, 2017) suggests that central executive functions play an important role in motor imagery that is not evident in overt actions. This model proposes that while executed movements rely on automatic processes that require little conscious control, the absence of physical movement during action simulation prevents the same processes from being used. Instead, action simulation is proposed to rely more heavily on consciously controlled cognitive processes. As such, the motor-cognitive theory proposes that motor imagery involves a network centered around the dorsolateral prefrontal cortex, with potential contributions from visuo-perceptual regions of the occipital lobe and the ventral visual stream. The present results provide mixed evidence in support of this theory. Our main analysis of Motor imagery was unique in recruiting the dorsolateral prefrontal cortex. However, contrast analyses indicated this region was not preferentially recruited during Motor Imagery when compared to Movement Execution. Additionally, our analyses provide no evidence to support the proposal that visuo-perceptual or ventral stream visual areas may be recruited during Motor Imagery.

The involvement of the primary motor cortex in action simulation has long been a subject of debate. Jeannerod (2001) argued that fMRI results show clear involvement of M1 in action simulation. In contrast, Grèzes and Decety (2001) proposed that M1 recruitment during action simulation was ambiguous, noting that PET studies generally showed no M1 activity, while fMRI studies report recruitment of sensorimotor cortex. However, neuroimaging meta-analyses provide evidence against the recruitment of M1 during action simulation. Caspers et al., (2010) found that M1 was only recruited during Action Observation when participants viewed actions with the intention to imitate them. Similarly, Hétu et al., (2013) found no evidence of consistent recruitment of M1 during Motor Imagery. Here we found no evidence of M1 recruitment during Motor Imagery or Action Observation. However, previous studies have argued that the effect size of such activations are very small (Grèzes and Decety, 2001; Jeannerod, 2001; Lotze and Halsband, 2006). Thus, this result could be further examined using a sufficiently powered sample of original neuroimaging data.

Conjunctions across the networks identified little consistent recruitment of subcortical structures, primarily because Action Observation did not recruit subcortical structures, and, contrary to proposed models, did not appear to directly recruit the cerebellum (Miall, 2003). Notably, Motor Imagery and Movement Execution both recruited the thalamus, putamen, and cerebellum, contrary to early reports that the basal ganglia are not involved in Motor Imagery (for review see Jackson et al., 2001). The consistent recruitment of subcortical structures associated with Movement Execution during Motor Imagery, but not during Action Observation, may have important implications for translational research (see below).

### 4.6. *Is co-activation across tasks evidence of functional equivalence?*

Previous research has proposed that overlapping activations during Motor Imagery, Action Observation, and Movement Execution provide evidence of 'functional equivalence'; that the same regions perform the same computations across the different tasks. This follows the intuitive logic that it would be inefficient to develop distinct networks for these similar tasks (Hétu et al., 2013), and could explain the majority of the overlap identified in our analyses. We note, however, that it is difficult to infer the exact processes that a region plays in a task on the basis of neuroimaging data (Poldrack, 2006). Furthermore, activation across multiple tasks is not necessarily consistent with functional equivalence. For example, our Motor Imagery subanalysis indicated that the same region of the right cerebellum was recruited regardless of whether the task was performed with the leg or arm, whereas our subanalysis of Movement Execution identified clear somatotopic cerebellar recruitment. While a conjunction across tasks identified a region of the cerebellum that was consistently implicated in both Motor Imagery and Movement Execution, it does not necessarily indicate that the cerebellum performs the same function across both tasks. Furthermore, the traditional BOLD contrast used in fMRI studies, and the haemodynamic response as measured in PET studies, provide only indirect evidence of functional equivalence. As each voxel contains many thousands of neurons, co-activation across tasks could represent responses of separate sub-populations. Studies using fMRI repetition suppression have attempted to address this limitation, which assumes that the firing response of neurons will attenuate if they are consistently presented with a stimulus to which they are sensitive. Studies attempting to identify mirror neurons in the human brain have probed for 'cross-modal' repetition suppression between Action Observation and Movement Execution with mixed results (for a review see Kilner and Lemon, 2013). Unfortunately, many of these studies used a limited search volume, and were therefore unsuitable for inclusion in the present meta-analyses. Therefore, while the co-activation of voxels across Motor Imagery, Action Observation, and Movement Execution can be seen as *broadly* consistent with the theory of functional equivalence, the question of how directly matched the processes underlying these activations are requires further investigation. Zabicki et al., (2017) recently provided evidence that the patterns of activity in premotor and parietal regions during motor imagery and action observation show a moderate-to-low level of similarity; thus, it appears reasonable to assume that a mixture of matched and unique processes occur in these regions during action simulation and execution.

### 4.7. *Implications for translational research*

While Motor Imagery and Action Observation recruited a consistent premotor-parietal network, Motor Imagery recruited more regions that were also involved in Movement Execution. This suggests that translational research that uses action simulation with the aim of recruiting circuits involved in Movement Execution may be best supported by Motor Imagery interventions. Despite the overlap between Motor Imagery and Movement Execution here, there is evidence that imagined actions can be limited by the same impairments that affect Movement Execution (Helmich et al., 2007; Heremans et al., 2011). Such limitations could be addressed by combining Motor Imagery (to recruit more circuits involved in Movement Execution) and Action Observation (to allow accurate control of the content of simulated action; Holmes and Calmels, 2008). Such a combination could therefore be of particular interest in clinical settings (Eaves et al., 2014; Vogt et al., 2013).

While there is considerable interest in using action simulation in rehabilitation after stroke, it has thus far provided mixed results. Initial studies in stroke provided promising effects (Ertelt et al., 2007), but larger clinical trials have indicated no effects (Ietswaart et al., 2011). As even extensive physical training has limited impact on motor abilities in the chronic phase of stroke recovery (Hardwick et al., 2017; Kitago and Krakauer, 2013), interventions using action simulation during this phase should be expected to have limited impact. Notably, the majority of recovery in stroke occurs not during the chronic phase, but in the acute period within the first three months (Xu et al., 2017). Animal models suggest physical training early after stroke may improve overall recovery (Zeiler and Krakauer, 2013). Critically, as patients are not cleared for physical activity in the early acute phase, action simulation may provide an alternate route to promote early motor recovery.

There is increasing interest in using emerging technologies such as brain computer interfaces and neurofeedback techniques in rehabilitation (Chaudhary et al., 2016; Liew et al., 2016). Recent work indicates that an individual's ability to produce Motor Imagery can be a determining factor in whether they can interact with such devices (Marchesotti et al., 2016). We propose that results from the our combined conjunction analyses represent the core brain network for action, and as such provide strong candidate regions of interest for future work in these fields.

### 4.8. *Strengths and limitations*

Individual neuroimaging studies typically involve 12–20 participants, and as such have relatively low statistical power. Meta-analytic techniques overcome this limitation by pooling data from previously published studies, allowing data from pools of thousands of participants to be examined. Furthermore, while review papers provide subjective, qualitative assessment of a body of literature, meta-analysis uses statistical testing to provide an objective, quantitative summary of a body of research. However, by their nature, the scope of meta-analyses are limited based on the pre-existing literature. As such, they face a number of limitations (e.g. age, sex, and task related effects).

The papers included in the present meta-analyses examined data from participants with a range of different ages. Notably, reporting of participant ages was not standardized across the sample of original experiments included; some studies reported only the mean age for the group, some studies reported only the range of ages for the participant group, some studies provided both the mean age and the range, and some studies provided no information on participant age. To provide an estimate of the ages of the participants involved in the study, we took an average value based on the group age for each experiment that included the mean age of the included participant group. We found that these ages were relatively well matched across our three analyses (Motor Imagery, 29.35 ± 10.69 years, Action Observation, 26.34 ± 6.11 years, Movement Execution, 29.87 ± 9.95, all values present Mean ± StDev of mean of group age). We conclude that the present results should generalize best to an adult population between the ages of approximately 20–40.

It is unclear to what extent sex differences may affect brain activity during the tasks examined in the present meta-analyses. We found the number of male and female participants included in our analyses (where this information was reported in the original manuscripts) to be relatively evenly distributed (Motor Imagery: 52% Male participants, 2342 Males, 2098 females, Action Observation, 48% Male participants, 4991 Male, 5279 females, Movement Execution: 55% Males, 1020 Males, 832 females). While there is some evidence that male participants provide higher self-reported scores when attempting to produce motor imagery (Richardson, 1991), these differences are relatively transient and disappear with only a few trials of practice (Koslow, 1987). Furthermore, there is, to our knowledge, no data that indicates such differences are present when motor imagery has been examined using neuroimaging techniques. We conclude that, as the ratio of male and female participants in the present meta-analyses was relatively equal, our results should generalize to both male and female participants.

A final consideration is that while a range of different movement tasks were examined the in experiments included in the meta-analyses, the majority of movement tasks were relatively simple (e.g. basic flexion/extension movements, simple button pressing tasks, etc). However, as many of the experiments used examined multiple action modalities (e.g. requiring the participant to imagine, observe, or execute the same movement), the complexity of the different movements was relatively well matched between the three main analyses. We conclude that the present results generalize best to actions involving relatively simple movements.

## 5. Conclusions

Previous comparisons between Motor Imagery, Action Observation, and Movement Execution have relied on the results of individual neuroimaging studies, or qualitative comparisons of their respective networks. Here for the first time we provide a quantitative comparison of the brain networks involved in these similar tasks. Our results provide an empirical answer to the longstanding debate over whether these tasks recruit similar brain regions by identifying a consistent premotor, parietal, and somatosensory network, while highlighting notable differences in their recruitment of subcortical structures.

## Data availability

Data from the present analyses are freely available at https://osf.io/3egd5/.

## Declarations of interest

None.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neubiorev.2018.08.003.

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