# The topographical organization of motor processing: An ALE meta-analysis on six action domains and the relevance of Broca's region

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## ARTICLE INFO

## ABSTRACT

Action is a cover term used to refer to a large set of motor processes differing in domain specificities (e.g. execution or observation). Here we review neuroimaging evidence on action processing (N = 416; Subjects = 5912) using quantitative Activation Likelihood Estimation (ALE) and Meta-Analytic Connectivity Modeling (MACM) approaches to delineate the functional specificities of six domains: (1) Action Execution, (2) Action Imitation, (3) Motor Imagery, (4) Action Observation, (5) Motor Learning, (6) Motor Preparation. Our results show distinct functional patterns for the different domains with convergence in posterior BA44 (pBA44) for execution, imitation and imagery processing. The functional connectivity network seeding in the motor-based localized cluster of pBA44 differs from the connectivity network seeding in the (language-related) anterior BA44. The two networks implement distinct cognitive functions. We propose that the motor-related network encompassing pBA44 is recruited when processing movements requiring a mental representation of the action itself.

## 1. Introduction

Humans perform numerous actions every day. Brain lesions, however, are known to hamper this ability (Binkofski et al., 1998; Haaland et al., 2000; Haaland and Harrington, 1996; Hoffman and Strick, 1995; Sirigu et al., 1999). Nevertheless, the specific relation between various sub-processes of actions and their brain basis is still a matter of debate. A large number of functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies have investigated different aspects of action including various levels of action planning down to motor execution of the movement (Ariani et al., 2015; Hanakawa et al., 2008; Mirabella et al., 2012; Monchi et al., 2006). Some of these have reported activation in Broca's area in the inferior frontal gyrus (IFG), also known to be involved in language processing (see Binkofski and Buccino, 2004). This has led to a discussion of the possible domain-generality of Broca's area as supporting both language and action (Fadiga et al., 2009; Nishitani et al., 2005). The aim of the present meta-analysis is to systemically review the available fMRI and PET studies on action, in order to characterize the activation specificities of the different action domains in the brain, and to more closely evaluate the functional nature of Broca's involvement in action experiments.

Prominent models of motor cognition classify actions into distinct domains used to accomplish intentions and goals. (1) Action Execution, the physical execution of an action (Grèzes and Decety, 2001); (2) Action Imitation, the physical execution of a previously or concurrently processed action (Koski et al., 2003); (3) Motor Imagery, the internal representation of an action that is not physically performed (Guillot et al., 2009; Kuhtz-Buschbeck et al., 2003) (4) Action Observation, the watching of an action performed by others (Decety and Grèzes, 1999); (5) Motor Learning, the acquisition of knowledge of an action (Bischoff-Grethe et al., 2004); (6) Motor Preparation/Planning, the process taking place before the physical execution of an action (Wong et al., 2015). The complexity of action processing—which crosses both abstract motor representation and physical realization of movement in space (Olivier et al., 2007)—has stimulated increasing scientific interest in a wide range of fields spanning from medical and rehabilitative neurology to neuropsychology and cognitive neurosciences (Chatterjee, 2018; Ertelt et al., 2007; Franceschini et al., 2010; Mulder, 2007; Pulvermüller, 2018; Salo et al., 2019).

At the neurocognitive level, the exploration of the brain networks for action processing is essential to understanding—first—how the different aspects of motor processes are implemented in the motor regions and in the higher cognitive areas of the cortex. Second, functional analyses of action processing can clarify whether higher cognitive areas involved for

action phenomena also comprise sets of domain-general neural populations, shared with other cognitive systems. Of major relevance here is the internal neural organization of Brodmann Area (BA) 44, the posterior part of Broca's area, in the left IFG, an area long-known to be involved during both motor and language tasks, and thus associated to contrasting neuronal hypotheses on the relationship between action and linguistic computational features (Corballis, 2010; Fiebach and Schubotz, 2006; Fitch and Martins, 2014; Fogassi and Ferrari, 2007; Greenfield, 1991; Häberling et al., 2016; Lametti and Mattar, 2006; Rizzolatti and Arbib, 1998).

Here we propose a meta-analytical review of studies on action processing reported in the neuroscientific literature by employing a different methodological and theoretical approach with respect to that of previous meta-analyses on action (Grèzes and Decety, 2001; Hardwick et al., 2018, 2013; Hétu et al., 2013; Molenberghs et al., 2009; Müller et al., 2018; Yang and Hofmann, 2016). The present approach is motivated by a long-lasting discussion whether both language and action are supported by the same brain structures, as the case of Broca's area might be, suggesting a related evolutionary emergence of the two faculties (Rizzolatti and Arbib, 1998). The answer to a possible relation between the two is complicated by the fact that the various functional MRI studies on action focus on different action (sub-)domains and features.

Here we will approach the current issues in three steps: (1) Characterizing the functional profile of six action domains using Activation Likelihood Estimation (ALE) meta-analysis; (2) Extracting the functional connectivity network for action processing, using the left BA44 as seed region for the Meta-Analytic Connectivity Modeling (MACM); (3) Comparing the functional connectivity network for action processing against the functional connectivity network for language, seeding in the same left BA44 region (Clos et al., 2013; Zaccarella and Friederici, 2017, 2015).

To date, Grèzes and Decety (2001) were among the first to use a meta-analytical approach to motor domain classification by investigating imagery, execution and observation. Such analysis only contained, however, a very small number of studies (only eight studies involving execution tasks were included) and, most importantly, it did not rely on specific statistical tests or validated procedures, but rather the authors identified commonalities across experiments by visually inspecting the foci of activation (Eickhoff et al., 2017; Garrison et al., 2019; Müller et al., 2018). Two current methodologies commonly used to ensure statistical reliability over large collections of functional data are image-based meta-analysis and coordinate-based meta-analysis (Laird et al., 2005b). Image-based meta-analyses use raw activation maps for the original studies as input for functional localization (Salimi-Khorshidi et al., 2009). The major drawback with image-based meta-analysis is the fact that the activation maps are often not published along the studies, thus drastically reducing the sample size of experiments to include in the analysis. Coordinate-based meta-analyses account for this drawback by using 3D localization peaks, which, conversely, are usually reported along the published study. Different approaches to coordinate-based meta-analysis exist (for recent overviews, Müller et al., 2018; Radua and Mataix-Cols, 2012): ALE (Eickhoff et al., 2012; Eickhoff et al., 2017; Eickhoff et al., 2009; Laird et al., 2005a; Turkeltaub et al., 2012); Gaussian-Process Regression (GPR; Salimi-Khorshidi et al., 2011); or Parametric Voxel-Based Meta-Analysis (PVM; Costafreda et al., 2009). ALE is by far the most commonly applied technique, as it allows easy reproducibility and direct comparisons of results across multiple meta-analyses (Graham et al., 2013). Methodologically, the ALE algorithm provides lower susceptibility to false positives (Eickhoff et al., 2016), by testing spatial convergence across experiments in the null space (Albajes-Eizagirre and Radua, 2018), and by modeling activation foci as centroids of a Gaussian probability distribution (Eickhoff et al., 2017). Subject information is weighted, so that foci belonging to studies with bigger sample sizes receive higher weight than the foci from studies with smaller sample sizes. The Gaussian distributions are iteratively summed, with the output being a simulated statistical parametric image

(Laird et al., 2005b). The resulting parametrical image is then anatomically mapped by using user-independent atlases to single locations at each point in a standard Montreal Neurological Institute (MNI; Collins et al., 1994) or Talairach (Talairach and Tournoux, 1988) three-dimensional space.

The ALE algorithm has been already employed for different meta-analyses on separate motor processing domains using large sets of functional data (Caspers et al., 2010; Hardwick et al., 2018, 2013; Kühn et al., 2013; Lesourd et al., 2018; Molenberghs et al., 2012; Yang and Hofmann, 2016; Zapparoli et al., 2017). These previous studies, however, appear to suffer from statistical as well procedural shortcomings (Müller et al., 2018). These may include the fact that region of interest (ROI) analyses, small volume correction (SVC) analyses or whole-brain analyses only reporting a subset of activation foci are not always excluded from the sample set: e.g., Frey and Gerry (2006) in Caspers et al. (2010) and Molenberghs et al. (2012); Nedelko et al. (2010) in Hétu et al. (2013); Lui et al. (2008) and Tanaka and Inui (2002) in Hardwick et al. (2018) and in Lesourd et al. (2018). Moreover, in previous meta-analyses, experiments performed on the same subject group have often been considered as independent (see 2.4), and contrasts not specifically focusing on the research question have been included, e.g. in Hardwick et al. (2018) an experiment in which participants were required to listen to the sound of footsteps (Bidet-Caulet et al., 2005) has been listed in the action observation studies. In Lesourd et al. (2018), not relevant contrasts have been included, e.g. "third-person imitation vs. first-person imitation" (Watanabe et al., 2011).

By following a more rigorous approach to meta-analytical investigations (Müller et al., 2018), our study therefore attempts to offer a comprehensive view of six different action domains simultaneously: Action Execution, Action Imitation, Motor Imagery, Action Observation, Motor Learning, and Motor Preparation. Most importantly, here we include comparative studies across all six action domains. We further seek to address one specific question regarding the role of BA44 in action processing, as raised in the literature (Fadiga et al., 2009; Johnson-Frey et al., 2003). According to Johnson-Frey et al. (2003) for instance, the inferior frontal cortex is suggested to participate to the processing of actions with subjects interacting with objects, as already observed in F5 for monkeys (Gallese et al., 1996). Conversely, following a rostro-caudal hierarchical organization of the frontal lobe (Badre, 2008; Badre and D'Esposito, 2009), object-directedness might not be the feature leading involvement in Broca's area. Rather, this area, and more specifically left BA44, might be involved in processing some more fundamental aspect of movement. In this respect, a long debate has seen the introduction of the concept of representation in the action domain, in a similar way to that of language (Fiebach et al., 2003; Huey et al., 2006; Nishitani and Hari, 2000; Wood and Grafman, 2003). Specifically, mental representations of actions are thought to be involved in abstracting information from events, in an implicit manner, and in selecting and retrieving the same abstract information from memory, according to the new context of application, either guiding or constraining action (Wood and Grafman, 2003). These processes are considered to be recruiting the left ventrolateral prefrontal cortex (VLPFC), spanning also BA44 (Badre and Wagner, 2007; Huey et al., 2006). Moreover, recent data suggest a functional distinction between more anteriorly located linguistic regions of BA44 and more posterior motor regions along BA6 (Clos et al., 2013). Such distinctiveness of the roles played by different sub-regions of BA44 is further supported by a MACM analysis (Clos et al., 2013), which employs user-specified regions as seeds of interest and looks for functional co-activations across the cortex, by providing connectivity models based on functional databases (Robinson et al., 2010; Yu et al., 2018). More specifically, Clos et al. (2013) used the anatomically-defined BA44 as search space (Amunts et al., 1999; Eickhoff et al., 2006; Eickhoff et al., 2005), and showed that the region could be internally subdivided into distinct functional clusters, on the basis of the corresponding co-activation patterns found across the brain for a wide range of functional neuroimaging experiments. To do so, they used all available

functional experiments included in the BrainMap database (Fox and Lancaster, 2002)—unrestricted with respect to cognitive domains. To note, such approach neither investigated the role played by different action domains in the involvement of BA44, nor it questioned the specific feature possibly leading to activity within that region, since it was beyond the focus of the study. On this account, here we provide, first, a comprehensive whole-brain functional profile of six action domains—Action Execution, Action Imitation, Motor Imagery, Action Observation, Motor Learning, and Motor Preparation. Second, since we expected to find convergence in the left IFG, we further assess which domains reliably involve BA44, and we explore the corresponding connectivity network for motor processing seeding in the region. On the basis of previous literature pointing at sub-regional functional differences inside BA44, alongside longstanding interest for action vs. language cognitive representations (Boeckx and Fujita, 2014; Clos et al., 2013; Fadiga et al., 2009; Fujita, 2009; Grafton and Hamilton, 2007; Leung, 2014; Martins et al., 2019; Moro, 2014b, 2014a; Pritchett et al., 2018; Pulvermüller, 2014), we also contrast the observed connectivity network for motor processing in the area against the network seeding in the anterior-ventral BA44. This cluster has been independently shown to be strongly associated to core aspects of human language processing using different criteria in previous studies (Clos et al., 2013; Zaccarella and Friederici, 2015). Moreover, this is to our knowledge the only anatomically-validated internal functional parcellation map for language in BA44 available in the literature. Overall, our goal here is to only use action-relevant studies, split into distinct domain datasets, to precisely explore the convergence for the different motor domains at the whole-brain level first and subsequently in BA44, and to study how the connectivity network in the region is cortically implemented for those specific motor domains.

## 2. Materials and methods

### 2.1. Literature searches

A systematic approach combining different bibliographic databases of life sciences and biomedical information together with previous meta-analyses was adopted to obtain a comprehensive paper selection of the existing literature on action domains. In a first phase, we used PubMed (http://www.ncbi.nlm.nih.gov/pubmed) as the main source for the relevant literature search. The database was screened using multiple search queries and additional filters. Preliminary filters were set up to include: (1) Papers only written in English; (2) Experiments performed on human subjects. The same multiple query search was adapted for each motor domain: (1) execution[Title/Abstract]; (2) imitation[Title/Abstract]; (3) observation[Title/Abstract] AND action[Title/Abstract] AND (fMRI[Title/Abstract] OR PET[Title/Abstract] OR functional magnetic resonance imaging[Title/Abstract] OR positron emission tomography [Title/Abstract]) NOT (MEG[Title/Abstract] OR EEG[Title/Abstract] OR disease[Title/Abstract] OR disorder[Title/Abstract] OR disorders[Title/Abstract] OR patient[Title/Abstract] OR patients[Title/Abstract] OR children[Title/Abstract]). In the case of preparation, an additional "[Title/Abstract]" field was included: (4) preparation[Title/Abstract] OR planning[Title/Abstract] AND action[Title/Abstract], followed by the same criteria. This additional procedure was applied here because of the often interchangeable use of the terms "preparation" and "planning" in the motor literature (e.g., Peters et al., 2018). For motor learning and imagery, a "[Title/Abstract]" field was deleted to avoid redundancy and extreme filtering due do the presence of both the words "motor" and "action". Therefore, we had: (5) motor learning[Title/Abstract], (6) motor imagery[Title/Abstract], followed by the same criteria, as above. The search was performed in May 2018 and produced, overall, 892 identified records. In a second phase, we screened the BrainMap database (May 2018; consisting of 3406 papers and 16901 experiments) using the Sleuth software (version 2.4; Sleuth, BrainMap) with the following criteria: "Normal Mapping", "Activation Only", "Imaging modality: Is

PET" or "Imaging modality: Is fMRI", "Behavioral Domain: Is Action: Execution" or "Behavioral Domain: Is Action: Observation" or "Behavioral Domain: Is Action: Imagination" or, finally, "Behavioral Domain: Is Action: Motor Learning". A list of 506 papers was retrieved. In a third phase, we finally screened previously published meta-analyses and included papers reported therein which were not found in the previous two searches, and which agreed with our current inclusion criteria. We screened the following relevant meta-analyses, in brackets: (1) Action Imitation (Caspers et al., 2010; Molenberghs et al., 2009); (2) Motor Imagery (Hardwick et al., 2018; Hétu et al., 2013); (3) Motor Learning (Hardwick et al., 2013); (4) Action Execution (Hardwick et al., 2018; Molenberghs et al., 2012); and (5) Action Observation (Caspers et al., 2010; Hardwick et al., 2018; Molenberghs et al., 2012). This search resulted in 799 additional papers. The final pool from the three different search procedures together, after duplicates removal, consisted of a total of 1575 articles on the different motor domains under analysis.

### 2.2. Inclusion and exclusion criteria

Abstracts were first screened one-by-one to exclude those articles that met our search criteria but were not directly investigating our current research questions. A graphical representation of the exclusion process is provided in Fig. 1. Experiment-based inclusion criteria were set up in turn. (1) Whole-brain analysis maps: since coordinate-based meta-analyses look for spatial convergence across experiments (Eickhoff et al., 2012), we were allowed to include only whole-brain general linear model analyses, and therefore forced to exclude ROI, SVC or psycho-physiological interaction (PPI) analyses. (2) Stereotactic coordinate systems: coordinates of activation foci had to be provided either in MNI or Talairach reference space. (3) Group age: age was taken into consideration through the exclusion of experiments performed on participant groups, whose mean age is either $< 18$ or $\geq 65$ years. (4) Neurological status: participants needed also to have no known neurological disorders. (5) Physical impairment: neurologically healthy but physically impaired subjects (e.g., amputees) were excluded. (6) Contrast of relevance: all studies were checked to include only those experiments in which at least one contrast was addressing our specific research question. For example, if one is interested in action observation per se, contrasts like "Observation of hand lifting vs. Observation of hand grasping object" should be excluded, in favor of more domain-general contrasts like "Observation of hand lifting vs. Rest" or "Observation of hand lifting vs. Observation of a static hand" (Müller et al., 2018). After the final screening was performed, our dataset included 378 papers (416 experiments; 8953 foci; 5912 subjects), organized in the following way: (1) Action Execution: 96 papers, 106 experiments, 2275 foci, 1266 subjects; (2) Action Imitation: 27 papers, 27 experiments, 747 foci, 415 subjects; (3) Action Observation: 98 papers, 103 experiments, 2409 foci, 1663 subjects; (4) Motor Imagery: 89 papers, 106 experiments, 2004 foci, 1637 subjects; (5) Motor Learning: 51 papers, 57 experiments, 1054 foci, 714 subjects; (6) Motor Preparation: 17 papers, 17 experiments, 464 foci, 217 subjects.

### 2.3. Data categorization

Data from each paper were classified according to the motor domain of investigation. For each contrast, the following relevant information was extracted: (1) Coordinates, classified according to the space in which they were reported (Talairach or MNI); (2) Number of participants; (3) Instructions received in order to correctly perform the task; (4) Description of the experimental stimuli (e.g., video of action, fixation cross, geometrical shapes, etc.); (5) Effector involved in the task (e.g., arm, tongue, hand, legs, etc.); (6) Type of object—if applicable—that the effector was required to work on (e.g., keyboard, button box, etc.); (7) Perspective—if applicable—of the stimulus or of the imagery procedure (i.e., first- or third-person perspective). A detailed summary of journal articles and detailed information concerning all the experiments included
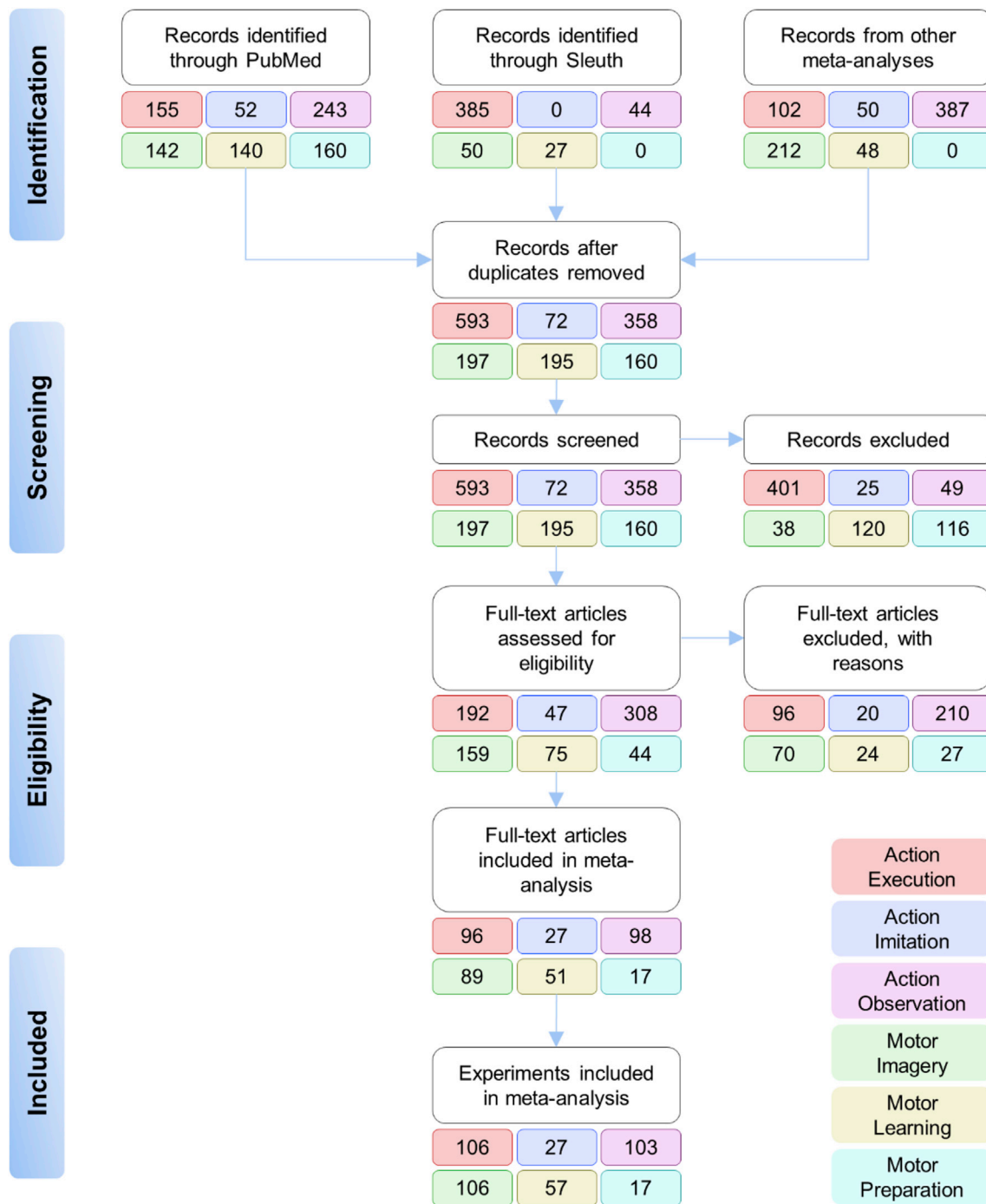
**Fig. 1.** Flowchart illustrating the inclusion-exclusion process leading to the datasets included in the meta-analyses. Each action domain is coded with a specific color: (1) Action Execution (red); (2) Action Imitation (blue); (3) Action Observation (purple); (4) Motor Imagery (green); (5) Motor Learning (yellow); (6) Motor Preparation (light blue).

in the current meta-analyses are reported in Supplementary Tables S1–S6. Experiments included follow the same criteria. They might involve familiar or unfamiliar tools, different effectors (e.g., fingers, hands, lips, mouth, foot, etc.), object-directed and non-object-directed movements, different viewing or imagery perspectives, meaningful and meaningless gestures. Speech (overt or covert) has not been considered, but only actions performed with the corresponding effectors (e.g., movement of the tongue). Sign language gestures have been considered actions in the cases in which subjects were non-signers. Furthermore, datasets were also classified following the same procedural steps. A detailed classification of the studies was performed to enrich the

understating of the phenomena under analysis and to check whether there was the possibility to compare different kind of action features, in accordance with our hypothesis. At the moment, this was not possible due to high differences in the number of studies on features of interest (e.g., effector used in the action).

### 2.4. Activation Likelihood Estimation

All Talairach coordinates were transformed into MNI space. This procedure was performed using the *icbm2tal* algorithm implemented in the GingerALE toolbox (Laird et al., 2010; Lancaster et al., 2007) and

available at https://www.brainmap.org/ale. Contrasts and their respective activation coordinates were pooled per subject group. Hence, two experiments in the same paper were considered as one in the case where the subject group was the same, or different if the two groups differed. This procedure was applied to control for non-independence effects in the same group of subjects being involved in similar cognitive processes across different experiments (Müller et al., 2018). Non-independence effects can have considerable negative impact on the statistical validity of the meta-analysis (Turkeltaub et al., 2012). The ALE algorithm was used to perform the coordinate-based meta-analysis (Eickhoff et al., 2009; Turkeltaub et al., 2002). GingerALE (version 2.3.6) was employed to run the ALE algorithm (Eickhoff et al., 2017). ALE algorithm tests for spatial convergence of neuroimaging findings against a null-distribution of random spatial association of experiments, assessing clusters where convergence is greater than expected by chance (Eickhoff et al., 2009; Müller et al., 2018; Turkeltaub et al., 2002). For each ALE calculation described below a more conservative mask size was selected as well as a more conservative Turkeltaub non-additive method (Turkeltaub et al., 2012), which correct for within-experiment effects derived from the proximity of foci reported by experiments (Eickhoff et al., 2012). Three types of analyses were conducted: Single and contrast studies of different action domains (2.4.1); Multi-domain overlap cluster analysis in BA44 (2.4.2); MACM localizing co-activation patterns of two different sub-regions of BA44 (2.4.3).

### 2.4.1. Studies of different action domains

Each action domain—Action Execution, Action Imitation, Action Observation, Motor Imagery, Motor Learning and Motor Preparation—was analyzed individually. This allowed us to have a general overview of the neural mechanisms involved in each specific domain using wide samples of data. For each domain, the following amount of experiments was analyzed: (1) Action Execution (N = 106); (2) Action Imitation (N = 27); (3) Action Observation (N = 103); (4) Motor Imagery (N = 106); (5) Motor Learning (N = 57); (6) Motor Preparation (N = 17). All domains included at least 17 experiments, which enabled us to have large enough datasets for sufficient statistical power and reliability, thus assuring that results were not driven by single experiments (Eickhoff et al., 2016; Müller et al., 2018). Significance was tested using 1000 permutations with a cluster forming threshold of p < 0.001 (uncorrected). In order to increase test sensitivity to false positives (Müller et al., 2018), significance was corrected with a cluster-level family-wise error threshold of p < 0.05 (cFWE; Eickhoff et al., 2016), as a gold standard approach used by other meta-analytic studies (Hardwick et al., 2018; Teghil et al., 2019).

Supplementary contrast studies were performed across all the domains (see Supplementary Tables S13–S48), with one single limitation. In order to compare two different datasets, these cannot have a large discrepancy in number of experiments. Specifically, a dataset A has to be maximum four times bigger than a dataset B, and vice versa, in order to be comparable (Eickhoff et al., 2016). Hence, of the 15 possible contrast studies, only 12 were performed. The three excluded contrasts are: (1) Motor Preparation (N = 17) vs. Action Observation (N = 103); (2) Motor Preparation vs. Action Execution (N = 106); (3) Motor Preparation vs. Motor Imagery (N = 106). Contrast studies and all their sub-steps were performed again with GingerALE (Eickhoff et al., 2011), according to the following procedure: (1) Single studies were performed; (2) The two single studies to compare were pooled together in a common foci list (the "merge & save foci" function was used); (3) A single study was performed on the pooled foci list, maintaining the same statistical features as for the previous single studies; (4) The three resulting single studies (the two original single studies and the pooled one) were loaded into the software; (5) The contrast analysis was executed. When performing contrast analyses, GingerALE randomly divides the pooled foci list into two datasets of the original size as the original datasets. In a second step, voxel-wise differences between them are recorded through a subtracting procedure: for each new dataset, an ALE image is produced, subtracted from the

other, and, finally, a comparison with the real data is performed. This procedure was repeated 10,000 times, introducing a higher number of permutations with respect to single studies (Alain et al., 2018; Yu et al., 2018). Given the absence of cluster-level inference in contrast analyses (Hoffman and Morcom, 2018), an uncorrected threshold of p < 0.05 was adopted. The minimum cluster volume was set to 100 mm$^3$.

### 2.4.2. Multi-domain overlapping cluster analysis in BA44

The goal of this analysis was to determine the location of convergence of the different motor processes in BA44, according to the hypothesis that the most posterior sub-region might be more consistently involved during motoric tasks. An overlapping cluster analysis was performed across domains for which we were able to identify at least one cluster of activity reaching a posterior portion of BA44. The FSL software (FMRIB, University of Oxford, UK) was used to import, binarize and multiply the single studies together, as well as for cluster indexing and center of mass extraction of the overlapping clusters. The degree of lateralization between left and right supra-thresholded BA44 voxels was further computed to evaluate interhemispheric asymmetry of action processing in the region. Laterality over ALE scores was assessed using AveLI (version 2017.4.3; Matsuo et al., 2012), available at http://aveli.we b.fc2.com, with laterality index ranging from 1 (completely left-lateralized) to −1 (completely right-lateralized). The cytoarchitectonically defined volume of interest (VOI) of left and right BA44 from the SPM Anatomy Toolbox (version 2.2c; Eickhoff et al., 2007, 2005) served as search space for this analysis (Trettenbrein et al., 2019).

### 2.4.3. Meta-Analytic Connectivity Modeling

A MACM analysis was performed to obtain relevant information about functional networks, through the identification of regions with above-chance covariance (Robinson et al., 2010; Yu et al., 2018). This was done using the BrainMap database (screened in January 2019). The purpose of MACM is to identify co-activation patterns associated with specific ROIs (Eickhoff et al., 2011; Yu et al., 2018). Here we wanted to confirm the hypothesis that anterior and posterior portions of BA44 are associated with differing cortical modules and different co-activation patterns (Clos et al., 2013; Laird et al., 2009). Specifically, we used the pBA44-centered cluster identified in the conjunction analysis of three action domains (Action Execution, Action Imitation, Motor Imagery) and Cluster 3 (C3) from Clos et al. (2013), as seed regions for the MACM analysis.

Using the anatomically-defined BA44 as search space (Amunts et al., 1999; Eickhoff et al., 2006; Eickhoff et al., 2005), Clos et al. (2013) employed MACM to show that BA44 could be internally subdivided into five different functional clusters, according to their corresponding co-activation patterns found across the brain for a wide range of functional neuroimaging experiments. The two posterior clusters were primarily associated with action processes (C1 and C4). Anteriorly, clusters C2 and C5, bordering the inferior frontal junction and sulcus respectively, were related to working memory processing and to some aspects of speech. Finally, the anterior-ventral cluster C3 was strongly associated with core aspects of language, including syntax, semantics and phonology. As for syntax, Zaccarella and Friederici (2015) found that only the most anterior-ventral cluster C3 was selectively involved in fundamental computations implementing syntactic processing in language (see also Zaccarella et al., 2017a). This is further supported by fact that cluster C3 forms a functional connectivity network, together with the left posterior temporal cortex and other subcortical regions, which is strongly sensitive to task-dependent linguistic manipulations (Clos et al., 2013). Thus, it appears that the anterior-ventral section of BA44 might be especially sensitive to language processes, and that it is part of a large-scale functional network at work during linguistic experiments. Cluster C3 was freely downloaded as NIfTI file at http://www.fz-juel ich.de/SharedDocs/Downloads/INM/INM-1/DE/Area44_Parcellation.ht ml?nn=534496.

Both masks were uploaded as seed regions into Sleuth in two separate

analyses, using the following command: "Locations", "MNI Image is". Further criteria were set: (1) "Normal Mapping" and (2) "Activations only". In this way, we were able to identify all the experiments from the database activating at least the foci within the given mask. The co-ordinates were automatically exported as a GingerALE text and converted into MNI space. As a standard procedure (Eickhoff et al., 2011; Molen-berghs et al., 2016; Yu et al., 2018), the new datasets were tested for significance using GingerALE with the same statistical criteria previously applied in the single studies of action domains (cFWE of $p < 0.05$, threshold of $p < 0.001$ (uncorrected), 1000 permutations), with the only difference being that the foci for MACM are not clustered together by subject group (Turkeltaub et al., 2012). The composition of the two datasets is the following: (1) motor-related cluster (151 experiments, 2310 subjects, 3592 foci) vs. (2) language-related cluster (178 experiments, 2659 subjects, 2834 foci). Once co-activation patterns were identified, a contrast analysis was performed, in which the results of the single studies were compared. The same statistical criteria were applied (uncorrected threshold of $p < 0.05$, minimum cluster volume was set to 100 mm$^3$, 10,000 permutations). Since the anterior-ventral cluster C3 from Clos et al. (2013) was validated thorough external post-hoc criteria not used in the present study, we run a supplementary MACM on a distinct BA44 cluster obtained from a recent meta-analysis on language processing (Zaccarella et al., 2017b). Our goal was to test whether the selection of the language-related cluster in BA44 is essentially independent of the criteria used to define the cluster. Thus, we expected high similarity between the co-activation patterns of the different seeds responding to language in BA44. Contrary to Clos et al. (2013), Zaccarella et al. (2017b) used the same procedure as the one we adopted in our study—the foci were first selectively extracted from the literature, and then fed into the ALE analysis to search for functional convergence at the whole-brain level. The meta-analysis pooled together functional studies (19 experiments, 295 subjects, 114 foci) contrasting grammatical linguistic sequences (sentences or phrases) against word-list sequences to identify areas of convergence for structure-building processes in language. In their main analysis, the authors showed strong convergence for language processing in different regions of the left-hemispheric linguistic network, the bigger cluster being in the IFG (7080 mm$^3$) and comprising both the pars opercularis (BA44) and the pars triangularis (BA45). For current purposes, we overlapped the IFG cluster from Zaccarella et al. (2017b) with the Area 44 from the SPM Anatomy Toolbox (Eickhoff et al., 2006, 2005). The resulting cluster served as seed for the MACM analysis. We further found that about 70% of all voxels of the BA44 cluster fell inside the C3 cluster from Clos et al. (2013), with the remaining ones minimally bordering the contiguous clusters. MACM procedure and statistical criteria were kept alike as above.

### 2.5. Reporting and displaying the results

ALE results were firstly automatically exported from GingerALE as NIfTI files (Belyk and Brown, 2014; Garrison et al., 2013; Zaccarella et al., 2017b), overlaid onto a standard MNI template (Col-in27_T1_seg_MNI; www.brainmap.org/ale/Colin27_T1_seg_MNI.nii.gz) and then displayed using the Mango brain visualization software (version 4.0.1; http://ric.uthscsa.edu/mango/). Consistent with previous meta-analyses, labels were automatically assigned using the Talairach atlas daemon (www.talairach.org) included in GingerALE (Lancaster et al., 2000; Luk et al., 2012; Sundermann et al., 2014; Wiener et al., 2010). In the results, two different coordinate sets are reported: the weighted center of the cluster and the location of the maximum ALE values. Further information that we report is: (1) Volume of the clusters; (2) ALE or Z scores; and (3) Location of the clusters. For what concerns the ALE and Z scores, the ALE score is made available for single studies and conjunction analyses; the Z score is used to show significance in all contrast analyses.

## 3. Results

In the following, we display the results of the ALE meta-analyses we conducted. These are: (1) Studies of six specific action domains; (2) Overlapping cluster analysis of domains with BA44 activity; (3) MACM analysis for Action and Language clusters centered in left BA44. Cluster localization and statistical information for contrast studies and conjunction analyses across domains can be found in Supplementary Tables S7–S59.

### 3.1. Studies of specific action domains

Single studies were conducted on separate datasets for the following six action domains: Action Execution, Action Imitation, Action Observation, Motor Imagery, Motor Learning and Motor Preparation (Fig. 2). The only two regions showing convergence within all six domains are, bilaterally, the premotor cortex (BA6) and to a much lesser extent the inferior parietal cortex (BA40; Supplementary Table S60). Domain specificities are reflected in regions of the occipital cortex, the parietal cortex and the inferior frontal cortex. Convergence in the most posterior left inferior frontal region of Broca's area (BA44) is found for Action Execution, Action Imitation and Motor Imagery only.

#### 3.1.1. Action execution

Action Execution primarily involves the left and right motor/pre-motor cortex (BA6/4) and the supplementary motor area (SMA), the ventral anterior cingulate cortex (BA24), and the right parietal cortex (BA40). Subcortically, additional clusters comprise areas of the thalamus, putamen and cerebellum (Fig. 2A and Supplementary Table S7). Marginal convergence is found in the insula and in the posterior left and right Broca's area (BA44; Supplementary Table S54).

#### 3.1.2. Action imitation

Action Imitation comprises the left and right premotor cortex (BA6), the supramarginal gyrus and precuneus in the parietal cortex (BA40/BA7), and occipital (BA19) and occipitotemporal regions (BA37; Fig. 2B and Supplementary Tables S8 and S55). Convergence is also found in the left and right BA44. Only in the right hemisphere, the cluster extends dorsally to include BA9.

#### 3.1.3. Motor imagery

Motor Imagery comprises the left and right premotor cortex (BA6), the left primary motor cortex (BA4), the bilateral medial prefrontal cortex (BA9), together with areas of the parietal cortex (BA7/40; Fig. 2C and Supplementary Tables S9 and S56). Spatial convergence is also found in the left and right BA44 along the insula. Subcortically, additional clusters comprise areas of the putamen and cerebellum.

#### 3.1.4. Action observation

Action Observation shows convergence in the left and right premotor cortex (BA6), the medial prefrontal cortex (BA9), occipital (BA18/19) and occipitotemporal regions (BA37), the superior temporal cortex (BA39) and the inferior parietal lobule (BA40; see Fig. 2D and Supplementary Table S10). No consistent convergence is reported in the left IFG, only a dorsal portion of BA44 is found in a cluster centered in BA9 (Supplementary Table S57). Subcortically, additional clusters comprise areas of the culmen as part of the cerebellum.

#### 3.1.5. Motor learning

Motor Learning shows a small network of cortical and subcortical areas, mainly spreading in the left hemisphere (Fig. 2E and Supplementary Tables S11 and S58). These include motor (BA4) and premotor areas (BA6) with bilateral precuneus (BA7). Subcortically, activations are found in the putamen and in the anterior nucleus of the thalamus.
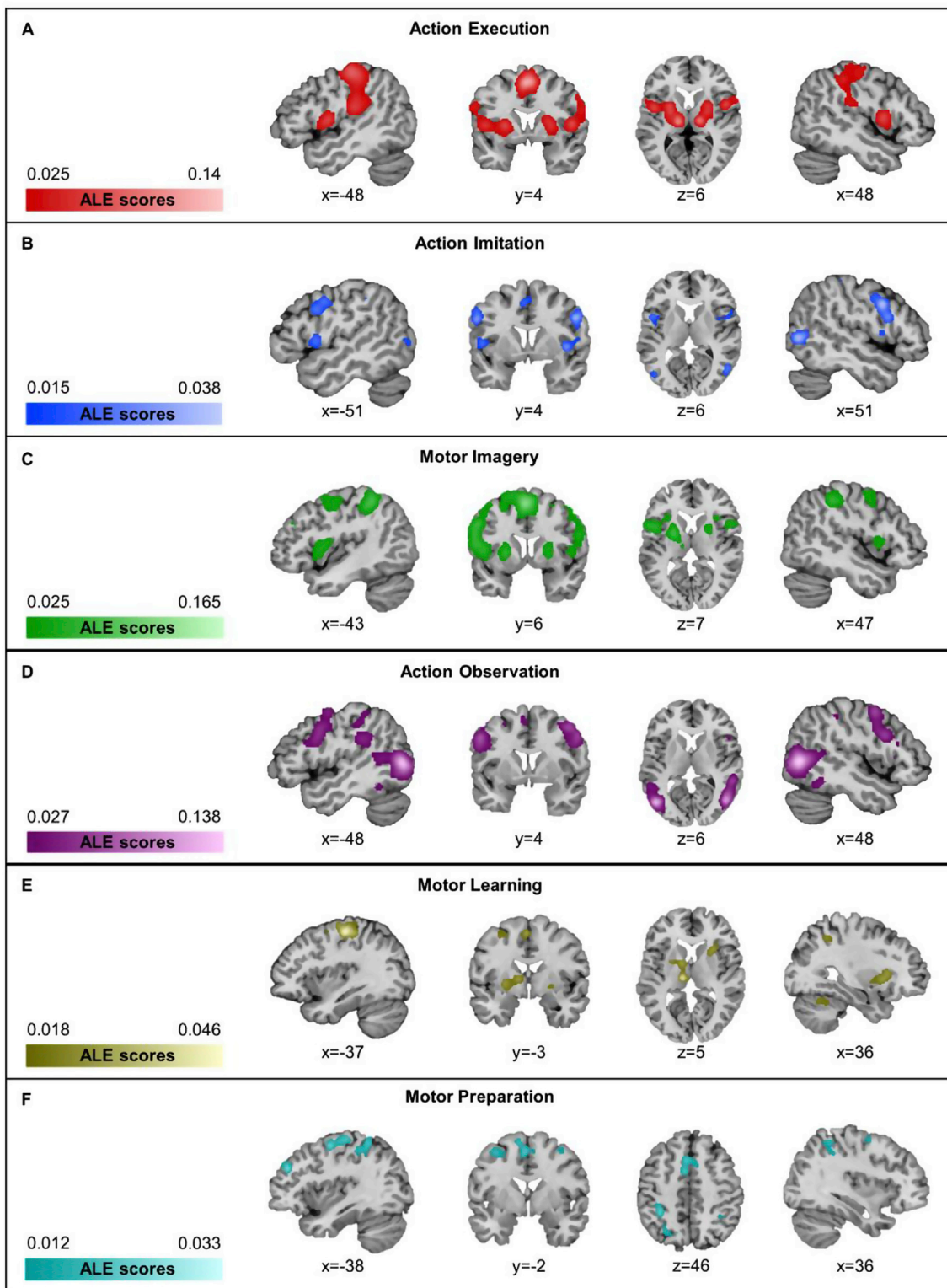
**Fig. 2.** Overview of significant clusters resulting from the single studies. Each domain is presented separately: (**A**) Action Execution; (**B**) Action Imitation; (**C**) Motor Imagery; (**D**) Action Observation; (**E**) Motor Learning; (**F**) Motor Preparation. Coordinates are in the MNI space.

### 3.1.6. Motor preparation or planning

Motor Preparation also shows involvement of motor (BA4) and premotor (BA6) areas together with the dorsal anterior cingulate (BA32) of the medial frontal gyrus (Fig. 2F and Supplementary Tables S12 and S58). Additional regions comprise the bilateral precuneus.

### 3.2. Overlapping cluster analysis in BA44

The three domains showing convergence in BA44 bilaterally—Action Execution, Action Imitation and Motor Imagery—overlap in the most posterior region of BA44, along BA6 (see Supplementary Fig. S1). Convergence in BA44 was not lateralized (AveLI score $< 0.1$). We also

found bilateral convergence in the SMA (BA6) and in the infero-parietal lobe (BA40).

## 3.3. MACM analysis: BA44 networks for action and language

The connectivity modeling was used to test co-activation differences between the motor-related cluster centered in posterior BA44 from the conjunction analysis across Action Execution, Action Imitation and Motor Imagery (see 3.2) and the anterior-ventral BA44 language-related cluster from Clos et al. (2013; see also Zaccarella et al., 2017a). In order to obtain brain areas that are selectively involved in the language network and in the action network, we performed a contrast analysis between the co-activation datasets for the two BA44 clusters. A representation of the contrast studies, as they will be discussed below, can be found in Fig. 3. Single studies, conjunction analysis and histograms representing the behavioral domain profiles can be found in the Supplementary Material (Supplementary Fig. S2 and Supplementary Tables S49–S53).

### 3.3.1. Co-activation patterns derived from the motor-related posterior sub-region of BA44

The motor co-activation map for the posterior sub-region of BA44 consists of a bilateral posterior-fronto-parietal cortical network comprising the premotor cortex and the SMA (BA6), the postcentral gyrus (BA2) and the parietal lobule (BA40). Additional subcortical co-activation comprises the putamen and the globus pallidus (see Supplementary Table S51).
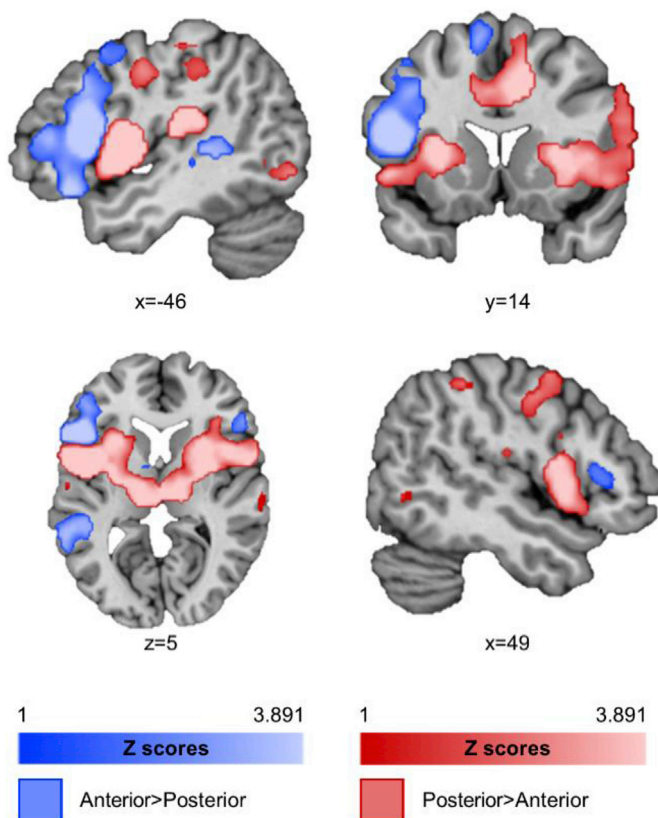


**Fig. 3.** Overview of significant clusters resulting from the MACM analysis. Two co-activation patterns were obtained from different sub-regions centered within BA44, one anterior and one posterior. Co-activations patterns resulting from anterior BA44 are contrasted with the patterns derived from the posterior cluster (blue); co-activations patterns resulting from posterior BA44 are contrasted with the patterns derived from the anterior cluster (red). Coordinates are in the MNI space.

### 3.3.2. Co-activation patterns derived from the language-related anterior sub-region of BA44

The language co-activation map for the anterior sub-region of BA44 consists of a bilateral anterior-fronto-temporal network including B45/46/47, the more dorsal BA9, and the left posterior superior temporal gyrus BA21/BA41 (see Supplementary Table S52). To note, the co-activation map seeding in the language-related BA44 cluster from Zaccarella et al. (2017b) revealed essentially identical results as the one obtained when seeding in the language-related C3 cluster from Clos et al. (2013; see Supplementary Fig. S3 and Supplementary Table S61). This suggests that the selection of the language-related cluster in BA44 is essentially independent of the approach used to define the cluster, and it confirms strong sensitivity of anterior-ventral BA44 to language-related processes (Zaccarella and Friederici, 2017).

## 4. Discussion

The current study set out to offer, first, a comprehensive functional profile of six action domains—Action Execution, Action Imitation, Motor Imagery, Action Observation, Motor Learning, and Motor Preparation—using quantitative meta-analytic estimations of the totality of the activation foci reported for motor experiments in the existing neuroscientific literature. Second, it aimed at more closely assessing supradomain specificities driving motor activity in a well-known high cognitive function area—BA44 in the left IFG. As such, we looked at the corresponding co-activation network between the left pBA44 and the other areas of the brain, and compared it to the co-activation network for language seeding in the same anatomical region, in aBA44 (Clos et al., 2013; Zaccarella and Friederici, 2017, 2015).

### 4.1. Different action domains

Within the present context, action domains have been studied independently from one another. The amount of controlled data available made it possible for us to delineate broad networks of convergence areas for each domain. This is the first time that six action domains have been studied as part of the same dataset. This improves the comparative quality of our work, being the same inclusion criteria and the same statistical features applied to each domain. To our knowledge, this is also the first time that the discussion on motor preparation or planning is taken from a meta-analytical perspective.

#### 4.1.1. Action execution

The actual execution of actions involves a bilateral infero-fronto-parietal network including the motor and premotor cortex, the SMA and the parietal lobule. Among the well-known motor areas being recruited during motor execution—the SMA, the primary somatosensory cortex and the primary motor cortex (Green et al., 2018; Grefkes et al., 2008; Roland et al., 1980)—the premotor cortex is especially thought to be involved in the preparation and organization of movements (Wise, 1985), and it is more generally linked to the presence of a motor output (Schubotz and Von Cramon, 2003; Schulz et al., 2015). In the IFG, right BA44 has been repeatedly considered to be involved in motor processes (Hoffstaedter et al., 2013; Sauvage et al., 2013). A recent parcellation study (Hartwigsen et al., 2018) proposed that at least two posterior sub-regions within the right BA44 share motor-related features, these being either prediction of motor outcomes or integration of visuomotor, auditory-motor, or somatosensory-motor information. A possible role for left pBA44 in action processing will be discussed in depth in 4.2. Furthermore, involvement of the right inferior parietal lobule during action execution has been strongly associated with the generation of sensory feedback (Chaminade and Decety, 2002) and motor intentions (Mattingley et al., 1998). As in Hardwick et al. (2018), we found a recruitment of a cerebello-thalamo-motor cortical network, consistent with previous models of coordination demands, motor planning or correction (Lehéricy et al., 2006; Sauvage et al., 2011; Schlerf et al., 2010).

### 4.1.2. Action imitation

Action Execution and Imitation of the same action share cognitive similarities, indeed a common involvement of the primary motor cortex, the premotor cortex, and the SMA is found. Compared to Action Execution, Action Imitation shows higher involvement of the left inferior and bilateral superior parietal lobules (Supplementary Table S14), which might suggest a source of specialization in the area, namely the implementation of perception-action matching processes transforming visual information into motor commands (Williams et al., 2007). In this sense, while the right inferior parietal lobule is likely to be associated with sensory feedback and with generating motor intentions, the left homologue has been more strongly associated with perspective taking in computing sensory-motor associations (Meltzoff and Decety, 2003). The specific involvement of the bilateral superior parietal lobule in Action Imitation finds convergence with a previous meta-analysis investigating the process (Lesourd et al., 2018). The superior parietal lobule has been proposed, indeed, to be part of a broader tool-use network encompassing also the bilateral IFG and the ventral premotor cortex as well as the middle temporal gyrus (Bi et al., 2015; Buxbaum, 2017). The specific role of the left pBA44, is discussed in a broader perspective in Section 4.2.

### 4.1.3. Motor imagery

Motor Imagery results show a clear involvement of the bilateral premotor cortex and of the left primary motor cortex. The last finding holds against previous models and meta-analytical studies (Annett, 1995; Hardwick et al., 2018; Hétu et al., 2013), according to which the primary motor cortex is not involved in action simulation. We propose, instead, a closer relationship between imagination and execution, since the processing of motor, temporal and spatial information is equally required in both (Collet and Guillot, 2005; Decety, 1996; Filgueiras et al., 2018; Jeannerod, 2001). In our analysis, the same cluster extended towards the IFG from its dorsal portion (BA9) to the more posterior one (BA44, also see Section 4.2). A similar pattern of activation can be found in the right hemisphere, with a further cluster reaching BA47. We would like to claim a cognitive-motor link arising in BA9 (Haker et al., 2013), which might be resulting in spatial attention processing, at least in the right hemisphere (Hartwigsen et al., 2018). Among the other convergent areas, we believe that the posterior portions of the right IFG are involved in inhibitory processes due to preventing an actual motor output (Rieger et al., 2017), as proposed also by recent parcellation and meta-analytical studies (Cieslik et al., 2015; Hartwigsen et al., 2018; Zhang et al., 2017).

### 4.1.4. Action observation

As expected, the main cluster involved during action observation spans across the occipital and temporal lobes, reaching the left inferior and superior temporal gyri, the fusiform gyrus and the insula. The occipito-temporal regions and the fusiform gyrus are thought to be involved in processing biological motion, of both conspecifics and non-conspecifics (Buccino et al., 2004; Georgescu et al., 2014; Jastorff et al., 2016). Consistently with the proposal of an action observation network (Grafton, 2009), we also found an involvement of the bilateral premotor cortex, BA9 and right-hemispheric convergence across BA44 and BA46. As seen before, the most dorsal part of the IFG, reaching the superior frontal gyrus, has been referred to as a link between cognitive and motor processes (Haker et al., 2013). However, a further function that BA9 might be playing in this context is the one of learning action patterns, as it has already been found involved in observation learning and spatial memory (Curtis, 2004; Leung et al., 2002; Wu et al., 2013). Two further clusters found convergence in the occipital cortex, in the bilateral visual association area (BA18), and in the right parieto-occipital BA7, including the precuneus, involved in integration of spatial information (Catalan et al., 1998; Grafton et al., 1992; Haslinger et al., 2002).

### 4.1.5. Motor learning

Learning movements involves both cortical and subcortical regions, mainly in the left hemisphere. Subcortically, convergence clustered in the putamen and in the thalamus. While the putamen was found to be extending bilaterally, the thalamus seems to be recruited only by the left hemisphere. Both the cerebellum and the basal ganglia are thought to be involved in different phases of the learning process. The cerebellum is thought to be recruited during the early stages of the learning process, while the basal ganglia comes into play only at a later stage (Debaere et al., 2004; Doyon et al., 2003; Floyer-Lea and Matthews, 2004).

### 4.1.6. Motor preparation

Motor Preparation shares large part of the network found for Action Execution and Action Imitation. Interestingly, in the left premotor cortex converge spans across the medial frontal gyrus (BA32). Indeed, the medial anterior prefrontal cortex has been reported in various monitoring experiments, especially when the task required movements at specific time points, and in anticipatory processes related to future actions to be performed (Koechlin et al., 2000; Ridderinkhof et al., 2004). As a matter of fact, we found strong convergence in a left-hemispheric portion of the dorsolateral prefrontal cortex and of the middle frontal gyrus (BA8 and BA9) when comparing Motor Preparation against Action Imitation. This involvement might be due to sustaining the attentional demands of the task (MacDonald et al., 2000) and to processing inhibitory mechanisms instantiated by participants during a phase in which the motor plan is available but still not executed (Blasi et al., 2006).

### 4.2. Supradomain processes underlying actions

We identified three domains sharing common convergence in left pBA44—Action Execution, Action Imitation and Motor Imagery. The left inferior frontal cortex is thought to be involved during the processing of actions in which there is an interaction with an object. This has been proposed for action observation of object-directed actions (Baumgaertner et al., 2007; Cattaneo and Rizzolatti, 2009), for execution of grasping or reaching movements involving complex or small objects (Binkofski et al., 1999; Di Bono et al., 2015; Ehrsson et al., 2001), for pantomimes of tool use (Goldenberg et al., 2007), and for action imitation (Nishitani and Hari, 2000). Because of this, Broca's area has been suggested to play an important role as a hub of the mirror neuron system, and as a homologue of the macaque's F5 (Di Bono et al., 2015; Gallese et al., 1996; Higuchi et al., 2009; Morin and Grèzes, 2008; Petrides et al., 2012; Petrides and Pandya, 2002; Rizzolatti and Arbib, 1998). However, the range of actions encoded in Broca's area, especially in BA44, seems to include also non-object-directed movements (e.g., Lui et al., 2008), although a preference for actions integrating objects is reported (Agnew et al., 2012; Muthukumaraswamy et al., 2004). To note, the relationship between Broca's area and F5 is still under debate. Recent studies, indeed, suggest a differentiation between F5 and a neighboring area in the fundus of the inferior arcuate sulcus, that might probably resemble BA44 of the human brain (Belmalih et al., 2009; Gerbella et al., 2011; Petrides, 2005; Petrides et al., 2005; Sharma et al., 2019). Activity within the sulcus has been reportedly associated with both hand and mouth movements or the combination of the two (Hage and Nieder, 2015; Petrides et al., 2005; Sharma et al., 2019). The heterogeneity of the tasks, stimuli and the small number of studies per effector so far available make it however difficult to employ ALE analyses to tackle effector-specific features in a comparative perspective between human and macaque's functionally homologous areas. From our meta-analysis, the six different action domains differentially involve BA44. While Action Execution, Action Imitation and Motor Imagery involve BA44 bilaterally, Action Observation, Motor Learning and Motor Preparation do not. At this point, the question arises what aspect of action requires the recruitment of BA44. We would like to suggest that, in the three domains, the respective studies all use tasks which require a mental representation of the action bridging the input/instruction to the action to be performed (Huey et al., 2006; Wood and Grafman, 2003). More specifically, action execution is often triggered by a verbal/auditory cue requiring access to a mental representation of the action. Action imitation is often triggered by a visual input that must be

imitated after perception has been completed, requiring a mental representation in short term memory. Motor imagery is triggered by a verbal or visual input (often instruction) requiring its mental representation.

Observation of an action, learning of sequences of movements or preparation of these do not necessarily require the mental-conceptual representation of the action and therefore these experimental domains might not need BA44 in addition to premotor and motor areas. Accessing a mental representation might not be necessary while perceiving a video or a picture of an action, since there is no motor/procedural information to be retrieved or selected. What is relevant during observation is more likely to be: (1) a forward model of the action and of its outcome; (2) an understanding of the action and the integration of the latter within a specific context. However, forward dynamic or output models are not specific to a single motor domain, but they are shared across these domains and they consist in the application of an intention to what observed (Blakemore and Decety, 2001; de Vignemont and Haggard, 2008). Being domain-general processes, and given the fact that forward models seem to be encoded in the posterior parietal cortex, it is unlikely that activity within BA44 reflects these forward processes (Gazzola et al., 2007). As in previous work investigating forward models across motor domains (Desmurget et al., 1999; Fontana et al., 2012; Gazzola et al., 2007; Mulliken et al., 2008), we identified a cluster in the posterior parietal cortex (BA7), especially evident for action observation. The present data suggest that posterior BA44 is involved in mental representations of actions. These representations are only needed in contexts in which the motor aspects of an action have to be directly retrieved, providing an explanation for the absence of involvement of the area in action observation. Furthermore, the recruitment of BA44 and BA45 in the motor domain has been often linked to processes related to object-directed actions, especially when observing these specific type of actions (de la Rosa et al., 2016; Johnson-Frey et al., 2003; Nishitani and Hari, 2000). However, these left IFG clusters are not consistently reported in the literature and moreover they are reported also for non-object-directed actions or actions with unclear intentions, also when performed with different effectors (Agnew et al., 2012; Ge et al., 2018; Lui et al., 2008; Wheaton et al., 2004). In addition, studies reporting activity within Broca's area, with regards to action observation, localize neural activity in an anterior portion of BA44 or directly in BA45 (de la Rosa et al., 2016; Decety et al., 1997; Grafton et al., 1996; Rizzolatti et al., 1996). Thus, considering exclusively meaningful object-directed actions in our meta-analysis would have introduced an unreasoned bias in focusing on a specific type of action. According to our hypotheses, activity within Broca's is functionally differentiated across its sub-regions. Involvement of BA45 and of the anterior portion of BA44 is indeed likely to reflect retrieval of information from semantic memory and the integration of an action with its context (Badre and Wagner, 2007; Hoeren et al., 2013), processes not necessarily required in the experiments included in our dataset. For what concerns motor preparation, many experiments (e.g., Beurze et al., 2007; Johnson-Frey et al., 2002) do not investigate the preparation of the action per se, but only some of the sub-processes involved. It is possible that sub-processes of planning do not require the same access to mental representations.

Finally, we would like to point out that each action domain might present different actions or action features within itself. This of relevance especially given the somatotopic organization of the premotor cortex (Penfield and Boldrey, 1937). Although all datasets tested here include actions performed with different effectors (i.e., upper limbs, lower limbs, face, whole body), our study does not allow for low-level effector-specific comparisons. As a matter of fact, contrast analyses between effectors across all six datasets would violate statistical requirements for meta-analytical contrast studies (Eickhoff et al., 2016; see also 2.4.1), given the reduced amount of experiments so far available for some of the effectors (e.g. legs; see also Supplementary Tables S1–S6: Effector). New studies investigating the use of different effectors are therefore awaited, before we can draw conclusions on the cortical representation of effector specificities. To note, when approaching lower-level features by looking

at the studies included in the current meta-analysis which support the involvement of BA44 in the Execution domain, we see an involvement of the area independently of the effector used (Brown et al., 2008; Ehrsson et al., 2000; Gerardin et al., 2003). On these data, we suggest that focusing on a single effector should not lead to different activation patterns with respect to BA44.

### 4.3. Differentiating action and language networks

Given that we found BA44 to be involved in some subdomains of action, the question is whether those parts of the area observed in subdomains of action are part of the same network as reported for language. A direct comparison between the present meta-analytical data for action and those of an earlier work on language (Clos et al., 2013) reveals a non-overlap of the crucial activation in BA44, with the activation pattern for language being more anterior, and the activation pattern for motor processing being more posterior. To note, the subdivision of BA44 into an anterior area and a posterior one is in line with a previous receptor-based parcellation of Broca's area which used multi-receptor mapping to assess density difference profiles of different neurotransmitters in post-mortem brains (Amunts et al., 2010; see also Zilles and Amunts, 2018). Such differentiation is strongly consistent with the first level of clustering (K = 2) in Clos et al. (2013), with the posterior part being more associated with action, and the anterior part, primarily associated with language. As put forward by Clos et al. (2013), given that transmitter receptors are key molecules for neurotransmission, their heterogeneity at the molecular level might lead to a similar differentiation at the functional level and at the connectivity level. Indeed, there is no overlap in the functional networks of action and language, and in the behavioral domain profiles associated with each seed region, especially when it comes to action, cognition, and perception. The co-activation pattern derived from aBA44 is mostly associated with language and memory when compared to the one derived from pBA44. The opposite is true for action execution and somesthesis. These results make the view of a joint neural basis of language and action as proposed earlier (Arbib and Rizzolatti, 1997; Binkofski and Buccino, 2004; Kühn et al., 2013; Martins et al., 2019; Rizzolatti and Arbib, 1998) less likely. Rather, it appears that language and action are supported by distinct neural networks. Furthermore, a sub-cortical differentiation is also evident, with cerebellum and basal ganglia functionally linked to pBA44. These two structures were observed at the single-domain level for Action Execution, Motor Imagery, Motor Learning and to a smaller extent for Action Observation. The cerebellum has been recently hypothesized to have a role in coordinated movements, i.e. bimanual hand movements, finger extension, arm-finger movements, precision grip, but also coordination of a motor rhythm with an external (visual or auditory) cue (Nair et al., 2003; Ramnani et al., 2001; Repp, 2005; Thach et al., 1992). Similarly, the basal ganglia has been proposed to be involved in coordination of motor behavior and on-line monitoring, especially in motor tasks requiring constant control, necessary to avoid erroneous responses (Lehéricy et al., 2006; Monchi et al., 2006; Puttemans et al., 2005). Hence, these sub-cortical structures confirm a purely motor behavior of the posterior cluster within BA44. However, the functional role played by this circuit cannot be explained further by the application of the MACM analysis, which only provides co-activation patterns and not proper functional networks (Eickhoff et al., 2011).

Before concluding, it is worth discussing potential issues in integrating the approach we used here with the one applied by Clos et al. (2013) with respect to aBA44 and pBA44 functional attributions. The anterior cluster obtained by Clos et al. (2013) is the result of the application of external stability criteria on the whole BrainMap dataset. The posterior cluster in our study is obtained from the conjunction analysis over three action domains, which we had tailored beforehand into distinct experimental datasets as input to the ALE algorithm. We have however shown that different approaches (Clos et al., 2013; Zaccarella et al., 2017b) reveal highly overlapping language-related clusters in the

more anterior-ventral region of BA44, with very similar functional co-activations maps across the brain. This thus suggests high specificity for language in aBA44, independently of the criteria used to define the cluster (Zaccarella and Friederici, 2017). The possibility to use comprehensive functional maps, like the one provided by Clos et al. (2013) for BA44 is to our point of view advantageous when testing fundamental questions regarding the specific sub-regional localization of cognitive functions within the area, as the goal of present study was. Such maps have been already used to test language and action processing in different fMRI studies in BA44 (Neef et al., 2016; Zaccarella and Friederici, 2015). Finally, we also note the presence of slight differences in the connectivity patterns for aBA44 as reported by Clos et al. (2013) and in our study. This difference is likely due to the large amount of data, compared to the earlier meta-analysis, available nowadays (see Supplementary Fig. S3). More importantly, co-activation patterns specific to each sub-cluster in Clos et al. (2013) were calculated by a conjunction analysis of the differences between a cluster and the other four. In our case, co-activation patterns were obtained by performing a contrast analysis between two single ALE analyses, since we only had two clusters to compare (Molenberghs et al., 2016; Yu et al., 2018).

## 5. Conclusions

Coordinate-based meta-analyses challenge quantity by providing evidence for significantly consistent results across experiments. Here we focused on motor processing, and more specifically on six action domains including: Action Execution, Action Imitation, Motor Imagery, Action Observation, Motor Learning and Motor Preparation. A coordinate-based ALE approach was employed to update previously published datasets available in the literature. The most recent guidelines for this specific statistical procedure were applied to make the results strongly reliable. Our results show distinct functional patterns for the different action domains, with cross-modal convergence for Action Execution, Action Imitation and Motor Imagery in different brain areas, including left posterior BA44 (pBA44) in Broca's area. Further, the functional connectivity network derived from seeding in the motor-based localized cluster of pBA44 differs from the connectivity network seeding in the (language-related) anterior BA44. Bringing the results together, we propose that the motor-related network encompassing pBA44 is recruited in specific action domains requiring a mental representation of the action itself.

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## Declaration of competing interest

None.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116321.

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