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Neural correlates of manual action language: Comparative review, ALE meta-analysis and ROI meta-analysis

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ABSTRACT

Despite decades of research, the nature of the involvement of the motor system in action language processing is still controversial, and little is known about how processing action language relates to observing, imaging and executing motor actions. This study combines a systematic review of the literature, an ALE meta-analysis and a region-of-interest (ROI) meta-analysis to provide the first complete (qualitative and quantitative) account of the motor-related functional network involved in action language processing in comparison to activation reported during motor observation, motor imagery and motor execution. The review of the literature revealed that the methodology of action language studies differed considerably from the methodology of other motor-related processes which may have contributed to blurring the interpretations over the years. The ALE and ROI meta-analyses showed that the functional network of action language was more similar to observation than imagery and finally execution, following a motor gradation. Overall, our results point towards a more cognitive, as opposed to purely motoric, involvement of the motor system during action language processing.

1. Introduction

The cerebral network of action language has been the focus of extensive research in the last decades and a wide range of theories on language embodiment have been developed (e.g. Binder and Desai, 2011; Gallese and Lakoff, 2005; Glenberg, 2015; Mahon and Caramazza, 2008; Pulvermüller, 2013; Zwaan, 2014). However, the specific role of the motor system in action language processing and the extent to which action language is embodied remain controversial (Meteyard et al., 2012; Zwaan, 2014). Functional magnetic resonance imaging (fMRI) studies have played an important part in demonstrating the involvement of the motor system during the processing of action language (e.g.Hauk et al., 2004; Kemmerer et al., 2008; Labruna et al., 2011; van Dam et al., 2012). Evidence has accumulated that suggests that the relationship between action language and the motor system varies as a function of several factors, including context, expertise, attentional focus and semantic control demand (Davey, 2015; Moody and Gennari, 2010; Yang, 2014; Zwaan, 2014). This suggests that the involvement of the motor system in action language processing is complex but important questions remain. What is the nature of this motor involvement? What are the motor-related neural mechanisms at play during action language? Of particular interest are the studies that directly compared action language with other motor-related processes. Such comparisons have revealed similarities between the action language network and the networks of motor observation (Aziz-Zadeh et al., 2006; Meister and Iacoboni, 2007), motor imagery (Yang and Shu, 2014) and motor execution (Moody-Triantis et al., 2014; Papeo et al., 2012; Peck et al., 2009). However, a lack of overlap between the neural networks of action language and these other motor-related processes has also been reported (Tomasino et al., 2007; Tremblay and Small, 2011; Willems et al., 2009; Zhang et al., 2018). Thus, agreement about the relationship between the neural networks supporting action language processing and those supporting other motor-related processes has not been reached yet.

Meta-analyses provide a quantitative methodology to summarize empirical data, which may help in reaching a consensus. Meta-analyses have been conducted to characterize the cerebral network of action language (Jirak et al., 2010), motor observation (Caspers et al., 2010) and motor imagery (Hétu et al., 2013), providing a comprehensive overview of the neural networks involved in each of these processes. A more recent meta-analysis compared motor observation, imagery, and execution (Hardwick et al., 2018) and revealed that motor execution shared more activation sites with motor imagery than with motor observation. A systematic meta-analysis comparing action language,

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motor observation, imagery, and execution would provide unique and important insights into the motor processes involved in action language processing.

The main objective of the present study was to provide a comprehensive analysis of the fMRI literature on action language processing and its links with other motor-related processes (motor observation, imagery, and execution) through a systematic review of the literature and a two-fold meta-analysis (ALE and ROI). The aims of the systematic review were to generate a clear portrait of research on the neural correlates of action language processing and to examine whether this literature has explored action/movement-related parameters that have been explored in other motor-related fields of research. The overall aim of the ALE meta-analysis was to characterize the motor-related network of action language processing in comparison to those of motor observation, imagery, and execution. The first specific objective was to compare action language, motor observation, and motor imagery to motor execution in order to confirm the existence of a gradation in the similarity of the neural networks associated with these processes to the motor execution network. Considering that the motor execution network is more similar to the network of motor imagery than motor observation (Hardwick et al., 2018), and that the network of action language is more similar to motor observation than execution (Rueschemeyer et al., 2014), we expected action language to be the least "motoric" of the following motor-related processes on a motor gradation: motor execution – motor imagery – motor observation – action language. The second specific objective was to determine to which motor-related process the action language network was most similar. Since the action language network has been shown to be more similar to motor observation than to motor execution (Rueschemeyer et al., 2014), we expected the degree of similarity between action language and other motor-related processes to follow the previously mentioned motor gradation: the neural network of action language would be more similar to that of motor observation, then to motor imagery and finally to motor execution. The third specific objective was to determine whether the action language network was more closely related to movement or action processing. We hypothesized that the action language network would be more similar to the action compared to the movement processing network. Finally, an anatomical ROI meta-analysis aimed to provide complementary information regarding the functional network for action language by comparing, region by region, the bilateral language activation to the profile for motor imagery, observation, and execution.

2. Systematic review of the literature

2.1. Search strategy

Four comprehensive electronic literature searches were performed using PubMed in January 2018 and updated in March 2019. The searches separately identified studies focusing on *manual* action language, motor observation, imagery, and execution. The following key search terms (in all fields) included: (1) (action language OR action verbs OR embodied language) AND (hand OR manual OR finger) AND fMRI, (2) action observation[2] AND (hand OR manual OR finger) AND fMRI, (3) (motor imagery OR kinesthetic imagery) AND (hand OR manual OR finger) AND fMRI, and (4) motor execution AND (hand OR manual OR finger) AND fMRI. In addition to the Pubmed search, the reference sections of pre-selected articles were screened for additional articles of interest. The title and abstract of all articles were screened. The pre-selected articles were then assessed thoroughly.

2.2. Selection criteria

Studies were selected if: (1) the main methodology was fMRI, (2) the study included at least one group of healthy right-handed participants (aged up to 50 years), (3) the study reported Talairach or MNI coordinates for the activation, (4) the study reported coordinates for the contrast of a condition of interest (i.e., language condition including action verbs) against a baseline condition (either rest or a non-action-related baseline), (5) the study reported activation patterns for right-handed physically possible action and/or movement conditions (language, observation, imagery or execution), with no object or tool held during the task for language, observation and imagery studies in order to avoid confounding motor activation linked to the sensorimotor processing of object/tool held in hand (response pads were accepted), (6) studies were published in peer-reviewed journals, and (7) articles were written in English.Language studies were included if they focused on action verbs, whether isolated or embedded in sentences, but studies of isolated tool nouns were excluded. Note that since action language studies rarely mentioned whether stimuli referred to uni-or bimanual actions, the right-hand inclusion criterion was applied to all categories with the exception of the language category. Connectivity and neurofeedback studies were not included. Studies reporting only region of interest analyses were also excluded. Considering that, in action language, motor observation and motor imagery, responses were always externally triggered, conditions involving self-triggered responses were excluded from the review of motor execution studies. Groups of motor or motor imagery experts and groups of participants who received intensive training in action language, motor observation, imagery, or execution were excluded (*i.e.,* training of an hour or more prior to testing). In order to avoid the confound associated with speech production – a motor act – and the confound of processing abstract action language, action language articles focusing exclusively on production or non-literal actions were also excluded. Both explicit (i.e., consciously performed) and implicit (i.e., unconsciously performed) motor imagery studies were included.

The identification of one exclusion criterium was judged sufficient to eliminate an article from further screening. The two authors independently assessed the content of the selected articles against the inclusion criteria. Discrepancies between judges were solved by consensus. The selected articles are listed in Tables 1–4. A detailed list of the exclusion/inclusion procedure for each article found through the systematic and additional searches is available in Supplementary Spreadsheet 1.

2.3. Data extraction

Data extraction was independently assessed by the two authors. Discrepancies were solved by consensus. The extracted data are presented in Tables 1–4. The following information was extracted for each study: sample size (Sample size), body part (finger, hand or arm) (Body part), contrast(s) of interest (Contrast), presence of a concomitant task (Concomitant task), stimuli type (action or movement) (Type, cf. Supplementary Table 1 for details), and association of stimuli to tools (Tool-related), or objects (Object-related) (cf. Supplementary Table 2 for details). The action/movement distinction is paramount because the underlying behaviours are distinct: while a movement is the result of planned muscle contractions (e.g., finger extension), an action is a *goal-oriented* sequence of movements (e.g., grasping a pen) (Rizzolatti et al., 1988). In this study, we characterized the association between each action/movement with a tool or an object as an alternative to the transitive/intransitive distinction that has been used in the literature to classify actions into using an item (i.e., transitive) or not (i.e., intransitive). This is because the use of the terms "transitive" and "intransitive" has generated some confusion regarding the use of tools or

[2] Throughout this article, we prefer to use the term "motor observation" because it includes both action observation and movement observation. However, the term "action observation" was used for the literature search because it is the term currently used in the field to refer to observation of both action and movement.

Table 1
Characteristics of studies included in the action language condition of the review and meta-analysis.

	Article	Sample size	Linguistic level	Modality	Task	Body part	Contrast[1]	Concomitant task[2]	Stimuli list[3]	Type[4]	Tool-related[5]	Object-related[6]	Hand[7]
1	Tyler et al. (2003) NeuroImage	12	word	visual	semantic relatedness judgement	hand	strings of letters	0	0	1	1	0	N/A
2	Hauk et al. (2004) Neuron	14	word	visual	passive reading	arm	strings of hashmarks	0	0	1	N/A	N/A	N/A
3	Noppeney et al. (2005) Cogn Brain res	12	word	auditory	semantic judgement	hand	gender identification	0	1*	1	–	–	–
		15	word	visual		hand							
4	Tettamanti et al. (2005) J Cogn Neurosci	17	word	auditory	passive listening	hand	abstract sentences*	0	1*	1	–	–	–
5	Rueschemeyer et al. (2007) J Cogn Neurosci	20	word	visual	pseudoword identification	hand/arm	abstract verbs*	0	1	1	–	–	–
6	Kemmerer et al. (2008) Brain Lang	16	word	visual	semantic judgement	hand/arm	strings of symbols	0	1	1	1	0	1
7	Boulenger et al. (2009) Cereb Cortex	18	sentence	visual	reading + questions	arm	strings of hashmarks	0	1*	1	N/A	N/A	N/A
8	Raposo et al. (2009) Neuropsyhcologia	22	word	auditory	passive listening	arm	non-action verbs*	0	0	1	N/A	N/A	N/A
9	Desai et al. (2010) Cereb Cortex	33	sentence	auditory	semantic judgement	hand	abstract sentences*	0	1	1	–	1	–
		33	sentence	auditory		hand							
10	Willems et al. (2009) J Cogn Neurosci	20	word	visual	infrequent lexical decision	hand	non-manual actions*	0	0	1	N/A	N/A	1
11	Desai et al. (2011) J Cogn Neurosci	22	sentence	visual	semantic judgement + recognition	hand	abstract actions*	0	1	1	0	1	–
12	Hauk and Pulvermüller (2011) Front Hum Neurosci	20	word	visual	passive reading	hand	strings of hashmarks	0	1	1	–	–	1,2
13	Desai et al. (2013) NeuroImage	28	sentence	visual	covert semantic judgement	hand	abstract sentences*	0	1	1	–	–	1,2
14	De Zubicaray et al. (2013) J Cogn Neurosci	21	word	visual	grammatical judgement	hand	non-body-related nouns*	0	1*	1	–	–	–
15	Di Cesare et al. (2017) Brain Cogn	22	word	auditory	passive listening	hand	silence	0	1*	1	0	1	–
		22	word	auditory	passive listening	hand	abstract words*	0	1*	1	0	1	–

Note.
[1] Contrast: * = selected contrasts for the restricted ALE meta-analysis.
[2] Concomitant task: 0 = no, 1 = yes.
[3] Stimuli list available: 0 = no, 1 = yes, 1* = upon request.
[4] Type: 0 = movement, 1 = action.
[5] Tool-related: 0 = no, 1 = yes, - = mixed tool-related and –unrelated; N/A = information not available.
[6] Object-related: 0 = no, 1 = yes, - = mixed object-related and –unrelated, N/A = information not available.
[7] Hand: 1 = unimanual, 2 = bimanual, - = mixed uni- and bi-manual, N/A = information not available.

Table 2
Characteristics of studies included in the motor observation condition of the review and meta-analysis.

	Article	Sample size	Stimuli	Body part	Contrast	Concomitant task[1]	Type[2]	Tool-related[3]	Object-related[4]
1	Buccino et al. (2001) Eur J Neurosci	12	movie	hand	static hand	0	1	0	0
		12	movie	hand	static hand	0	1	0	1
2	Wheaton et al. (2004) NeuroImage	12	movie	hand	static hand	0	0	0	0
3	Costantini et al. (2005) Cereb Cortex	13	movie	finger	static hand	0	0	0	0
4	Molnar-Szakacs et al. (2005) Cereb Cortex	58	images	finger	rest	unclear	0	0	0
5	Grosbras and Paus (2006) Cereb Cortex	20	movie	hand	non-biological motion	0	1	–	–
6	Hamilton et al. (2006) NeuroImage	19	movie	hand	bouncing ball	1	1	0	1
7	Pierno et al. (2006) J Cogn Neurosci	14	movie	hand	movie of non-moving person	0	1	0	1
8	Filimon et al. (2007) NeuroImage	15	movie	hand	static object	0	1	0	1
9	Jonas et al. (2007) NeuroImage	19	picture	finger	static hand	0	0	0	0
10	Meister and Iacoboni (2007) PlosOne	14	movie	hand	rest	1	1	0	1
11	Adamovich et al. (2009) Restor Neurol Neurosci	13	movie	finger	static hand	1	0	0	0
12	Pierno et al. (2009) Cereb Cortex	15	picture	hand	static hand (with object)	0	1	0	1
13	Turella et al. (2009) NeuroImage	17	movie	hand	static hand (with object)	0	1	0	1
14	Biagi et al. (2010) Brain Res Bull	12	movie	hand	static hand (with object)	0	1	–	–
15	Tremblay and Small (2011) Cereb Cortex	21	movie	hand	rest	0	1	–	–
16	Tubaldi et al. (2011) Hum Brain Mapp	15	movie	hand	static hand (with object)	0	1	0	1
17	Heitger et al. (2012) J Neurophysiol	19	movie	hand	static hand (with object)	0	1	0	1
		19	movie	hand	static hand (with object)	0	1	0	1
18	Turella et al. (2012) Cereb Cortex	19	movie	hand	static hand (with object)	1	1	0	1
19	Vingerhoets et al. (2012) Neuropsychol Rehab	17	movie	hand	static object	1	1	1	0
20	Di Dio et al. (2013) NeuroImage	14	movie	hand	static arm	1	1	0	1
		16	movie	hand	static arm	1	1	0	1
21	Liew et al. (2013) Front Hum Neurosci	16	movie	hand	static hand	1	1	0	1
22	Plata Bello et al. (2013) PlosOne	19	movie	finger	static hand	0	0	0	0
23	Plata Bello et al. (2014) Neuroscience	31	movie	finger	static hand	0	0	0	0
24	Simos et al. (2017) NeuroImage	21	movie	hand	static hand (with dot)	0	0	0	0

[1] Concomitant task: 0 = no, 1 = yes.
[2] Type: 0 = movement, 1 = action.
[3] Tool-related: 0 = no, 1 = yes, - = mixed tool-related and –unrelated.
[4] Object-related: 0 = no. 1 = yes, - = mixed object-related and –unrelated.

objects. For instance, they have been used in reference to the association or lack of association of actions with objects (e.g. Pokorny et al., 2015; Press et al., 2008; van Dam and Desai, 2016; Wamain et al., 2014) and tools (e.g. Bonivento et al., 2014) separately, as well as objects or tools indistinctly (Carmo and Rumiati, 2009; Króliczak and Frey, 2009; Villarreal et al., 2008). However, tool-related and object-related actions are distinct. In an object-related action, the action is conducted *on* the object while in a tool-related action, the tool is used to *perform* an action. More specifically, when one grasps or throws an object, the object can only have an impact on some parameters of the action (e.g., whether a ball is light or heavy may impact the strength or the trajectory of the movement). In contrast, the tool that is used impacts the very nature of the action (e.g., a pen will usually be used to write rather than to cut a piece of paper). Therefore, the object/tool distinction is useful to specify the nature of the action.

Additional, category-specific data were also extracted. For language studies, we extracted the linguistic level of the stimuli (word, phrase or sentence) (Linguistic level), the modality (visual, auditory or audio-visual) (Modality), the nature of the linguistic task (Task), the availability of the stimuli list (Stimuli list) and the nature of the manual task (uni- or bimanual actions) (Hand). For observation studies, we extracted the modality of stimuli (movie or picture) (Stimuli). For motor imagery studies, we extracted the imagery type (implicit or explicit) (Imagery type) and whether the imagery task was immediately preceded by verbal instructions (Verbal instructions). Note that in 18 out of the 21 motor imagery studies, there were no action language instructions prior to motor imagery, since motor imagery cues were abstract words such as “imagine” or “ideate”, or a symbol such as a circle. Thus, a possible overlap between action language and motor imagery could not be attributed to the presence of action language during motor imagery tasks.

2.4. Results

Electronic literature searches identified a total of 905 studies matching the search terms. Initial screening of title and abstract was performed against the selection criteria. When the title and abstract did not provide sufficient information, the entire article was read. After excluding 369 studies from the initial screening, and adding 166 studies identified through references, full-text versions of 702 records were screened for eligibility. A total of 89 studies were included in the systematic review and the following meta-analyses; 15 of which focused on action language, 24 on motor observation, 21 on motor imagery and 29 on motor execution (Fig. 1).

Several patterns emerged from the systematic review regarding the stimuli used in the studies reviewed. First, while hand laterality (i.e., unimanual vs. bimanual) was systematically reported in motor observation, imagery, and execution studies, most action language studies omitted to consider this factor. Another major difference involved the object/tool distinction. In the observation, imagery, and execution studies, either the distinction was made, or it could be inferred from the stimuli description, while it was rarely reported in action language studies. Examination of the stimuli lists in language studies, when available, further revealed that the distinction was often not considered: object- and tool-related action words were indistinctly used in a unique experimental action condition. A list of all available stimuli used in the selected action language studies is available in Supplementary Table 3. Finally, all language studies focused on action (e.g. “play the piano”), as opposed to movements (e.g., “bend a finger”) while the other categories of studies (motor observation, imagery, and execution) included either actions or movements. Fig. 2 illustrates the distribution of studies focusing on action vs. movement in each of the studied motor-related fields.

Table 3
Characteristics of studies included in the motor imagery condition of the review and meta-analysis.

	Article	Sample size	Imagery type[1]	Verbal instructions[2]	Body part	Contrast	Concomitant task[3]	Type[4]	Tool-related[5]	Object-related[6]
1	Gerardin et al. (2000) Cereb Cortex	8	0	0	finger	rest	0	0	0	0
2	Vingerhoets et al. (2002) NeuroImage	12	1	0	Hand	Non-rotated hand	0	0	0	0
3	Dechent et al. (2004) Cogn Brain Res	6	0	0	Finger	Imagery of static scenery	0	0	0	0
4	Seurinck et al. (2004) NeuroImage	22	1	0	hand	Non-rotated hand	0	0	0	0
5	Filimon et al. (2007) Eur J Neurosci	15	0	0	hand	Object viewing	0	1	0	1
6	Szameitat et al. (2007) Eur J Neurosci	17	0	0	hand	rest	0	1	–	–
7	De Vries et al. (2008) Clin Neurol Neurosurg	9	0	0	Hand	rest	0	0	0	0
8	Guillot et al. (2008) NeuroImage	13	0	0	finger	Rest (with sounds)	0	0	0	0
		15	0		finger	Rest (with sounds)	0	0	0	0
9	Guillot et al. (2009) Hum Brain Mapp	13	0	0	finger	Rest (with sounds)	0	0	0	0
10	Sauvage et al. (2011) Brain Imaging Behav	8	0	0	finger	rest	0	0	0	0
11	Szameitat et al. (2012) PlosOne	17	0	0	hand	rest	0	1	–	–
12	Mizuguchi et al. (2013) Neurosci Res	18	0	0	hand	rest	0	1	0	1
13	Bartolo et al. (2014) Eur J Neurosci	14	1	0	hand	Scrambled images	0	1	0	1
14	Mizuguchi et al. (2014a) Front Hum Neurosci	16	0	0	hand	rest	0	0	0	0
15	Mizuguchi et al. (2014b) Neurosci Lett	17	0	0	hand	rest	0	0	0	0
16	Zapparoli et al. (2014) Exp Brain Res	2	1	0	hand	rest	1	0	0	0
17	Gardini et al. (2016) Brain Topogr	15	0	0	finger	rest	0	0	0	0
18	Lu et al. (2016) Neural Regen Res	10	0	–	finger	rest	0	0	0	0
19	Zanardi et al. (2016) Brain Cogn	14	1	0	hand	Visual mental rotation	0	0	0	0
20	Simos et al. (2017) NeuroImage	21	0	–	finger	rest	0	1	0	0
21	Hamada et al. (2018) Brain Imaging Behav	26	0	–	hand	fixation cross	0	0	0	0
		26	1	0	hand	fixation cross	1	0	0	0

[1] Imagery type: 0 = explicit motor imagery, 1 = implicit motor imagery.
[2] Action language priming: 0 = no, 1 = yes, - = information not available.
[3] Concomitant task: 0 = no, 1 = yes.
[4] Type: 0 = movement, 1 = action.
[5] Tool-related: 0 = no, 1 = yes, - = mixed tool-related and –unrelated.
[6] Object-related: 0 = no, 1 = yes, - = mixed object-related and –unrelated.

Table 4
Characteristics of studies included in the motor execution condition of the review and meta-analysis.

	Article	Sample size	Body part	Contrast	Concomitant task[1]	Type[2]	Tool-related[3]	Object-related[4]
1	Rao et al. (1997) J Neurosci	13	finger	rest	0	0	0	1
2	van Oostende et al. (1997) NeuroImage	7	finger	rest	0	0	0	0
3	Binkofski et al. (1999) Eur J Neurosci	12	hand	rest	0	1	0	1
4	Sakai et al. (1999) J Neurosci	6	finger	control tone sequence	0	0	0	1
5	Jäncke et al. (2001) Cereb Cortex	12	hand	rest	0	1	0	1
6	Cunnington et al. (2002) NeuroImage	12	finger	rest	0	0	0	1
7	Rowe et al. (2002) NeuroImage	15	finger	rest	0	0	0	1
8	Kuhtz-Buschbeck et al. (2003) Eur J Neurosci	12	hand	visual imagery (static landscape)	0	1	0	1
9	Maguire et al. (2003) NeuroImage	6	finger	rest (with fixation)	0	1	0	1
10	Dechent et al. (2004) Cogn Brain Res	6	finger	rest (with fixation)	0	0	0	0
11	Kudo et al. (2004) NeuroImage	12	finger	rest (with fixation)	0	0	0	0
12	Wenderoth et al. (2005) Eur J Neurosci	10	hand	rest	0	1	1	0
13	Filimon et al. (2007) NeuroImage	16	hand	rest (with fixation)	0	1	0	1
14	Suminski et al. (2007) J Neurophysiol	10	wrist	rest (with fixation)	0	0	0	1
15	de Vries et al. (2008)Clin Neurol Neurosurg	9	wrist	Rest	0	0	0	0
		9	hand	Rest	0	0	0	0
16	Guillot et al. (2008) NeuroImage	13	finger	rest (with sounds)	0	0	0	0
		15	finger	rest (with sounds)	0	0	0	0
17	Hanakawa et al. (2008) Cereb Cortex	13	finger	rest	0	0	0	0
18	Turella et al. (2009) NeuroImage	17	hand	rest (with fixation)	0	1	0	1
19	Kim et al. (2010) Neurol Res	20	elbow	rest	0	0	0	0
20	Sauvage et al. (2011)Brain Imaging Behav	8	finger	rest	0	0	0	0
21	Akhlaghi et al. (2012) Brain Res	13	finger	rest (with fixation)	0	0	0	0
22	Specogna et al. (2012) Radiol Med	15	finger	rest	0	0	0	0
23	Moody-Triantis et al. (2014) Front Hum Neurosci	18	finger	rest	0	1	0	1
24	Plata Bello et al. (2014) Neuroscience	31	finger	rest (with fixation)	0	0	0	0
25	Plata Bello et al. (2015) Brain Imaging Behav	20	finger	rest (with fixation)	0	0	0	0
26	Gardini et al. (2016) Brain Topogr	20	finger	rest	0	0	0	0
27	Rousseau et al. (2016) Neuroscience	19	wrist	rest	0	0	0	0
28	Adhikari et al. (2018)Brain Connect	9	finger	rest (with fixation)	0	0	0	1
29	Turesky et al. (2018) Hum Brain Mapp	15	finger	rest (with fixation)	0	0	0	0

[1] Concomitant task: 0 = no, 1 = yes.
[2] Type: 0 = movement, 1 = action.
[3] Tool-related: 0 = no, 1 = yes.
[4] Object-related: 0 = no, 1 = yes.

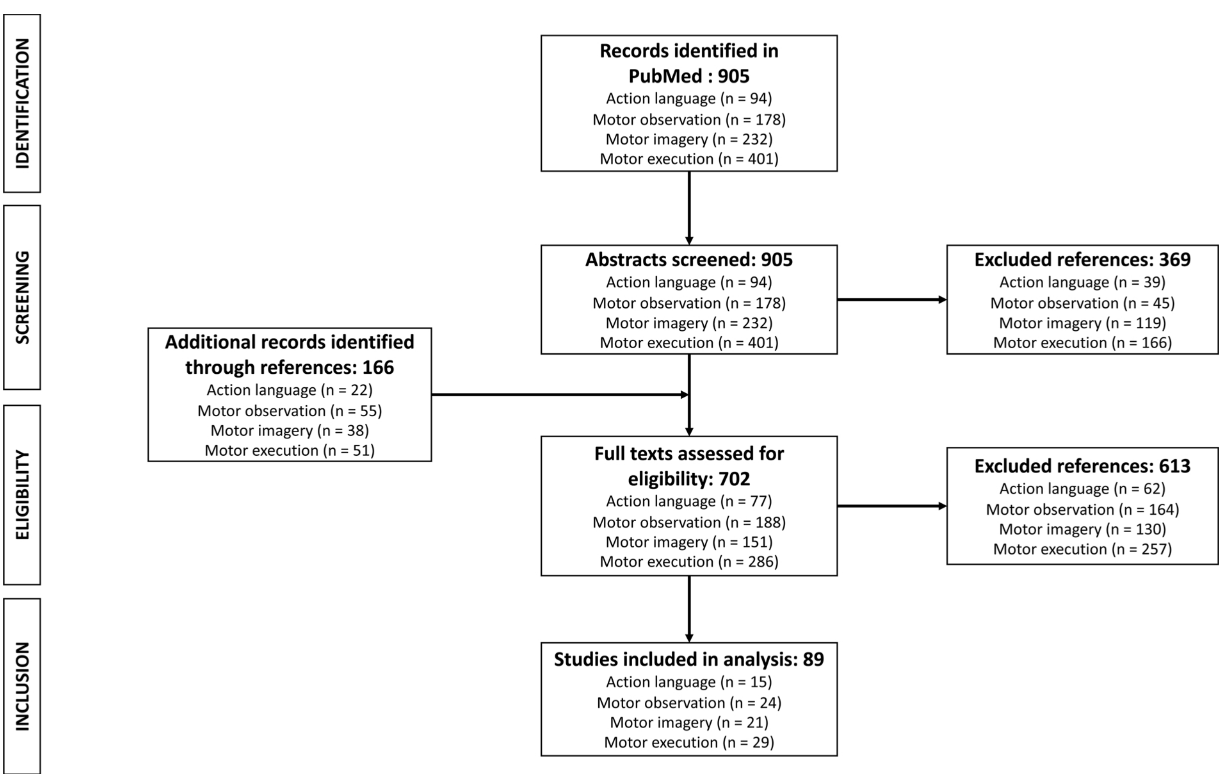

Fig. 1. Article selection diagram.

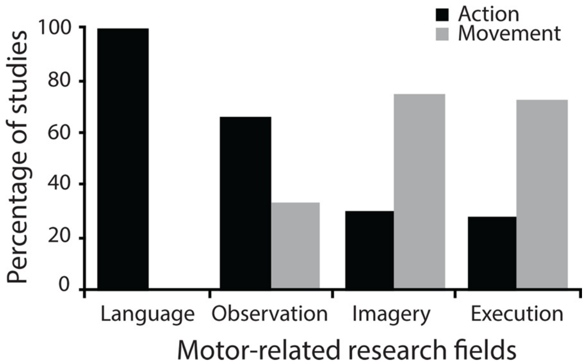

Fig. 2. Proportion of articles in each motor-related research field focusing on action and movement.

As can be seen in Tables 1 through 4, there was some heterogeneity within each category of studies with regards to the stimuli and tasks used. Regarding the nature of the tasks, in the action language category, some studies used semantic while others used non-semantic tasks, and in the motor imagery category, most studies focused on explicit motor imagery and only four focused on implicit motor imagery. Regarding the nature of stimuli, in the action language category, most studies focused on isolated words and only four focused on whole sentences. In motor imagery and motor execution, some studies focused on hand while others on fingers. Because the nature of the task and stimuli used could influence the functional network for these processes, a series of exploratory ALE analyses was first run to determine whether the differences in task and/or stimuli within category influenced the general activation map for action language, motor imagery and motor execution.

3. Meta-analysis

The general objective of the meta-analysis was to characterize the brain networks involved in action language processing and to compare these networks to those of motor observation, imagery, and execution as a way to gain further knowledge about the mechanisms involved in action language processing. The analysis was divided into two components: a series of activation likelihood estimation (ALE) analyses and an anatomical region of interest (ROI) analysis. The ALE analyses allowed for the direct comparison of activation peaks in action language with those in the other motor-related processes. The ROI analysis allowed us to calculate the percentage of fMRI studies reporting activation in each ROI for each of the motor-related processes and to compare activation distributions in action language and each of the other motor-related processes.

3.1. General method

For each study, coordinates were converted in MNI space using the BioImage Suite MNI/Talairach converter (Yale University: http://sprout022.sprout.yale.edu/mni2tal/mni2tal.html). Series of ALE meta-analyses were run to determine whether the action language network is comparable to those of motor observation, imagery, and execution. In addition, a ROI meta-analysis looked into the percentage of studies reporting activation in ROIs during each motor-related process.

The list of all coordinates as well as all activation maps are openly available on the Scholar Portal Dataverse (https://doi.org/10.5683/SP2/BRB00Z)[3].

[3] https://doi.org/10.5683/SP2/BRB00Z.

3.2. ALE meta-analyses

3.2.1. Methods

ALE meta-analyses were conducted using the GingerAle software (version 2.3.6, on an iMac computer). Coordinates of interest were manually selected, verified and then imported into GingerAle. For the computation of single maps and contrast analyses, significant clusters were identified at an uncorrected *p*-value threshold of .001 and with a minimum volume of 120 mm[3] (Hétu et al., 2013). For contrast analyses, a *p*-value permutation of 10 000 was used.

First, an activation map was computed for action language, motor observation, imagery, and execution (Fig. 3), and conjunction analyses were conducted to test our hypotheses. Because there was some heterogeneity within each category of studies with regards to the stimuli and tasks used, a set of exploratory analyses was conducted to examine the potential impact of these differences on functional networks. For the language studies, some studies explicitly required semantic processing of language stimuli (e.g., in a semantic judgment task) while in other studies no semantic processing was explicitly required (i.e., passive reading or listening tasks). To examine the impact of the semantic nature of tasks used in action language studies, the activation maps of studies using semantic tasks and of those not using a semantic task were compared to the general map for all action language studies. In addition, some language studies used single words as stimuli while others used whole sentences. Hence, the activation map for the action language focusing on single words and those focusing on sentences were compared to the general map for all action language studies. For motor imagery, some studies used implicit imagery while others used explicit imagery. We thus compared the activation maps for explicit and implicit motor imagery to the general map for all motor imagery studies. Finally, in motor imagery and motor execution categories, a large proportion of studies focused on finger actions/movements rather than hand actions/movements. We therefore compared the activation maps for hand and finger tasks of motor imagery to the general map for all motor imagery studies, and the activation maps for hand and finger tasks of motor execution to the general map for all motor execution studies.

Next, to confirm the existence of a “motor gradation” in the neural networks associated with motor-related processes, we compared the activation pattern of *motor execution* to those of motor imagery, motor observation and action language. Then, to determine to which motor-related process the action language network was most similar, we compared the activation pattern of *action language* to those of motor observation, imagery, and execution.

To determine whether the action language network is more closely related to the processing of action or movement, action and movement-related studies were separately collapsed across observation, imagery, and execution studies to form one general map for action and one general map for movement. Action language processing was then compared to action and movement. Next, studies on motor observation, imagery, and execution were divided into two subcategories: action and movement. Action language was then compared to action observation, action imagery, action execution, movement observation, movement imagery and movement execution. Similarly, action execution was compared to action language, action observation, action imagery and movement execution was compared to movement observation and movement imagery.

A final analysis was conducted, which aimed to determine whether the activation pattern observed during action language was *exclusively* linked to motor-related processes: a restricted analysis was run that focused on a subset of the action language studies that controlled for more general aspects of language processing during the processing of action language (Table 1). This restricted activation map of action language was compared to each motor-related process.

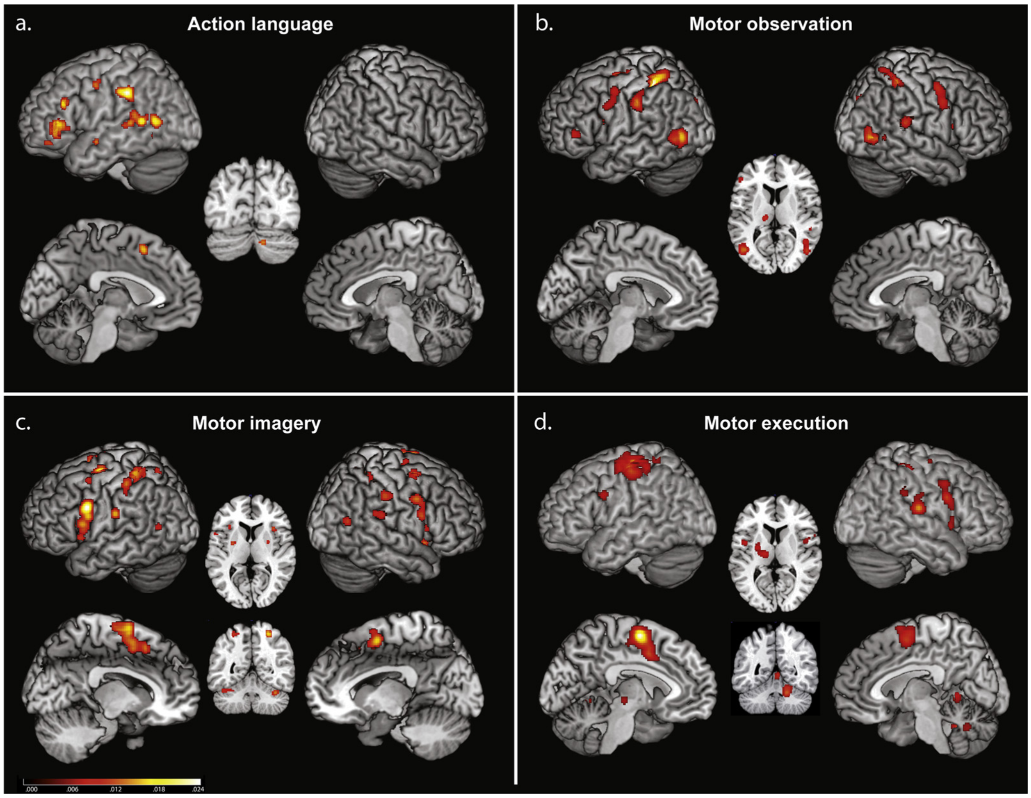

Fig. 3. Functional networks for **a.** action language, **b.** motor observation, **c.** motor imagery, and **d.** motor execution.

3.2.2. Results

3.2.2.1. Exploratory analyses. The analyses presented in this section aimed to determine whether some differences in stimuli or tasks used in the selected studies should be integrated to the main meta-analysis (section *3.2.2.2)*.

For the language studies, we tested two parameters: the nature of the task (semantic, not semantic) and the type of stimuli (words, sentences). The activation maps for semantic and non-semantic tasks were very similar to the general network of action language (Supplementary Fig. 1). Likewise, the activation map for studies using single words and those using sentences were similar to the general network of action language (Supplementary Fig. 2). Perhaps surprisingly, the network for studies focusing on sentences was more restricted than that of single word studies. This was potentially due to a lack of power induced by the small number of studies (N = 4). Because of the similarity, all action language studies were included in the main analyses, regardless of the task or stimuli used.

For the imagery studies, we also tested two parameters: the nature of the task (implicit, explicit) and the modality (hand, finger). The activation maps for implicit and explicit motor imagery were both similar to the general map for motor imagery (Supplementary Fig. 3). Of note, the activation map for implicit motor imagery was more restricted than the map for explicit motor imagery, possibly due to a lack of power resulting from the small number of studies (N = 4). The activation maps for hand and finger motor imagery were similar to the general map for motor imagery (Supplementary Fig. 4). Because of the similarity among the resulting maps, all motor imagery studies were included in the main analyses, regardless of the task or modality.

Finally, the activation maps for hand and finger motor execution were similar to the general map of motor execution (Supplementary Fig. 5); all motor execution studies were therefore included in the main analyses.

3.2.2.2. Main analyses. The first series of ALE analyses aimed to determine whether there was a motor gradation in the neural networks supporting motor-related processes. All activation maps are publicly available on the Scholars portal Dataverse[2]. Execution was compared to each motor-related process (Fig. 4) as well as to subcategories of action and movement (Supplementary Figures 6 & 7). Results revealed that execution was most similar to imagery. Their common network included bilateral central and inferior precentral regions, left mSFG, left putamen, right ventral postcentral region, right pars opercularis (POp) and right posterior portion of the medial superior frontal gyrus (i.e., pmSFG, also called supplementary motor area / SMA). The common network of motor execution and observation was slightly less extended and included bilateral central sulcus, ventral precentral region, left putamen, right ventral postcentral region, and right POp. The only common area to motor execution and action language was a small cluster in the left ventral postcentral region. The activation map for motor execution was more similar to that of movement execution than action execution, possibly due to the number of articles included in each sub-category (for more details, see Supplementary Figures 6 & 7). Regardless of this difference, a similar gradation in network similitude between execution and the other processes was observed when considering action and movement separately.

In a second series of analyses, action language was compared to motor observation, imagery, and execution (Fig. 5). It was then separately compared to the general maps of action and movement (Fig. 6). Finally, it was compared to the action and movement subcategories of each of the three motor-related processes (Supplementary Figure 8). Results for all these analyses were circumscribed to the left hemisphere. Specifically, the results revealed that the action language network included areas traditionally considered as pertaining to the language system: the pars triangularis of the IFG (PTr) and posterior portions of the superior and middle temporal gyri (pSTG and pMTG). In addition, clusters were found in the precentral and postcentral regions, as well as in the anterior portion of the medial superior frontal gyrus (amSFG),

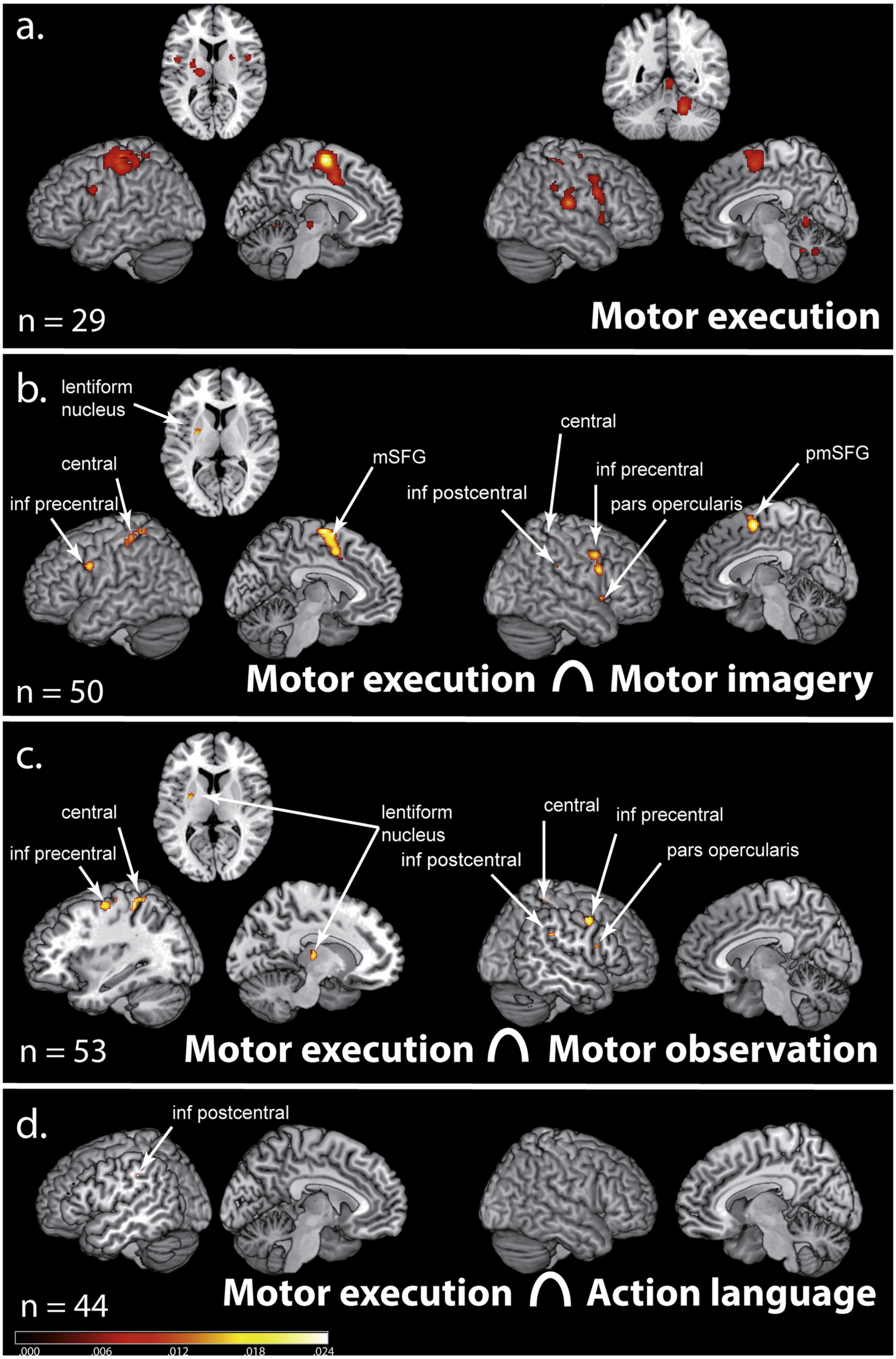

Fig. 4. Functional networks resulting from the execution-centered ALE analyses. Both action and movement studies were included within each category. **a.** Functional network of motor execution. **b.** Network overlap between motor execution and imagery. **c.** Network overlap between motor execution and observation. **d.** Network overlap between motor execution and action language. inf postcentral = inferior postcentral area; inf precentral = inferior precentral area; pmSFG = postero-median superior frontal gyrus (i.e. supplementary motor area); mSFG = median superior frontal gyrus, including supplementary motor area and pre-supplementary motor area.

corresponding to the pre-SMA (Fig. 5a). The conjunction analyses showed that the action language network was most similar to that of observation (Fig. 5c), both of them including activation in the PTr, the precentral and postcentral regions and the pMTG. Action language shared activations in pMTG and amSFG with imagery (Fig. 5b) and a circumscribed activation in the postcentral region with execution (Fig. 5d). Action language and the general map of action commonly recruited PTr, precentral and postcentral regions and pMTG, while action language and the general map of movement commonly recruited the postcentral region and the amSFG. Cortical areas common to action language and the subcategory of *action* observation were identical to those shared between action language and motor observation: PTr, precentral and postcentral regions and pMTG. The pMTG was also common to action language and movement observation and action imagery. Action language and movement imagery shared an activation of the amSFG. Action language and action execution shared an

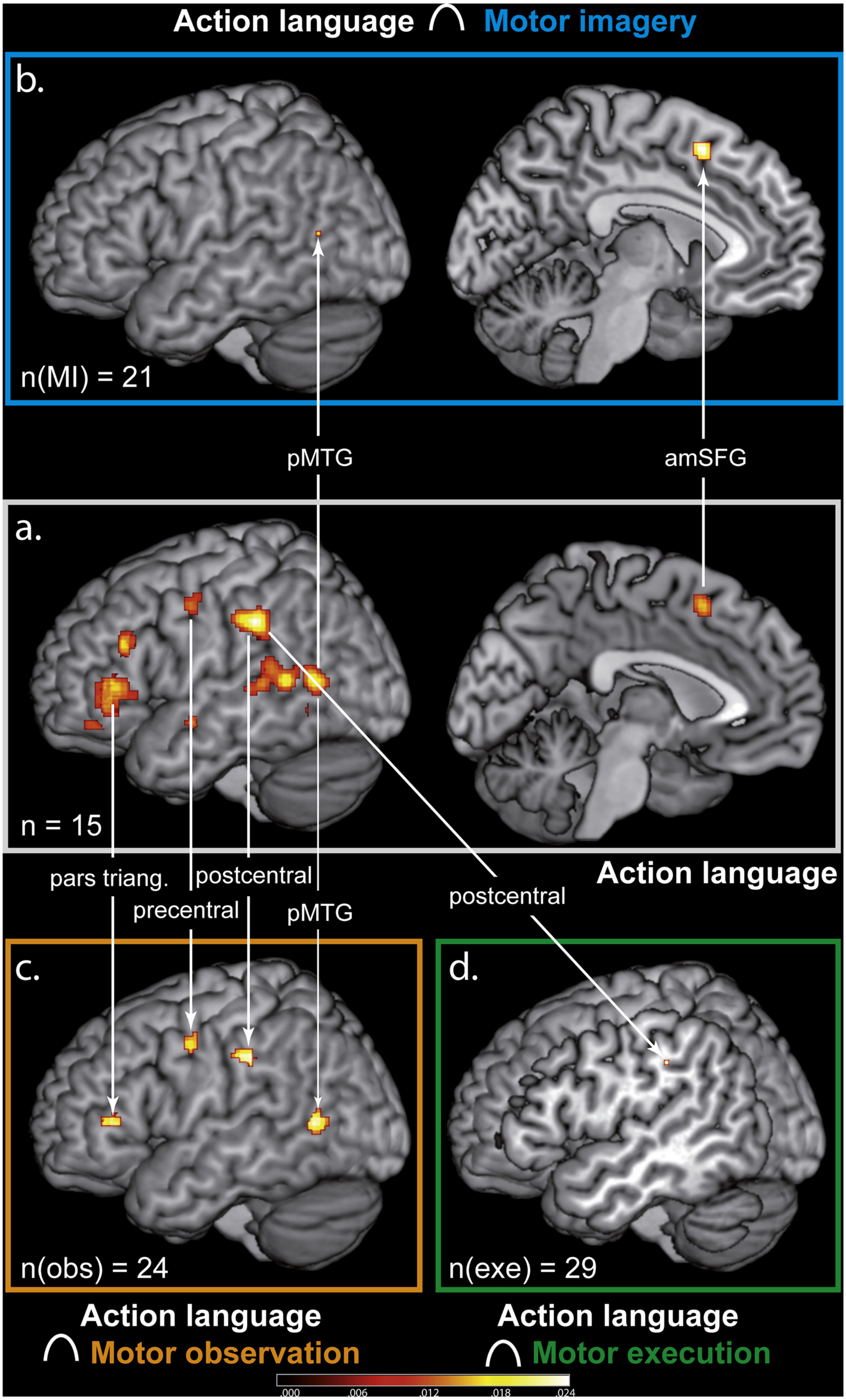

Fig. 5. Functional networks resulting from the language-centered ALE analyses. Both action and movement studies were included within each category. **a.** Functional network of action language. **b.** Network overlap between action language and motor imagery. **c.** Network overlap between action language and motor observation. **d.** Network overlap between action language and motor execution. pMTG = posterior middle temporal gyrus; amSFG = antero-median superior frontal gyrus (i.e. pre-supplementary motor area); pars triang. = pars triangularis.

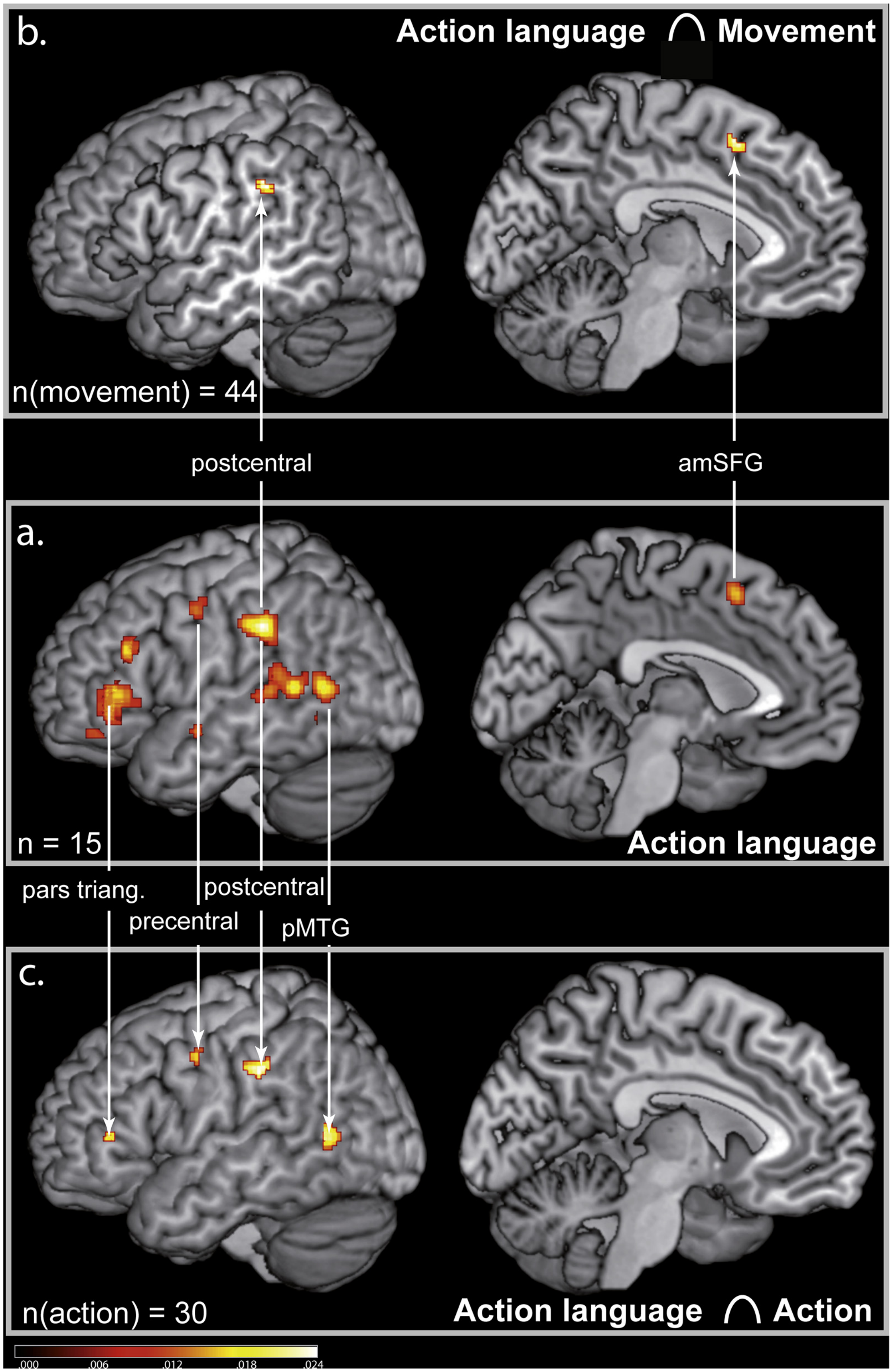

Fig. 6. Results from the action/movement series of analyses. **a.** Functional network of action language. Network overlap between **b.** action language and action processing, and **c.** action language and movement processing. pMTG = posterior middle temporal gyrus; amSFG = antero-median superior frontal gyrus (i.e. pre-supplementary motor area); pars triang. = pars triangularis.

activation of a very small portion of the postcentral region.

The additional analysis, controlling for general aspects of language processing, revealed that a single area was commonly activated for action language and the other motor-related processes: the left postcentral region (Supplementary Figure 9).

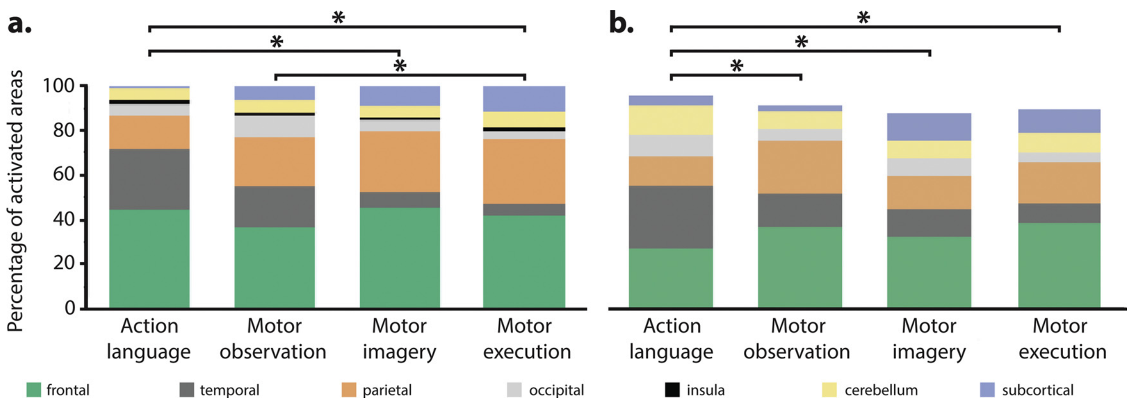

Fig. 7. Distributions of activation for action language, motor observation, imagery, and execution in the a. left and b. right hemispheres.

3.3. ROI meta-analysis

3.3.1. Labelling of coordinates

All coordinates reported in the selected articles were located on the non-linear T1 MNI brain template using Brainsight (version 2.3.10) and labelled based on the atlas of the human brain, 4th edition (Mai et al., 2016) and the MRI atlas of the human cerebellum (Schmahmann et al., 2000). All coordinates were verified by the two authors. Coordinates located outside of the cortex (i.e., more than 2 mm away from gray matter) and those that grossly mismatched their label, were excluded from the analysis (between 3.42 % and 7.66 % of labels were excluded in each study category). When a coordinate was located in the central sulcus, whether on the precentral or postcentral side, the coordinate was labelled “central”. The medial superior frontal gyrus (mSFG) was divided into three areas based on the macro-anatomical markers proposed by Picard and Strick (2001). Coordinates located posterior to the vertical anterior commissure (VAC) line were labelled as posterior medial SFG or pmSFG (i.e., supplementary motor area or SMA), coordinates located anterior to the VAC line and posterior to a vertical line going through the anterior border of the corpus callosum were labelled as anterior medial SFG or amSFG (i.e., pre-supplementary motor area or pre-SMA), and coordinates located anterior to the anterior border of the corpus callosum vertical line were labelled medial prefrontal cortex or mPFC. To enhance anatomical precision, the cingulate cortex was divided using the same macro-anatomical markers, with an additional area located in the parietal cortex and labelled parietal cingulate area. Lateral SFG and MFG were divided into three segments: anterior, middle and posterior. The line separating the anterior and middle areas of SFG and MFG was drawn perpendicular to the inferior frontal sulcus, going through the intersection of the ascending ramus and the horizontal ramus of the lateral fissure, and through the following y and z MNI coordinates: (18, -5) and (43, 21). The line separating the middle and posterior areas of the SFG and MFG was drawn perpendicular to the inferior frontal sulcus, going through the intersection of the inferior frontal sulcus and the inferior precentral sulcus, and through two points each spatially defined by the y and z MNI coordinates: (22, 44) and (13, 30). The STG, MTG and ITG were each divided into two segments: anterior and posterior. The dividing line was drawn perpendicular to temporal sulci and going through the middle of the transverse gyrus, and through the following y and z MNI coordinates: (-15, 10) and (-36, -29). Dividing lines for the frontal and temporal ROIs can be found in Supplementary Figure 10. Finally, the precentral, central and postcentral regions were divided into a ventral (i.e. z coordinate below 50) and a dorsal area (i.e., z coordinate of 50 or above). Coordinates falling within cerebellar hemispheres were grouped under three labels: the superior cerebellum, which included lobules IV, V and VI, the middle cerebellum, which included lobules Crus I and Crus II, and the inferior cerebellum which included lobules VII, VIII, IX and X. The vermis was labelled separately. The percentage of reported coordinates in the left hemisphere was of 71.30 % for action language, 49.82 % for motor observation, 52.90 % for motor imagery and 56.95 % for motor execution. The percentage of articles reporting activation in each cortical and subcortical area for action language, motor observation, imagery, and execution is summarized in Supplementary Table 4, separately for each hemisphere.

3.3.2. Statistical analyses

The number of reported activations in each of seven zones (i.e., frontal, temporal, parietal and occipital lobes, insula, cerebellum and subcortical) was calculated for each motor-related process and each hemisphere. For action language, 77 coordinates were reported in the left hemisphere across the 15 action-language articles including 34 in the frontal lobe, 21 in the temporal lobe, 12 in the parietal lobe, 4 in the occipital lobe, 1 in the insula, 4 in the cerebellum and 1 in subcortical areas. These numbers were then converted into percentages of the total reported activations within each motor-related process and each hemisphere, resulting in left and right distributions of activation for each motor-related process (Fig. 7). For action language, the left distribution was as follows: 44.16 % in the frontal lobe, 27.27 % in the temporal lobe, 15.58 % in the parietal lobe, 5.19 % in the occipital lobe, 1.30 % in the insula, 5.19 % in the cerebellum and 1.30 % in subcortical areas. The right distribution for action language was: 28.57 % in the frontal lobe, 28.57 % in the temporal lobe, 14.29 % in the parietal lobe, 9.52 % in the occipital lobe, 0 % in the insula, 14.29 % in the cerebellum and 4.76 % in subcortical areas. Fisher’s exact tests (r x 2) were used to compare the distributions for each process in each hemisphere. For analyses run in the right hemisphere, the insula was excluded because of a 0 % rate in the action language category.

3.3.3. Results

The left hemisphere distribution of activation for action language was significantly different from those of motor imagery ($p = 0.001$, $V = 0.33$) and motor execution ($p < 0.001$, $V = 0.38$), but not motor observation ($p = 0.17$, $V = 0.21$). The distributions for motor observation and execution differed significantly ($p = 0.02$, $V = 0.29$), whereas the distribution of motor imagery did not significantly differ from those of motor observation ($p = 0.17$, $V = 0.21$) and motor execution ($p = 0.94$, $V = 0.10$). In the right hemisphere, the distribution of activation for action language was significantly different from those of motor observation ($p = 0.05$, $V = 0.24$), imagery ($p = 0.05$, $V = 0.24$) and execution ($p = 0.002$, $V = 0.31$). The distribution for motor observation did not significantly differ from imagery ($p = 0.07$, $V = 0.23$) or execution ($p = 0.21$, $V = 0.20$). The distributions of motor imagery and motor execution were not significantly different ($p = 0.55$, $V = 0.15$).

4. Discussion

The general objective of this study was to provide a systematic and statistically supported account of the state of research on the neural correlates of action language processing. To this aim, a systematic review of the literature and two kinds of meta-analyses were conducted (ALE and ROI-based). Four main findings emerged: (1) the motor parameters that are frequently considered in motor observation, imagery, and execution studies are rarely considered in action language research, (2) there is a motor gradation among the neural networks of motor-related processes, (3) the network of action language is most similar to motor observation and least similar to motor execution, and (4) the neural network of action language is more similar to the network of action processing than movement processing.

4.1. Systematic review of the literature

The systematic review of the literature revealed the existence of important methodological differences between research on action language and research on other motor-related processes. Different parameters were explored: hand laterality, object/tool distinction and action/movement distinction. In contrast to studies on motor observation, imagery, and execution, action language studies did not take these parameters into consideration in their experimental design. Yet, the literature reports that unimanual and bimanual movements are associated with different cerebral activation patterns (Goerres et al., 1998; Nair et al., 2003): bimanual movements are associated with greater activity in areas such as the primary motor cortex, sensorimotor cortex, SPL, SMA and cerebellum. Regarding the object/tool distinction, a few studies have suggested that tools and non-tool objects have distinct brain representations, as shown by the activation of specific cerebral networks for tools and non-tool objects during observation (Mruczek et al., 2013) and motor planning (Przybylski and Króliczak, 2017) tasks. Results from these studies suggest that tool-related conditions engage several areas more strongly, including the SPL, premotor areas and SMA in comparison to non-tool objects conditions. Finally, regarding the action/movement distinction, though, to the best of our knowledge, the functional networks of action and movement have not been directly compared, results from our meta-analysis suggest that action and movement rely upon partially distinct networks (see Section 3.2.2 and Supplementary Figure 11). In order to achieve a better understanding of the role of motor areas in action language processing, these parameters will need to be considered in future studies.

4.2. ALE meta-analysis

An activation map was generated for each of the four motor-related processes: action language, motor observation, imagery, and execution (Fig. 3). Examination of these maps reveals a few salient differences. The functional network for motor execution included a cluster in the left primary motor cortex (M1), as well as clusters located in the periphery of M1, in frontal and parietal lobes, such as SMG and SMA. In contrast, the functional networks for action language, motor observation and motor imagery did not include M1 but clusters in the periphery of M1, such as the ventral premotor cortex (PMv), the SMG and the somatosensory cortex. This suggests that the motor system is only partially involved in motor-related processes that do not include motor execution, which is congruent with previous fMRI meta-analyses on action language (Jirak et al., 2010), motor observation (Caspers et al., 2010; Hardwick et al., 2018) and motor imagery (Hardwick et al., 2018; Hétu et al., 2013).

Second, a global analysis of lateralization reveals that action language differs from other motor-related processes. Indeed, the activation map for action language, with the exception of a limited activation in the right cerebellum, is circumscribed to the left hemisphere, whereas the activation maps for motor observation, imagery, and execution are bilateral at the cortical and subcortical levels. Considering that all participants were right-handed, which implies a mainly left-lateralized language network, this observation suggests that the involvement of the motor system in action language processing is influenced by language lateralization.

4.2.1. Motor gradation

Results from the first series of ALE meta-analyses and from the ROI analysis show that motor execution is more similar to motor imagery than to motor observation, which is consistent with the findings of a previous meta-analysis that compared these processes (Hardwick et al., 2018). Our meta-analysis shows that motor execution is least similar to action language, thus completing the motor gradation, from most to least motoric: motor execution – motor imagery – motor observation – action language (Fig. 4). The network activated during motor execution was only partially activated during motor imagery and motor observation. Motor execution and motor imagery shared a network comprised of bilateral central (i.e. primary motor cortex or M1) and inferior precentral (i.e., PMv) areas, the right inferior postcentral area (i.e. somatosensory cortex), POp, left pre-SMA and SMA, right SMA and left putamen (Fig. 4b). The common network of motor execution and motor observation was less extended as it included the same areas with the exception of the medial frontal region. Finally, at the end of the gradation, the only region common to motor execution and action language was the ventral postcentral region (Fig. 4d), corresponding to the somatosensory cortex. Thus, our results show that the core network for motor execution is *not* recruited during action language processing, providing evidence that action language processing does not rely, for the most part, on motor processes used in motor execution. If the involvement of motor structures can be considered an indicator of embodiment, and in line with the notion that “embodiment is a graded rather than a binary concept” (Arbib et al., 2014), then action language could be considered the least embodied of these motor-related processes.

4.2.2. Action language network

Results of the second series of ALE meta-analyses showed that the functional network of action language was more similar to motor observation and least similar to motor execution, which is consistent with the literature (Rueschemeyer et al., 2014) and also with our ROI analysis. In this action-centered series of analyses, all activation sites were left lateralized. This is not surprising since language in most right-handers shows a relative left lateralization (Catani et al., 2007) and the right hand is mainly controlled by the left hemisphere. The processing of action language recruited a fronto-temporo-parietal network composed of the PTr, PMv, postcentral areas (i.e., somatosensory cortex and aSMG) and pMTG. This network is very similar to the network reported in an earlier meta-analysis of action language, though it is more focal (Jirak et al., 2010). The difference in network extent between these two meta-analyses most likely results from differences in the inclusion and exclusion criteria (i.e., control of contrast baseline and exclusion of foot/leg actions in our meta-analysis). The action language network consists in areas typically associated with language functions, namely PTr and pMTG (Geranmayeh et al., 2014; Hagoort, 2014), and parts of the motor system: PMv and sensory cortex (Hardwick et al., 2018). The aSMG has been reported to play a role in both language processing (Deschamps et al., 2014; Oberhuber et al., 2016; Sliwinska et al., 2012) and motor planning (Johnson-Frey et al., 2005; Randerath et al., 2017). The overlap between action language and motor observation (Fig. 5) included all the cortical areas of the action language network, which are also known to be part of the action observation network (AON) (Caspers et al., 2010). Consistent with previous findings (Rueschemeyer et al., 2014), this overlap was wider than the overlaps of action language with motor imagery and motor execution, which suggests that neural mechanisms that are engaged during action language processing may be shared with motor observation and, to a lesser extent, with motor imagery.

The limited overlap between action language and motor imagery may be explained by the distribution of implicit and explicit motor imagery studies within our sample. Since most motor imagery studies focused on explicit rather than implicit imagery processes (cf. section 3.2.2.1), it is likely that the functional network obtained for motor imagery was driven by explicit motor imagery studies. It has been argued that if action language relied, at least in part, on motor imagery, it would more likely rely upon implicit rather than explicit imagery processes (Willems et al., 2009). Future studies directly addressing this question are needed to test this hypothesis.

Although the neural network of action language has been directly compared to those of motor observation (Pritchett et al., 2018; Zhang et al., 2018) and motor imagery (Papeo et al., 2012; Tomasino et al., 2007; Willems et al., 2009; Yang and Shu, 2014), the literature lacks experimental research investigating the precise role that specific motor-related areas may play in both action language and motor observation or imagery. However, studies on motor observation and studies on motor imagery have investigated the roles of specific areas in each of these two motor-related processes. For instance, such studies have shown that, during motor observation, aSMG participates in monitoring spatiomotor information (Bach et al., 2010) and processing meaning, intent and plausibility of action (Buccino et al., 2007; Costantini et al., 2005; Newman-Norlund et al., 2010). It is therefore possible that the involvement of aSMG in action language processing reflects a role for these motor-related cognitive mechanisms in action language processing. Relatedly, the role of PTr in action language could be related to processing action goals (Bach et al., 2010; Möttönen et al., 2016; Wurm et al., 2014), while PMv may be matching visuospatial information onto motor representations (Pilgramm et al., 2010), the somatosensory motor cortex may be processing somatosensory properties of objects (Turella et al., 2012; Valchev et al., 2017), pMTG may be involved in processing the meaning of action (Reader and Holmes, 2019) and pre-SMA may be involved in generating motor representations (Cunnington et al., 2005). Empirical investigations are needed to test these hypotheses, which could reveal the neural mechanisms underlying action language processing.

4.2.3. Action/movement distinction

The comparison of the functional network of action language with those of action and movement revealed that action language is more similar to action than movement processing. The overlap between action language and movement processing was circumscribed to the pre-SMA and aSMG. This suggests that, during action language processing, pre-SMA and aSMG are involved in the processing of the movements that compose the action expressed through language. The overlap between action language and action was larger and included PTr, PMv, somatosensory cortex, aSMG and pMTG (Fig. 6). This finding is consistent with the fact that language studies included in the meta-analysis exclusively focused on action (Table 1). These results support the notion that action and movement are different concepts (Rizzolatti et al., 1988) that rely upon partly different functional cortical networks (Hoeren et al., 2013). Conceptually, action differs from movement in that the processing of an action implies the processing of a goal towards which the action is oriented (Rizzolatti et al., 1988). The goal of an action, the intention that lies behind it, and the meaning it bears are all part of a more cognitive sphere of action processing, *action semantics*, that has been defined as “the representational foundation of action-related percepts, thoughts, simulation and intention” (Prinz, 2014). PTr, aSMG and pMTG have been reported to play a part in the processing of the goal and meaning of action. We therefore suggest that the involvement of these areas in action language reflects the processing of action semantics.

The concept of action is strongly associated with those of tools and non-tool objects. Indeed, tools and non-tool objects are often studied in action research (e.g., Bach et al., 2010; Chong et al., 2008; El-Sourani et al., 2018; Fiori et al., 2018) and some cortical areas pertaining to the motor system seem to play a particular part in their processing. For instance, SMG participates in the processing of actions in relation to tools and objects (Johnson-Frey et al., 2005; Koch et al., 2010; McDowell et al., 2018; Randerath et al., 2017; Tunik et al., 2008), the primary somatosensory cortex is especially involved if there is an object in the observed action (Turella et al., 2012), and PMv plays a role in target-directed hand shaping and fine motor control of fingers, which is key to successfully grabbing an object or tool (Fiori et al., 2018; Reader and Holmes, 2018). However, research has also shown that the processing of tools and non-tool objects is associated with different neural correlates (Mruczek et al., 2013; Przybylski and Króliczak, 2017). The study of the differential involvement of motor areas in the processing of tools and non-tool objects during action language in comparison to motor observation and/or motor imagery will provide additional cues into the neurobiological underpinning of action language processing.

4.3. ROIs meta-analysis

Consistent with the literature (Hardwick et al., 2018; Rueschemeyer et al., 2014) and our ALE meta-analysis, the ROI meta-analysis showed that action language was similar to motor observation in the left hemisphere. In addition, this analysis allowed for the study of the right hemisphere activation pattern during action language processing. Consistent with the notion of a relative left lateralization (Catani et al., 2007), our data showed that a considerable proportion of the action language network (28.7 %) is located in the right hemisphere. Interestingly, the right network of action language was significantly different from those of all other motor-related processes, suggesting that the involvement of the right action language network is less related to motor processing than the left network. Consistent with this notion, it has been suggested that the involvement of the right hemisphere in language processing is related to the processing of more abstract semantic content (Gainotti, 2016). Although the right hemisphere has been largely neglected historically, the focus of future studies on the role of right cerebral areas in language processing will contribute to a better understanding of all cerebral networks at play during action language processing.

4.4. What future for action language?

The action language literature has been characterized by a particularly heated debate focusing on whether action language processing should be considered to be embodied (Glenberg, 2015;Hauk et al., 2004 Pulvermüller and Fadiga, 2010) or not (Mahon, 2015; Mahon and Caramazza, 2008). The present meta-analysis does not aim to close or fuel this debate. Rather, it aims to offer an objective analysis of the existing literature and new directions for future research to compare action language to other motor-related processes. It is from this future work that an answer may emerge.

The comparison of action language with motor-related processes offers a unique perspective on the neural architecture of action language. Recently, action language has been compared to motor observation (Aziz-Zadeh et al., 2006; Meister and Iacoboni, 2007; Tremblay and Small, 2011; Zhang et al., 2018), imagery (Tomasino et al., 2007; Willems et al., 2009; Yang and Shu, 2014), and execution (Moody-Triantis et al., 2014; Papeo et al., 2012; Peck et al., 2009). Future investigations comparing action language with each of these processes, particularly observation and imagery, while focusing on a specific mechanism (such as action selection, generation of motor representations or motor inhibition) will provide important new knowledge about the role of different structures of the broadly defined motor system in action language processing. Action language will need to be compared to motor observation and motor imagery by controlling for similar parameters, such as hand laterality, the action/movement and the tool/object distinctions, and by elaborating a priori hypotheses regarding the role of specific cerebral regions involved in more than one motor-related process. This recommendation relies upon the notion that if bridges are to be built across research fields, common denominators have to be found. These common denominators may consist in more basic processes. It has recently been argued that language studies tend to be very language-centric, because they often explain cerebral activation observed during language tasks by language-specific processes only (Hasson et al., 2018; Tremblay and Dick, 2016). Hasson et al. propose that "*linguistic processes [can be] explained by basic computations that are not limited to language comprehension*" (page 136). Future research on the neural correlates of action language and the role of motor areas in language processing should therefore include a search for basic processes, in addition to potentially language-specific ones, in order to begin elaborating more neurobiologically plausible models of language processing.

4.5. Limits

In the present study, we analyzed the literature on action language processing. All studies were carefully selected, evaluated by the two authors and described in multiple tables and figures. A large number of analyses were conducted, including both hypothesis-based and exploratory-based analyses, the former aiming to address concerns about the heterogeneity of the selected articles. Despite this careful procedure, the present study is not without limitations. The main limitation of the study is the relatively small number of action language studies. Several studies were excluded because of missing information or failure to report activation coordinates resulting in a relatively small sample size. Another concern is that most of the studies that have been conducted have focused on word-level processing, which is not naturalistic, given that, in most day-to-day uses of language, sentences and even discourse are preferred rather than single words. The very nature of literature reviews and meta-analyses is that they are limited to studies that have been published, and the limits of a field of research become the limits of the review and meta-analysis. As such, our work highlights many of the limits of the previous studies, but also provides direction for future work into this important research question. We hope that future work includes more naturalistic language stimuli to pursue the investigation into the neural bases of action language processing.

Another limit is that response pads held by participants in some language, observation and imagery studies might have induced a confound associated with sensorimotor processing. Although the presence of objects or tools in hand was an exclusion criterium, the presence of response pads had to be accepted because of the large number of studies relying on them to collect participants' responses. However, to limit this possible confound, only articles in which the language, observation or imagery task did not focus on pressing the response pad buttons were included.

Finally, the absence of an analysis on the object/tool distinction is another limitation of the present meta-analysis. This distinction could not be addressed for two reasons. First, in action language studies, there was either insufficient information regarding this notion, or an absence of distinction between tool and object concepts. Second, the imbalance in the proportion of object-related and tool-related stimuli within motor observation, imagery, and execution categories would have limited the power of analyses.

5. Conclusion

The present research is the first to compare the functional network of action language to those of motor observation, imagery, and execution using three different approaches: a systematic review of the literature, an ALE whole-brain meta-analysis and a ROI-based meta-analysis. The review of the literature highlighted the experimental standards in research on motor observation, imagery, and execution, that action language research needs to adopt if bridges are to be built across research fields. Both the ALE and ROI-based meta-analyses showed that action language, at least in terms of word and sentence-level processing, is more similar to observation than to imagery and execution. The ALE meta-analysis further revealed that the core network for motor execution is not involved in action language processing and suggests that the involvement of "motor" areas in action language processing is more cognitive in nature, as opposed to purely motoric. Future study of cognitive mechanisms that participate in several motor-related processes, including action language processing, will be key to establishing more plausible, less language-centric neurobiological models of language processing.

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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.2020.06.025.

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