ALE meta-analysis of action observation and imitation in the human brain

Svenja Caspers [a,b,*], Karl Zilles [a,b,c], Angela R. Laird [d], Simon B. Eickhoff [a,b,e]

[a] Institute of Neuroscience and Medicine (INM-2), Research Centre Jülich, 52425 Jülich, Germany
[b] JARA-BRAIN, Jülich-Aachen Research Alliance, 52425 Jülich, Germany
[c] C. and O. Vogt Institute for Brain Research, Heinrich-Heine-University Düsseldorf, 40001 Düsseldorf, Germany
[d] Research Imaging Institute, University of Texas Health Science Center, San Antonio, TX, USA
[e] Department of Psychiatry and Psychotherapy, RWTH Aachen University, 52074 Aachen, Germany

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ABSTRACT

Over the last decade, many neuroimaging studies have assessed the human brain networks underlying action observation and imitation using a variety of tasks and paradigms. Nevertheless, questions concerning which areas consistently contribute to these networks irrespective of the particular experimental design and how such processing may be lateralized remain unresolved. The current study aimed at identifying cortical areas consistently involved in action observation and imitation by combining activation likelihood estimation (ALE) meta-analysis with probabilistic cytoarchitectonic maps. Meta-analysis of 139 functional magnetic resonance and positron emission tomography experiments revealed a bilateral network for both action observation and imitation. Additional subanalyses for different effectors within each network revealed highly comparable activation patterns to the overall analyses on observation and imitation, respectively, indicating an independence of these findings from potential confounds. Conjunction analysis of action observation and imitation meta-analyses revealed a bilateral network within frontal premotor, parietal, and temporo-occipital cortex. The most consistently rostral inferior parietal area was PFt, providing evidence for a possible homology of this region to macaque area PF. The observation and imitation networks differed particularly with respect to the involvement of Broca's area: whereas both networks involved a caudo-dorsal part of BA 44, activation during observation was most consistent in a more rostro-dorsal location, i.e., dorsal BA 45, while activation during imitation was most consistent in a more ventro-caudal aspect, i.e., caudal BA 44. The present meta-analysis thus summarizes and amends previous descriptions of the human brain networks related to action observation and imitation.

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Introduction

The neural bases of action observation and action imitation in the human brain have been a longstanding interest of neuroscientific research. Increasing attention was focused on these functions and their neuronal correlates when "mirror neurons" were identified in the macaque brain using single-cell recordings (Gallese et al., 1996; Fogassi et al., 2005). These neurons are active not only when performing an action but also when observing another subject performing the same action (Gallese et al., 1996). This discovery in the macaque brain raised the question of whether a comparable system also exists in humans (e.g., Rizzolatti et al., 2001). However, since single-cell recordings are rarely feasible in humans, a direct demonstration of mirror properties for individual human neurons has not yet been provided. Consequently, evidence for possible "mirror" areas in humans is predominantly based on the results of functional

neuroimaging experiments. Over the last decade, several studies using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have investigated different aspects of action processing in the human brain (e.g., Buccino et al., 2004b; Iacoboni et al., 1999) that are conceptually related to "mirror" properties, in particular action observation and imitation.

Investigation into the human action observation network directly relates to the properties of mirror neurons as defined in nonhuman primates. It is assumed that observing actions enables the mirror neuron system to understand the actions themselves as well as the underlying intentions (e.g., Fabbri-Destro and Rizzolatti 2008; Rizzolatti 2005; Rizzolatti and Fabbri-Destro 2008). By understanding the action with one's own motor system, it is possible to infer on the intentions behind a motor act (e.g., Prinz 2006; Schütz-Bosbach and Prinz, 2007), a mechanism that already has been proposed long before the discovery of mirror neurons (e.g., Viviani and Terzuolo, 1973). Such ability is then seen as a crucial step towards the development of complex interpersonal and social interactions as witnessed in humans but also other primates (Iacoboni 2009; Rizzolatti and Fabbri-Destro, 2008).

* Corresponding author. Institut für Neurowissenschaften und Medizin, INM-2, Forschungszentrum Jülich, 52425 Jülich, Germany. Fax: +49 2461 612990.
E-mail address: s.caspers@fz-juelich.de (S. Caspers).

Understanding an action and its intention might also provide an important link between the sole observation of an action and its subsequent imitation by directly copying the observed action (e.g., Fabbri-Destro and Rizzolatti, 2008; Rizzolatti and Craighero, 2004; Rumiati et al., 2005). Furthermore, imitation offers a potential mechanism for learning from the early stages of life. The motor system can learn how specific actions are carried out by imitating them (e.g., Bandura and Wood, 1989; Brass and Heyes, 2005; Iacoboni, 2005), a mechanism that has long been discovered much earlier in human neonates (Meltzoff and Moore, 1977). Furthermore, just like action understanding, imitation processes play an important role during social interactions: people also tend to imitate behaviours of their social partners (either consciously or subconsciously) to adapt to a given social situation (e.g., Bargh et al., 1996; Iacoboni, 2009; Niedenthal et al., 1985; Schilbach et al., 2008a).

Therefore, assessment of the neural substrates of both action observation and action imitation is not only important for understanding action-related processes but also holds further implications for cognitive and social neuroscience. In spite of the considerable number of neuroimaging studies on these action-related topics, the organisation of the respective networks in the human brain and their anatomical correlates are still disputed (Dinstein et al., 2008; Iacoboni, 2005, 2009; Keysers and Gazzola, 2009). One controversial aspect is the role of Broca's region in action- related processes (Brass and Heyes, 2005; Molenberghs et al., 2009; Molnar-Szakacs et al., 2005; Vogt et al., 2007). Another is the hemispheric dominance of such functions, as arguments have been made for a leading role of either hemisphere as well as for a bilateral distribution (e.g., Iacoboni and Dapretto, 2006). Finally, since observation and imitation are closely related, the question of whether they are sustained by the same neuronal networks or engage different brain areas is still disputed (e.g., Heyes, 2001; Brass and Heyes, 2005; Turella et al., 2009a,b).

One reason for the diverging evidence on the involvement of different brain regions in these networks is the heterogeneity of the experimental approaches, such as paradigms and effectors (e.g., hand/fingers, face, feet), that have been used to delineate the neural correlates of these functions. To identify those areas in the human brain that are consistently implicated in action processing, the results of these different studies should be synopsized in a quantitative, unbiased fashion. Previous summaries of published studies on action observation or imitation have consisted of qualitative reviews of the reported activation sites (e.g., Brass and Heyes, 2005; Fabbri-Destro and Rizzolatti, 2008; Iacoboni, 2005, 2009; Rizzolatti et al., 2001). However, a promising new approach for identifying the neural substrates of action observation and imitation in humans is the use of coordinate-based meta-analysis. These analyses aim at revealing areas that are consistently activated in a particular class of paradigms (Laird et al., 2005a, 2009; Eickhoff et al., 2009).

The aim of the present study was to provide a quantitative meta-analysis of the current neuroimaging literature to delineate consistently activated cortical regions associated with action observation and imitation. In a first step, the neural correlates of these processes were analysed separately. Additional subanalyses that assessed the effects of potential confounds, such as effectors or instructions, were carried out to evaluate the consistency of the findings. Conjunction and contrast analyses were performed to reveal divergent and convergent areas for action observation and imitation. Using probabilistic cytoarchitectonic maps of cortical areas, activations identified in each analysis were specifically allotted to the most probable brain area.

Material and methods

Data used for the meta-analysis

Functional imaging studies included in the meta-analysis were obtained from the BrainMap database (www.brainmap.org; Fox and Lancaster, 2002, Laird et al., 2005b) and a PubMed literature search (www.pubmed.org, search strings: "mirror neurons", "imitation", and "action observation") on functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) experiments. The literature cited in the obtained papers was also assessed to identify additional neuroimaging studies dealing with action observation or imitation processing. Only studies that reported results of whole-brain group analyses as coordinates in a standard reference space (Talairach/Tournoux, MNI) were analysed, while single-subject reports were excluded. Based on these criteria, 87 articles (reporting 83 fMRI and 4 PET studies) were designated as suitable for meta-analysis. Together, these studies included data from 1289 subjects and reported 139 experiments with 1932 activation foci (Table 1).

The reported tasks were subsumed into two main categories: "action observation" and "action imitation": 104 experiments reported action observation tasks (1061 subjects, 1390 activation foci), and 35 reported imitation tasks (459 subjects, 542 activation foci). Action observation comprised those experiments in which subjects were instructed to observe the action performed by others without performing their own motor act. In this first analysis, the general action observation brain network was assessed. There are, however, several possible confounds that may influence the analysis across the whole sample of observation and imitation experiments, like effectors, instructions or the involvement of an object. To explore the effects of these potential confounds, we subdivided the studies into several subgroups. These were then analysed separately to reveal the neural correlates of different forms of action observation and compared among each other by contrast and conjunction analyses: observation of hand actions ('right hand' (37 experiments), 'left hand' (2 experiments), 'both hands', or 'hand not specified' (23 experiments)), observation of right hand actions, observation of face actions, observation of non-hand actions (either 'face', 'body', or 'leg/foot'), observation of object-related hand actions, and observation of non-object-related hand actions. A further analysis was performed within those areas which were found to be consistently active for observation of hand actions: observation of hand actions with instruction 'passively observe', and observation of hand actions with instruction 'observe to imitate' (Table 2).

Action imitation comprised all those tasks in which subjects were asked to imitate actions performed by a visual model as exactly as possible. As for the action observation category, general effects associated with action imitation were analyzed first. Then, subgroups of the imitation studies were analysed separately for imitation of hand actions (either 'right hand' (15 experiments), 'left hand' (2 experiments), 'both hands', or 'hand not specified' (11 experiments)), imitation of right hand actions, and imitation of non-object-related hand actions (Table 2). A subgroup of studies on imitation of object-related hand actions could not been analysed due to an insufficient sample size.

Differences in coordinate spaces (MNI vs. Talairach space) were accounted for by transforming coordinates reported in Talairach space into MNI coordinates using a linear transformation (Lancaster et al., 2007).

Meta-analysis algorithm

Meta-analysis was carried out using the revised version (Eickhoff et al., 2009) of the activation likelihood estimation (ALE) approach for coordinate-based meta-analysis of neuroimaging results (Turkeltaub et al., 2002; Laird et al., 2005a,b). The algorithm aims at identifying areas showing a convergence of activations across different experiments, and determining if the clustering is higher than expected under the null distribution of a random spatial association between the results obtained in the experiments. The key idea behind ALE is to treat the reported foci not as single points, but rather as centers for 3D Gaussian probability distributions capturing the spatial uncertainty

Table 1
Overview of the 87 studies included in the meta-analysis on action observation and imitation.

Publication	Subjects	Mode	Experiment (rep. foci)	Effector (o/no)	Instruction	Contrast	Stimulus
Adamovich et al., 2009	13	fMRI	OBS (24)	Hand (o)	Observe to imitate	Task>rest	Hand manipulating objects
			IMI (14)	Hand (o)	Imitate as observed	Task>rest	Hand manipulating objects
Agnew and Wise, 2008	20	fMRI	OBS (5)	Right hand (no)	Passively observe	OBS motion>OBS static	Hand static or moving
			OBS (11)	Right hand (no)	Passively observe	OBS motion>EXE motion	Hand static or moving
Aziz-Zadeh et al., 2006a	12	fMRI	IMI (25)	Hand (o)	Imitate as observed	Task>rest	Finger movement
			IMI (30)	Left hand (o)	Imitate as observed	Task>rest	Finger movement
Aziz-Zadeh et al., 2006b	12	fMRI	OBS (9)	Hand/foot/face (o)	Passively observe	Task>rest	Combination of lower three
			OBS (4)	Foot (o)	Passively observe	Task>rest	Foot pressing on objects
			OBS (4)	Hand (o)	Passively observe	Task>rest	Hand reaching/grasping objects
			OBS (6)	Face (o)	Passively observe	Task>rest	Mouth biting fruits
Baumgaertner et al., 2007	19	fMRI	OBS (2)	Right hand (o)	Passively observe	OBS action>OBS nonaction	Hand manipulating objects
Bidet-Caulet et al., 2005	10	fMRI	OBS (15)	Body (no)	Listen to action sound	Task>rest	Hearing human footsteps
Blakemore et al., 2005	12	fMRI	OBS (11)	Hand (o)	Rate intensity of touch	OBS touch>OBS object	Touch to human neck or face
Buccino et al., 2001	12	fMRI	OBS (9)	Face (o)	Passively observe	OBS motion>OBS static	Mouth biting fruits
			OBS (6)	Hand (o)	Passively observe	OBS motion>OBS static	Hand reaching/grasping objects
			OBS (4)	Foot (o)	Passively observe	OBS motion>OBS static	Foot pressing on objects
			OBS (5)	Face (no)	Passively observe	OBS motion>OBS static	Mouth chewing
			OBS (2)	Hand (no)	Passively observe	OBS motion>OBS static	Hand mimicking object actions
			OBS (2)	Foot (no)	Passively observe	OBS motion>OBS static	Foot mimicking object actions
Buccino et al., 2004a	12	fMRI	OBS (10)	Left hand (o)	Observe to imitate	Task>rest	Left hand playing guitar chords
			OBS (17)	Left hand (o)	Passively observe	Task>rest	Left hand playing guitar chords
			IMI (13)	Left hand (o)	Imitate as observed	Task>rest	Left hand playing guitar chords
Calvert and Campbell, 2003	8	fMRI	OBS (27)	Face (no)	Read lips	OBS motion>OBS static	Mouth moving
Calvo-Merino et al., 2005	20	fMRI	OBS (23)	Body (no)	Rate tiring capacity	Task>rest	Ballet/capoeira movements
Calvo-Merino et al., 2006	24	fMRI	OBS (20)	Body (no)	Rate symmetry	Gender-specific>gender-common motion	Ballet movements
Carr et al., 2003	11	fMRI	IMI (32)	Face (no)	Imitate as observed	Task>rest	Emotional faces
			OBS (22)	Face (no)	Passively observe	Task>rest	Emotional faces
Chaminade et al., 2002	10	PET	IMI (6)	Hand (o)	Imitate as observed	IMI>EXE	Hand manipulating Lego blocks
Chaminade et al., 2005	12	fMRI	IMI (20)	Hand (no)	Imitate as observed	IMI>EXE	Hand/foot moving
Cheng et al., 2007	20	fMRI	OBS (15)	Right hand (o)	Passively observe	OBS motion>OBS scramble	Hand reaching/grasping objects
Chong et al., 2008	16	fMRI	OBS (14)	Hand (o)	Discriminate grip type	OBS motion>OBS figure	Hand reaching/grasping objects
Costantini et al., 2005	13	fMRI	OBS (8)	Right hand (no)	Passively observe	OBS motion>OBS object	Moving finger/object, possible
			OBS (16)	Right hand (no)	Passively observe	OBS motion>OBS object	Moving finger/object, impossible
Cross et al., 2006	10	fMRI	OBS (23)	Body (no)	Passively observe	Task>rest	Dance movements
Cross et al., 2009	17	fMRI	OBS (12)	Body (no)	Passively observe	OBS familiar>OBS untrained	Dance movements
Cunnington et al., 2006	14	fMRI	OBS (10)	Right hand (no)	Observe to imitate	OBS>EXE	Finger gestures
Decety et al., 2002	18	PET	IMI (17)	Hand (o)	Imitate as observed	IMI>EXE	Hand manipulating objects
Dinstein et al., 2007	13	fMRI	IMI (6)	Right hand (no)	Imitate as observed	Task>rest	Finger gestures
			OBS (6)	Right hand (no)	Passively observe	Task>rest	Finger gestures
Engel et al., 2008	18	fMRI	OBS (20)	Hand (no)	Passively observe	OBS motion>OBS static	Hand movements
Filimon et al., 2007	16	fMRI	OBS (14)	Right hand (o)	Passively observe	OBS motion>OBS object	Hand reaching objects
Frey and Gerry, 2006	19	fMRI	OBS (6)	Hand (o)	Observe to imitate	Task>rest	Hand constructing objects
Galati et al., 2008	11	fMRI	OBS (26)	Body (no)	Listen to action sound	Task>rest	Hearing action sounds with primer
Gazzola et al., 2006	16	fMRI	OBS (8)	Hand (o)	Listen to action sound	Sound action>environment	Hand action sounds
			OBS (20)	Face (o)	Listen to action sound	Sound action>environment	Mouth action sounds
Gazzola et al., 2007	16	fMRI	OBS (22)	Right hand (o)	Passively observe	OBS motion>OBS static	Human/robotic hand reaching/grasping objects
German et al., 2004	16	fMRI	OBS (18)	Hand (o)	Rate completeness	OBS pretend>OBS real	Everyday actions
Grèzes et al., 2003	12	fMRI	IMI (8)	Hand (o)	Imitate as observed	Task>rest	Hand reaching/grasping objects
			IMI (7)	Hand (no)	Imitate as observed	Task>rest	Hand movements
Grèzes et al., 2004	6	fMRI	OBS (5)	Body (o)	Rate expectation	OBS self>OBS other	Carrying boxes of different weight
Grosbras and Paus, 2006	20	fMRI	OBS (24)	Hand (o)	Passively observe	OBS neutral>OBS control	Hand reaching/grasping objects
			OBS (32)	Hand (o)	Passively observe	OBS angry>OBS control	Hand reaching/grasping objects
			OBS (28)	Face (no)	Passively observe	OBS neutral>OBS control	Moving faces
			OBS (25)	Face (no)	Passively observe	OBS angry>OBS control	Emotional faces
Hamzei et al., 2003	6	fMRI	OBS (3)	Right hand (o)	Passively observe	OBS motion>OBS static	Hand reaching/grasping objects
Haslinger et al., 2005	12	fMRI	OBS (26)	Right hand (o)	Passively observe	OBS motion>OBS static	Playing piano/moving hand
			OBS (26)	Left hand (o)	Passively observe	OBS motion>OBS static	Playing piano/moving hand
Hermsdörfer et al., 2001	7	fMRI	OBS (6)	Right hand (no)	Decide same/different	OBS motion>OBS control	Hand gestures
			OBS (8)	Right hand (no)	Decide same/different	OBS motion>OBS control	Finger gestures
Iacoboni et al., 1999	12	fMRI	IMI (3)	Right hand (no)	Imitate as observed	IMI>EXE	Finger movements
Iacoboni et al., 2001	12	fMRI	IMI (1)	Right hand (no)	Imitate as observed	IMI>EXE	Finger movements
Iacoboni et al., 2004	13	fMRI	OBS (16)	Body (no)	Passively observe	OBS interaction>OBS single	Everyday actions
Iacoboni et al., 2005	23	fMRI	OBS (36)	Right hand (o)	Passively observe	OBS motion>OBS object	Hand reaching/grasping objects
Iseki et al., 2008	16	fMRI	OBS (11)	Body (no)	Passively observe	OBS motion>OBS scramble	Stepping movements
			OBS (10)	Body (no)	Passively observe	OBS motion>OBS scramble	Stepping movements
Jackson et al., 2006	16	fMRI	IMI (16)	Hand/foot (no)	Imitate as observed	IMI>OBS	Hand/foot movements
Johnson-Frey et al., 2003	18	fMRI	OBS (9)	Right hand (o)	Recognize duplicate	OBS motion>OBS touch	Hand touching/grasping objects

Table 1 (continued)

Publication	Subjects	Mode	Experiment (rep. foci)	Effector (o/no)	Instruction	Contrast	Stimulus
Jonas et al., 2007	19	fMRI	OBS (3)	Right hand (no)	Recognize oddball	Task>rest	Finger movements
			IMI (5)	Right hand (no)	Imitate as observed	Task>rest	Finger movements
Keysers et al., 2004	14	fMRI	OBS (5)	Foot (o)	Passively observe	OBS touch>OBS object	Touch to human leg with objects
Koski et al., 2002	14	fMRI	IMI (15)	Hand (no)	Imitate as observed	IMI with goal>without goal	Finger movements with goals
Koski et al., 2003	8	fMRI	IMI (26)	Hand (no)	Imitate as observed	IMI>EXE	Mirrored finger movements
Leslie et al., 2004	15	fMRI	IMI (23)	Face (no)	Imitate as observed	Task>rest	Emotional faces
			OBS (16)	Face (no)	Passively observe	Task>rest	Emotional faces
Lewis et al., 2005	20	fMRI	OBS (9)	Hand (o)	Listen to action sound	Sound tool>sound animal	Tool action/animal sounds
Lotze et al., 2006	20	fMRI	OBS (7)	Right hand (o)	Passively observe	OBS body-referred action>OBS isolated action	Everyday actions
			OBS (16)	Right hand (no)	Imagine being addressed	OBS emotional action>OBS isolated action	Emotional gestures towards observer
Lui et al., 2008	16	fMRI	OBS (7)	Hand (no)	Passively observe	OBS motion>imagine motion	Finger gestures
Makuuchi 2005	9	fMRI	IMI (2)	Right hand (no)	Imitate as observed	IMI>EXE	Finger gestures
Makuuchi et al., 2005	22	fMRI	IMI (23)	Left hand (no)	Imitate as observed	IMI>EXE	Finger gestures
Manthey et al., 2003	12	fMRI	OBS (23)	Hand (o)	Passively observe	OBS meaningful action>OBS meaningless action	Hand manipulating objects
Meister and Iacoboni, 2007	14	fMRI	OBS (25)	Right hand (o)	Count no. of fingers	Task>rest	Hand manipulating objects
Molnar-Szakacs et al., 2005	58	fMRI	OBS (5)	Hand (no)	Passively observe	Task>rest	Finger movements
			IMI (4)	Hand (no)	Imitate as observed	Task>rest	Finger movements
Molnar-Szakacs et al., 2006	12	fMRI	OBS (72)	Right hand (o)	Passively observe	Task>rest	Hand manipulating objects
Menz et al., 2009	15	fMRI	OBS (5)	Right hand (o)	Observe to imitate	Task>rest	Hand manipulating objects
			IMI (15)	Right hand (o)	Imitate as observed	Task>rest	Hand manipulating objects
Montgomery et al., 2007	14	fMRI	OBS (16)	Right hand (no)	Observe to imitate	Task>rest	Finger gestures
			IMI (18)	Right hand (no)	Imitate as observed	Task>rest	Finger gestures
			OBS (16)	Right hand (o)	Observe to imitate	Task>rest	Finger gestures
			IMI (18)	Right hand (o)	Imitate as observed	Task>rest	Finger gestures
Montgomery and Haxby, 2008	12	fMRI	OBS (16)	Face (no)	Observe to imitate	Task>rest	Emotional faces
			IMI (18)	Face (no)	Imitate as observed	Task>rest	Emotional faces
			OBS (11)	Right hand (no)	Observe to imitate	Task>rest	Finger gestures
			IMI (16)	Right hand (no)	Imitate as observed	Task>rest	Finger gestures
Morris et al., 2008	8	fMRI	OBS (7)	Body (no)	Passively observe	OBS motion>OBS object	Everyday actions
Mouras et al., 2008	10	fMRI	OBS (14)	Body (no)	Passively observe	Task>rest	Sexual intercourse
Mühlau et al., 2005	12	fMRI	IMI (24)	Hand (no)	imitate as observed	IMI variable>IMI stereotype	Hand/finger gestures
Pierno et al., 2006	14	fMRI	OBS (9)	Right hand (o)	Passively observe	OBS motion>OBS static	Hand reaching/grasping objects
Pierno et al., 2009	15	fMRI	OBS (4)	Right hand (no)	Passively observe	OBS motion>OBS static	Hand pointing to objects
			OBS (8)	Right hand (o)	Passively observe	OBS motion>OBS static	Hand reaching/grasping objects
Rocca et al., 2008a	14	fMRI	OBS (6)	Right hand (no)	Passively observe	OBS>EXE	Finger movements
Rocca et al., 2008b	11	fMRI	OBS (12)	Right hand (no)	Passively observe	OBS>EXE	Finger movements
			OBS (11)	Left hand (no)	Passively observe	OBS>EXE	Finger movements
Rumiati et al., 2005	10	PET	IMI (9)	Hand (no)	Imitate as observed	IMI>OBS	Meaningful/meaningless hand movements
Sakreida et al., 2005	19	fMRI	OBS (10)	Hand/foot/face (no)	Passively observe	OBS distal>OBS proximal	Hand/foot/mouth movements
			OBS (11)	Hand/foot/face (no)	Passively observe	OBS proximal>OBS distal	Hand/foot/mouth movements
			OBS (14)	Body (no)	Passively observe	OBS axial>OBS distal + proximal	Axial rotation of body
Schaefer et al., 2009	10	fMRI	OBS (4)	Right hand (o)	Passively observe	OBS touch>OBS non-touch	Hand being touched by brush
Schubotz and von Cramon, 2008	18	fMRI	OBS (14)	Hand (o)	Passively observe	Task>rest	Hand writing and pretending to
Schulte-Rüther et al., 2007	26	fMRI	OBS (12)	Face (no)	Focus on emotion	OBS emotion>OBS person	Emotional faces
Shmuelof and Zohary, 2005	11	fMRI	OBS (13)	Hand (o)	Passively observe	OBS hand + contralat. object>OBS contralat. hand + object	Hand reaching/grasping objects
Tai et al., 2004	7	PET	OBS (3)	Hand (o)	Passively observe	OBS motion>OBS static	Human hand grasping object
			OBS (2)	Hand (o)	Passively observe	OBS motion>OBS static	Non-human hand grasping object
Tanaka et al., 2001	9	fMRI	IMI (12)	Right hand (no)	Imitate as observed	Task>rest	Finger movements
			IMI (8)	Right hand (no)	Imitate as observed	Task>rest	Finger gestures
Tanaka and Inui, 2002	12	fMRI	IMI (6)	Right hand (no)	Imitate as observed	IMI>OBS	Finger gestures
Tettamanti et al., 2005	17	fMRI	OBS (5)	Face (o)	Listen to action sound	Sentence face>abstract	Action-related sentences
			OBS (8)	Hand (o)	Listen to action sound	Sentence hand>abstract	Action-related sentences
			OBS (5)	Foot (o)	Listen to action sound	Sentence foot>abstract	Action-related sentences
Turella et al., 2009a	17	fMRI	OBS (16)	Right hand (no)	Passively observe	OBS motion>OBS static	Hand reaching/grasping objects
Uddin et al., 2005	10	fMRI	OBS (5)	Face (no)	Decide self/different	OBS self>OBS other	Faces of self and familiar person
van der Gaag et al., 2007	17	fMRI	IMI (57)	Face (no)	Imitate as observed	Task>rest	Emotional faces
			OBS (29)	Face (no)	Passively observe	Task>rest	Emotional faces
			OBS (35)	Face (no)	Decide same/different	Task>rest	Emotional faces
			OBS (26)	Face (no)	Observe to imitate	Task>rest	Emotional faces
Villarreal et al., 2008	17	fMRI	OBS (24)	Hand (o)	Rate type of motion	Task>rest	Hand manipulating objects
			OBS (29)	Hand (no)	Rate type of motion	Task>rest	Finger gestures

Table 1 (*continued*)

Publication	Subjects	Mode	Experiment (rep. foci)	Effector (o/no)	Instruction	Contrast	Stimulus
Vogt et al., 2007	32	fMRI	OBS (13)	Left hand (o)	Observe to imitate	OBS practised action>OBS non-practised action	Left hand playing guitar chords
			IMI (5)	Left hand (o)	Imitate as observed	IMI practised action>IMI non-practised action	Left hand playing guitar chords
Wheaton et al., 2004	12	fMRI	OBS (5)	Face (no)	Passively observe	OBS motion>OBS static	Mouth movements
			OBS (5)	Right hand (no)	Passively observe	OBS motion>OBS static	Right hand movements
			OBS (14)	Foot (no)	Passively observe	OBS motion>OBS static	Leg movements
Willems et al., 2007	16	fMRI	OBS (3)	Right hand (no)	Rate match	OBS gesture mismatch>OBS correct match	Spoken and sign language
Williams et al., 2006	16	fMRI	IMI (6)	Right hand (no)	Imitate as observed	Task>rest	Finger movements
Williams et al., 2007	12	fMRI	IMI (34)	Right hand (no)	Imitate as observed	IMI>EXE	Finger movements
Zentgraf et al., 2005	10	fMRI	OBS (12)	Body (no)	Observe to imagine	Task>rest	Gymnastic movements
			OBS (9)	Body (no)	Observe to evaluate	Task>rest	Gymnastic movements

The column "Mode" refers to the type of data acquisition used in the respective study (fMRI, PET). The column "Experiment" reports the meta-analysis category with which each experiment of the respective study was labelled. The count of reported foci is added in brackets. The column "Effector" reports the effector used during action observation or imitation as reported in the respective study, with "hand" meaning either "both hands" or "a non-specified hand". The involvement of an object during the observed or imitated action is added in brackets (o object, no non-object).

OBS: action observation, IMI: action imitation, EXE: action execution without visual model (in contrast to imitation).

associated with each focus. The width of these uncertainty functions was determined based on empirical data on the between-subject and between-template variance, which represent the main components of this uncertainty. Importantly, the applied algorithm weights the between-subject variance by the number of examined subjects per study, accommodating the notion that larger sample sizes should provide more reliable approximations of the 'true' activation effect and should therefore be modelled by 'smaller' Gaussian distributions (Eickhoff et al., 2009).

The probabilities of all activation foci in a given experiment were combined for each voxel, resulting in a modelled activation map (MA map). Taking the union across these MA maps yields voxel-wise ALE scores describing the convergence of results at each particular location. Since neurophysiologically, activation should predominantly be localized within the grey matter, all analyses were restricted to those voxels where a probability of at least 10% for grey matter could be assumed based on the ICBM tissue probability maps (Evans et al., 1994).

To distinguish 'true' convergence between studies from random convergence, i.e., noise, the ALE scores were compared to an empirical null distribution derived from a permutation procedure. This null distribution reflects a random spatial association between experiments, while regarding the within-experiment distribution of foci as fixed. Thus, a random-effects inference is invoked, focussing inference on the above-chance convergence between different experiments, not the clustering of foci within a particular experiment. Computationally,

Table 2
Details of analyses and subanalyses carried out in the present meta-analysis.

		Experiments	Subjects	Activation foci
Observation		104	1061	1390
	of hand actions	62	804	823
	–with instruction 'passively observe'	38	459	516
	–with instruction 'observe to imitate'	8	131	111
	of right hand actions	37	477	475
	of non-hand actions	32	364	508
	of face actions	17	188	291
	of object-related hand actions	37	516	587
	of non-object-related hand actions	25	318	236
Imitation		35	459	542
	of hand actions	30	405	396
	of right hand actions	15	211	193
	of non-object-related hand actions	19	320	245

deriving this null hypothesis involved sampling a voxel at random from each of the MA maps and taking the union of these values. The ALE score obtained under this assumption of spatial independence was recorded and the permutation procedure iterated 10^{11} times to obtain a sufficient sample of the ALE null distribution. The 'true' ALE scores were tested against the ALE scores obtained under the null distribution and thresholded at a cluster-level corrected threshold of $p < 0.05$ for each separate meta-analysis performed.

Conjunction analysis was carried out to determine the intersection between the meta-analyses on observation and imitation. Results are reported for a corrected p-value of <0.05. Contrast analyses were calculated by means of ALE subtraction analysis, accounting for potential differences in sample size. To increase the specificity of the results, the analysis of differences was restricted to those voxels that showed an effect in main action observation or imitation meta-analyses. The reported contrasts were also thresholded at a corrected p-value of <0.05.

The resulting areas were anatomically labeled by reference to probabilistic cytoarchitectonic maps of the human brain using the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007). Using a Maximum Probability Map (MPM), activations were assigned to the most probable histological area at their respective locations. Previous studies have provided details about the cytoarchitecture, intersubject variability, and borders of the areas implicated in the current analysis that can be found in the following publications, such as Broca's region (BA 44, BA 45: Amunts et al., 1999), inferior parietal areas (PFop, PFt, PFcm, PF: Caspers et al., 2006, 2008), primary motor cortex (4a; Geyer et al., 1996), premotor cortex (BA 6; Geyer, 2004), primary somatosensory areas (BA 2: Grefkes et al., 2001; BA 1: Geyer et al., 1999, 2000), secondary somatosensory area OP1 (Eickhoff et al., 2006a,b), visual area V5 (Malikovic et al., 2007), superior parietal area 7A, intraparietal area hIP3 (Scheperjans et al., 2008a,b), and intraparietal area hIP1 (Choi et al., 2006).

Results

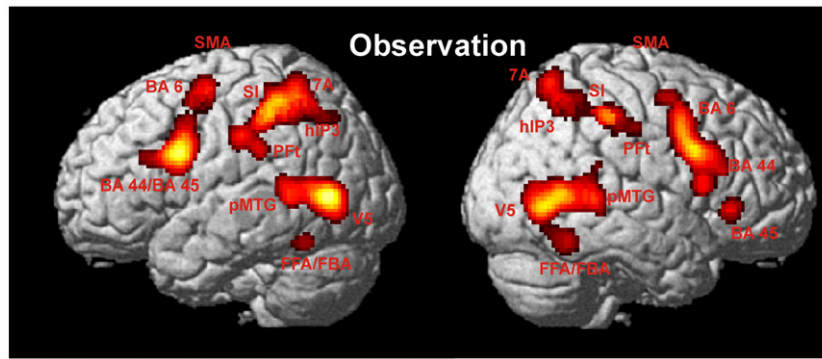### Individual meta-analyses of action observation and imitation networks

Action observation network

Brain regions showing consistent activation across the 104 action observation experiments were observed symmetrically across both hemispheres in frontal areas BA 44/45, lateral dorsal premotor cortex (dPMC, BA 6), supplementary motor area (SMA, BA 6), rostral inferior parietal lobule (IPL, area PFt), primary somatosensory cortex (SI, BA 1/2), superior parietal (SPL, area 7A), intraparietal cortex (IPS, area hIP3), posterior middle temporal gyrus (pMTG) at the transition to

Fig. 1. Significant meta-analysis results for action observation, summarized over all effectors. All results are displayed on the left and right lateral surface view of the MNI single subject template. pMTG posterior middle temporal gyrus, SMA supplementary motor area (hidden within the interhemispheric fissure); BA 44, 45: Broca's area (Amunts et al., 1999); BA 6: lateral premotor cortex (Geyer 2004); SI: primary somatosensory cortex (BA 2, Grefkes et al., 2001); 7A: superior parietal area (Scheperjans et al., 2008a,b); PFt: inferior parietal area (Caspers et al., 2006, 2008); hIP3: intraparietal area (Scheperjans et al., 2008a,b); V5: extrastriate visual area (Malikovic et al., 2007).

visual area V5, and fusiform face area/fusiform body area (FFA/FBA; Fig. 1). Coordinates of the activation maxima of the meta-analysis on action observation are given in Table 3.

Table 3
Peaks of activation for the two categories "action observation", and "action imitation."

Macroanatomical location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Action observation				
L IFG / PrG	BA 44 / BA 45 / vent-lat BA 6	−50	9	30
L lat dPMC	dors-lat BA 6	−26	−4	56
L med PMC (SMA)	med BA 6	−2	18	50
L SI / IPS / SPL	BA 2 / hIP3 / 7A	−34	−44	52
L IPL	PFt / PFop	−60	−24	36
L STS / pMTG		−54	−50	8
L lat occipital	V5	−46	−72	2
L fusiform (FFA/FBA)		−44	−56	−18
R IFG	BA 44	52	12	26
R IFG	BA 45	56	30	−2
R lat dPMC / MFG	dors-lat BA 6	34	−2	54
R med PMC (SMA)	med BA 6	4	12	58
R SI	BA 1 / 2	60	−20	40
R IPL	PFt	44	−34	44
R SPL	7A	22	−62	64
R IPS	hIP3	30	−54	48
R STS / pMTG		56	−40	4
R lat occipital	V5	52	−64	0
R fusiform (FFA/FBA)		44	−54	−18
Action imitation				
L IFG / PrG	BA 44 / vent-lat BA 6	−60	12	14
L lat dPMC	dors-lat BA 6	−36	−14	62
L med PMC (SMA)	med BA 6	−1	12	52
L SI / IPS	BA 2 / hIP3	−38	−40	50
L STS / pMTG		−54	−50	10
L lat occipital	V5	−52	−70	6
R IFG	BA 44 / 45	58	16	10
R lat dPMC / MFG	dors-lat BA 6 / MFG	42	4	56
R med PMC (SMA)	med BA 6	14	6	66
R anterior insula		42	4	1
R SI / IPL	BA 2 / PFt	52	−36	52
R SII / IPL	OP1 / PFcm	60	−26	20
R lat occipital	V5	54	−64	4
R fusiform (FFA/FBA)		44	−54	−22

All peaks are assigned to the most probable brain areas as revealed by the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007).
FFA/FBA: fusiform face area/fusiform body area, IFG: inferior frontal gyrus, IPL: inferior parietal lobule, IPS: intraparietal sulcus, MFG: middle frontal gyrus, PMC: premotor cortex, pMTG: posterior middle temporal gyrus, PrG: precentral gyrus, SI: primary somatosensory cortex, SII: secondary somatosensory cortex, SMA: supplementary motor cortex, SPL: superior parietal lobule, STS: superior temporal sulcus, dors-lat: dorso-lateral, med: medial, lat: lateral, vent-lat: ventro-lateral.
For further naming details, see Materials and Methods and Results sections.

To assess the effects of potentially confounding factors, additional subanalyses for different effectors and instructions were carried out, revealing a comparable brain network to that of the general analysis across all experiments. Brain areas consistently active during the observation of hand actions include: frontal BA 44, dPMC (BA 6), IPL area PFt, SPL area 7A, IPS area hIP3, SI cortex (BA 2), and pMTG at the transition to visual area V5 bilaterally. BA 45 was only found to be consistently active in the right hemisphere. In contrast to the analysis based on all action observation experiments, activation of FFA/FBA was not found in the observation of hand actions alone (Fig. 2A and Table 4).

When only including right hand actions in the analysis, the same areas were consistently found to be activated across studies (Fig. 2B and Table 4). That is, while the smaller number of studies resulted in lower statistical power and hence smaller clusters of convergence, results were replicated when testing across all action observation, observation on hand actions, and observation of right hand actions.

In contrast to hand-related actions, the analysis of observation of non-hand actions (e.g., involving the face or the whole body) showed consistent activations within frontal and temporo-occipital areas bilaterally, including BA 44, PMC and SMA (BA 6), pMTG and V5. FFA/FBA was only active in the right hemisphere, whereas the only consistent parietal activation, which was located within the IPS (hIP3), was found in the left hemisphere (Fig. 2C and Table 4). The same activation pattern was found for the analysis of observation limited to face actions, except for SMA which did not show consistent activation (Fig. 2D and Table 4).

Contrasting observation of hand and non-hand actions revealed a higher consistency of activations within BA 44 for non-hand actions. In contrast, a higher convergence of reported activations evoked by the observation of hand actions was found in the PMC (BA 6), SI (BA 2), the IPL (area PFt), and the pMTG at the border to V5 (Fig. 2E).

A further subanalysis assessed the effects of different instructions that were given to the subjects in the various action observation tasks. The observation of hand actions with the instruction to 'passively observe' recruited a comparable network as the main analysis on action observation, consisting of lateral premotor, IPL, SPL, and IPS cortex, SI, and pMTG (Fig. 3A). In contrast, observation of hand actions with the instruction 'observe to imitate' mainly led to consistent activations in lateral premotor and posterior temporal and extrastriate visual cortex, without consistent activation of parietal areas (Fig. 3B).

Contrast analysis between different instructions provided to subjects revealed more consistent activation within IPL (area PFt) bilaterally as well as in left BA 44, SI, and intraparietal sulcus (area hIP3) for the instruction 'passively observe' whereas the instruction 'observe to imitate' revealed no stronger association in any region (Fig. 3C and Table 4). However, we note that the subanalysis on
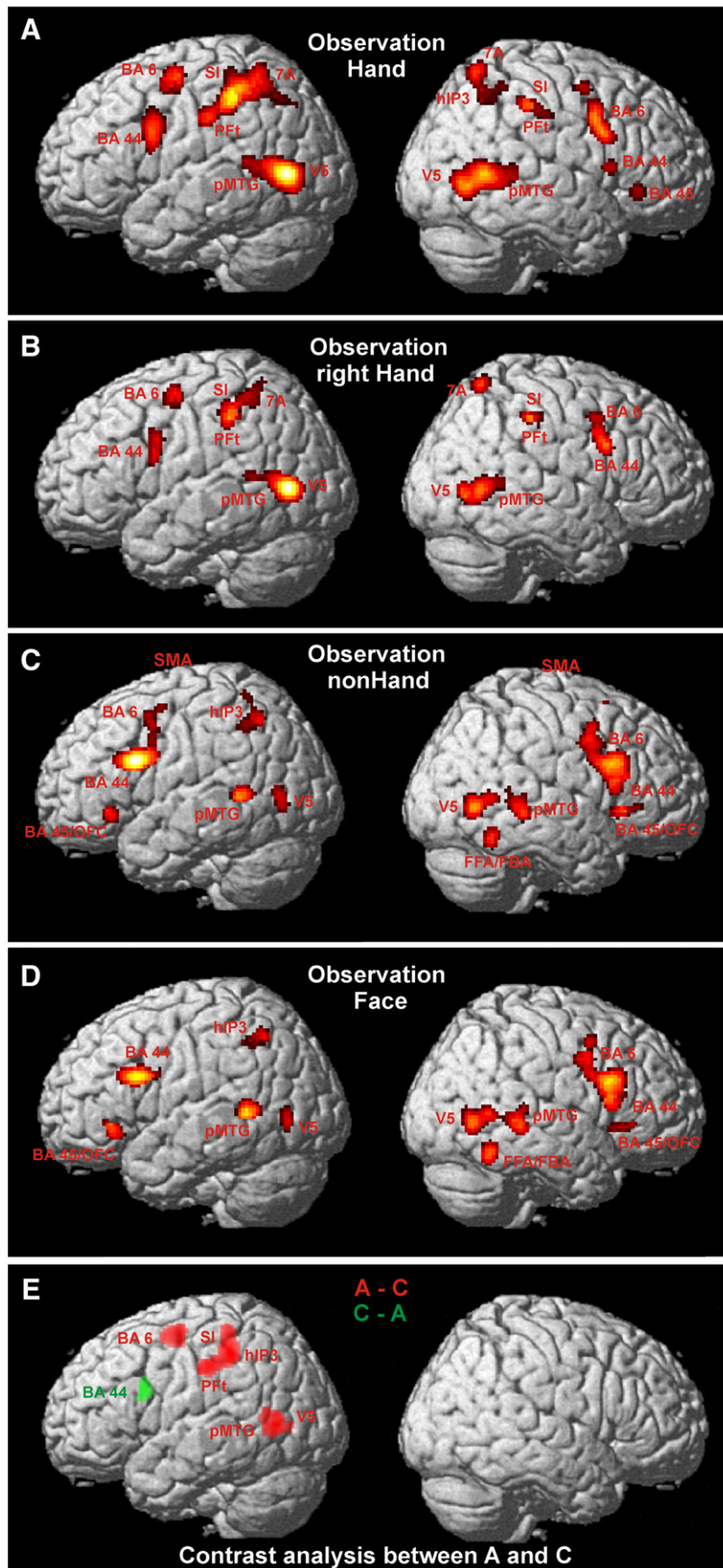
Fig. 2. Significant meta-analysis results for (A) observation of hand actions, (B) observation of right hand actions, (C) observation of non-hand actions, (D) observation of face actions, and (E) contrast analysis between observation of hand actions and observation of non-hand actions (colour-coding of respective contrasts within the figure). For other conventions, see Fig. 1.

Table 4
Peaks of activation for the subanalyses within the observation sample.

Macroanatomical location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Observation hand				
L IFG / PrG	BA 44 / vent-lat BA 6	−50	6	30
L lat dPMC	dors-lat BA 6	−26	−4	56
L SI / IPS	BA 2 / hIP3	−36	−42	36
L IPL	PFt	−58	−24	36
L STS / pMTG		−56	−48	10
L lat occipital	V5	−46	−70	4
R IFG / PrG	BA 44 / vent-lat BA 6	52	8	36
R IFG	BA 45	56	30	−4
R lat dPMC / MFG	dors-lat BA 6 / MFG	36	0	54
R SI	BA 2	42	−34	46
R IPL	PFt	60	−26	42
R SPL	7A	22	−62	64
R STS / pMTG		52	−60	4
R lat occipital	V5	50	−66	0
Observation right hand				
L IFG / PrG	BA 44 / vent-lat BA 6	−51	5	29
L lat dPMC / MFG	dors-lat BA 6 / MFG	−26	−4	54
L IPL / SI	PFt / BA 2	−44	−36	42
L SI / SPL	BA 1 / 2 / 7A	−32	−48	56
L STS / pMTG		−56	−50	12
L lat occipital	V5	−46	−70	4
R IFG / PrG	BA 44 / vent-lat BA 6	−54	8	36
R IPL / SI	PFt / BA 2	49	−32	47
R SPL	7A	22	−62	64
R lat occipital / pMTG	V5 / pMTG	52	−72	4
Observation non-hand				
L IFG / PrG	BA 44 / BA 45 / vent-lat BA 6	−49	11	31
L IFG / OFC	BA 45 / OFC	−44	28	−6
L med PMC (SMA)	med BA 6	4	10	58
L SPL / IPS	7A / hIP3	−32	−54	51
L pMTG / STS		−52	−48	6
L lat occipital / pMTG	V5 / pMTG	−48	−70	6
R IFG / PrG	BA 44 / BA 45 / vent-lat BA 6	53	13	29
R IFG / OFC	BA 45 / OFC	46	20	2
R med PMC (SMA)	med BA 6	−4	10	58
R pMTG / STS		56	−38	0
R lat occipital / pMTG	V5 / pMTG	54	−64	0
R fusiform (FFA/FBA)		46	−54	−18
Observation face				
L IFG / PrG	BA 44 / BA 45 / vent-lat BA 6	−48	15	27
L IFG / OFC	BA 45 / OFC	−44	28	−6
L med PMC (SMA)	med BA 6			
L SPL / IPS	7A / hIP3	−32	−56	48
L pMTG / STS		−52	−48	6
L lat occipital / pMTG	V5 / pMTG	−49	−71	2
R IFG / PrG	BA 44 / BA 45 / vent-lat BA 6	53	13	27
R IFG / OFC	BA 45 / OFC	50	24	−1
R med PMC (SMA)	med BA 6			
R pMTG / STS		56	−38	0
R lat occipital / pMTG	V5 / pMTG	54	−64	0
R fusiform (FFA/FBA)		46	−54	−18
Observation hand passively observe				
L IFG / PrG	BA 44 / vent-lat BA 6	−51	6	31
L lat dPMC / MFG	dors-lat BA 6 / MFG	−26	−4	54
L SI / IPL	BA 2 / PFt	−52	−28	40
L lat occipital	V5	−46	−70	4
R IFG / PrG	BA 44 / vent-lat BA 6	52	9	36
R SI / IPL	BA 2 / PFt	42	−32	44
R SPL	7A	22	−62	64
R pMTG		52	−58	4
R lat occipital	V5	44	−70	2
Observation hand observe to imitate				
L IFG / PrG	BA 44 / vent-lat BA 6	−51	8	39
L lat dPMC	dors-lat BA 6	−34	−14	60

Table 4 (*continued*)

Macroanatomical location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Observation hand observe to imitate				
L M1	4a	−40	−28	58
L pMTG		−55	−51	12
L lat occipital / pMTG	V5 / pMTG	−52	−70	6
R IFG	BA 44	58	14	10
R anterior insula		42	5	−1
R SPL	7A	9	−63	64
R pMTG		52	−48	8
R lat occipital / pMTG	V5 / pMTG	54	−72	2
Observation hand object				
L IFG / PrG	BA 44 / vent-lat BA 6	−51	7	30
L lat dPMC / MFG	dors-lat BA 6 / MFG	−26	−4	56
L SI / IPS	BA 2 / hIP3	−36	−42	52
L IPL	PFt	−58	−24	36
L lat occipital / pMTG	V5 / pMTG	−46	−70	4
R IFG / PrG	BA 44 / vent-lat BA 6	54	9	34
R SI / IPL	BA 2 / PFt	42	−34	46
R SPL	7A	22	−62	64
R pMTG		52	−60	4
R lat occipital	V5	44	−72	4
Observation hand non-object				
L SI / IPS	BA 2 / hIP1	−37	−46	50
L IPL	PF	−54	−36	46
L pMTG		−56	−50	6
L lat occipital / pMTG	V5 / pMTG	−50	−64	6
R IFG / PrG	BA 44 / vent-lat BA 6	51	8	37
R pMTG		54	−40	8
R lat occipital / pMTG	V5 / pMTG	50	−68	2

All peaks are assigned to the most probable brain areas as revealed by the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007). For naming conventions, see Table 3.

observation with instruction 'observe to imitate' was based on only 8 experiments. The meta-analysis algorithm accommodates for such differences in sample size. But with such large differences as found here, a potential confounding effect due to sample size cannot fully be excluded. Thus, it cannot be ruled out that a lack of consistent activation within parietal cortex might have resulted from the small number of studies. Further subdividing the studies according to the other instructions only yielded very low numbers of studies for different categories, thus not providing enough data for further subanalyses.

Dividing the experiments on hand action observations into those that presented object-related actions and those that did not revealed a further differentiation within the observation network. The observation of object-related hand actions was more consistently associated with activations in BA 44, lateral PMC (BA 6), IPL area PFt, SPL area 7A, the pMTG and V5 bilaterally, as well as with activations in SI (BA 2) and the anterior IPS (area hIP3) on the right hemisphere (Fig. 4A and Table 4). In contrast, observation of non-object-related hand actions was mainly associated with activations in the temporo-occipital areas (Fig. 4B and Table 4).

Contrast analysis between observation of object- and non-object-related actions revealed a stronger association of activation with object-related actions within left BA 44, lateral PMC (BA 6), and inferior parietal area PFt, and in right superior parietal area 7A and temporo-occipital cortex (Fig. 4C).

Action imitation network

Action imitation tasks also most consistently evoked activation in an extended bilateral network comprising frontal BA 44, the PMC (BA 6) and adjacent superior frontal gyrus (SFG), the SMA (BA 6), SI (area 2), IPL (area PFt), and visual area V5. The pMTG was found to be consistently activated only in the left hemisphere, whereas ventral IPL area PFcm at the border to the secondary somatosensory cortex (SII) area OP1, the FFA/FBA, and the frontal aspect of the insular cortex
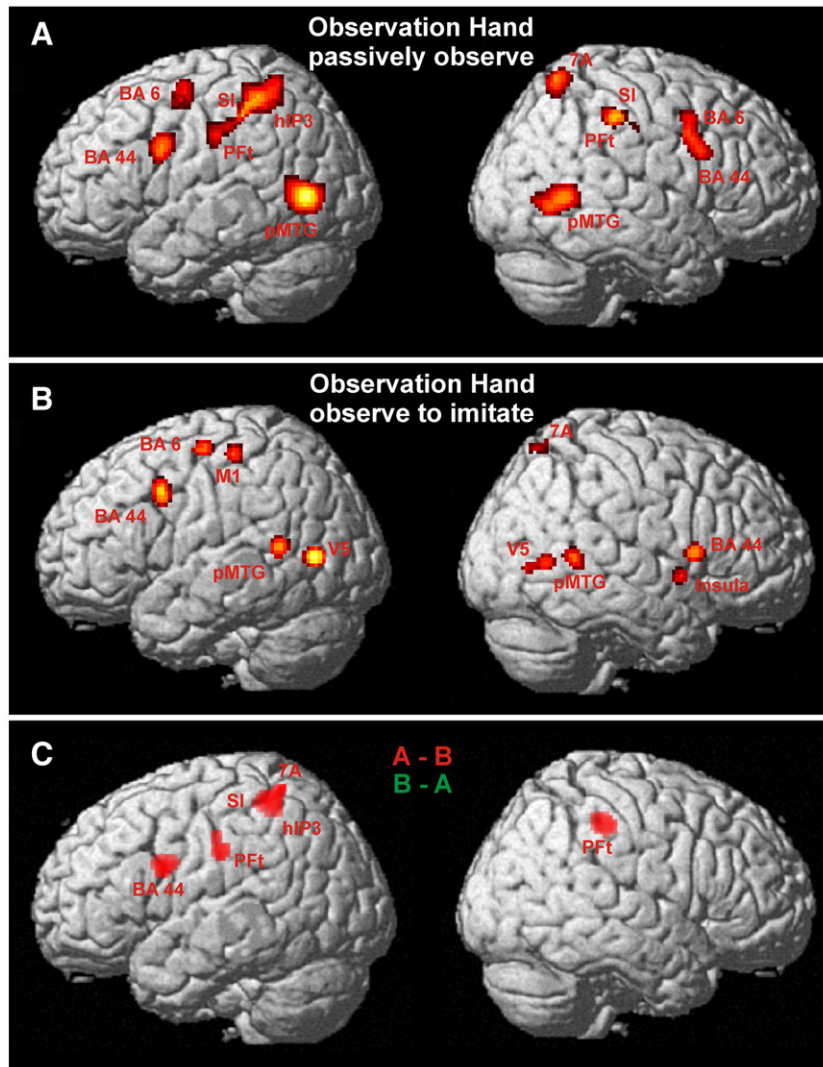
Fig. 3. Significant meta-analysis results for (A) observation of hand actions with instruction 'passively observe,' (B) observation of hand actions with instruction 'observe to imitate,' and (C) contrast analysis between both categories (colour-coding of respective contrasts within the figure). For other conventions, see Fig. 1.

were only consistently activated in the right hemisphere (Fig. 5). Coordinates of the activation maxima for the main meta-analysis on action imitation are given in Table 3.

Additional subanalyses were carried out on the imitation of hand actions, right hand actions, and non-object-related hand actions. Imitation of hand actions and right hand actions both revealed patterns of activation that were highly comparable to action imitation across all experiments. A major difference was only found with respect to imitation of right hand actions: here, the pMTG was not only consistently activated in the left, but also in the right hemisphere (Figs. 6A, B and Table 5).

Imitation of non-object-related actions, however, only evoked consistent activation of the motor and lateral premotor areas, like BA 44, BA 6, and adjacent SFG (Fig. 6C and Table 5), but not in temporo-occipital areas.

Conjunction and contrast analyses

Conjunction analysis

To identify brain regions that are consistently activated by action observation as well as action imitation tasks, a conjunction analysis of the two meta-analyses reported above was performed.

Common significant activations were found bilaterally in frontal BA 44, lateral PMC (BA 6), the SMA (BA 6), rostral IPL (areas PFop and PFt),

SI (BA 2), and visual area V5. Moreover, the left hemispheric pMTG was also found in both networks whereas activation of the right FFA/FBA was commonly found in the right hemisphere (Fig. 7A and Table 6).

Contrast analysis

To assess which areas were more consistently associated with action observation or imitation, an ALE subtraction was performed on those voxels where either of the two analyses showed a significant activation to determine the relative divergence of these tasks. In comparison with imitation tasks, action observation tasks were more associated with activations in a rostro-dorsal part of BA 44, lateral PMC, the pMTG and V5 bilaterally as well as with activation in left IPL areas PFt/PFop and in right SPL area 7A (Fig. 7B and Table 7).

In contrast, activations in action imitation experiments were more consistently found in a caudo-ventral part of left BA 44 (at the border to caudally adjacent BA 6) bilaterally, and in the SI (BA 2), the adjacent IPL (area PFt), and the FFA/FBA within the right hemisphere (Fig. 7B and Table 7).

Comparable results could be found when performing separate conjunction and contrast analyses for the subsamples on effectors, involvement of an object, and instructions that have been reported in the previous sections. Small differences were only found with respect to the size of the activation clusters whereas the location remained stable.
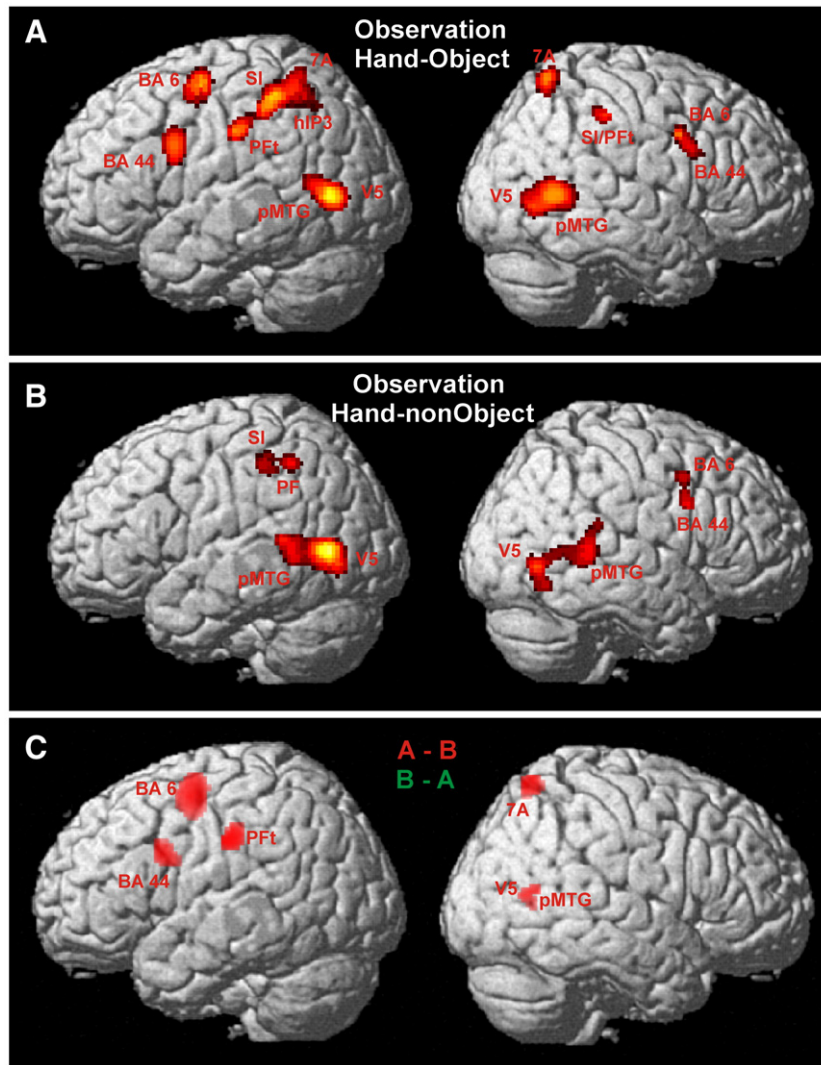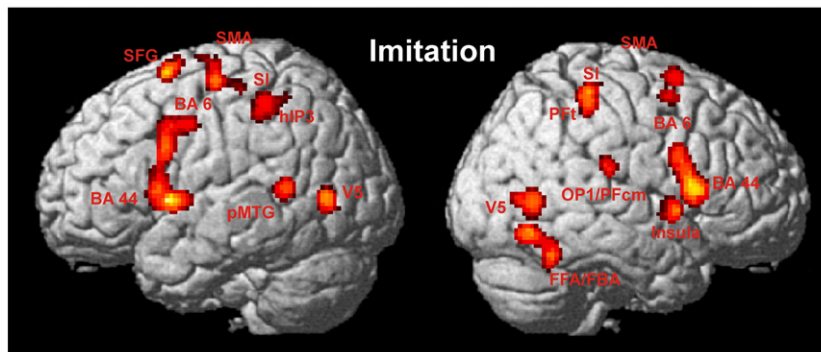
Fig. 4. Significant meta-analysis results for (A) observation of object-related hand actions, (B) observation of non-object-related hand actions, and (C) contrast analysis between both categories (colour-coding of respective contrasts within the figure). For other conventions, see Fig. 1.

Discussion

The present study assessed the action observation and imitation networks in the human brain in a meta-analysis of 139 fMRI and PET experiments. Both action observation and imitation experiments were consistently associated with activation in a largely bilateral network of premotor, primary somatosensory, inferior parietal, and intraparietal as well as temporo-occipital areas. Further analysis revealed that this activation pattern is largely independent from possible confounds, such as effectors. However, activation in Broca's area (BA 44, BA 45) differed between the observation and the imitation of an action: while activation due to observation was more consistent in a rostro-dorsal aspect (BA 45), activation due to imitation consistently recruited the caudo-ventral part (BA 44). Another notable difference pertained to the posterior middle temporal cortex: While action observation involved this cortical

Fig. 5. Significant meta-analysis results for action imitation. MI: primary motor cortex (areas 4a, 4p; Geyer et al., 1996). For other conventions, see Fig. 1.
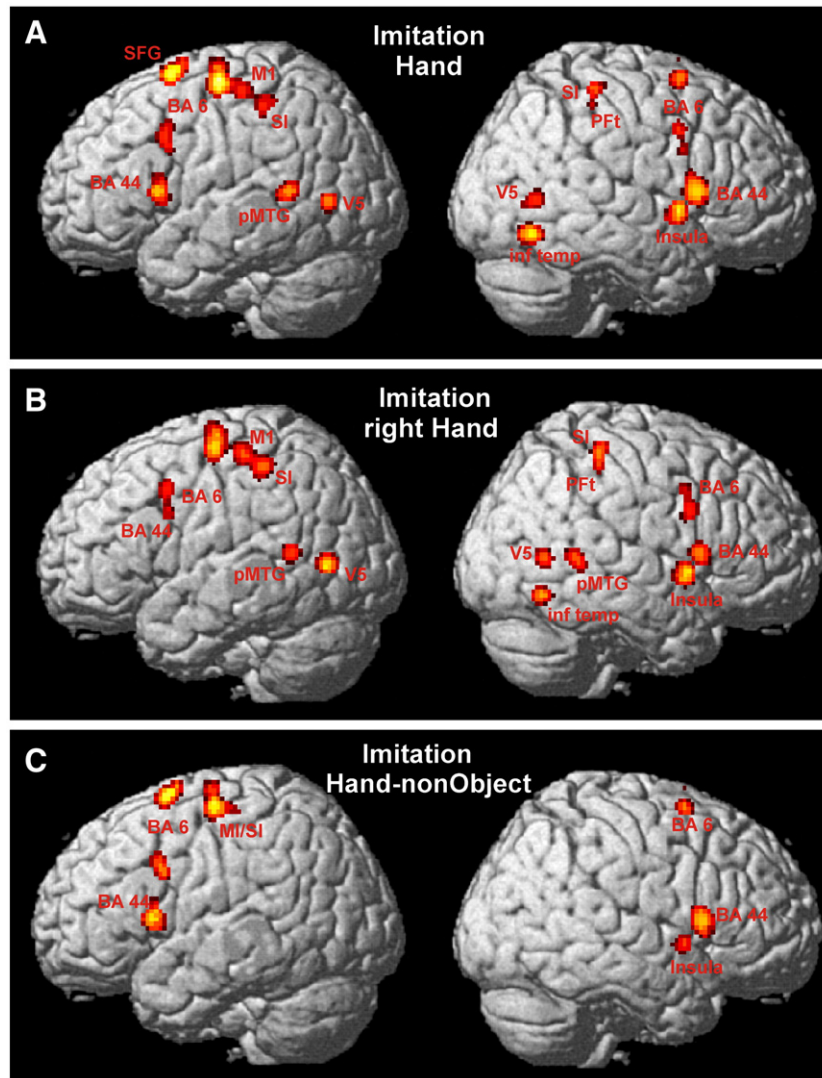
Fig. 6. Significant meta-analysis results for (A) imitation of hand actions, and (B) imitation of right hand actions, and (C) imitation of non-object-related hand actions. For other conventions, see Fig. 1.

region bilaterally, imitation tasks only involved the left pMTG. In the context of imitation, activation in right pMTG was only found for imitation of right hand actions.

Methodological considerations

The results of any given neuroimaging experiment are influenced by various study-specific idiosyncrasies, including the experimental design, implementation of the paradigm, task requirements, included subjects and the analysis of the data. Hence, the results of any particular experiment can rarely yield generalisable inference on the cortical substrates of a particular cognitive process. One way to overcome these drawbacks is to integrate the results from several neuroimaging studies by means of quantitative meta-analyses (Eickhoff et al., 2009; Laird et al., 2009; Turkeltaub et al., 2002). Hereby, inference is directed towards identifying those regions where previous experiments showed converging evidence for activation. Significant results in a meta-analysis are achieved if convergence across studies occurs more likely than expected by chance, even though this does not require all or even the majority of the studies to activate at that particular location. Using the revised version of the ALE meta-analysis algorithm (Eickhoff et al., 2009) provided objective modelling of spatial uncertainty relative to sample sizes within different studies and testing for convergence across

different experiments. Therefore, possible drawbacks of former coordinate-based meta-analysis approaches (Laird et al., 2005a,b; Turkeltaub et al., 2002) were avoided. Nevertheless, differences in sample size between different meta-analyses (e.g., on action observation and action imitation) may influence the obtained results, in particular with respect to the size of the significant clusters. Furthermore, it has to be noted that meta-analyses on the basis of ALE algorithms only reveal a consistency of activations across studies. Information about strength of a resulting activation cluster is not considered, as these are reported inconsistently and by incompatible measures in the original publications (e.g., percent signal change vs. contrast estimates vs. Z-scores). Consequently, a task which evokes stronger activation in any particular experiment than another may result in less significant and/or extended activation on meta-analyses, if the convergence between studies is less pronounced.

Also, coordinate-based meta-analyses only use reported peak activations for the analysis, thus discarding a large amount of spatial information from the original statistical parametric images. To address this problem, image-based meta-analyses have been proposed, which use the full statistic images of the experiments (e.g., Schilbach et al., 2008b). While such approaches use more information from the original data, their applicability is quite limited since they require comparable contrast images and error estimates for every

Table 5
Peaks of activation for the subanalyses within the imitation sample.

Macroanatomical location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Imitation hand				
L IFG / PrG	BA 44 / vent-lat BA 6	−52	10	38
L IFG	BA 44	−54	14	8
L lat dPMC	dors-lat BA 6	−36	−14	62
L M1	4a	−40	−28	58
L SFG		−16	8	66
L SI	BA 2	−36	−38	52
L STS / pMTG		−54	−50	10
L lat occipital / pMTG	V5 / pMTG	−52	−68	6
R IFG / PrG	BA 44 / vent-lat BA 6	56	7	38
R IFG	BA 44 / 45	58	15	11
R lat dPMC / SFG	dors-lat BA 6 / SFG	16	6	64
R anterior insula		44	6	0
R SI	BA 1 / 2	48	−34	60
R IPL	PF / PFt	54	−36	52
R lat occipital / pMTG	V5 / pMTG	54	−64	6
R inf temporal		44	−66	−10
Imitation right hand				
L IFG / PrG	BA 44 / vent-lat BA 6	56	8	34
L lat dPMC	dors-lat BA 6	−34	−14	62
L M1	4a	−40	−28	58
L SI	BA 2	−36	−38	54
L pMTG		−54	−52	10
L lat occipital / pMTG	V5 / pMTG	−52	−70	6
R IFG	BA 44	58	14	8
R SI	BA 1 / 2	46	−36	58
R IPL	PF / PFt	54	−36	52
R anterior insula		44	6	−2
R pMTG		52	−48	6
R lat occipital / pMTG	V5 / pMTG	54	−62	6
R inf temporal		−44	−64	−11
Imitation hand non-object				
L IFG / PrG	BA 44 / vent-lat BA 6	−53	10	35
L IFG	BA 44 /45	−54	14	8
L lat dPMC / M1	dors-lat BA 6 / 4a	−40	−16	62
L lat dPMC / SFG	dors-lat BA 6 / SFG	−18	6	68
R IFG	BA 44 / 45	60	16	8
R lat dPMC / SFG	dors-lat BA 6 / SFG	16	6	64
R anterior insula		42	6	−2

All peaks are assigned to the most probable brain areas as revealed by the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007). M1 primary motor cortex, for other naming conventions, see Table 3.

included study. That is, image-based analyses may use more data from each individual experiment but the number of experiments that can be included is generally greatly reduced. However, a recent comparison of image- and coordinate-based meta-analyses (Salimi-Khorshidi et al., 2009) revealed good agreement between meta-analyses based on full statistical contrast images and reduced 3D coordinates. Given this evaluation and the difficulties of obtaining full image data from a sufficient amount of published experiments, it seems that coordinate-based approaches such as ALE represent the most practical tool for meta-analyses on neuroimaging data.

An important caveat for the interpretation of meta-analyses is the potential presence of confounding factors in the assessed experiments. Meta-analyses pool across many studies to identify convergent findings while disregarding experiment-specific variability in design and analysis. However, the averaging effects of meta-analyses that allow for the influence of confounding factors to be ignored only pertain to unsystematic study variations. If, however, an additional cognitive process is present in a significant number of the included experiments, the ensuing activations may confound the meta-analysis. In this case, activation in a certain area would not be attributable to the process of interest but to processes that were concurrently present in the included experiments. For example, it has been argued that activation of Broca's area during imitation tasks

could result from covert speech (e.g., Brass and Heyes, 2005). Assuming that vocalisation is present in the majority of the imitation experiments, vocalisation-related activity will be indistinguishable from an imitation-related one. This scenario, however, also raises the fundamental question, whether two processes that co-occur consistently in neuroimaging experiments should actually be distinguished from each other. That is, covered vocalisation and the corresponding activation of BA 44 may be an intrinsic part of action imitation rather than a confound that must be excluded. Evidence for such a genuine role of BA 44 in imitation processes, for example, is provided by recent transcranial magnetic stimulation (TMS) and lesion studies, which showed that lesions (artificial or pathological) in BA 44 led to imitation failure (Fazio et al., 2009; Heiser et al., 2003).

Areas involved in both networks

Overall, the current meta-analysis revealed a network for the observation and imitation of actions that expands both hemispheres and reaches far beyond the 'classical' mirror neuron areas within ventral premotor and inferior parietal cortex. This view of an "expanded MNS" involving similar areas as revealed by the current meta-analysis, has recently been assumed based on human imaging studies (Fabbri-Destro and Rizzolatti, 2008; Iacoboni, 2009) and with respect to possible homologies to the macaque mirror neuron system (Keysers and Gazzola, 2009). The present meta-analysis could provide further evidence to this discussion regarding the involvement of these networks in processing of observed and imitated actions. The results showed that areas other than the 'classical' mirror neuron areas vPMC and rostral IPL were consistently activated across studies, i.e., dPMC, SMA, pMTG, and V5.

Among the commonly activated areas are BA 44 and the rostral IPL/anterior IPS (areas PFt/hIP3). These two regions are thought to be the human homologues of macaque ventral premotor area F5 and rostral inferior parietal areas PFG and PF, i.e., those areas where mirror neurons were discovered using invasive recordings (e.g., Fogassi et al., 2005; Gallese et al., 1996; Rozzi et al., 2008). Activation of these regions by action observation tasks is not surprising, since "activation during action observation" is one of the key properties defining a mirror neuron (e.g., Rizzolatti, 2005). Thus, if BA 44 and the rostral IPL are indeed the homologues of the mirror neuron areas in other primates, they should be activated by action observation tasks. Activation during action imitation, however, is not a typical mirror neuron characteristic. Rather, it has been stressed that monkeys are not able to imitate in a comparable way as humans (e.g., Iacoboni, 2009; Rizzolatti, 2005). In human neuroimaging studies on imitation paradigms, however, robust activation of BA 44 and the rostral IPL have been reported (e.g., Hamilton and Grafton, 2008; Iacoboni, 2009; Iacoboni and Dapretto, 2006; Rizzolatti et al., 2001) and are confirmed in the current meta-analysis. A straightforward explanation for these findings could be provided by the experimental setup of most action imitation experiments. Typically these involve concurrent execution of an observed action, i.e., both properties that define mirror neurons. It has, however, also been argued that potential mirror neurons in the human brain may have an independent relevance for imitation tasks, even though they don't hold the same function in non-human primates (e.g., Brass and Heyes, 2005; Culham and Valyear, 2006; Heyes, 2001). This view is largely based on conceptualising mirror properties as a matching between sensory input and motor acts (e.g., Kilner et al., 2007; Jakobs et al., 2009) and stressing the importance of such a mechanism for action observation, execution, and crucially also imitation (e.g., Fabbri-Destro and Rizzolatti, 2008). Rizzolatti (2005) moreover stressed the possibility that in particular the caudal aspect of BA 44 may represent the putative homologue of macaque area F5. Our meta-analysis confirms and extends this view in a quantitative analysis over a large number of individual experiments. Since imitation and observation recruited the very caudal aspect of BA 44
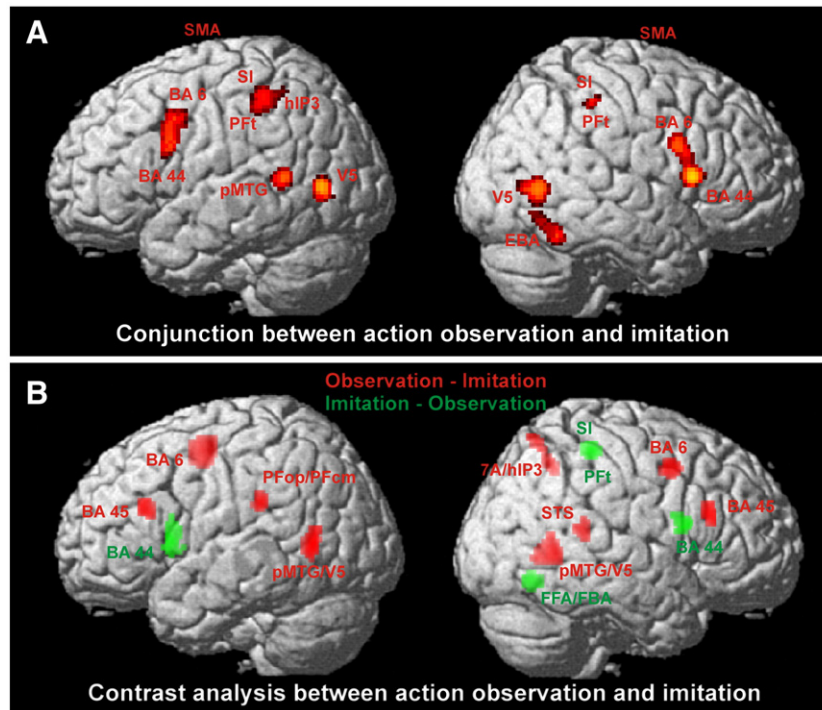
Fig. 7. Significant results for (A) the conjunction and (B) the contrast analysis between the main categories action observation and action imitation (colour-coding of respective contrasts within the figure). For other conventions, see Fig. 1.

at the border to BA 6, the same region was activated during imitation as thought to be a human mirror region (Rizzolatti, 2005). With respect to the parietal cortex, the current meta-analysis could provide new evidence for the discussion of potential homologies between humans and monkeys by showing that human area PFt seems to be most consistently involved in processes that have been ascribed to area PF of the macaque.

Importantly, the location of the convergent activation within Broca's area (BA 44, BA 45) differed between action observation and action imitation tasks. Only the caudo-dorsal part of BA 44 was involved in both networks, whereas a higher consistency of activation for imitation was found in a more caudo-ventral aspect of BA 44. In turn, more consistent activation by observation tasks was found in the rostro-dorsal aspect of Broca's region (BA 45). This dissociation has already been noted in previous experiments and was interpreted as deriving from the requirements of forward modelling processes during imitation (e.g., Molnar-Szakacs et al., 2005; Morin and Grèzes,

2008, Brass and Heyes, 2005; Vogt et al., 2007). Furthermore, an explicit model for this differentiation within Broca's region was introduced by Koechlin et al. (2003) and Koechlin and Jubault (2006): Within this model, Broca's region is most likely involved in context specific recognition of stimuli. Further differentiation regarding the amount of cognitive control results in a bipartition: Activation within BA 44 was seen as being responsible for the initiation and termination of simple actions whereas activation in BA 45 was more likely ascribed to the supraordinate aspect of the action (Koechlin and Jubault, 2006). Following this model and the works by Molnar-Szakacs et al. (2005) and Vogt et al. (2007), the differentiation within Broca's region found in the present meta-analysis could be interpreted as follows. Actions shown during the observation experiments were generally more complex, whereas actions in the imitation experiments were kept simpler. This difference is owed to feasibility constraints in the scanner for imitation but not for observation studies. Thus, the

Table 6
Peak activations for the conjunction between "action observation" and "action imitation."

Macroanatomical location	Cytoarchitectonic location	Anatomical MNI coordinates		
		x	y	z
L IFG / PrG	BA 44 / vent-lat BA 6	−56	8	28
L vPMC	vent-lat BA 6	−54	6	40
L SMA	med BA 6	−1	16	52
L SI / IPS	BA 2 / hIP3	−38	−40	50
L STS / pMTG		−54	−50	10
L lat occipital	V5	−52	−70	6
R IFG	BA 44	58	16	10
R SMA	med BA 6	4	12	56
R IPL	PFt	51	−36	50
R SPL	7A / 7PC	30	−62	63
R fusiform (FFA/FBA)		44	−54	−20
R lat occipital	V5	54	−64	4

All peaks are assigned to the most probable brain areas as revealed by the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007). For naming details, see Table 3.

Table 7
Peak activations for contrast analysis.

Macroanatomical location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Imitation > observation				
L IFG	BA 44	−56	12	9
R IFG	BA 44	58	10	20
R SI / IPL	BA 2 / PFt	50	−36	54
R inf. temporal		42	−66	−12
Observation > imitation				
L IFG	BA 45	−52	28	22
L lat dPMC / SFG	dors-lat BA 6 / SFG	−20	−6	52
L IPL	PFop / PFcm	−50	−34	24
L pMTG		−46	−60	6
R IFG	BA 45	54	28	22
R lat PMC / PrG	lat BA 6	48	4	46
R SPL / IPS	7A / hIP3	28	−60	54
R STS		54	−40	16
R pMTG / lat occipital	pMTG / V5	47	−57	4

All peaks are assigned to the most probable brain areas as revealed by the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007). For naming details, see Table 3.

dominance of the rostro-caudal part of Broca's region (BA 45) during action observation might result from the processing of more complex movements. As such, there is a high need for integrating and assessing the context of the whole action. This is less the case for the more simple actions used during the imitation experiments. These, however, pose higher needs for control and forward modelling provided by caudal BA 44.

The supplementary motor area (SMA) was also consistently found to be active during action observation as well as action imitation tasks. Whereas action-related activations in BA 44 were linked to, e.g., motor sequence learning, motor imagery, and action preparation (e.g., Binkofski et al., 1999; Johnson-Frey et al., 2003; Krams et al., 1998; Mecklinger et al., 2002) or recognition of abstract motor behaviour and associative motor learning (e.g., Binkofski et al., 2000; Hazeltine et al., 1997; Seitz and Roland, 1992), one function of SMA was seen in temporally sequencing different parts of a complex movement (e.g., Tanji, 1994; Mita et al., 2009). Tankus et al. (2009) ascribed SMA activation to the encoding of speed and direction of a movement. Furthermore, it has been shown that lesions in SMA lead to deficits in sequencing actions (Gentilucci et al., 2000). Following these previous studies, the association of SMA activation with observation and imitation tasks can be interpreted as reflecting the temporal sequencing of the action. After disassembling a complex action into different executable parts, the individual parts have to be put into a temporal sequence to imitate the observed action correctly. For observation alone, this step might as well be necessary to capture all parts of the observed action for subsequent understanding of the action as a whole. This is supported by the notion that the activation within SMA during observation was mainly driven by the observation of non-hand actions which included whole body movements which are much more complex than simple finger and hand movements. To further enlighten the role of the SMA in temporal sequencing, the observation experiments have been subdivided into those with video (i.e., moving) and those with static stimuli, assuming that static stimuli would not require the involvement of the SMA. Both subanalyses revealed a comparable network as the overall observation analysis, with a higher consistency of activations for the video subsample. But since the sample sizes were largely unequal (79 video, 15 static), a potential bias toward the video sample could not fully be excluded. Furthermore, the static sample also involved complex actions which required a disassembly of the actions into different executable parts. Therefore, the need for temporal sequencing, and thus, the involvement of the SMA in this subsample could not completely be ruled out by conceptual reasons, either.

Furthermore, the posterior middle temporal gyrus/superior temporal sulcus (pMTG/STS), anterior and dorsal to V5, was consistently involved in action observation and imitation. This region is known to be involved in the processing of biological motion (e.g., Buccino et al., 2001; Puce and Perrett, 2003; Morris et al., 2008). Since the majority of all action observation and imitation experiments included in the present meta-analysis featured the display of video clips showing natural human movements, the activation of the pMTG/STS is well explained by this role.

Extrastriate visual area V5 has been involved within both networks revealed by the present meta-analysis. Activations in V5 have been reported in previous studies due to recognition and early processing of visually presented motion stimuli (e.g., Seymour et al., 2009; Thompson et al., 2009; Vaina et al., 2001). In the context of action observation and imitation, the involvement of area V5 could be explained in line with these previous reports, serving as an encoder of the dynamic aspect of the movement.

A part of the fusiform gyrus was also involved in both networks, most probably the fusiform face area / fusiform body area (FFA/FBA). The name of this region refers to the involvement of FFA and FBA in recognition of faces and bodies. (e.g., Downing et al., 2006; Kitada et al., 2009). In the current meta-analysis, activation in FFA/FBA was

primarily found during observation of face actions and, more generally, non-hand actions, which also involved, e.g., the whole body. No activation in this region was found for the observation of hand actions. The same holds true for the imitation sample: Whereas the total analysis which also contained imitation of face actions revealed activation in FFA/FBA, the analysis of imitation of hand actions did not reveal such an activation (there, the activation is located more rostro-dorsally). Thus, in both networks, FFA/FBA most likely serves as an encoder of facial and body stimuli. Furthermore, both networks only involved right FFA/FBA which is also in line with recent studies on the lateralization of visual perception areas, arguing in favour of a specialization of hemispheres with respect to different levels of processing which results in a specialization of the right hemisphere for tasks where spatial metrics and conjoining features play an essential role, like in the recognition of faces and bodies (e.g., Willems et al., 2009; Umiltá et al., 1985; for review: Dien, 2009).

Both action observation and imitation were also robustly associated with activations of the primary somatosensory cortex (SI). While an involvement of sensorimotor cortices during action observation has been demonstrated in a recent study explicitly dealing with this issue (Gazzola and Keysers, 2009), other studies provide evidence that somatosensory cortical regions also respond to the sight of touch (Blakemore et al., 2005; Carlsson et al., 2000; Keysers et al., 2004). But still, the neurobiology of this phenomenon remains elusive. Given that primary or unimodal sensory cortices such as SI are driven by modality-specific thalamic input, these activations should be attributable to top-down modulation from associative areas. One interpretation for SI activation during action observation is that this region may act as a simulator of "what it could feel like to act as seen." This idea of SI as providing a proprioceptive and tactile matching of seen actions has recently been advanced (Gazzola and Keysers, 2009; Keysers and Gazzola, 2009), saying that an action needs to be mapped onto one's own sensorimotor system to fully understand the motor components of the observed action. It could be speculated that this simulatory processes in SI might be coordinated by the ventral premotor cortex (BA 44 and adjacent BA 6) which has been assumed to be responsible for forward modelling processes, especially during imitation experiments (Molnar-Szakacs et al., 2005).

Neural correlates of action observation

The action observation network, as delineated by the present meta-analysis of 104 functional neuroimaging experiments, spanned both hemispheres in a largely symmetrical manner, consisting of frontal, parietal, and posterior temporal areas as assumed previously (e.g., Culham and Valyear, 2006; Fadiga et al., 2005; Lui et al., 2008; Rizzolatti and Craighero, 2004). The involvement of frontal premotor, parietal, and extrastriate visual areas within this network was also further supported by transcranial magnetic stimulation (TMS) studies. It has been shown that transient inactivation ("virtual lesions") over these areas may result in an impaired action observation ability (for review, e.g., Fadiga and Craighero, 2004), e.g., for the discrimination of biomechanically possible actions (Candidi et al., 2008) or for the correct rearrangement of a sequence of actions (Gangitano et al., 2008).

A main question of our analysis regarding the organization of this network relates to the effect of possible confounds such as effectors, use of an object, or instructions given to the subject.

Different locations of the activations when observing actions performed by different effectors raised the question of a possible somatotopic organization within the involved areas. Buccino et al. (2004b) reported a somatotopy within the fronto-parietal part of the observation network, with observation of mouth movements activating most ventral parts (BA 44 and rostral IPL, respectively), observation of foot actions more dorsal parts, and observation of hand actions in between. With focus on the lateral premotor cortex,

similar findings were reported by Sakreida et al. (2005) as well as Wheaton et al. (2004). Besides these findings on visual action processing, Gazzola et al. (2006) found a comparable somatotopical arrangement of activations in the premotor cortex for the processing of action sounds, indicating a topic arrangement of concepts rather than sensory representations. In contrast, a recent meta-analysis on action observation by Morin and Grèzes (2008) did not find a clear somatotopical arrangement of activations within the lateral premotor cortex. By comparing MNI coordinates and counting the number of hits in the macroanatomically defined lateral premotor cortex and BA 44 for different effectors, they found association of activations within BA 44 slightly more often for observation of whole body and leg movements than for observation of mouth or finger movements. In contrast, the meta-analysis by Van Overwalle and Baetens (2009) did report a somatotopic arrangement comparable to that found by Buccino et al. (2004b) and confirmed in the present, more extended analysis.

Our meta-analysis on action observation revealed a bilateral network with pronounced involvement of the lateral premotor and parietal cortex, which was confirmed to be largely independent of the effector by subanalyses on observation of hand actions, right hand actions, and non-hand actions. Contrasting observation of hand and non-hand actions, however, revealed a notable difference with regard to possible somatotopy: whereas observation of non-hand (i.e., whole body, face, and leg) actions were more associated with activation in BA 44, observation of hand actions was more consistently associated with activations in a more dorsal part of premotor cortex (BA 6). For the parietal lobe, our meta-analysis did not provide such a possible somatotopical arrangement: whereas observation of hand actions was consistently associated with activations within parietal cortex, the observation of non-hand actions was not. The difference to the results of Morin and Grèzes (2008) might be caused by the difference in sample size, which was considerably larger in our study, or the applied method. Nevertheless, it must be pointed out that meta-analyses may not be ideally suited to investigate somatotopy since pooling of data from very different studies could diminish or even delete such effects (Morin and Grèzes, 2008), especially when somatotopic organization is not very pronounced, as in the parietal cortex (e.g., Buccino et al., 2004b; Rizzolatti and Arbib, 1998).

Another potential influencing factor for the organization of the action observation brain network is the involvement of an object within the observed action. Separating the experiments on observation of hand actions into object-related and non-object-related ones revealed a major difference: whereas activation within the temporo-occipital cortex (pMTG, V5) was consistently found within both subanalyses, activation within the fronto-parietal part of the observation network was mainly driven by observation of object-related actions.

It has been proposed that activation in these regions reflects visually guided feedback control of an action (e.g., Shmuelof and Zohary, 2007). This hypothesis, however, was mainly inferred from imitation or grasping studies. The involvement of the SPL and adjacent IPS in somatosensory and visuomotor integration, reaching movements in particular, as well as object recognition has frequently been demonstrated in neuroimaging studies (e.g., Battaglia-Mayer and Caminiti, 2002; Grèzes and Decety, 2001; Hahn et al., 2006; Pellijeff et al., 2006; Rizzolatti and Matelli, 2003, Buccino et al., 2001). Moreover, it is also supported by lesion studies of patients suffering from optic ataxia, a syndrome with deficits in the online control of visually guided actions (e.g., Glover 2003). It was assumed that these superior and adjacent intraparietal areas form a human parietal reach region (e.g., Connolly et al., 2003), referring to the comparable region in macaques (for review, e.g., Grefkes and Fink, 2005). Other authors, however, reported the parietal cortex active also for the observation of non-object-related actions (e.g., Montgomery et al., 2007). These discrepant findings indicate that there apparently is no strict and exclusive neurophysiological distinction between object and non-object-related actions. Rather, the type of the observed movement and/or its spatio-temporal properties may drive neurons in some grasp-related areas.

For the lateral premotor cortex additional strong association with actions aiming at a certain target have been found. This was also interpreted as providing additional information to the visuomotor integration process required for object-related actions (for review, e.g., Hoshi and Tanji, 2007). This correlation was supported by a recent meta-analysis on the involvement of the premotor cortex in different types of action observation (Morin and Grèzes, 2008), which revealed a less consistent activation within premotor areas during non-object-related actions. Buccino et al. (2004b), however, reported that observation of object- as well as non-object-related actions activates lateral premotor areas to a comparable degree.

The data of our meta-analysis on 104 individual experiments also provide evidence that activation in the fronto-parietal part of the action observation network may not only be related to the observation of an action per se but also particularly involved in the (implicit) processing of object features and their integration within the observed motor act. For the parietal part of the network, this is in line with the concept of a human parietal reach region. For the frontal part, a stronger association with object- and goal-directed actions was assumed when considering one of these areas as a possible human homologue of macaque area F5 since macaque mirror neurons more strongly responded to such actions as compared to non-goal- and non-object-related actions (e.g., Morin and Grèzes, 2008). Our meta-analysis results support this notion, providing a further aspect for future research on such possible homologies between humans and macaques (Morin and Grèzes 2008; Nelissen et al., 2006).

For this frontal part of the network, another notable involvement was found: this part of the cortex, together with the temporo-occipital visual areas, was constantly involved when passively observing a movement, but also when intending to imitate the observed movement. Furthermore, the primary motor cortex was consistently activated during active observation. In an early study, Grèzes et al. (1999) studied a possible differentiation between active and passive observation. They also found increasing activity within premotor cortex and on the precentral gyrus (presumably primary motor cortex), but also in inferior and superior parietal cortices, which was interpreted as reflecting the information processes needed for subsequent action. The results of the present meta-analysis did not show any involvement of the parietal cortex. But the samples of active and passive observation experiments considerably differed in sample size. Thus, even with the meta-analysis algorithm covering for such differences, such larger difference could still have introduced potential bias to the present analysis. This could have led to detection failure of parietal activations during active observation since only 8 experiments could have been involved in this analysis. Thus, the present meta-analysis provides first hints that especially primary and premotor areas might consistently be involved in active observation, whereas involvement of the parietal cortex could not finally be resolved.

Another consistently activated region during action observation was the dorso-lateral premotor cortex (dPMC; BA 6). Activation of this region was also found consistently in imitation experiments, but the exact location differed between the observation and imitation sample, leading to no common activation being detected in the conjunction analysis.

Summarizing previous reports, recent reviews suggested that the dPMC is involved in learning appropriate motor responses based on arbitrary cues (Chouinard and Paus, 2006), and thus, motor planning and preparation (Hoshi and Tanji, 2004). Furthermore, it was proposed that the dPMC integrates different pieces of sensorimotor information to formulate the appropriate motor program (Hoshi and Tanji, 2007). Given this current knowledge on the dPMC, we would

assume that within the action observation and action imitation networks, the dPMC might provide the composition of the appropriate motor program during movement preparation. Such a step should be required during action observation particularly to understand the observed action (e.g., Grafton and Hamilton, 2007), and certainly, for the realization of the observed action by imitation.

Neural correlates of action imitation

The action imitation network as revealed by the present meta-analysis recruited frontal, parietal, and temporo-occipital areas as previously assumed in qualitative reviews (e.g., Brass and Heyes, 2005; Heyes, 2001; Iacoboni, 2005, 2009; Turella et al., 2009a,b).

One issue of controversial discussion is a possible lateralization within activations of the action imitation network since previous studies have provided conflicting evidence on this issue. Since imitation is one form of higher-order motor processing, it could be assumed that it recruits a bilateral brain network rather than showing a hemispheric lateralisation (e.g., Iacoboni and Dapretto, 2006). Support for this assumption is provided by functional (e.g., Aziz-Zadeh et al., 2006a; Molnar-Szakacs et al., 2005) and virtual lesion studies (e.g., Aziz-Zadeh et al., 2002; Heiser et al., 2003), arguing in favour of a bilateral organization of an imitation network, in particular for frontal premotor areas.

Predominant right hemispheric activations during imitation have also been reported, e.g., within right occipito-temporal junction (Binkofski et al., 2000; Iacoboni et al., 1999, 2001), even disregarding the used hand (Aziz-Zadeh et al., 2006a), or in temporal and frontal areas for right hand movements (Biermann-Ruben et al., 2008) as well as imitation of emotional faces Carr et al., 2003).

Other studies, however, reported a dominance of left hemispheric areas during imitation tasks, which was interpreted in reference to the lateralisation of language functions (e.g., Aziz-Zadeh et al., 2004; Rizzolatti and Arbib, 1998; Iacoboni et al., 2005). Moreover, Goldenberg and Karnath (2006) argued in favour of a left-lateralisation of imitation-related processes based on lesion studies.

The quantitative results of the present meta-analysis argue in favour of a bilateral activation pattern for action imitation. Most of the included imitation experiments involved the imitation of hand movements with either the right or an unspecified hand (29 out of 35). Since action imitation contains a major component of motor execution, it could have been assumed that this imbalance would result in a dominance of left hemispheric activations, for frontal motor areas in particular. Instead, activations within these areas were evenly found in both hemispheres. Our data are thus in line with the idea of imitation being a higher-order motor process supported by a bilateral network as assumed by Iacoboni and Dapretto (2006).

Within this context, one idiosyncrasy of the imitation network could be noted: only the subanalysis 'imitation of right hand actions' revealed consistent activation within the right pMTG while imitation in general and imitation of hand actions did not. The importance of the right pMTG/STS for imitation processes was first pointed to by Iacoboni et al. (2001), based on an imitation study on right hand actions. In this study, activation of the pMTG for imitation was even stronger than the pure observation of the respective action.

Furthermore, it has to be noted that imitation studies included in the present meta-analysis involved online ($n = 24$) as well as delayed imitation experiments ($n = 11$). Comparison of these two subsets revealed largely comparable brain networks between both subsamples and compared to the imitation analysis including all experiments. Moreover, direct comparison revealed a higher consistency of activations for delayed as compared to simultaneous imitation in all of the activated brain areas. This could most likely be interpreted as resulting from a higher difficulty of the delayed imitation paradigms, thus a higher cognitive demand, as compared to the online imitation paradigms (e.g., Buccino et al., 2004a). A comparable effect is known for the imagery of action where strong activations can be found in premotor and visual areas in particular, in the absence of a visual model. The imagination of an action also requires a higher cognitive demand, thus resulting in stronger activations (e.g., Creem-Regehr and Lee, 2005; David et al., 2006; Grafton et al., 1996; Johnson-Frey et al., 2005). Thus, further investigation seems required to detect possibly subtle differences between on- and off-line performances of imitative behaviour.

Reference to recent meta-analyses

Two recent smaller meta-analyses (Molenberghs et al., 2009; Van Overwalle and Baetens, 2009) also reported a largely bilateral activation pattern for imitation tasks. Both these meta-analyses, however, used a region of interest (ROI)-based approach and assessed only activations which fell within predefined regions of the lateral premotor and parietal (Molenberghs et al., 2009) and posterior temporal cortex (Van Overwalle and Baetens, 2009). The definition of these ROIs was based either on estimates of the location of anatomical areas using the Talairach atlas (Molenberghs et al., 2009) or on manually delineated ones based on previous knowledge from the literature (Van Overwalle and Baetens, 2009) which could have confounded the results. Since the delineation of cortical areas should only reliably be possible by means of cytoarchitectonic investigation (not by means of macroanatomical anatomy; Amunts et al., 2007; Zilles et al., 2002), the areal definition within these previous studies might potentially introduce bias towards a misinterpretation of areal boundaries. Our meta-analysis used a different approach, assessing the action imitation network as a whole, without any a priori assumptions or focus on ROIs.

Since, in general, our findings on the action imitation network are well in line with those of previous meta-analyses as discussed above, the present meta-analysis could confirm and amend the findings of previous smaller analyses using an unbiased quantitative algorithm to synthesise results from a larger sample of primary studies.

One major difference to the analysis of Molenberghs et al. (2009) relates to the involvement of BA 44 within the action imitation network which is controversially discussed in the literature (e.g., Brass and Heyes 2005; Iacoboni 2005). The difference between our and Molenberghs' result might on the one hand be due to a methodological difference. Since we used the revised version of the ALE algorithm (Eickhoff et al., 2009), potential drawbacks of previous approaches which were used by Molenberghs et al., could be avoided. On the other hand, activation within BA 44 might have failed reaching significance in their analysis, especially considering the fact that the respective activation is located at the very caudal part of BA 44 (as stated above). This fact might have resulted in a failure of detection in an ROI-based approach as performed by Molenberghs. Furthermore, we were able to include a larger amount of imitation experiments within our analysis. For the ROI within BA 44 in Molenberghs' analysis, an even smaller amount of activations was found since several studies did not seem to report respective activation foci within their predefined ROI. This small number of activation foci provides difficulties for the interpretation of their negative result for BA 44. The larger sample of studies within our analysis increased the power of the ALE analysis. By objectively analysing reported activations without any preallocation to a certain ROI, our analysis was able to find activation within BA 44, with a major focus in its most caudal aspect. This provides further evidence for the role of BA 44 in imitation as stated in the section about the areas involved in both networks.

Conclusions

In the present quantitative meta-analysis of neuroimaging data, we identified the cortical regions that are consistently implicated in the human observation and imitation networks. Hereby, the findings

of 139 individual experiments could, for the first time, objectively be generalized in an unbiased fashion.

It was shown that action observation and imitation are sustained by a bilateral network spanning fusiform, posterior temporal, parietal, and premotor areas including BA 44. These activation patterns are largely independent from possible confounds, such as effector, involvement of an object, or instructions given to the subjects. There was, however, evidence for a somatotopical organization of activations within the lateral premotor cortex (cf., Buccino et al., 2001) as well as for a stronger association of fronto-parietal areas with observation of object- as compared to non-object-related actions. Moreover, we found a three-way differentiation within Broca's region. The caudo-dorsal part of BA 44 is involved in both action observation and imitation; a more rostro-dorsal aspect within BA 45 was more consistently activated by observation tasks and a more caudo-ventral part of BA 44 was primarily involved in the imitation network.

Thus, the current meta-analysis on action observation and imitation provides objective evidence for common neural correlates of these networks across different experiments. Furthermore, evidence on putative homologies between humans and macaques was provided by the observation that human inferior area PFt showed most consistent activation across all analyses carried out in the present meta-analysis and hence seems to match the functional properties of primate area PF.

Acknowledgments

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