

## RESEARCH ARTICLE

# Neural processing of social interaction: Coordinate-based meta-analytic evidence from human neuroimaging studies

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## Abstract

While the action observation and mentalizing networks are considered to play complementary roles in understanding others' goals and intentions, they might be concurrently engaged when processing social interactions. We assessed this hypothesis via three activation-likelihood-estimation meta-analyses of neuroimaging studies on the neural processing of: (a) social interactions, (b) individual actions by the action observation network, and (c) mental states by the mentalizing network. Conjunction analyses and direct comparisons unveiled overlapping and specific regions among the resulting maps. We report quantitative meta-analytic evidence for a "social interaction network" including key nodes of the action observation and mentalizing networks. An action-social interaction-mentalizing gradient of activity along the posterior temporal cortex highlighted a hierarchical processing of interactions, from visuomotor analyses decoding individual and shared intentions to in-depth inferences on actors' intentional states. The medial prefrontal cortex, possibly in conjunction with the amygdala, might provide additional information concerning the affective valence of the interaction. This evidence suggests that the functional architecture underlying the neural processing of interactions involves the joint involvement of the action observation and mentalizing networks. These data might inform the design of rehabilitative treatments for social cognition disorders in pathological conditions, and the assessment of their outcome in randomized controlled trials.

## KEYWORDS

action observation network, activation likelihood estimation, amygdala network, mentalizing network, meta-analysis, mirror network, social cognition rehabilitation, social interaction network

## 1 | INTRODUCTION

Decoding others' intentions, to understand and predict their behavior, is a core component of social cognition. Despite increasing evidence on the neural bases of social understanding (Arioli, Crespi, & Canessa, 2018; Spunt & Lieberman, 2012a), it is still debated how intentions, and particularly social intentions in interactive contexts, are neurally represented, and whether this process recruits dedicated brain structures (Frith, 2007). Most of the relevant evidence in this respect

involves the mirror (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and mentalizing ("theory of mind"; Frith & Frith, 2006) networks.

The former includes areas recruited both when observing and when performing actions, that is, the posterior portion of inferior frontal gyrus, dorsal and ventral premotor cortex, inferior parietal lobule (IPL), superior parietal lobule, and intraparietal sulcus (IPS), alongside the posterior portion of the superior temporal sulcus (pSTS) (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs, Cunnington, & Mattingley, 2012). A subset of its key fronto-parietal and occipito-

temporal nodes, collectively termed “action observation network” (e.g., Gardner et al., 2015), is considered to embody a neural representation of *action meaning*, allowing its direct understanding via automatic simulation routines (Buccino, Vogt, et al., 2004; Buccino, Lui, et al., 2004; Gallese & Sinigaglia, 2011). In contrast, the mentalizing network is recruited when people reflect on others’ *mental states* without directly attending their biological motion or available visual cues, for example, when reading stories or watching cartoons, and in false-belief tasks (Wimmer & Perner, 1983). This type of process involves the medial precuneus and temporoparietal junction (TPJ), as well as ventromedial and dorsomedial prefrontal cortex (Saxe, 2006).

The role of these networks in intention understanding revolves around three related notions, that is, action, goal and intention, which can be ordered hierarchically according to their level of abstractness (Hamilton & Grafton, 2006; Van Overwalle & Baetens, 2009). A distinction can thus be made among the processing of simple movements (e.g., opening and closing fingers), immediate action goal (often requiring the motion sequence to interact with an object, e.g., grasping a glass), the final action goal (e.g., grasping the glass to drink), intention (reflecting the “why” of the action, e.g., grasping a glass to drink in order to rehydrate after exercise), up to a social intention (when the “why” of the action involves other individuals, e.g., grasping a glass to make a toast in a party). The mirror/action observation and mentalizing networks play different roles in processing intentions along this hierarchy (Grafton, 2009; Van Overwalle & Baetens, 2009). The former underpins the meaning of simple movements, actions and their associated goals, embodied in their neural representations along the fronto-parietal networks underlying action organization (Rizzolatti & Luppino, 2001), which are automatically activated when attending others’ actions and their goals (Fogassi et al., 2005; Iacoboni et al., 2005). The mentalizing network is recruited when others’ intentions cannot be automatically derived from available visuomotor cues, and must thus be inferred in terms of internal mental states such as thoughts, desires, and beliefs (Van Overwalle & Baetens, 2009).

Considerable evidence on the neural processing of *individual actions* has supported a functional segregation between the complementary roles of the action observation and mentalizing networks, driven by, respectively, (a) biological actions versus verbal/abstract information; (b) implicit versus explicit tasks; and (c) processing “what” and “how” a person is doing (behavioral states) versus “why” (mental states) (Chiavarino, & Humphreys, 2012; Spunt, Kemmerer, & Adolphs, 2016; Spunt & Lieberman, 2012a, 2012b). However, this segregation conflicts with their joint activation when processing *social interactions*, regardless of stimuli type (Arioli et al., 2018; Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Iacoboni et al., 2004; Kujala, Carlson, & Hari, 2012). Their concurrent engagement might reflect the greater complexity of understanding interactions, which, compared with individual actions, would require both the recognition of joint actions, and a representation of their multiple actors’ mental states (Catmur, 2015). We have recently shown that the relative activation and connectivity pattern of the action observation and mentalizing networks indeed depend on different dimensions expressed by interactions, such as their degree of cooperativity and

affectivity, respectively (Arioli, Perani, et al., 2018; Canessa et al., 2012; Proverbio et al., 2011). Within a network for “social intention understanding” activated regardless of these dimensions, observed cooperativity increases connectivity between pSTS and both SPL and vPMC, while affectivity increases connectivity between pSTS and vmPFC (Arioli, Perani, et al., 2018). Therefore, the complexity of interactions reflects in divergent but interconnected neural pathways associated with the bottom-up visuomotor processing of action meaning and the top-down attribution of affective/mental states, depending on the weight of specific dimensions underlying shared action goals.

Alongside fMRI evidence of a brain network dedicated to the visual processing of social interactions in the primate brain (Sliwa & Freiwald, 2017), these considerations highlight the need to take into account the specific features of interactions, compared with individual actions, when discussing the available evidence on the neural bases of decoding social intentions (Quadflieg & Koldewyn, 2017). Further insights into this issue might come from coordinate-based meta-analyses, that is, a quantitative unbiased approach unveiling the areas that are consistently activated in a particular class of paradigms (Laird et al., 2005).

On this basis, we performed a quantitative meta-analysis of the available neuroimaging literature to unveil: (a) the regions specifically associated with the neural decoding of social interactions, over and beyond the processing of single individuals’ actions and mental states by the action observation and mentalizing networks, respectively and (b) the shared and specific contribution of these networks to such processing. We first expected to replicate previous meta-analytic evidence on the role of the mirror/action observation (Caspers et al., 2010; Molenberghs et al., 2012) and mentalizing (Bzdok et al., 2012; Molenberghs, Johnson, Henry, & Mattingley, 2016; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; van Veluw & Chance, 2014) networks in processing others’ actions versus mental states, respectively. Based on our previous evidence (Arioli, Perani, et al., 2018), we additionally predicted an involvement of both networks in processing interactions, that is, to observe overlapping and specific brain regions between a “social interaction network” and both the action observation and mentalizing networks.

## 2 | MATERIALS AND METHODS

### 2.1 | Rationale of the meta-analytic approach

Despite the well-known contribution of the action observation and mentalizing networks to social understanding (Arioli, Perani, et al., 2018), quantitative meta-analytic evidence is still needed to identify the most consistent findings and thus overcome the limitations inherent in single neuroimaging studies. We thus aimed to identify the brain regions consistently associated with the neural processing of interactions, over and beyond the processing of single individuals’ actions and mental states by the action observation and mentalizing networks, respectively. To this purpose, we used activation likelihood estimation (ALE), a coordinate-based meta-analytic approach using the Montreal Neurological Institute (MNI) coordinates of peak

locations to summarize and integrate published findings (Turkeltaub, Eden, Jones, & Zeffiro, 2002).

We defined “social interaction” a situation in which *two or more persons* act together, as opposed to single individuals’ behaviors traditionally ascribed to the action observation and mentalizing networks for the processing of their actions or mental states, respectively. We focused, however, on the neural bases of *representing* interactions, rather than those associated with actual behavior. Therefore, we included in a first ALE analysis the studies addressing a passive exposure to interactions (vs. single individuals’ motor or mental activity), regardless of positive–negative valence, experimental paradigm or stimulus type (e.g., videos, pictures, auditory, etc.) (Section 2.2.1).

Based on previous related evidence (Arioli, Perani, et al., 2018; Centelles et al., 2011; Iacoboni et al., 2004; Kujala et al., 2012), we expected a common, although possibly non-exhaustive, involvement of the action observation and mentalizing networks in the neural processing of interactions. This hypothesis is grounded in recent evidence for their combined role in this process, suggesting that fronto-temporo-parietal areas in charge of action recognition might provide sensorimotor information supporting and constraining inferential processes of intention understanding by the mentalizing network (Catmur, 2015; Arioli, Perani, et al., 2018). To quantify this contribution in terms of the overlap between the neural processing of interactions and either the action observation or mentalizing networks (Catmur, 2015), we performed two additional ALE analyses addressing the neural processing of *single individuals’* actions or mental states, respectively. Since most fMRI studies on social interaction are limited to visual processing without an explicit engagement, we used the same constraints when selecting studies on individual action, that is, we focused on action representation rather than motor mirroring. As with the decoding of interactions, however, we aimed to investigate the neural bases of processing an abstract high-order representation of actions or mental states, transcending specific kinds of stimuli. To this purpose, the “action observation” and “mentalizing” data sets included experiments addressing the neural bases of these processes regardless of the experimental paradigm or stimulus type (e.g., videos, pictures or verbs, and pictures or verbal stories, respectively) (Sections 2.2.2 and 2.2.3). The studies included in the three meta-analyses did not differ with respect to the presence of stimuli involving object-directed actions or an object representation (Table S1a–c).

Based on current prescriptions for ALE meta-analyses (Eickhoff et al., 2016), we aimed to include at least 17–20 experiments (contrasts) in each data set, to achieve sufficient power for moderate effects and ensure that results would not be driven by single experiments. To this purpose, for each data set, we selected a specific process of interest and the types of contrast/experiment fitting our research question (Section 2.2). A stringent selection of the studies fulfilling these criteria resulted in a comparable number of experiments for each data set, while keeping this number close to 30 in order to ensure enough power for reliable results (Muller et al., 2018). All the inclusion criteria for each data set were selected by the first author, and then checked by the last author. This procedure, entailing

a double check by two independent investigators, was aimed to reduce the chances of a selection bias (Muller et al., 2018).

## 2.2 | Literature search and study selection

A systematic online database search was performed in December 2017–February 2018 on PubMed (<https://www.ncbi.nlm.nih.gov/pubmed/>), Google scholar (<https://scholar.google.it/>), and Neurosynth (<http://neurosynth.org/>), by entering various combinations of relevant search items as detailed below.

### 2.2.1 | Social interaction

Papers pertaining to the first ALE analysis were initially identified using the following terms: “social interaction,” “social scene,” “social intention,” “social perception,” “social observation,” “watching social,” “social action,” and “social stimuli.” This first search was expanded by looking for (a) authors of related articles, (b) similar articles, or (c) review papers, and by carefully examining (a) the references of each retrieved paper, and (b) the studies that have cited each retrieved paper. The selection criteria for this search procedure led to select only:

1. Published studies written in English.
2. Empirical fMRI studies, while excluding review articles and behavioral studies, as well as those employing other techniques to ensure comparable spatial and temporal resolution.
3. Studies including non-clinical and drug-free participants, to prevent possible differences in brain activation associated with neuropsychiatric disease or pharmacological manipulations.
4. Studies with adult subjects (age range: 18–55 years).
5. Studies reporting the MNI coordinates of the activations, as well as detailed information about results, tasks, and subjects.
6. Studies reporting whole-brain activation coordinates, rather than results limited to regions of interest (ROIs). A prerequisite for coordinate-based meta-analyses is indeed that convergence across experiments is tested against a null hypothesis of random spatial associations across the entire brain under the assumption that each voxel has the same a priori chance of being activated (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). Studies based on ROI analyses should therefore be excluded from meta-analyses (Muller et al., 2018).
7. Studies investigating brain activity related to the *processing of social interactions*, as opposed to single individuals’ motor or mental activity. To this purpose, we selected only specific types of contrast in which the subject passively attends interactions (vs. no interaction), and that were clearly aimed to elicit a representation of interactions and underlying social intentions, over and beyond single individuals’ behavior, that is:
  - a. interaction > individual action (i.e., only one acting person);
  - b. interaction > parallel action (i.e., presence of more than one acting person, but without interaction);

**TABLE 1** Overview of the 27 studies included in the meta-analysis on the neural bases of processing social interactions. N = progressive study number; Sub = subjects; IAPS = International affective picture system (Lang et al., 2008)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
1	Akitsuki and Decety (2009)	NeuroImage	Social context and perceived agency affects empathy for pain: An event-related fMRI investigation	26 sub (mean age: 24.4)	Animated visual images	Social interactions > individual actions	23
2	Arioli, Perani, et al. (2018)	Human Brain Mapping	Affective and cooperative social interactions modulate effective connectivity within and between the mirror and mentalizing systems	36 sub (mean age: 24/25)	Photographs	Social interactions > other	46
3	Becchio et al. (2012)	NeuroImage	Social grasping: From mirroring to mentalizing	16 sub (mean age: 23.3)	Video clips	Social interactions > individual actions	6
4	Beyer, Munte, and Kramer (2014)	Biological Psychology	Increased neural reactivity to socio-emotional stimuli links social exclusion and aggression	40 sub (mean age: 22.5)	Black and white drawings	Social interactions > individual actions	3
5	Canessa et al. (2012)	PLoS One	The neural bases of social intention understanding: The role of interaction goals	27 sub (mean age: 24–26)	Photographs	Social interactions > other	34
6	Centelles et al. (2011)	PLoS One	Recruitment of both the mirror and the mentalizing networks when observing social interactions depicted by point lights: A neuroimaging study	14 sub (mean age: 29.4)	Point-light displays, videos	Social interactions > parallel actions	24
7	Chambon et al. (2017)	Scientific Reports	Neural coding of prior expectations in hierarchical intention inference	18 sub (mean age: 24–54)	Videos	Social interactions > individual actions	5
8	Deuse et al. (2016)	Social Cognitive and Affective Neuroscience	Neural correlates of naturalistic social cognition: Brain-behavior relationships in healthy adults	42 sub (mean age: 23.88)	Photographs	Social interactions > other	30
9	Dolcos, Sung, Argo, Flor-Henry, and Dolcos (2012)	Journal of Cognitive Neuroscience	The power of a handshake: Neural correlates of evaluative judgments in observed social interactions	18 sub (age range: 18–34)	Videos	Social interactions > individual actions (unanimated host)	17
10	Ebisch et al. (2011)	Journal of Cognitive Neuroscience	Differential involvement of somatosensory and interoceptive cortices during the observation of affective touch	19 sub (age range: 22–34)	Videos	Social interactions > individual actions	1
11	Eskenazi, Rueschemeyer, de Lange, Knoblich, and Sebanz (2015)	Cortex	Neural correlates of observing joint actions with shared intentions	21 sub (mean age: 22)	Dialogs and actions	Social interactions > individual actions	14

(Continues)

TABLE 1 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
12	Georgescu et al. (2014)	Human Brain Mapping	Perceiving nonverbal behavior: Neural correlates of processing movement fluency and contingency in dyadic interactions	21 sub (mean age: 26.86)	Videos	Social interactions > other	20
13	Göttlich, Ye, Rodriguez-Formels, Munte, and Kramer (2017)	NeuroImage	Viewing socio-affective stimuli increases connectivity within an extended default mode network	17 sub (mean age: 27.8)	Drawings	Social interactions > individual actions	10
14	Iacoboni et al. (2004)	NeuroImage	Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline	13 sub (mean age: 27.2)	Videos	Social interactions > individual actions	16
15	Krämer, Mohammadi, Donamayor, Samii, and Munte (2010)	Brain Research	Emotional and cognitive aspects of empathy and their relation to social cognition—An fMRI study	17 sub (mean age: 27.8)	Drawings	Social interactions > individual actions	8
16	Kujala et al. (2012)	Human Brain Mapping	Engagement of amygdala in third-person view of face-to-face interaction	18 sub (mean age: 28.3)	Photographs	Social interactions > parallel actions; social interactions > other	44
17	Pierro, Becchio, Turella, Tubaldi, and Castiello (2008)	Social Neuroscience	Observing social interactions: The effect of gaze	17 sub (mean age: 26)	Photographs	Social interactions > parallel actions	11
18	Powers, Chavez, and Heatherton (2016)	Social Cognitive and Affective Neuroscience	Individual differences in response of dorsomedial prefrontal cortex predict daily social behavior	33 sub (age range: 18–21)	Photographs from the IAPS database	Social interactions > other	9
19	Powers, Wagner, Norris, and Heatherton (2013)	SCAN	Socially excluded individuals fail to recruit medial prefrontal cortex for negative social scenes	34 sub (age range: 18–21)	Photographs from the IAPS database	Social interactions > other	19
20	Quadflieg, Gentile, and Rossion (2015)	Cortex	The neural basis of perceiving person interactions	12 sub (mean age: 26)	Photographs	Social interactions > parallel actions	4
21	Saarela and Hari (2008)	Social Neuroscience	Listening to humans walking together activates the social brain circuitry	12 sub (mean age: 27)	Sounds	Social interactions > individual actions	4
22	Sapey-Triomphe et al. (2017)	Social Cognitive and Affective Neuroscience	Deciphering human motion to discriminate social interactions: a developmental neuroimaging study	16 sub (mean age: 28.8)	Point-light displays and stitch lights	Social interactions > parallel actions	22
23	Shibata, Inui, and Ogawa (2013)	Cognitive Neuroscience and Neuropsychology	Role of the dorsolateral prefrontal cortex in recognizing hand actions performed in social contexts: a functional MRI study	18 sub (mean age: 26.9)	Videos	Social interactions > individual actions	5

(Continues)

TABLE 1 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
24	Van den Stock, Hortensius, Sinke, Goebel, and de Gelder (2015)	Scientific Report - Nature	Personality traits predict brain activation and connectivity when witnessing a violent conflict	15 sub (mean age: 23.6)	Videos	Social interactions > other	12
25	Vrticka, Sander, and Vuilleumier (2011)	Neuropsychologia	Effects of emotion regulation strategy on brain responses to the valence and social content of visual scenes	19 sub (mean age: 24.82)	Photographs from the IAPS database	Social interactions > other	18
26	Wagner, Kelley, and Heatherton (2011)	Cerebral Cortex	Individual differences in the spontaneous recruitment of brain regions supporting mental state understanding when viewing natural social scenes	48 sub (mean age: 20)	Photographs	Social interactions > other	16
27	Walter et al. (2004)	Journal of Cognitive Neuroscience	Understanding intentions in social interaction: The role of the anterior paracingulate cortex	exp1: 13 sub (mean age: 25.15) exp2: 12 sub (mean age: 24.75) TOT SUB: 612	Stories	Social interactions > other	18
					Stories	Social interactions > other	15
					TOT FOCI		454

- c. interaction > stimuli without persons (e.g., fixation cross, landscapes, or objects).
8. Studies entailing a passive exposure to interaction, rather than an active involvement in real online interactions.
9. Studies addressing human interactions, that is, real persons (in videos, photographs, or verbal stories) or stimuli representing human beings (such as point light displays).

Although most of the selected studies already compared brain activity associated with processing interaction versus individual action, here we moved this comparison to the meta-analytic level to unveil consistent commonalities/differences transcending study-specific experimental manipulations. To this purpose, we included studies fulfilling the above criteria regardless of: (a) type of stimuli (e.g., video, audio, picture, verbal, etc.), and (b) the nature of interaction (e.g., positive, negative, affective, dance, sport, games, etc.). Our aim was indeed to pool across different experimental paradigms to ensure both generalizability and consistency of results, within the above constraints inherent in our research question (Radua & Mataix-Cols, 2012).

This procedure led to include in the ALE meta-analysis 27 previously published studies (Table 1), resulting from 28 experiments (individual comparisons reported) with 612 subjects and 454 foci. Importantly, the inclusion of multiple contrasts/experiments from the same set of subjects can generate dependence across experiment maps and thus decrease the validity of meta-analytic results. To prevent this issue, we adjusted for within-group effects by pooling the coordinates from all the relevant contrasts of a paper into one experiment (Turkeltaub et al., 2002).

## 2.2.2 | Action representation

Our search for the coordinates associated with the action observation network started from two previously published meta-analyses by Caspers et al. (2010) and Molenberghs et al. (2012). Within the BrainMap database (Laird et al., 2009), we selected these works because they explicitly address action representation by the mirror network in healthy adults. We then expanded our search for other potentially relevant studies by carefully examining both the studies quoting, and those quoted by, each of the two meta-analyses.

While the methodological selection criteria for the included studies are the same as above (1–6), here we selected only studies reporting brain activations interpreted by the authors as related to the *perception or representation of human individual actions*. To this purpose, we selected only specific types of contrast in which the subject passively attends to stimuli depicting human actions by single individuals, and that were aimed to elicit brain activations interpreted by the authors in terms of action representation, that is:

1. human action > static (someone who is not acting);
2. human action > nonhuman action (e.g., object motion);
3. human action > sensory aspects without persons and/or action (e.g., scrambled images, objects, context, or abstract sentences).

Importantly, we aimed to assess the spatial overlap between a network associated with the processing of interactions and the action observation network associated with *perceiving or representing individual actions*. To ensure the specificity of this analytical approach, we excluded from this ALE analysis the studies addressing other functions ascribed to the mirror network, such as action imitation (i.e., action observation for subsequent replication), action execution, or an affective resonance to others' sensory or emotional experiences (e.g., Canessa et al., 2009; Canessa, Motterlini, Alemanno, Perani, & Cappa, 2011; Keysers et al., 2004; Singer et al., 2004; Wicker et al., 2003).

We included studies fulfilling these criteria regardless of stimuli type (e.g., video, audio, and sentences) to ensure the generalizability of results. This procedure led to include in the ALE meta-analysis 34 previously published studies (Table 2), resulting from 34 experiments (individual comparisons reported) with 598 subjects and 712 foci. As with the first ALE analysis, we adjusted for within-group effects by pooling the coordinates from all the relevant contrasts with the same subjects into one experiment (Turkeltaub et al., 2002).

Importantly, 12 out of 27 papers included in the meta-analysis on social interaction used "individual action" as an explicit baseline condition. However, only one of them reported activations resulting from the "individual versus social" contrast (involving the precentral gyrus, medial prefrontal cortex, and cerebellum), while the others reported either no information on this contrast (8/12) or no significant results (3/12) (Table S2). Therefore, these studies were not used to investigate the regions associated with the action observation network.

### 2.2.3 | Mental state representation

We searched for the coordinates associated with mentalizing starting from four previously published meta-analyses by Molenberghs et al. (2016), van Veluw and Chance (2014), Spreng, Mar, and Kim (2009), and Bzdok et al. (2012). Within the BrainMap database (Laird et al., 2009), we selected these works because they explicitly address the representation of others' mental states by the mentalizing network in healthy adults. We then expanded our search for other potentially relevant studies by carefully examining both the studies quoting, and those quoted by, each of the four meta-analyses.

While the methodological selection criteria for the included studies are the same as above (1–6), here we selected only studies reporting brain activations interpreted by the authors as related to *making inferences on single individuals' mental states*. To this purpose, we selected only specific types of contrast that were aimed to elicit brain activations interpreted in terms of "mentalizing network" underpinning the representation or attribution of mental states, that is:

1. inferences on beliefs > inferences on physic or perceptual aspects other than mental states;
2. attribution of mental states > gender inferences (based on the "reading the mind in the eyes" task [Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001]).

In particular, we included only the studies which:

1. investigated the representation of a single person's mental states;
2. isolated mental states, via a "mental versus nonmental" comparison;
3. entailed no difference between the two conditions in terms of "social" processing. That is, studies in which an interaction, if present, involves both the "mental" and control conditions.

Moreover, we excluded studies that addressed mentalizing during real interactions.

Importantly, we aimed to assess the spatial overlap between a network associated with the processing of interactions and the sectors of the mentalizing network specifically associated with *the representation or attribution of single individuals' mental states*. We thus excluded studies addressing other facets of mentalizing, such as empathy and emotional processing, moral cognition or self-representations. To ensure the specificity of this analytical approach, we additionally excluded studies investigating the neural correlates of processing false beliefs versus true beliefs, or jokes versus literal sentences, since they both involve the processing of mental states. We also excluded contrasts which, rather than isolating the neural processing of mental states, compare different facets of such processing, for example, desires versus beliefs, cognitive versus affective mentalizing, or beliefs versus preferences.

We included studies fulfilling these criteria regardless of stimuli type (e.g., photographs, vignettes, and sentences) to ensure the generalizability of results. This procedure led to include in the ALE meta-analysis 29 previously published studies (Table 3), resulting from 30 experiments (individual comparisons reported) with 652 subjects and 450 foci. As with the other ALE analyses, we adjusted for within-group effects by pooling the coordinates from all the relevant contrasts with the same subjects into one experiment (Turkeltaub et al., 2002).

### 2.3 | Activation likelihood estimation

We performed different ALE analyses, using the GingerALE software (Eickhoff et al., 2009), to identify consistently activated regions for all the three domains under investigation, that is, processing (a) interactions, (b) individual actions (action observation network), and (c) individual mental states (mentalizing network).

For these analyses, activation foci were initially interpreted as the centers of three-dimensional Gaussian probability distributions, to capture the spatial uncertainty associated with each individual coordinate. All coordinates were reported in the MNI space. The three-dimensional probabilities of all activation foci in a given experiment were then combined for each voxel, resulting in a modeled activation (MA) map. The union of these maps produces ALE scores describing the convergence of results at each brain voxel (Turkeltaub et al., 2002). To distinguish "true" convergence across studies from random convergence (noise), the ALE scores are compared with an empirically defined null distribution derived from a permutation procedure (Eickhoff et al., 2012). This null distribution reflects a random spatial association between experiments, with the within-experiment distribution of foci being treated as a fixed property. Thus, a random-effects inference is invoked, by focusing on the above-chance

**TABLE 2** Overview of the 34 studies included in the meta-analysis on the neural bases of processing others' individual actions via the action observation network. N = progressive study number; Sub = subjects

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
1	Agnew and Wise (2008)	The Journal of Neuroscience	Separate areas for Mirror responses and agency within the parietal operculum	20 sub (mean age: 29)	Actions performed by the experimenter	Obs actions > static	5
2	Baumgaertner, Buccino, Lange, McNamara, and Binkofski (2007)	European Journal of Neuroscience	Polymodal conceptual processing of human biological actions in the left inferior frontal lobe	19 sub (mean age: 27.3)	Action videos and sentences	Obs actions > nonhuman action (cd spinning in cd player); sentences actions > nonhuman actions (wind)	11
3	Biagi, Cioni, Fogassi, Guzzetta, and Tosetti (2010)	Brain Research Bulletin	Anterior intraparietal cortex codes complexity of observed hand movements	12 sub (mean age: 31)	Action videos	Obs actions > static	22
4	Buccino et al. (2001)	European Journal of neuroscience	Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study	12 sub (age range: 25–38)	Action videos	Obs actions > static	19
5	Buccino, Lui, et al. (2004)	Journal of Cognitive neuroscience	Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study	14 sub (age range: 23–33)	Action videos	Obs actions > static	19
6	Calvert and Campbell (2003)	Journal of Cognitive neuroscience	Reading speech from still and moving faces: The neural substrates of visible speech	8 sub (mean age: 26)	Action videos	Obs actions > static	56
7	Cheng, Meltzoff, and Decety (2007)	Cerebral Cortex	Motivation modulates the activity of the human Mirror-neuron system	20 sub (age range: 19–38)	Action videos	Obs actions > scrambled	37
8	Costantini et al. (2005)	Cerebral Cortex	Neural systems underlying observation of humanly impossible movements: An fMRI study	13 sub (mean age: 24)	Action videos	Obs actions > nonhuman actions	24
9	Cross, Hamilton, and Grafton (2006)	NeuroImage	Building a motor simulation de novo: Observation of dance by dancers	10 sub (mean age: 20.7)	Dance videos	Obs actions > baseline	23
10	Di Cesare, Errante, Marchi, and Cuccio (2017)	Brain and Cognition	Language for action: Motor resonance during the processing of human and robotic voices	22 sub (age range: 22–32)	Action verbs	Audio of actions > silence	23
11	Emmorey, Xu, Gannon, Goldin-Meadow, and Braun (2010)	NeuroImage	CNS activation and regional connectivity during pantomime observation: No engagement of the mirror neuron system for deaf signers	14 sub (mean age: 24.3)	Pantomimes and ASL verbs	Obs actions > baseline (fixation)	46

(Continues)



TABLE 2 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
12	Engel, Frum, Puce, Walker, and Lewis (2009)	NeuroImage	Different categories of living and nonliving sound sources activate distinct cortical networks	32 sub (age range: 19–29)	Action sounds	Action sounds human > nonhuman action sounds	18
13	Filimon, Nelson, Hagler, and Sereno (2007)	NeuroImage	Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery	16 sub (age range: 19–48)	Action videos	Obs actions > obj	14
14	Hanzei et al. (2003)	NeuroImage	The human action recognition system and its relationship to Broca's area: An fMRI study	6 sub (age range: 20–30)	Action pictures	Obs actions > static	3
15	Hetu, Mercier, Eugene, Michon, and Jackson (2011)	PLoS One	Modulation of brain activity during action observation: Influence of perspective, transitivity, and meaningfulness	18 sub (mean age: 25)	Action videos	Obs > baseline	16
16	Iacoboni et al. (2005)	PLoS Biology	Grasping the intentions of others with one's own mirror neuron system	23 sub (mean age: 26.3)	Action videos	Obs actions > obj	36
17	Iseki, Hanakawa, Shinozaki, Nankaku, and Fukuyama (2008)	NeuroImage	Neural mechanisms involved in mental imagery and observation of gait	16 sub (mean age: 34.3)	Action videos	Obs actions > scrambled	21
18	Jonas et al. (2007)	NeuroImage	Do simple intransitive finger movements consistently activate fronto-parietal mirror neuron areas in humans?	19 sub (mean age: 25.2)	Action videos	Obs actions > static	6
29	Marsh, Mullett, Ropar, and Hamilton (2014)	NeuroImage	Responses to irrational actions in action observation and mentalizing networks of the human brain	25 sub (mean age: 21.48)	Action videos	Obs actions human > nonhuman actions	6
20	Mazzarella, Ramsey, Conson, and Hamilton (2013)	Social Neuroscience	Brain systems for visual perspective taking and action perception	20 sub (mean age: 27.7)	Action pictures	Obs actions > static; obs actions > obj	22
21	Meister and Iacoboni (2007)	PLoS One	No language-specific activation during linguistic processing of observed actions	14 sub (mean age: 25.1)	Action videos	Obs actions > rest	25
22	Mizuguchi, Nakata, and Kanosue (2016)	Scientific Reports	The right TPJ encodes efforts of others during action observation	22 sub (mean age: 23)	Action videos	Obs actions > rest	18

(Continues)

TABLE 2 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
23	Molinari et al. (2013)	Cerebral Cortex	Human Parietofrontal networks related to action observation detected at rest	16 sub (mean age: 23.3)	Action videos	Obs actions > rest; obs actions > static	6
24	Molnar-Szakacs, Kaplan, Greenfield, and Iacoboni (2006)	NeuroImage	Observing complex action sequences: The role of the fronto-parietal mirror neuron system	12 sub (mean age: 27.8)	Action videos	Obs actions > rest	72
25	Molnar-Szakacs, Iacoboni, Koski, and Mazziotta (2005)	Cerebral Cortex	Functional segregation within pars opercularis of the inferior frontal gyrus: Evidence from fMRI studies of imitation and action observation	58 sub (mean age: 26.16)	Action pictures	Obs actions > rest	7
26	Plata Bello, Modrono, Marciano, and Gonzalez-Mora (2013)	PLoS One	Observation of simple intransitive actions: The effect of familiarity	19 sub (mean age: 22.7)	Action videos	Obs actions > static	34
27	Pierro et al. (2006)	Journal of Cognitive Neuroscience	When gaze turns into grasp	14 sub (mean age: 28)	Action videos	Obs actions > static	9
28	Pierro et al. (2009)	Cerebral Cortex	Neurofunctional modulation of brain regions by the observation of pointing and grasping actions	15 sub (mean age: 34)	Action pictures	Obs actions > static	12
29	Schubotz and von Cramon (2009)	Journal of Cognitive Neuroscience	The case of pretense: Observing actions and inferring goals	18 sub (mean age: 26.4)	Action videos	Obs actions > rest	14
30	Tettamanti et al. (2005)	Journal of Cognitive neuroscience	Listening to action-related sentences activates fronto-parietal motor circuits	17 sub (mean age: 25.3)	Action sentences	Audio of action > abstract sentences	19
31	Turella, Erb, Grodd, and Castiello (2009)	NeuroImage	Visual features of an observed agent do not modulate human brain activity during action observation	17 sub (mean age: 27.8)	Action videos	Obs actions > static	16
32	Wheaton, Thompson, Syngoniatis, Abbott, and Puce (2004)	NeuroImage	Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex	12 sub (mean age: 29.6)	Action videos	Obs actions > static	24

(Continues)

TABLE 2 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
33	Whitehead, Marchant, Craik, and Frith (2009)	SCAN	Neural correlates of observing pretend play in which one object is represented as another	15 sub (mean age: 24.85)	Action videos	Obs actions > obj context	20
34	Zentgraf et al. (2005)	NeuroImage	Differential activation of pre-SMA and SMA proper during action observation: Effects of instructions	10 sub (mean age: 24.1)	Action videos	Obs actions > rest	9
				TOT SUB			TOT FOCI
				598			712

Abbreviations: ASL = American sign language; N = progressive study number; Obj = object; Obs = observation; sub = subjects.

convergence between different experiments, and not on the clustering of foci within a specific experiment. From a computational standpoint, deriving this null hypothesis involved sampling a voxel at random from each of the MA maps and taking the union of the resulting 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 false discovery rate (FDR) of  $p < .05$  and cluster size of  $100 \text{ mm}^3$  (Laird et al., 2005). For exploratory purposes, we also assessed voxels surviving the FDR correction in the absence of a cluster-based threshold.

The second step was to unveil the common and specific contributions of action and mental state representation to the neural processing of interactions. To this purpose, direct comparisons and conjunction analyses were performed, within GingerALE, to identify commonalities and differences between: (a) action observation and mentalizing maps; (b) interaction and action observation maps; and (c) interaction and mentalizing maps.

For each of these contrasts, a conjunction image was created, using the voxel-wise minimum value of the included ALE images, to display the similarity between the data sets (Eickhoff et al., 2011). In the same analysis, two ALE contrast images were created for each of the data sets, and compared by directly subtracting one input image from the other. To correct for sampling errors, GingerALE creates such data by polling the foci in each data set and randomly dividing them into two new groupings equivalent in size to the original data sets. An ALE image is created for each new data set, then subtracted from the other and compared with the true data. Permutation calculations are then used to compute a voxel-wise  $p$ -value image indicating where the values of the “true data” fall within the distribution of values in any single voxel. To simplify the interpretation of ALE contrast images, significant ALE subtraction scores were converted to Z scores. For contrast analyses, clusters were thresholded at  $p < .05$  FDR corrected and cluster size of  $100 \text{ mm}^3$  (Laird et al., 2005).

### 3 | RESULTS

#### 3.0.1 | Neural processing of individual actions by the action observation network

Activations associated with the neural processing of human individual actions encompassed the regions typically associated with the action observation network (Figure 1a, Table 4). These included the posterior portion of the inferior frontal gyrus, as well as the ventral premotor cortex and precentral gyrus, bilaterally. Further activations involved the superior parietal lobule and IPS bilaterally, alongside the left IPL. The occipito-temporal and inferior-middle temporal cortex, extending in the pSTS, were also bilaterally associated with this network.

### 3.0.2 | Neural processing of individual mental states by the mentalizing network

The neural processing of another's mental states involved consistent activation in the typical nodes of the mentalizing network (Figure 1b, Table 5). These included the dorsomedial and ventromedial prefrontal cortex, as well as the posterior cingulate cortex and the TPJ bilaterally.

### 3.0.3 | Neural processing of social interaction

The neural processing of interactions was associated with consistent activations in the dorsomedial and ventromedial prefrontal cortex alongside posterior cingulate cortex, as well as in the right premotor cortex and left cerebellum (Figure 1c, Table 6). Further activations encompassed the posterior portion of middle temporal cortex and the pSTS, extending into the TPJ, alongside the amygdala, bilaterally.

### 3.0.4 | Common activations to processing individual actions and mental states

Conjunction analyses unveiled a significant overlap between the meta-analytics maps of the action observation and mentalizing networks in a cluster encompassing the right pSTS and TPJ (Figure 2a, Table 7).

### 3.0.5 | Common activations to processing individual actions and social interaction

Processing interactions and human individual actions was associated with consistent common activations encompassing the right premotor cortex, alongside the posterior portion of middle temporal cortex extending into the pSTS bilaterally (Figure 2b,d, Table 8).

### 3.0.6 | Common activations to processing individual mental states and social interaction

Processing interactions and another's mental states reflected in consistent common activations in the dorsomedial prefrontal and posterior cingulate cortex, as well as in the TPJ bilaterally (Figure 2c,d, Table 9).

### 3.0.7 | Differential activations associated with processing individual actions versus mental states

Compared with representing another's mental states, the neural processing of human individual actions was associated with stronger bilateral activity in the typical nodes of the action observation network, that is, ventral premotor cortex, IPL, and IPS, alongside the posterior portion of inferior and middle temporal cortex plus the cerebellum (Figure 2a, Table 7).

### 3.0.8 | Differential activations associated with processing mental states versus individual actions

The neural processing of another's mental states, compared with human individual actions, reflected in stronger activity in the typical nodes of the mentalizing network, that is, dorsomedial and ventromedial prefrontal cortex, posterior cingulate cortex and the TPJ bilaterally (Figure 2a, Table 7).

### 3.0.9 | Differential activations associated with processing individual actions versus social interaction

The neural processing of human individual actions, compared with interactions, was associated with stronger activity in the IPL bilaterally (but with a left hemispheric dominance), alongside the left ventral premotor and inferior temporal cortex (Figure 2b, Table 8).

### 3.0.10 | Differential activations associated with processing social interaction versus individual actions

Compared with representing human individual actions, the neural processing of interactions reflected in stronger activations in the dorsomedial and ventromedial prefrontal cortex, posterior cingulate cortex and left pSTS (Figure 2b, Table 8).

### 3.0.11 | Differential activations associated with processing mental states versus social interaction

The neural processing of another's mental states, compared with interactions, was associated with stronger bilateral activity in the TPJ (Figure 2c, Table 9).

### 3.0.12 | Differential activations associated with processing social interaction versus mental states

Compared with representing another's mental states, the neural processing of interactions reflected in stronger bilateral activity in the posterior portion of middle temporal cortex and pSTS (Figure 2c, Table 9).

## 4 | DISCUSSION

We performed three quantitative meta-analyses to investigate the contribution of action and mental state representation to the neural processing of social interaction. This goal was pursued via the ALE approach, highlighting both common and specific regions associated with the neural processing of interactions and either single individuals' actions or mental states by, respectively, the action observation or mentalizing networks.

**TABLE 3** Overview of the 29 studies included in the meta-analysis on the neural bases of processing others' mental states via the ToM, or mentalizing, network. N: Progressive study number; sub: Subjects; RMET: reading the mind in the eye task (Baron-Cohen et al., 2001)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
1	Abraham, Rakoczy, Werning, von Cramon, and Schubotz (2010)	Social Neuroscience	Matching mind to world and vice versa: Functional dissociations between belief and desire mental state processing	22 sub (mean age: 26.14)	Verbal scenarios and questions	Mental > logic reasoning	14
2	Aichhorn et al. (2009)	Journal of Cognitive Neuroscience	TPJ activity in tToM tasks: Falseness, beliefs, or attention	21 sub (median age: 24)	Vignettes (2 sentence) and questions	Belief > physic	15
3	Baron-Cohen et al. (1999)	European Journal of Neuroscience	Social intelligence in the normal and autistic brain: An fMRI study	12 sub (mean age: 25.5)	RMET	Emotional mind state > gender	53
4	Bodden et al. (2013)	Advances in Cognitive Psychology	Comparing the neural correlates of affective and cognitive ToM using fMRI: Involvement of the basal ganglia in affective ToM	30 sub (mean age: 25.3)	Sentences and colored pictures	Belief > physic	15
5	Castelli et al. (2010)	Neuropsychologia	Effects of aging on mindreading ability through the eyes: An fMRI study	12 sub (mean age: 25.2)	RMET	Emotional mind state > gender	18
6	Cheung et al. (2012)	International Journal of Psychophysiology	False belief and verb nonfactivity: A common neural basis?	20 sub (mean age: 23.5)	Stories and pictures	Belief > physic	25
7	Dodell-Feder, Koster-Hale, Bedny, and Saxe (2011)	NeuroImage	fMRI item analysis in a ToM task	62 sub (mean age: 22)	Verbal stories	Belief > physic	27
8	Dohnel et al. (2012)	NeuroImage	Functional activity of the right TPJ and of the medial prefrontal cortex associated with true and false belief reasoning	18 sub (mean age: 24.72)	Pictures and questions	Belief > reasoning about reality	16
9	Dufour et al. (2013)	PLoS One	Similar brain activation during false belief tasks in a large sample of adults with and without autism	27 sub (mean age: 30.6)	Verbal stories	Belief > physic	14
10	Ferstl and von Cramon (2002)	NeuroImage	What does the frontomedian cortex contribute to language processing: Coherence or theory of mind?	9 sub (age range: 22-27)	Audio sentences	Belief > pseudo-worded sentences	13
11	Focquaert, Steven-Wheeler, Vanneste, Doron, and Platek (2010)	Brain Research Bulletin	Mindreading in individuals with an empathizing versus systemizing cognitive style: An fMRI study	24 sub (mean age: 27)	RMET	Emotional mind state > gender	13

(Continues)

TABLE 3 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
12	Gallagher et al. (2000)	Neuropsychologia	Reading the mind in cartoons and stories: An fMRI study of "ToM" in verbal and nonverbal tasks	6 sub (mean age: 30)	Cartoons/stories	Belief > physic	16
13	Gobbini, Koralek, Bryan, Montgomery, and Haxby (2007)	Journal of Cognitive Neuroscience	Two takes on the social brain: A comparison of ToM tasks	12 sub (mean age: 22)	Stories	Belief > physic	19
14	Gweon, Dodel-Feder, Bedny, and Saxe (2012)	Child Development	Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts	8 sub (mean age: 21.5)	Stories	Belief > physic	6
15	Herve, Razafimandimby, Jobard, and Tzourio-Mazoyer (2013)	PLoS One	A shared neural substrate for Mentalizing and the affective component of sentence comprehension	42 sub (mean age: 30.9)	Sentences	Mental > reasoning about the plausibility	20
16	Jenkins and Mitchell (2010)	Cerebral Cortex	Mentalizing under uncertainty dissociated neural responses to ambiguous and unambiguous mental state inferences	15 sub (mean age: 19.8)	Stories	Belief > physic	9
17	Jimura, Konishi, Asari, and Miyashita (2010)	Brain Research	Temporal pole activity during understanding other persons' mental states correlates with neuroticism trait	44 sub (age range: 20–28)	Stories	Belief > physic	4
18	Kobayashi, Glover, and Temple (2006)	Brain and Language	Cultural and linguistic influence on neural bases of "ToM": An fMRI study with Japanese bilinguals	32 sub (mean age: 28.42)	Stories	Belief > physic	13
19	Lombardo et al. (2010)	Journal of Cognitive Neuroscience	Shared neural circuits for Mentalizing about the self and others	33 sub (mean age: 27.97)	Vignettes requiring to make judgments	Mental > physics	23
20	Mitchell (2008)	Cerebral Cortex	Activity in right TPJ is not selective for ToM	20 sub (mean age: 23)	Vignettes (stories and questions)	Mental > physics	4
21	Ochsner et al. (2005)	NeuroImage	The neural correlates of direct and reflected self-knowledge	Exp 1:17 sub (mean age: 29) Exp 2:16 sub (mean age: 22.95)	Trait adjectives Trait adjectives	Mental (attribution) > physics (n of syllables) Mental (attribution) > physics (perceptual features)	8 23

(Continues)

TABLE 3 (Continued)

N	Authors (year)	Journal	Title	Sub (mean age)	Stimuli	Contrast	Foci
22	Otsuka, Osaka, Ikeda, and Osaka (2009)	Neuroscience Letters	Individual differences in the ToM and superior temporal sulcus	24 sub (mean age: 24)	Sentences	Mental > grammar reasoning	6
23	Saxe and Powell (2006)	Psychological Science	It's the thought that counts: Specific brain regions for one component of ToM	12 sub (age range: 19–26)	Stories	Belief > physic	9
24	Sebastian et al. (2012)	SCAN	Neural processing associated with cognitive and affective theory of mind in adolescents and adults	15 sub (mean age: 28.88)	Cartoon stories	Belief > physic	13
25	Seger, Stone, and Keenan (2004)	Neuropsychologia	Cortical activations during judgments about the self and another person	12 sub (mean age: 23.6)	Food words	Mental (decide if they/other like the food) > physic (n of voxel in the word)	20
26	Vogel et al. (2001)	NeuroImage	Mind reading: Neural mechanisms of theory of mind and self-perspective	42 sub (age range: 21–32)	Stories	Belief > physic	7
27	Vollm et al. (2006)	NeuroImage	Neuronal correlates of ToM and empathy: A functional magnetic resonance imaging study in a nonverbal task	13 sub (mean age: 24.9)	Nonverbal stories	Belief > physic	8
28	Young, Dodel-Feder, and Saxe (2010)	Neuropsychologia	What gets the attention of the TPJ? An fMRI investigation of attention and ToM	17 sub (age range: 18–31)	Stories	Belief > physics	9
29	Zaitchik et al. (2010)	Neuropsychologia	Mental state attribution and the TPJ: An fMRI study comparing belief, emotion, and perception	15 sub (mean age: 22.4)	Sentences	Belief > syntax reasoning; belief > physic (perception)	10
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				652			450

Abbreviations: ToM = theory of mind; TPJ, temporoparietal junction.

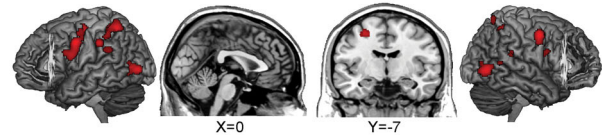
#### 4.1 | Neural processing of individual actions and mental states

First, our results confirmed previous meta-analytic evidence on the distinct neural bases of the action observation and mentalizing systems. Processing human individual actions, compared with mental states, was associated with stronger activity in a bilateral fronto-temporo-parietal network encompassing the ventral premotor and inferior frontal cortex, alongside the aIPS and IPL, and the cerebellum (Caspers et al., 2010; Molenberghs et al., 2012) (Figures 1d and 2). This network is considered to receive higher order perceptual inputs from other regions highlighted by our analysis, such as the occipito-temporal and posterior inferior-middle temporal cortex, extending into the pSTS containing polysensory neurons that respond to biological motion (Barraclough, Xiao, Baker, Oram, & Perrett, 2005). The lack of evidence for the cingulate gyrus, previously associated with the vicarious processing of emotional and somatosensory experiences (Fan, Duncan, de Greck, & Northoff, 2011; Lamm & Singer, 2010; Molenberghs et al., 2012), is likely explained by our focus on the neural bases of “action representation,” which lead to exclude activations associated with empathy-related processes. The reverse contrast highlighted the typical nodes of the mentalizing network, that is, the dorsomedial and ventromedial prefrontal cortex plus the posterior cingulate cortex in the midline, alongside TPJ bilaterally (Bzdok et al., 2012; Molenberghs et al., 2016; van Veluw & Chance, 2014) (Figures 1d and 2).

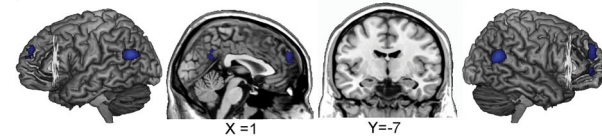
These networks are considered to provide different contributions to the processing of social intentions. Understanding the goal of observed actions involves a well-known fronto-parietal network mediating the access to an experiential knowledge in terms of their motor consequences, with no need for a conceptual interpretative neural mechanism (Rizzolatti & Sinigaglia, 2010). Instead, the lack of visuomotor cues requires intentions to be inferred in terms of internal mental states such as thoughts, desires, and beliefs (Van Overwalle & Baetens, 2009). While the computational mechanisms underlying mentalizing are still debated (e.g., Saxe & Kanwisher, 2003 vs. Mitchell, 2008), possible cues into this issue come from the ubiquitous involvement of multiple brain areas spanning the right pSTS and TPJ in a variety of social cognitive processes (Bahnmann, Dziobek, Prehn, Wolf, & Heekeren, 2010; Yang, Rosenblau, Keifer, & Pelphrey, 2015), i.e., perceiving biological motion (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Peelen, Wiggett, & Downing, 2006), mentalizing (Schneider, Slaughter, Becker, & Dux, 2014; Wolf, Dziobek, & Heekeren, 2010), and making moral judgments (Heekeren et al., 2005; Prehn et al., 2008). These data have suggested a two-stage model in which the right pSTS underpins an initial parsing of visuospatial information into meaningful discrete elements, whose communicative significance for interpreting others' behavior involves more complex computations associated with hierarchically increasing activity in the TPJ “mentalizing” node (Bahnmann et al., 2010; Redcay, 2008).

This hypothesis fits both with the present meta-analytic data on the common involvement of the right pSTS—bordering the TPJ—in action observation and mentalizing (Figure 2), and with our recent connectivity evidence highlighting this region as the input of visual social information, modulating activity in both networks while

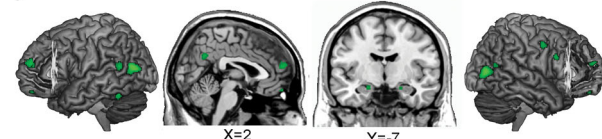
#### (a) Action observation network



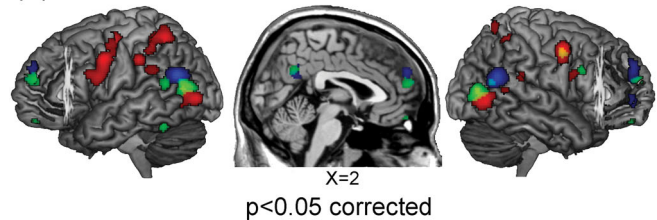
#### (b) ToM network



#### (c) Interaction network



#### (d) All networks



**FIGURE 1** Action observation, mentalizing, and social interaction brain networks. From top to bottom, the figure reports the brain structures consistently associated with processing others' individual actions (action observation network, red), others' mental states (theory of mind [ToM], or mentalizing, network, blue) and social interactions (interaction network, green), either in isolation or superimposed onto the same brain render and slices. All the reported activations survived a statistical threshold of  $p < .05$  corrected for multiple comparisons. A = action observation; I = interaction; T = theory of mind (mentalizing) [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

observing social interactions characterized by different degrees of cooperativity or affectivity (Arioli, Perani, et al., 2018). This combined evidence supports the role of pSTS in decoding different kinds of intentions inherent in others' actions (Gao, Scholl, & McCarthy, 2012; Yang et al., 2015), via distinct but interrelated pathways connecting this region to (a) the key nodes of the action observation network for the bottom-up visuomotor processing of action meaning, and (b) the ventromedial prefrontal cortex for the top-down attribution of affective/mental states (Arioli, Perani, et al., 2018). We thus expected the pSTS to be included in the meta-analytic ALE map associated with processing interactions.

#### 4.2 | The social interaction network

The neural processing of interactions involved regions known to be associated with representing individual actions and mental states,



**TABLE 4** Neural bases of processing others' actions

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	Label
1	6,576	-50	4	36	Left frontal precentral gyrus
		-26	-8	54	Left frontal precentral gyrus
		-52	10	20	Left inferior frontal gyrus
		-38	-2	46	Left middle frontal gyrus
		-46	6	24	Left frontal precentral gyrus
		-48	-4	50	Left frontal precentral gyrus
2	4,360	-36	-52	56	Left superior parietal lobule
		-38	-38	46	Left inferior parietal lobule
3	2,664	46	-64	-2	Left middle temporal gyrus/pSTS
4	2,144	-48	-76	2	Left inferior temporal gyrus
		-42	-70	4	Left middle occipital gyrus
		-50	-64	10	Left middle temporal gyrus/pSTS
5	1,976	48	2	46	Right frontal precentral gyrus
6	992	34	-48	52	Right precuneus
7	568	-60	-24	36	Left inferior parietal lobule
8	304	-50	-38	26	Left insula
9	240	46	14	24	Right inferior frontal gyrus
10	232	24	-60	66	Right superior parietal lobule
11	152	56	-32	22	Right parietal operculum-supramarginal gyrus
12	104	52	-46	8	Right superior temporal gyrus

Abbreviation: pSTS = posterior sector of superior temporal sulcus.

Note. From left to right, the table reports the size (in mm<sup>3</sup>), stereotaxic coordinates of local maxima and anatomical labeling of the clusters consistently associated with representing others' actions (action observation network).

**TABLE 5** Neural bases of processing others' mental states

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	Label
1	2,856	-52	-58	22	Left TPJ
2	2,464	54	-52	20	Right TPJ
3	1,392	0	56	30	Left medial frontal gyrus
4	864	2	-58	28	Left posterior cingulate
		0	-54	36	Left precuneus
5	344	-8	-58	18	Left posterior cingulate
6	328	-8	52	0	Left medial frontal gyrus

Abbreviations: TPJ, temporoparietal junction.

Note. From left to right, the table reports the size (in mm<sup>3</sup>), stereotaxic coordinates of local maxima and anatomical labeling of the clusters consistently associated with representing others' mental states (mentalizing, or ToM, network).

alongside the amygdala bilaterally (Figure 1d). Conjunction analyses and direct comparisons provided formal evidence for commonalities and differences between this set of regions and either the action observation or mentalizing networks (Figure 2).

#### 4.2.1 | Social interaction and action observation networks

Processing individual actions (vs. interactions) was specifically associated with bilateral activity in the occipito-temporal cortex, IPL, and

ventral premotor cortex (Figure 2). The opposite comparison highlighted the dorsomedial and ventromedial prefrontal cortex, alongside the posterior cingulate cortex and left TPJ (Figure 2). Common activations to the two networks encompassed the posterior middle temporal cortex and pSTS bilaterally, alongside the right premotor cortex (Figure 2). As previously discussed, the common involvement of areas associated with representing action meaning (Caspers et al., 2010; Molenberghs et al., 2012) might reflect the visuomotor decoding of shared motor goals in social interactions (Arioli, Perani, et al., 2018).

**TABLE 6** Neural bases of processing social interactions

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	Label
1	1,800	-46	-66	14	Left middle temporal gyrus
2	1,736	50	-70	8	Right middle temporal gyrus
3	944	6	54	20	Right medial frontal gyrus
4	392	2	-58	32	Left cingulate gyrus
5	384	-42	-48	-22	Left cerebellum
6	384	-54	-48	14	Left superior temporal gyrus
7	336	44	2	42	Right frontal precentral gyrus
8	240	54	20	26	Right middle frontal gyrus
9	168	46	-58	16	Right middle temporal gyrus
10	144	-20	-8	-18	Left amygdala
11	112	20	-6	-20	Right amygdala
12	112	2	54	-20	Right medial frontal gyrus

Note. From left to right, the table reports the size (in mm<sup>3</sup>), stereotaxic coordinates of local maxima and anatomical labeling of the clusters consistently associated with processing social interactions (social interaction network).

This hypothesis is supported by recent fMRI data from monkeys engaged in the visual processing of interactions (Sliwa & Freiwald, 2017), in which planned contrasts allowed to ascribe the recruitment of classical visuomotor areas to the decoding of agents' actions. Instead, medial prefrontal regions displayed a selective response to interactions. The spatial overlap between these regions and the human mentalizing network suggested a role for such “*exclusively social interaction network*” in drawing inferences about the intentional states underlying the observed interactions, which in turn might have represented a potential evolutionary pressure to the development of mentalizing skills (Sliwa & Freiwald, 2017). We thus assessed whether available evidence from published studies supports the existence of “*exclusively social*” brain activations also in the human brain, or rather the neural processing of interactions can be reduced to the joint engagement of the mirror and mentalizing networks. Based on our initial evidence that processing interactions recruits regions beyond the action observation network, we thus performed further analyses to assess whether such additional activations can be fully ascribed to the mentalizing network, or they rather involve regions exceeding both networks.

#### 4.2.2 | Social interaction and mentalizing networks

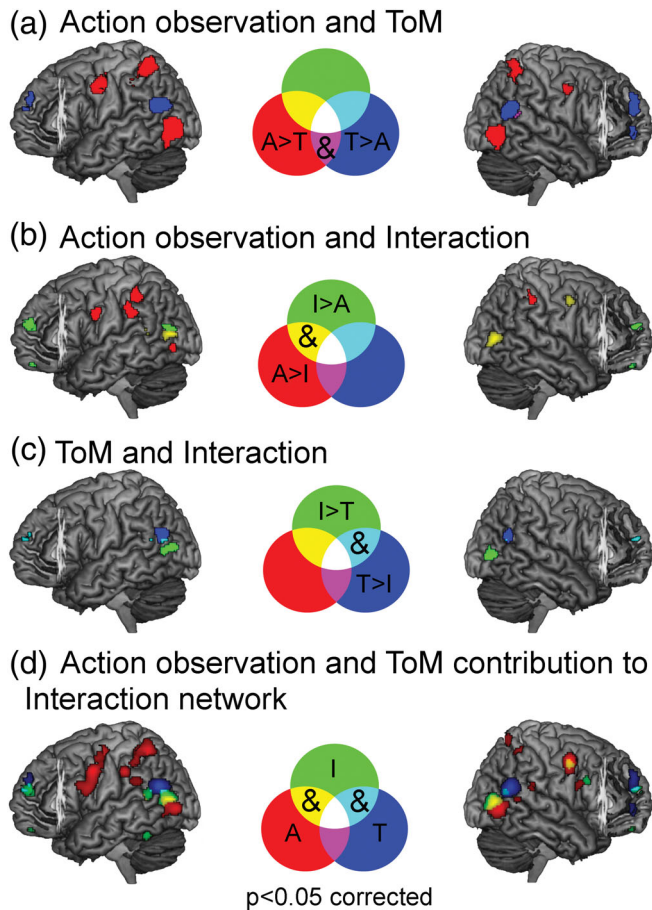
Mentalizing and processing interactions were associated with consistent common activations in the dorsomedial prefrontal cortex and posterior cingulate cortex, alongside the TPJ bilaterally (Figure 2). While all these areas have been associated with inferences on others' mental states (van Overwalle, 2009; Van Overwalle & Baetens, 2009), Sliwa and Freiwald's (2017) data from the monkey brain strongly suggest a role of these regions, and particularly the dorsomedial prefrontal cortex, in decoding shared social intentions over and beyond the visuomotor analyses associated with the action observation network (Arioli, Perani, et al., 2018; Iacoboni et al., 2004; Van Overwalle & Baetens, 2009).

Compared with interactions, processing another's mental states selectively involved the TPJ bilaterally (Figure 2), which lesion-based studies highlight as a key node of the mentalizing network in the human brain (Samson et al., 2004). The reverse comparison highlighted the posterior middle temporal cortex and pSTS bilaterally (Figure 2), likely underpinning the deeper visuomotor analyses required by processing joint, compared with individual, actions. While the outcome of such analyses might provide the mentalizing network with sensorimotor information supporting and constraining inferential processes of shared intention understanding (Arioli, Perani, et al., 2018; Catmur, 2015), these results seem to provide limited evidence for “*exclusively social*” areas, exceeding the contribution of action observation and mentalizing networks, in the human brain.

#### 4.3 | The neural processing of social interaction

The present meta-analytic data suggest that a putative “social interaction network” can be largely reduced to the joint contribution of the action observation and mentalizing networks in representing action meaning and others' mental states, respectively. This evidence allows to refine previous hypotheses, based on studies addressing the processing of single individuals, that the two networks underpin complementary social cognitive functions (Van Overwalle & Baetens, 2009).

The involvement of both networks in processing interactions is strongly suggested by the progression of activity, along the posterior lateral temporal cortex, associated with representing individual actions (bilateral inferior-middle temporal cortex plus the right pSTS; red), social interactions (bilateral middle temporal cortex and pSTS extending into TPJ; green), and mental states (bilateral TPJ; blue) (Figures 1 and 2). This parcellation fits with Redcay (2008) two-stage model, distinguishing between the analysis of biological motion in the right pSTS (associated with parsing a stream of visuospatial information) and subsequent mentalizing in the bilateral TPJ (Bahnmann et al., 2010). Moreover, our data suggest that this model might be extended to



**FIGURE 2** Commonalities and differences across action observation, mentalizing, and social interaction brain networks. From top to bottom, the figure depicts with different colors the common and specific brain structures across the action observation and mentalizing networks (a), action observation and interaction networks (b), as well as mentalizing and interaction networks (c). In the bottom panel, the three networks are depicted onto the same brain render alongside the common voxels across the interaction network and either the action observation (yellow) or mentalizing (cyan) networks. All the reported activations survived a statistical threshold of  $p < .05$  corrected for multiple comparisons. A = action observation; I = interaction; T = theory of mind (mentalizing) [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

include the visual processing of interactions as a further component, partially overlapping, at the anatomical and functional levels, with both the action observation and mentalizing networks. The progressive transition from action-specific activity in the posterior middle temporal cortex (Figure 2) to overlapping action-interaction (yellow) and finally interaction-specific (green) activations in the pSTS might underpin the transition from the visuomotor decoding of the single agents' actions to processing the "how" and "what" of the observed interaction (Spunt & Lieberman, 2012a, 2012b). Then, in the TPJ, the spatial overlap between activations associated with processing interactions and mentalizing (Figure 2) might reflect the progressive transition from the visuomotor decoding of action-related intentional states to intention reading in terms of mental states detached from visuomotor information. Once relayed to the TPJ (Figures 1 and 2), a key node for detaching from one's own

attentional perspective (Mitchell, 2008), this hierarchical processing might promote further in-depth inferences on the social actors' intentional states (i.e., in terms of the "why" of the [inter]action; Chiavarino et al., 2012; Vogeley, 2017; Spunt & Lieberman, 2012a, 2012b). The output of this process is then likely relayed to the dorsomedial prefrontal cortex (Arioli, Perani, et al., 2018), which has been shown to play a role in forming impressions of people (Ferrari et al., 2016) and in their accuracy (Spunt & Adolphs, 2015; Wagner, Kelley, Haxby, & Heatherton, 2016).

Such a process would be expected to include the amygdala, which both neuroimaging (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011; Schultz, 2005) and lesional (Bickart, Dickerson, & Barrett, 2014; Emery et al., 2001; Rutishauser, Mamelak, & Adolphs, 2015) studies highlight as a key modulator of social perception and behavior. This hypothesis was supported by the inclusion of amygdala among the structures recruited by processing interactions (Figure 1). However, despite the lack of previous evidence for its involvement in the action observation (Caspers et al., 2010; Molenberghs et al., 2012) or mentalizing (Bzdok et al., 2012; van Veluw & Chance, 2014) networks, direct comparisons failed to highlight a significantly stronger involvement of the amygdala in processing interactions than individual actions or mental states. Therefore, its possible "exclusively social" engagement remains speculative, and in need of additional evidence, at this stage. It is noteworthy that this research question reflects current debates on the domain specificity versus generality of amygdala computations in social cognition, due to inconsistent data supporting its specific involvement in the automatic (and even subliminal) processing of social stimuli (Öhman, 2002) versus its generic role in processing salient stimuli (Herry et al., 2007; Whalen, 2007). This debate has suggested the existence of a specific "amygdala" network associated with a more general function, that is, processing the current value of stimuli based on their salience and behavioral relevance in terms of affiliation or aversion (Bickart et al., 2014). This domain-general role would explain its involvement in a variety of functions and contexts, including judgments of trustworthiness and approachability (Adolphs, 2010) which are inherent in the processing of social interactions (Kujala et al., 2012).

Overall, a hierarchical neural processing of social interactions and intentions seems thus to involve the progressive transition from visuomotor decoding to mentalizing in the posterior lateral temporal cortex (Figures 1d and 2), plus further contributions by specific nodes of the action observation and mentalizing networks in the right premotor and medial prefrontal cortex, respectively. Alongside recent evidence on the role of the latter region in the visual processing of interaction in the monkey brain (Sliwa & Freiwald, 2017), these data strengthen the hypothesis that this stimulus might have represented an evolutionary pressure toward the development of mentalizing skills. Our results thus highlight several directions for future studies aiming to address the specific roles played by these brain regions in normal and impaired social cognition.

#### 4.4 | Conclusions and limitations

We reported novel meta-analytic evidence of a network of areas associated with the processing of social intentions, including key nodes of the well-established action observation and mentalizing

**TABLE 7** Common and specific regions across the action observation and mentalizing networks

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	Label
Action observation and mentalizing					
1	24	54	-46	16	Right superior temporal gyrus
2	16	52	-44	18	Right TPJ
3	8	54	-48	14	Right superior temporal gyrus
Action observation > mentalizing					
1	5,280	-45	-71	-0	Left cerebellum. Posterior declive
2	3,824	49	-67	-3	Right cerebellum. Posterior declive
3	3,384	-37	-49	58	Left inferior parietal lobule
		-38	-42	46	Left inferior parietal lobule
4	1,784	32	-51	54	Right inferior parietal lobule
5	1,304	-55	-1	39	Left frontal precentral gyrus
6	376	49	-2	41	Right frontal precentral gyrus
7	376	-30	-5	48	Left middle frontal gyrus
Mentalizing > action observation					
1	2,896	-52	-58	22	Left TPJ
2	2088	55	-54	21	Right TPJ
3	1,360	-1	55	25	Left medial frontal gyrus
4	848	2	-57	29	Left posterior cingulate
5	360	-7	-58	18	Left posterior cingulate
6	336	-8	52	-0	Left medial frontal gyrus

Abbreviation: TPJ, temporoparietal junction.

Note. From left to right, the table reports the size (in mm<sup>3</sup>), stereotaxic coordinates of local maxima and anatomical labeling of the clusters which were commonly (top) and specifically (bottom) associated with the action observation and mentalizing networks.

**TABLE 8** Common and specific regions across the action observation and social interaction networks

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	Label
Social interaction and action observation					
1	1,040	48	-70	6	Right middle occipital gyrus
2	688	-48	-68	10	Left middle temporal gyrus/pSTS
3	336	44	2	42	Right frontal precentral gyrus
4	8	-54	-46	10	Left middle temporal gyrus/pSTS
5	8	54	-44	14	Left superior temporal gyrus
Social interaction > action observation					
1	944	3	56	18	Left medial frontal gyrus
2	464	-44	-67	16	Left middle temporal gyrus/pSTS
3	392	2	-59	32	Left precuneus
4	112	1	54	-19	Left medial frontal gyrus
Action observation > social interaction					
1	1,264	-42	-37	47	Left parietal supramarginal gyrus
2	984	39	-36	46	Right inferior parietal lobule
3	728	-55	3	29	Left frontal precentral gyrus
4	728	-54	-29	32	Left inferior parietal lobule
5	120	-53	-70	-2	Left inferior temporal gyrus

Abbreviation: pSTS = posterior sector of superior temporal sulcus.

Note. From left to right, the table reports the size (in mm<sup>3</sup>), stereotaxic coordinates of local maxima and anatomical labeling of the clusters which were commonly (top) and specifically (bottom) associated with the action observation and social interaction networks.

**TABLE 9** Common and specific regions across mentalizing and social interaction networks

Cluster #	Volume (mm <sup>3</sup> )	x	y	z	Label
Social interaction and mentalizing					
1	208	2	-58	30	Left cingulate gyrus
		0	-56	36	Left precuneus
2	128	0	58	20	Left medial frontal gyrus
3	40	-46	-62	18	Left middle temporal gyrus
4	16	-56	-50	18	Left TPJ
5	8	-48	-62	16	Left TPJ
6	8	48	-58	18	Right TPJ
7	8	2	56	22	Left medial frontal gyrus
8	8	2	54	24	Left medial frontal gyrus
9	8	4	56	24	Right medial frontal gyrus
Social interaction > mentalizing					
1	904	-47	-70	10	Left middle temporal gyrus/pSTS
2	784	48	-73	2	Right inferior occipital gyrus
		54	-74	8	Right middle occipital gyrus
Mentalizing > social interaction					
1	1,016	-52	-61	24	Left TPJ
2	464	57	-56	22	Right TPJ

Abbreviations: pSTS = posterior sector of superior temporal sulcus; TPJ, temporoparietal junction.

Note. From left to right, the table reports the size (in mm<sup>3</sup>), stereotaxic coordinates of local maxima and anatomical labeling of the clusters which were commonly (top) and specifically (bottom) associated with the mentalizing and social interaction networks.

networks for representing action meaning and others' mental states, possibly in conjunction with an amygdala network underlying evaluations on affective salience. While fitting with available evidence on the specific role played by the action observation and mentalizing networks in processing individual agents' actions versus mental states, the present results highlight their joint contribution in the analysis of a qualitatively different stimulus such as social interaction.

In the light of the centrality of social cognition in several neuropsychiatric disorders (DSM-5), characterizing the neural bases of this key ability of the social brain entails both scientific and translational implications. On the one hand, even in healthy young individuals the lack of interaction, that is, loneliness, has been shown to reflect in increased connectivity within the cingulo-opercular network associated with tonic alertness (Layden et al., 2017). Moreover, social cognitive functions can be disrupted in neurological (e.g., frontotemporal dementia or amyotrophic lateral sclerosis; Cerami et al., 2014a, 2014b; Crespi et al., 2014, 2016, 2018; Dodich, Cerami, Crespi, et al., 2016; Dodich, Cerami, Iannaccone, et al., 2016), psychiatric (e.g., schizophrenia; Fujiwara, Yassin, & Murai, 2015) and developmental (e.g., autism; Fett, Shergill, & Krabbendam, 2015) disorders, as well as after acute brain damage (e.g., stroke or traumatic brain injury; Henry, von Hippel, Molenberghs, Lee, & Sachdev, 2016). Moreover, such deficits are critical predictors of functional outcomes because they affect the ability to form and sustain interpersonal relationships, thereby eliminating the benefits that interactions have for patients or at-risk individuals (Stephoe, Shankar, Demakakos, & Wardle, 2013). An advancement of knowledge on the neural bases of social cognition is

thus crucial in several respects, including the development of novel tools for assessing related abilities in pathological conditions (e.g., Dodich et al., 2014, 2015).

The present evidence is limited by the relatively low number of contrasts included in each data set, which, although in line with current recommendations for ALE meta-analyses (Eickhoff et al., 2016; Muller et al., 2018), did not allow to compare the regions underlying the processing of different types of interaction. In the trade-off between sensitivity and specificity, however, we opted for stringent criteria which, while fulfilling well-established prescriptions, might allow to unveil subtle differences between largely overlapping neural computations. Further limitations of this study reflect those inherent in the relevant literature, and particularly the frequent use of different types of stimuli, that is, verbal versus visual, when addressing the neural bases of processing mental states versus individual actions and interactions, respectively. The present data should thus be considered to provide a preliminary evidence which will require further support from novel empirical studies.

While the fast growth of this research field will likely help filling these gaps, the present results strengthen the notion of a joint involvement of the action observation and mentalizing networks in social intention understanding (Arioli, Perani, et al., 2018; Centelles et al., 2011; Iacoboni et al., 2004; Kujala et al., 2012), and pave the way for further in-depth investigations on the brain mechanisms underlying the processing of social interaction. These insights may also prove useful in future studies assessing the status of the interaction network as a neural marker of impaired social cognition, or the

effects of cognitive remediation procedures (Kurtz & Richardson, 2012), in different pathological conditions (Henry et al., 2016).

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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