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The Interactive ‘Social Brain’: Behavioral and Neural Substrates for the Processing of Potential Engagement in Motor Interactions.

Coordinatore:

Chiar.mo Prof. Luca Bonini

Tutore:

Chiar.mo Prof. Vittorio Gallese

Dottorando: Edoardo Arcuri

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Abstract

Over the past three decades, the ‘Social Brain’ has become a prominent construct in cognitive neuroscience, often divided into abstract mentalization processes, correlated with a ‘Mentalizing’ (MENTA) brain network, and sensorimotor encoding of others’ bodily displays, associated with the ‘Mirror Neuron System’ (MNS). This dualistic view limits our understanding of social cognition, especially in contexts of direct interaction. ‘Second-person Neuroscience’ have demonstrated that direct (or potential) engagement in interpersonal interactions determines both different involvements of neural resources and different deployment of behavioural patterns related to decoding others’ intentions. Yet what features of social cues are critical to signal or decode a potential interaction and how this dimension is mapped onto the social brain is not fully understood.

To unveil potential markers of social intentions in motor acts and facial signals, we conducted a series of behavioural experiments focusing on the execution and perception of a basic motor act—grasping an object—comparing actions executed with individualistic (grasp to place) or social (grasp to pass) intentions. Employing hand kinematics analyses and classification techniques, we found that grasping with social intent resulted in slower, more precise, and more predictive for observers compared to individualistic actions. Hand positioning on objects was a key indicator of social intention, possibly linked to social affordance processing. An eye-tracking analysis also revealed the face as the most attended feature during action observation.

In a follow-up fMRI experiment, we employed action stimuli from the previous experiment to explore brain responses to engagement-relevant features of observed actions. We focused on social intention, action-directedness, and gaze monitoring. Whole-brain analysis revealed that action-directedness, rather than social nature, primarily drove neural activity in premotor, temporal, and occipital areas, likely related to kinematic processing and social affordance encoding. Parametric analysis based on perceived engagement ratings highlighted opercular somatosensory and superior parietal areas, indicating increased monitoring and simulation of sensorimotor features during higher engagement.

Lastly, a Representational Similarity Analysis (RSA) revealed similar coding of engagement-related features between MNS’s fronto-parietal areas and the Temporo-Parietal Junction (TPJ). Functional lateralization was observed, with right-lateralized regions (e.g., IPL, Premotor cortex, TPJ) mostly encoding action engagement and action directedness and a left-lateralized cluster (e.g., IPL, ST, TPJ) coding for the action goal.

These results demonstrate the integration of bodily cues in predicting potential interactions and highlight the neural underpinnings of perceived engagement in observed actions.

1. The Human ‘Social Brain’: Past and Present.

1.1. The ‘Social Brain’: where are we at?

The term ‘Social Brain’ is widely used today to refer to putative neural mechanisms, networks, and cognitive functions involved in the processing of information related to other agents and interactions with them in a variety of different species (cf. Adolph, 2009; Prounis and Ophir, 2020). Traditionally, however, its early establishment as a specific concept and object of research was initially set by the emergence, around the 90s, of a rather specific research program aimed at unravelling primates’ social behaviour, characterized by a complex relational and societal life (cf. Reader and Laland, 2001; Van Schaik and Burkart, 2011) thought to peak in the human species (Tomasello, 2014). This program’s foundational hypothesis asserted the progressive refinement along the primates’ clade of brain networks specialized in mapping conspecifics’ ‘psychological facts’ (i.e., internal mental states) posited as a necessary capacity for solving crucial tasks like accurately reading and predicting others’ behaviour (Humphrey, 1978; Brothers, 1990a) or achieving mutual understanding among individuals for successful interpersonal coordination (Vogeley, 2017).

Influential in this peculiar formulation of the main function of primates’ Social Brain’ was the convergence of developmental psychology, evolutionary psychology, and neurophysiology breakthroughs. First, behavioural experiments in children provided convincing evidence to set around the 4th year from birth the acquisition of the ability to “pass” the ‘false-belief task’ (cf. Wimmer and Perner, 1983), in which an agent is required to represent another agent’s experience and perspective for succeeding. The discovery of a potential ontogenetic behavioural marker for the development of humans’ (apparently) unique ability to represent other agents’ subjective beliefs, known as ‘Theory of Mind’ (ToM) (cf. Premack and Woodruff, 1978; Dennett, 1987), quickly set a gold standard for what, to many, constituted the core of social cognition: the ability to perform ‘social inferences’, that is representing others as agents with their own mental states, knowledge, and perspective, and to use these representations to frame causal relationship among internal states and displayed behaviour. With the advent of non-invasive neuroimaging techniques like fMRI, researchers could repeatedly test participants during false-belief or intention-attribution tasks, revealing specific brain regions such as the dorsomedial prefrontal cortex (dmPFC) and temporoparietal junction (TPJ) that were active during these tasks (Saxe and Powell, 2006; Frith & Frith, 2006).

At the same time, comparative evidence from non-human primates began to highlight potential correlates and precursors of this ability and its connection with other brain systems. First, studies on the evolution of the central nervous system in vertebrates highlighted a co-linearity between increased neocortex development and a greater number of long-term relationships with other conspecifics, i.e., social group size, peaking in primates (cf. Dunbar, 1998). To explain this correlation, it was proposed (Byrne and Whiten, 1988; Dunbar, 2003; Dunbar and Schulz, 2007) that cognitive demands derived from managing long-term bondings in big groups favoured the selection and development of neurobiological substrates for dealing with the complexity and uncertainty of the primates' social bonds. Supporting this idea, neurophysiological findings in the temporal cortex of macaques reported single neurons' selective responses to complex social stimuli such as faces, bodily movements, and goal-directed actions (see Emery and Amaral, 2000 and Jellema and Perrett, 2005 for an overview). Notably, this was taken to suggest that specific information processing in the primates' brain was devoted to the tracking of goal-oriented and communicative overt bodily behavior. More specifically, it was suggested that these neuronal representations might support the capacity to reconstruct conspecifics' internal intentions and dispositions (Brothers, 1990).

The discovery in 1992 of similar neuronal responses in macaques' Mirror Neurons (MNs), a class of premotor neurons active during both the execution and perception of goal-oriented actions (Di Pellegrino et al., 1992), added a further essential piece, highlighting the involvement of systems devoted to the control of self-related bodily motor acts during the observation of others' behavior. A major insight derived from this discovery was that others' behavior is not only processed in purely sensory or metacognitive terms but appears to involve resources from the covert activity of body-monitoring and bodily-control neuronal systems (see Gallese, 2001, 2003; Keysers and Gazzola 2006). Supporting this idea, in the last 30 years several key structures involved in primarily self-related bodily processes have been found to play a role in social perception, such as the amygdala and insula, determining affective and emotional recognition deficits when damaged (Leigh et al. 2013; Boucher et al. 2015); the anterior cingulate cortex, involved in both encoding others' pain (Lamm, Decety, and Singer, 2011; Jauniaux et al., 2019; Keysers et al., 2022) and strategic decision-making integrating emotional and economic aspects (Chang, Gariépy, and Platt, 2013); parieto-frontal visuomotor circuits, like the human Mirror Neuron System (MNS), active during the observation of others' actions and involved in interpersonal action coordination (Rizzolatti and Craighero 2004; Bonini and Ferrari 2011); finally, somatosensory regions, involved in the modulation of prosocial behavior (Keysers, Kaas, and Gazzola, 2010; Gallese and Ebisch, 2013).

Despite these developments, a major outcome of the early 'Social Brian' project has been a significant and hardly conciliable fracture in the current view of how other agents' are represented in the brain. In particular, the received view maintains a fundamental distinction between a 'high-level' and a 'low-level' social cognition (cf. Shamay-Tsoory, 2011; Preckel, Kanske, and Singer, 2018; Alcalà-López et al., 2019; Frith and Frith, 2021), with the former indicating metacognitive processes for belief attributions, and the latter related to the processing of emotional and bodily features of other agents, possibly involved in affective empathy or forms of motor contagion (see De Waal and Preston 2017).

While this dualistic framework of the human 'Social Brain' is often tacitly assumed as a proper depiction of the computations and neural substrates involved in social cognition, today, almost 30 years later, there are several reasons to regard such a view as problematic and, ultimately, with inherent limitations. First, it has not met the initial promise of providing a phylogenetic account of the development of social skills, as 'high-level' belief attribution is mostly studied in humans through specific tasks (e.g., 'false-belief' tasks), offering poor comparative resources to understand this ability and its neural correlates in non-verbal animals. Secondly, despite its tacit acceptance, ToM-based explanation of humans' social capacities has encountered widespread requests for methodological, taxonomical and conceptual clarity from researchers and scholars within diverse fields of the cognitive sciences, leaving the ecological status of ToM research in constant questioning. Finally, by assuming ToM-like 'social inferencing' as the basic model for testing social capacities in both humans and animals, the received view has not offered valid tools to correctly assess the relevance and functional role of embodied processes, shared among species, in underpinning fundamental social skills like empathy, prosocial behavior, and adaptive cooperative or competitive behavior.

In the next sections, I will discuss these major limitations by showing how accrued data in the last 10 years is pushing for revising the dichotomization of social cognition in abstract mentalization and sensorimotor encoding of others' behavior, together with its received anatomo-functional view. Moreover, I will show how the study of the 'Social Brain' is transitioning from its initial status as a science of 'social inferencing' to that of skilful interaction management. In particular, I will discuss the relevance of adopting a different theoretical model to frame social computations based on 'second-person' approaches in neuroscience, and will show how a growing body of literature is highlighting the involvement of traditionally regarded as either strictly ToM-related or sensorimotor networks in both 'high' and 'low' level information processing and behavioural control.

1.2. Flaws in the 'dualistic' social brain

Since the pivotal study of Wimmer and Perner on the 'false-belief' tasks, it has been proposed that the core capacity of attributing beliefs to other agents, also called '*mentalising*' (cf. Quesque et al., 2024), represents a core psychological function. Fostered by evidence of impaired false-belief attribution in psychopathologies like autism (cf. Baron-Cohen, Leslie, and Frith, 1985; Perner et al., 1989), attempts to isolate a neurological substrate for this skill have heavily relied on fMRI recording to evaluate brain regions active during diverse tasks requiring attributions of a range of diverse mental states like intentions, emotional states, and beliefs.

Initial evidence highlighted several regions, like the orbital, ventral, and dorsal parts of the mesial PFC, the TPJ, the Superior Temporal Sulcus (STS), the Precuneus, and the temporal poles (cf. Gallagher and Frith, 2003; Amodio and Frith, 2006; Overwalle, 2009). However, meta-analyses which considered the diverse methodologies used to measure belief attribution evidenced the mesial PFC (in particular, its dorsal part) and the TPJ as "core regions" (see Figure 1.1) of a potential mentalizing (MENTA) network surrounded by peripheral regions spanning frontal, temporal, and parietal lobes involved at diverse degrees in different tasks (Carrington Bailey 2009; Schurz et al., 2014).

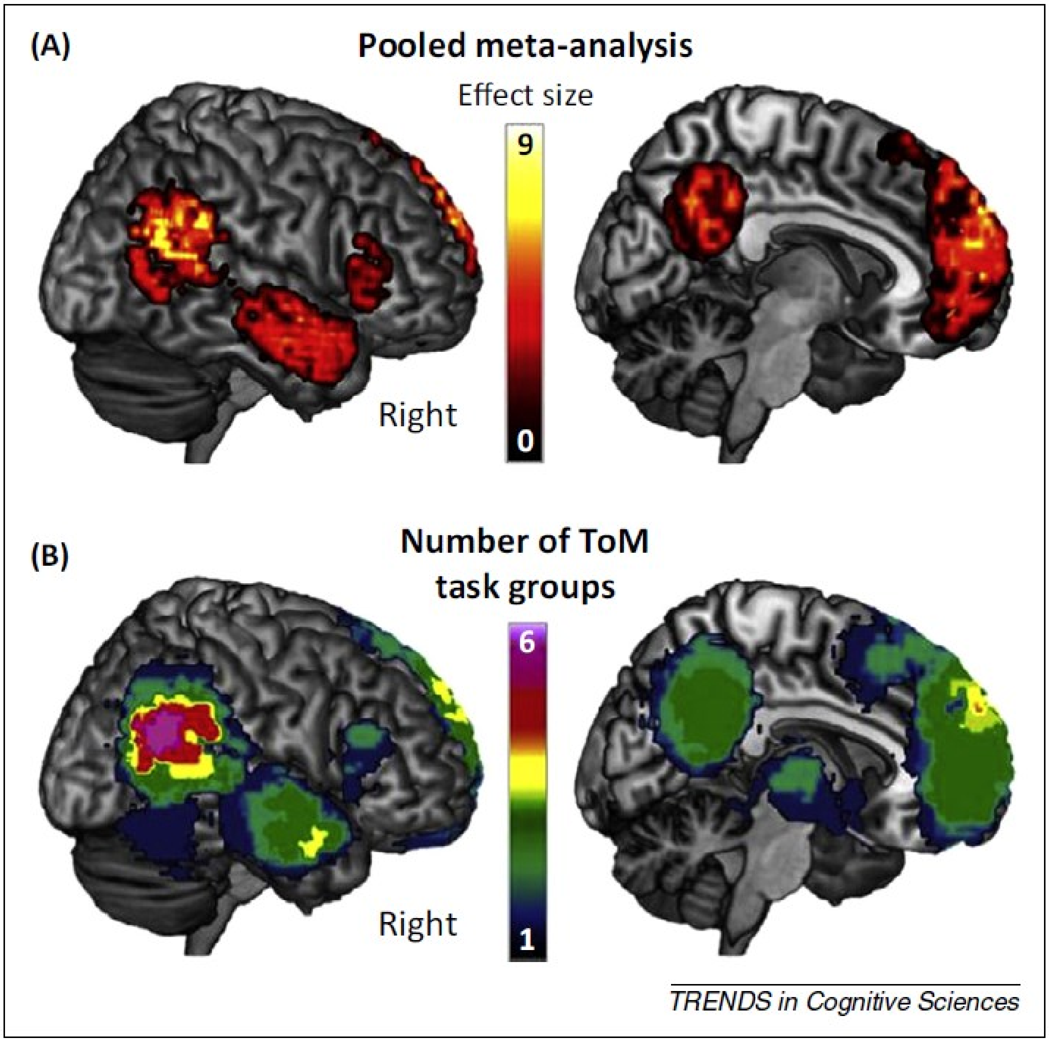

Figure 1.1 | 'Core' regions of the MENTA network. Activation maps the meta-analysis of Schultz et al., 2014. (A) Meta-analysis results pooling 73 neuroimaging studies employing different tasks to measure ToM skills. (B) Sum of results from six independent meta-analyses conducted for task groups. The color map indexes the number of the tasks that reliably produce activation at a given voxel. *Figure from Schaafsma et al., 2015.*

The detection of a core network active transversely in tasks requiring some kind of mental state attribution seems prima facie to favor the early hypothesis of a ToM module in the human brain (Leslie, Friedman, and German, 2004). However, the accrued functional data is counterbalanced by a severe lack of causal evidence from studies in lesions. For example, while initial evidence demonstrated a correlation between ToM abilities and lesions in the bilateral mesial frontal cortices (Rowe et al., 2001) and TPJ (Samson et al., 2004), further assessments strongly contradicted those initial findings. For example, Bird et al. (2004) demonstrated the poor reliability of the cohort and methodologies used to isolate brain damage in the frontal cortices in initial studies and reported the eloquent case of a patient with vast bilateral mesial frontal and temporal regions displaying no deficits in classic ToM measurement. Moreover, brain injuries involving the mesial PFC usually have vast effects beyond ToM capacities, often affecting self-related processes related to personal evaluation (McDonald and Genova, 2021) and emotion regulation (Maggio et al., 2022). Similarly, a lesion-mapping meta-analysis revealed no consistent association between the TPJ and belief attributions (Cohen-Zimerman et al., 2021). Finally, strong evidence has been shown for poor performances in ToM tasks and regions outside the core networks evidenced by fMRI studies, like the dorsolateral PFC (Jenkins et al., 2014; Corradi-Dell’Acqua et al., 2020) and eminently sensorimotor structures such as the Inferior Parietal Lobule (IPL), the Middle Frontal Gyrus, and the Cerebellum (Cohen-Zimerman et al., 2021; Beuriat et al., 2022).

While these data speak against the initial hypothesis of a ‘belief attribution’ module, it emphasizes the highly distributed processing of others’ mental states. Moreover, it hints at the link between ToM and self-related cognition. Indeed, it has been noted that regions of the MENTA networks, especially the dmPFC, are also implied in the processing of self-related emotional and autobiographical information (Mitchell, Banaji, and Macrae, 2005; Spreng, Mar, and Kim, 2009; Liebermann et al., 2019). Moreover, MENTA regions fundamentally overlap with another network, the so-called ‘Default-Mode Network’ (DMN), implied in introjected attention and self-reflection (see Vogeley, 2017, and Yesurun, Nguyen, and Hasson, 2021, for an overview). The “blurred boundaries” of mentalizing capacities are also testified by robust functional data which reported the involvement of regions from the sensorimotor regions and the Mirror Neuron System (MNS) in belief and emotional states attribution (Thye et al. 2018; Schmidt et al., 2021; Boccadoro et al., 2019).

Establishing the existence of an independent mentalizing process in the brain becomes even more challenging when considering other experimental paradigms commonly used to measure this capacity, such as emotion recognition and intention recognition (or prediction) during tasks like story-listening or exposure to visual stimuli depicting interactions between agents. Indeed, when thoroughly decomposing these diverse measurements, meta-analyses on fMRI data reported the broad involvement of areas related to affective processing, multimodal association, and sensorimotor processing (Schurtz et al., 2014; Schurtz et al., 2021; Maliske 2023). Thus, recurrent themes in the study of ToM abilities have become those of properly outlining the different components involved in mental states attribution (cf. Schfaasma et al., 2015; Molapour et al., 2021) and achieving taxonomical and methodological clarity (cf., Quesque and Rossetti, 2020; Quesque et al., 2024).

While the idea that mental state attribution is not a monolithic and modular process has found broad consensus, the exact weight and relevance of putative 'high-level' components of ToM are still a matter of debate. In particular, the complex picture that has emerged from studies in humans has pushed many to question the validity of the construct of 'belief attribution' from both an operational and a conceptual point of view. Early critical considerations emphasized that the original construct together with its main methodological assessment, i.e., the 'false-belief task', cover more basic processes required for the ability to attribute mental states, like inhibiting self-centred perspective (Apperly, Samson, and Humphreys, 2005), separating information about the self and other (Corbetta, Patel, and Shulman, 2008), and simulating others' perspective and mental states (Waytz and Mitchell 2011; Mitchell and Philips, 2015).

Lastly, the 'false-belief task' in its classic form presents a crucial limitation in relying on verbal reports from human participants. For this reason, it has been noted that such a paradigm offers very poor comparative resources for understanding social behavior in both humans and other animals (cf. Emery and Clayton, 2009) and prevents an evolutionarily grounded account of the emergence of 'high-level' mentalizing capacities in the brain (cf. Gallese, 2007). Many scholars have instead argued in favor of more behaviorally sound measurements and for non-verbal assessment of 'false-belief' attribution to assess sensorimotor precursor of this capacity. Of particular interest in this regard are the abilities to engage in joint attention and processing other people's gaze and facial expression, as it is known that deficits in these skills often correlate with deficits in ToM, especially in autism (Stone and Gerrans, 2006). Crucially, as noted above, studies employing gaze-tracking have demonstrated behavioral markers of false-belief understanding in children below the canonical 4th year of age (already within the 2nd year, cf. Scott, 2017, for an overview) and in non-human primates (cf. Ferrari et al., 2000; Rochat et al., 2008; Krupenye 2016: Dureux et al., 2023). Interestingly, the involvement of the dmPFC in this skill has been highlighted by comparative studies exploring attention monitoring in macaques (Lanzilotto et al., 2017; Dal Monte et al., 2022) and humans (see Pfeiffer et al., 2013 and Hamilton, 2016, for an overview), together with the demonstration that chemical inhibition of this area impairs macaques' ability to anticipate humans' behavior in false-belief scenarios (Hayashi et al., 2020). Thus, it has been proposed that attention monitoring and gaze coordination (see Figure 1.2) might be key phylogenetic precursors of explicit mentalizing abilities (cf. Freiwald, 2020).

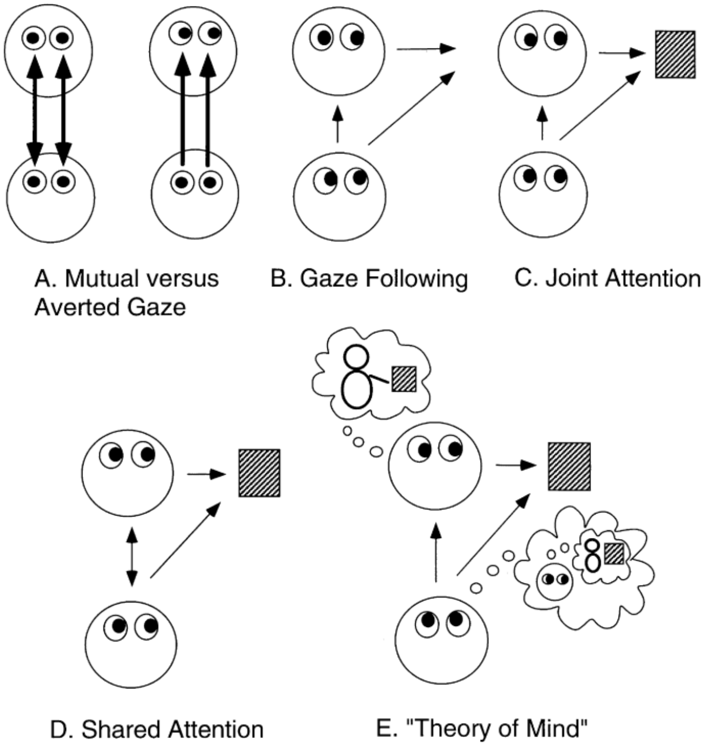

Figure 1.2 | Gaze monitoring as a scaffold for belief attribution skills. The figure represents a progressive model for the development of ToM skills, starting from simple averted-mutual gaze processing to full-fledged "mental reasoning". As reported by Emery, 2000, "Gaze direction provides a number of potential social cues which may be utilized by an individual to learn about the external (other individuals, objects, events, etc.) or internal (emotional and intentional) states". It is suggested that 'Mental state attribution' "uses a combination of the previous A-D attentional process" together with other cognitive process related to cognitive strategies, empathy, and the subject's expertise. *Figure from Emery, 2000.*

Notably, a role in the processing of other people's gaze and attention has been also attributed to the other 'core' MENTA region, the TPJ. While it is well-known that lesions in this region result in attentional deficits (cf. Vallar and Calzolari, 2018), studies employing causal approaches like transcranial magnetic stimulation (TMS) have demonstrated its causal role in both implicit (Bardi, Six, and Brass 2016) and explicit (Martin et al., 2019; Bio et al., 2022) processing of the visual perspective of other agents, which some suggest being related to TPJ's role in reconstructing attentional orientation (cf., Schurz et al., 2015; Guterstam et al., 2021). Crucially, reconstructing another agent's perspective requires accurately distinguishing, or inhibiting, one's own perspective from that of the other. In this context, it is important to highlight that although the TPJ is both anatomically and functionally a highly heterogeneous area (cf. Graziano and Igelstrom 2017; Patel, Sestieri, and Corbetta, 2019), it plays a key role in sensorimotor integration (Carter and Huettel 2013) of visual, motor, and somatosensory signals. This function is not only relevant for oculomotor control but also for constructing internal models of the body (cf. Decety et al., 2016) and its position in space (Wang et al., 2016; Martin et al., 2020). Thus, it has been proposed that the involvement of this region in social cognition might be critical for Self-Other distinction (cf. Lamm et al., 2016; Quesque and Brass, 2019). Indeed, several fMRI meta-analyses confirm TPJ's activity during the processing of conflictual mental representations regarding self and other's perspectives, action, or beliefs (Arioli et al., 2019; Deschrijver and Palmer, 2020; Bang et al., 2022). Interestingly, both the TPJ and the dmPFC have been shown to play a role in modulating the relevance of self-related information when evaluating other people's mental states, as highlighted by TMS studies exploring the Self-Other "mergence" phenomenon (Wittmann et al., 2021; Sun et al., 2023).

Collectively, the accrued evidence pushes to re-think both the major components involved in mapping other mental states and the functional role of areas of the MENTA network, highlighting their crucial involvement in sensorimotor processes for gaze coordination and multimodal processing of self- and other-related information. In the next section, I will discuss how the other major 'Social Brain' network, i.e., the Mirror Neuron System (MNS), is undergoing a revision and evolution of its original framework, prompting a redefinition of its functional properties and an expanded role in social cognition.

1.3. The pragmatic Mirror Mechanism

In October 1992, it was published the first description of a special class of cells in the monkey ventral premotor cortex exhibiting the fascinating property of discharging both when the animal performed a goal-directed hand movement (e.g. grasping a food morsel) and when it observed an experimenter (Di Pellegrino et al., 1992) or another monkey (Rizzolatti et al., 1996), performing the same or a similar goal-directed manual action. A few years later, these cells were named “mirror neurons” (MNs) (Gallese et al., 1996), to emphasize the capacity of the motor system to “reflect” other’s observed actions by recruiting the same neuronal substrates involved in action planning and execution.

Thirty years after their discovery, a large body of evidence has confirmed the involvement of motor regions in the processing of a wide range of other-related bodily displays, including motor actions, whole-body movements, facial expressions, and vocalization (Naish et al. 2014; Hamzei et al., 2015; Hardwick et al., 2018; Borgomaneri et al., 2020; Zhang et al., 2021). A comprehensive picture of the brain regions in which action-related MNs have been found in primates is shown in figure (Figure 1.3B) and includes, in addition to the ventral premotor cortex, the other premotor and primary motor areas, inferior parietal regions, and possibly the lateral prefrontal cortex. Moreover, a large body of evidence indicates that human brain regions involved in the control and regulation of emotions become active also when witnessing emotional displays of others. Studies using a variety of approaches have provided robust evidence that a network (Figure 1.3B) including the amygdala (Wang et al., 2017), the insula (Woolley et al., 2015), and the cingulate cortex (Caruana et al., 2020) plays a role in both the expression, experience and perception of facial and bodily emotional displays (cf. de Gelder et al., 2015). These advances provided robust evidence regarding the essential feature of the mirror mechanism: other-related information is mapped onto the neural substrates primarily involved in the encoding of self-related processes in an extended network of brain areas (Gallese, 2014; Bonini et al., 2017; Bruni et al., 2018; Albertini et al., 2017) that encompass multiple domains – from motor actions, sensations, and emotions to decisions and spatial representations – and multiple animal species (Figure 1.3A).

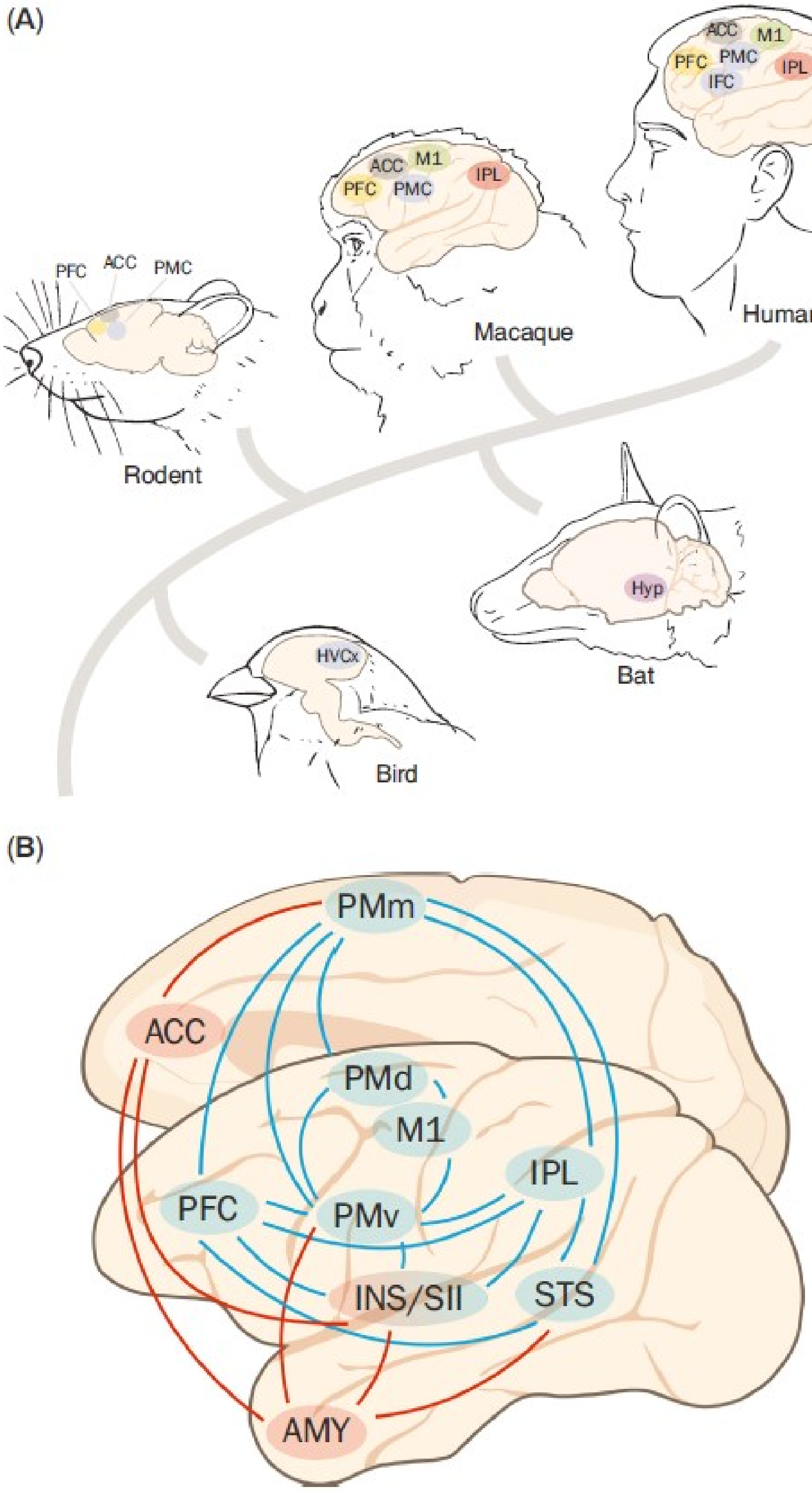

Figure 1.3 | Species and brain areas with evidence of mirror neurons, and the mirror networks in the primate brain. (**A**) Mirror neuron regions across species and brain areas. ACC, anterior cingulate cortex; HVCx, caudal nucleus of the ventral hyperstriatum projecting to area X; Hyp, hippocampus; IFC, inferior frontal cortex; IPL, inferior parietal lobule; M1, primary motor cortex; PFC, prefrontal cortex; PMC, premotor cortex. The same color code for different areas suggests possible homologies across species. (**B**) Organization of primate sensorimotor (light blue) and emotional (red) MN networks based on macaque neuroanatomical studies on areas in which neurons with mirror

properties have been found. The MN sensorimotor network includes, beyond the ventral premotor cortex, the inferior parietal lobule (Fogassi et al., 2005; Bonini et al., 2010), particularly area AIP (Maeda et al., 2015; Lanzilotto et al., 2019); the dorsal (Cisek and Kalaska, 2004; Papadourakis and Raos, 2017) and mesial (Mukamel et al., 2010; Yoshida et al., 2011; Livi et al., 2019) premotor cortex; the primary motor cortex (Dushanova and Donoghue 2010; Vigneswaran et al., 2013); and the secondary somatosensory cortex (Hihara et al., 2015). Furthermore, data from imaging in macaques (Nelissen et al., 2011) and anatomical tracing (Borra et al., 2011; Gerbella et al., 2013) suggest the presence of neurons with mirror properties in the dorsolateral prefrontal cortex. *Figure from Bonini et al., 2022.*

The 'mirror' property of monkey premotor neurons, recorded through electrophysiological techniques, was the kickstarter to the study of the role of the motor system in social cognition (cf. Gallese, 2001, 2003). Several works through the years have produced a progressive expansion of the knowledge about the functional profiles of MNs, highlighting a more complex picture than the one initially portrayed. They demonstrated the existence of different types of mirror neurons, from interneurons to cortico-spinal and cortico-striatal cells, exhibiting different functional properties in response to action observation, possibly related to diverse functions such as motor simulation, action inhibition, and motor learning (see Bonini et al., 2022). Moreover, agent-specific cells encoding others' actions are recruited along with 'classic' mirror neurons displaying 'shared' coding of self and other actions (Ferrucci et al., 2022), with animal data indicating that interplay of these cells with self-related neurons to produce adaptive coordination during interactions (Kingsbury et al., 2019).

Following years of debate on the origin and functions of MNs (see Cook et al., 2014), researchers have finally reached a basic agreement regarding the involvement of MN brain regions in the perception of motor actions, human speech discrimination, and imitative responses (cf. Heyes and Catmur, 2021). The current research directions aim mainly to determine what features of observed actions are primarily (or specifically) processed by the observer's motor system and why (Kemmerer et al., 2021). The mainstream view on the mirror mechanisms classically focused on agent-shared representations as a ground for social perception. However, a new framework is proposing that a hallmark function of the mirror mechanisms, phylogenetically preserved across vertebrate species, appears to be also related to social interaction, besides social perception (cf. Bonini et al., 2023).

Areas subserving action planning and execution do play a role in others' action perception and prediction. Lesion-symptom-mapping studies in human patients have shown that impairments in the perceptual judgments regarding others' observed actions typically occur in association with lesions involving the left inferior frontal, inferior parietal, and middle-superior temporal cortex (Urgesi et al., 2014). Moreover, apraxic patients, whose ability to perform gestures is impaired, also exhibit impairments in recognition of familiar gestures more marked than that of non-apraxic patients, and the greater recognition deficits are associated with the involvement of the opercular and triangularis portions of the left inferior frontal gyrus (Pazzaglia et al., 2008). Additional causal evidence of the involvement of the motor system in recognizing others' actions comes from continuous theta-burst stimulation (cTBS) experiments: when applied over the hand and lip areas of healthy humans' left premotor cortex, cTBS produced a double dissociation reducing the participants' accuracy in recognizing pantomimed hand or mouth actions, respectively (Michael et al., 2014). When cTBS was applied over IPL regions whose fMRI activity could predict the intention behind reach-to-grasp actions, subjects were impaired in their capacity to exploit the readout of hand kinematics for the purpose of attributing intentions to others' actions (Patri et al., 2020). Finally, a recent ultra-high-field fMRI study demonstrated that the observation of complex everyday action sequences in their natural order triggers an increased information flow from frontal premotor output layers to parietal input layers; this did not occur when the very same actions were randomly arranged in a sequence that hindered predictions (Cerliani et al., 2022). This finding provides anatomo-functional support for the hypothesis that frontal areas feed expected perceptual outcomes of others' actions back to parietal areas, which in turn integrate incoming sensory signals about the ongoing observed action in the form of a prediction error (Friston et al., 2011).

According to the recently proposed 'Social Affordance Framework' (Figure 1.4), these perceptual and predictive functions of the human motor system may be primarily linked with its evolutionarily conserved role in the planning and coordination of behavioral responses to others' actions; not surprisingly, one of the most widely accepted roles of the human MN mechanism is its mediation of imitative phenomena. However, when subjects witness another's action, they have a variety of options that are known to recruit the main nodes of the MNS: 1) faithfully imitating or emulating the observed action (Charpentier et al., 2020), 2) avoiding doing so (Darda et al., 2019), or 3) executing a complementary (Newman-Norlund et al., 2007; Sacheli et al., 2015) or alternative (Cross et al., 2013) action.

But how are others' actions mapped onto one's own motor system to achieve motor coordination? It is known that observing others' actions triggers subthreshold muscular responses, detectable through TMS-induced Motor-Evoked Potentials (MEPs) which reflect congruent motoric features of the observed action of both specific (e.g. kinaematics, somatotopy) and general (e.g. goal) features (a phenomenon known as 'motor resonance'; cf. Rizzolatti et al., 1999; Senna et al., 2014; Finisguerra et al., 2015; Hilt et al., 2017). However, evidence has accumulated that these evoked motor responses do not rigidly and stereotypically reflect features of observed actions, but can show specific modulations (in terms of increased or inhibited activity) as a function of many relevant contextual elements, like expectations about the outcome of an action (Craighero et al., 2014; McCabe et al., 2015) or previously learned associative responses and rules (Catmur et al., 2007; Cavallo et al., 2014); subjective features such as knowledge and motor expertise (Amoruso et al. 2014; Markis and Urgesi, 2015; Pedullà et al., 2020): attention (Puglisi et al., 2018; Wright et al., 2018); and current emotional state (Galang et al., 2017; Pool-Goudzwaard et al., 2018). Some studies focusing on the temporal dynamic of these modulations demonstrated the ongoing update of an initial (and less somatotopically organized) motor resonance toward a more specific, contextually modulated motor response which reflects subjects' expertise and contextual constraints requiring the adaptive enhancement or inhibition of the motor response (Barchiesi and Cattaneo, 2013; Amoruso, Finisguerra, and Urgesi, 2016, 2018). Moreover, recent studies are starting to highlight that recruitment of incongruent effectors can happen as fast as congruent ones when these are related to actions affording complementary interactions (Betti et al., 2017), indexing a parallel, pluripotent motor coding of the observed action.

This suggests that mirroring in humans is sensitive to the demands of the action context, and that observed motor configurations are processed and exploited for preparing appropriate actions. Causal manipulations of fronto-parietal MNs areas bolster this view. For example, cTBS

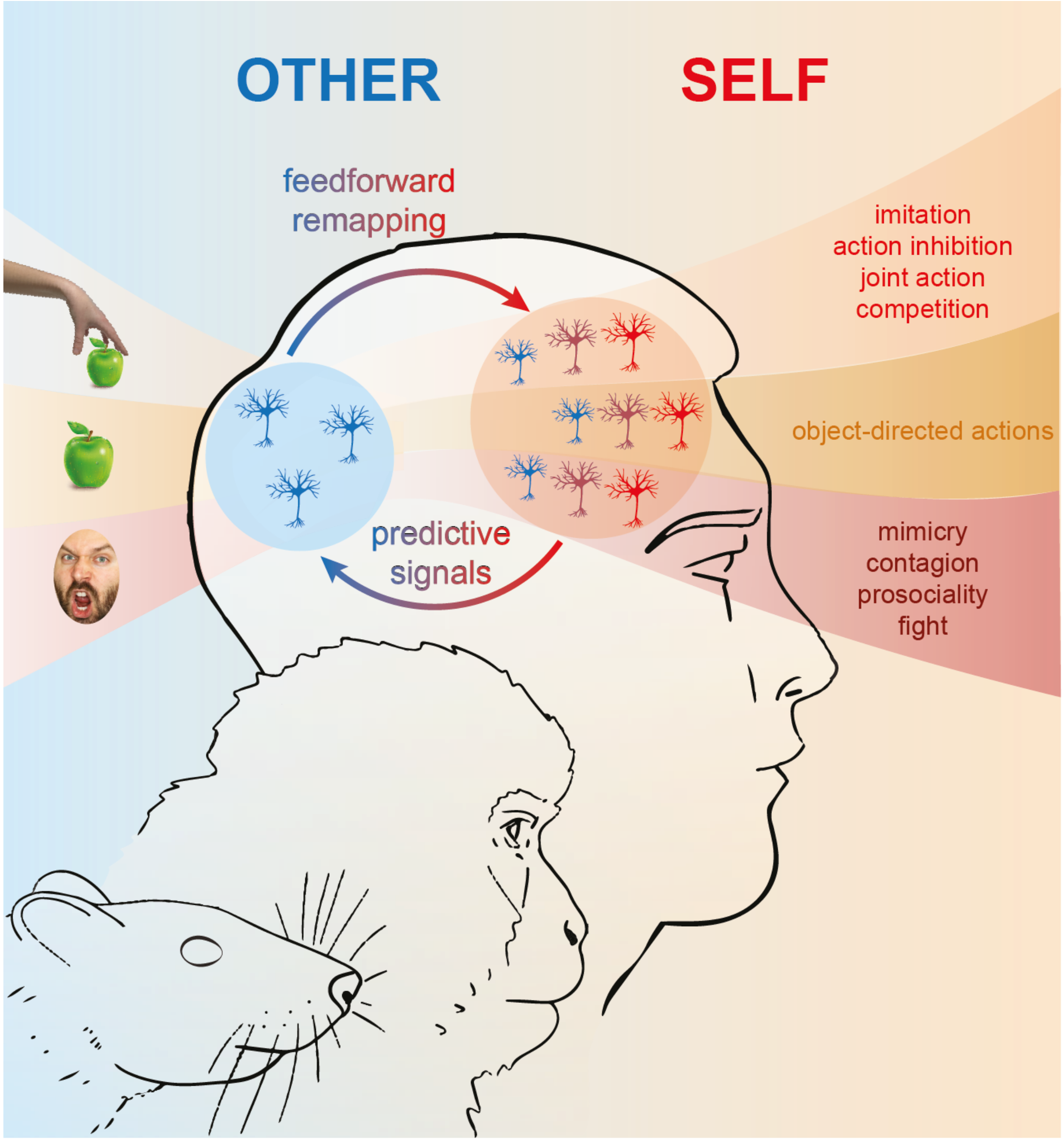

Figure 1.4 | Social perception and social interaction in mammals in the social affordance framework. Information about goal-directed actions of others, real objects, and the facial/bodily expressions of others, is processed along specific visual streams. Feedforward connections with frontal and subcortical motor/visceromotor regions remap this information on a variety of neuronal subpopulation that (1) gradually specify potential classes of motor action, to be possibly selected and executed/released by the observer with the contribution of additional prefrontal/subcortical brain regions; and (2) generate predictive feedback signals to guide the proactive research of information in the environment by the subject, especially when biological motion of others is the focus. Color codes in the figure schematize other-type (blue), self-type (red), and mirror type (purple) neurons. *Figure from Bonini et al., 2023.*

over the aIPS lowers the efficiency in executing both congruent and complementary actions in response to an observed action, while this does not happen if the action to be executed is pre-planned in advance regardless of the kind of match (Era et al., 2018). Interestingly, enhancing the cortical excitability of the IFC through tDCS improves individuals’ ability to control imitative behaviour in a task-dependent way, enhancing the inhibition of imitative gestures when requested while also increasing individuals’ propensity to spontaneously imitate in naturalistic interactions (Hogeveen et al., 2015; Nobusako et al., 2017). Importantly, an fMRI study demonstrated that multiple observed actions can be decoded from the motor cortex BOLD signal (Cracco et al., 2019), suggesting that internal models for the self and others’ actions are processed together within parieto-frontal systems.

Altogether, these data suggest a role for the human MNS in updating the motor response through constant remapping of both perceptually driven and contextually driven action cues. They suggest that social stimuli drive sensorimotor responses whose role is to promote optimal interaction. Moreover, mirror phenomena are not only tied to the demands of social interaction; they participate in the proper monitoring and control of one’s actions while mapping and discriminating those of others, making them a fundamental component of brain mechanisms involved in the coordination of embodied processes and social information.

1.4. From ‘Social Inferencing’ to Interaction Management

As discussed earlier, the traditional literature and debate on social cognition posited high-level and low-level processing of other agents’ representations as neatly separated and subserved by different neural systems. However, the evidence reviewed so far offers a perspective that significantly differs from this 'dualistic view'. On the one hand, beyond being active during mental states attribution, areas like the dmPFC and TPJ appear to be strongly involved in the multimodal integration and management of bodily signals, including the differentiation of self- and other-related bodily perspectives On the other hand, the mirror mechanism is modulated by the subject's relation with the action observed, tied to action features and contextual elements that afford diverse possibilities of interacting with the social environment. Finally, both the MENTA system and the mirror mechanisms appear to be involved in managing the coordination of self-related and other-related representations, hinting at a possibly complementary role in the online updating of internal models of self and others for adaptive behavior.

This expanded view of the functional properties of networks of the ‘Social Brain’ has promoted a progressive shift in how social cognition is conceived and approached. Some scholars have criticized the traditional approach to social cognition as being overly reliant on a “detached”, “passive”, and ultimately “isolated” view of how cognitive systems process the social environment (Gallagher and Hutto, 2008; Schilbach et al., 2013; Tylen et al 2012). According to these criticisms, the original emphasis on understanding others’ minds through an internally resolved process (i.e., ‘social inferencing’) overshadowed the physical and cognitive dynamics that most social interactions in a naturalistic context entail, together with the fundamental effects interacting with others produces on the individual. Real-time social interactions are characterized by complex, dynamic, and non-linear reciprocal relationships (Port and van Gelder, 1995; Thelen and Smith, 1994; Tylen and Allen, 2009), where the perception of socially relevant information triggers (or requires) actions that are, in turn, processed and responded to. Moreover, cooperative interactions involve the ability to build shared representations of common goals at least at a basic level (Gallese, 2003; Bekkering et al., 2009; Hasson et al., 2012). Under an evolutionary lens, this emphasizes sensorimotor coordination among individuals in the physical space as the primary context for the development of intersubjective skills (cf. Cisek 2019; Barrett et al., 2022). Thus, the problem posed by interacting with other agents most closely resembles a form of ‘embodied decision-making’ (Gordon et al., 2021; Viale, Gallagher and Gallese 2023) where encoding potential affordances and outcomes of dynamic interactions require rapid and efficient coding of information about the self, the other, and their joint effect. For this reason, an alternative approach has been called for considering the management and processing of the ongoing interaction, rather than the reconstruction of another agent’s internal state, as the building block of social computations and neural correlates (De Jaegher et al., 2010; Rusch et al., 2020; Dingenmanse et al., 2023).

Adopting this focus on active, contextualized interaction, research has begun focusing on how interactions are represented in the brain. Evidence has shown that single actions and agents are processed as a single unitary representation when they are complementary and interacting. For example, behavioral studies demonstrated a “social chunking” of observed actions in working memory and recall abilities: people's performance in memorising observed individual actions doubled in accuracy when these entailed a potential social interaction (Ding et al., 2017), regardless of asking to focus on task-irrelevant elements like spatiality or semantic features unrelated to actions (Lu et al., 2022). With a different paradigm, Fedorov et al. (2018) demonstrated that individual actions automatically prime participants' perceptions of contingent actions, like taking from giving and catching from throwing. More evidence for unitary coding of interactions comes from an fMRI-guided TMS study which demonstrated that categorization of pictures representing facing dyads is more negatively affected by inversion of facing direction than non-facing dyads, and that the faciliatory effect in coding facing dyads is cancelled when perturbing a previously identified sector of the lateral extrastriate cortex (Gandolfo et al., 2024). Finally, several neuroimaging studies comparing the perception of social interactions against actions which do not entail potential interactions demonstrated that activity from several occipital and temporal areas could be used efficiently to decode the 'social' nature of the actions observed, regardless of the task or specific social context (for an overview, see McMahon and Isik, 2022).

While these data demonstrate that interactions are a form of perceptual "primitive" (whose sensibility is already detectable in infancy, cf. Stahl and Feigenson, 2014; Bosseler et al., 2024), further studies showed that there is more to social processing than just vision. In particular, areas of the 'Social Brain' including both MENTA and MNS regions are robustly shown to encode the perceived sociality of interactions (Varrier and Finn, 2022), with decoding techniques showing that activity patterns from the dmPFC (Wagner et al., 2016) and the TPJ (Walbrin, Downing, and Koldewyn, 2018) can be used to discriminate if an observed interaction has a social nature or not. Evidence from neuroimaging in monkeys (Sliwa and Freiwald, 2017; Cléry et al., 2021) during the observation of conspecifics demonstrated the specific involvement of the dmPFC and stronger activation of premotor sectors with mirror properties in the processing of motor interactions as opposed to simple goal-oriented actions. Moreover, a study showed increased connectivity between these frontal sectors and temporal areas when processing ambiguous social interactions (Ainsworth et al., 2021), possibly hinting at predictive processes. Finally, a recent study (Guidali et al., 2023) demonstrated that MEPs in the hand and the arm of participants viewing grasping actions were stronger for grasping actions involving a partner than individual actions or intransitive actions, and that the evoked motor activity followed a specific temporal pattern involving the initial activation and subsequent inhibition of motor resonance, linked to action control.

These studies mainly focused on the perception of third-party interactions, demonstrating widespread neural selectivity for this kind of stimuli in the brain and differential involvement of motor processes. As discussed before, however, the core idea of the new approach to the study of social cognition is that selectivity to social content is scaffolded by computations developed for managing direct involvement in interaction. In this regard, an expanding corpus of studies adopting 'Second-person' approaches in neuroscience (Gallese, 2014) in which interactive stimuli or paradigms are used to study brain activity in social interactions (cf. Redcay and Schilbach, 2019; Fan et al., 2021), are demonstrating that agent-related and agent-shared representations in the social brain are (inter)action-oriented.

Indeed, the same selectivity in premotor and prefrontal areas found for third-party social interactions has been shown by neuroimaging studies in macaques (Sheperd and Freiwald, 2018) and humans (Schulte-Ruther et al., 2007; Nagels et al., 2015; Trujillo et al., 2020; Begliomini et al., 2017) when observing a same facial expression or a same movement directed toward the observer, signaling potential engagement in interaction. Interactive paradigms demonstrated that BOLD signal from the dmPFC and premotor cortex encodes whether the same grasping action is executed to pass an object to a partner rather than put it into a box (Di Bono et al., 2017), showing that potentially engaging in a joint action modulate motor control by integrating social information. This has been further confirmed by neurophysiological recordings in macaques which demonstrated both shared and agent-specific coding of self and other actions during motor interactions in macaques' dorsal premotor (Ferrari Toniolo et al., 2019) and posterior dorsomesial prefrontal cortices (Falcone et al., 2017). Notably, a further study proved that unidirectional inactivation of information flow from premotor to dorsomesial prefrontal cortices impairs monkeys' ability to employ visual information from the observation of a conspecific's action to adapt their motor response in a cooperative task (Ninomiya et al., 2020), demonstrating that premotor cortices are causally involved in feedforwarding information relevant for adaptive executive control.

A final corpus of evidence highlighting online interaction processing as a core feature of the social brain is found in studies employing hyper-scanning techniques, or “two-brain” paradigms (cf. Shamay-Tsoory et al., 2021; Carollo and Esposito, 2024), in which the real-time reciprocal interactions of a pair or even a group of subjects can be investigated as a single system. Employing dual fMRI scanning, studies demonstrated that motor, somatosensory, and limbic areas of the brains of interactive partners strongly synchronize, i.e., correlates in their pattern of activation, during coordination tasks requiring monitoring the other’s face (Koike et al., 2016; Hirsch et al., 2017; Koike et al., 2019) or actions (Sperduti et al., 2014; Miyata et al., 2021). Similarly, a study which required participants to either share or not biographical information in front of a partner demonstrated higher facial display production and monitoring in the sharing condition, and that this was correlated with stronger activations of the IFG, the dorsal PFC, the IPL and the TPJ, with activity in the right TPJ predictive of the activation in the partners’ dorsolateral PFC (Canigueral et al., 2021). A possible interpretation, based on current knowledge of the mirror mechanism and interbrain synchrony phenomena in animals (Kingsbury et al. 2019; Bonini et al., 2022), is that interbrain synchrony might guide social interaction by means of remapping of other-related information onto neural substrates for self-related control in the brain of Subject 1, whose produced bodily displays subsequently drives other-selective responses in the brain of Subject 2, which finally leads to an adaptive behavioural response of Subject 2 by activating self-related neurons.

Considering the reviewed evidence, the new approach to social cognition is fruitfully reframing computations of the ‘Social Brain’ as devoted to the efficient encoding and processing of social cues to prepare the individual for adaptive interactions. As seen, interactive contexts and stimuli affording engagement represent key drivers of neural activity in MENTA and MNS regions. In particular, ‘Second-person’ social interactions are contexts where information between one's own and others’ behavior requires rapid and efficient prediction, on the one hand, and differentiation and monitoring, on the other. Contrary to the proposed dichotomy between abstract mentalization and sensorimotor encoding of others’ behavior, data pushes to reframe the received dualistic anatomo-functional map of the Social Brain. Classically regarded ToM-specific regions and sensorimotor networks are better understood as part of a distributed processing involving, on the one hand, remapping processes of sensorimotor information for action prediction and preparation and, on the other, Other vs. Self information processing for correct Self-Other distinction and long-term interaction managing.

2. Aim of the current research

As seen, the latest data and new theoretical frameworks are pushing to revise both the methodology and the conceptual taxonomy traditionally employed to address social cognition. In particular, new trends in social neuroscience underscore the necessity of understanding the behavioral and neural correlates linked to adaptive control of intersubjective physical interactions to guide the investigation of the functional roles of key brain systems traditionally related to processing other agents.

Therefore, the current research aims at extending previous knowledge about the cognitive processes involved during the observation of other agents' goal-directed actions. In particular, the goal is to investigate if and how the pragmatic relevance of a social context, i.e., its potentiality for involvement in direct interaction, is a fundamental feature driving the perception and processing of other agents. Data from existing literature support the perceptual saliency of actions affording potential engagement, and studies employing neurophysiological measurements demonstrated that either direct or potential engagement in interpersonal interaction determines both the different involvement of neural resources and different behavioral patterns related to the decoding of others' intentions, providing evidence that detection of social intentions in observed bodily displays has a strong impact in the processing of others' actions. However, a thorough investigation of how engagement is coded from observed actions is still lacking, and different socially relevant features (i.e., communication, gaze behavior, context, action goal, etc.) are often conflated due to the dynamic nature of naturalistic interactions.

In the current study, we investigated engagement processing during the observation of a basic motor act extensively studied in the literature on action observation, that is a grasping action. We first studied behavioral correlates of social intention in the execution of grasping actions and then assessed their saliency and specificity during observation. Then, we assessed what features of the observed action played specific roles in modulating neural activity related to the perception of potential engagement. In line with the idea that basic sensorimotor cognition is the fundamental scaffold for social cognition, we investigated the functional involvement of brain regions of the 'Social Brain' in different processes underlying the encoding and control of interpersonal motor interaction, including the encoding of the social nature of an action from its motor goal, the encoding of first-person involvement in an observed action, and the role of basic bodily cues (e.g., the visibility of gaze).

3. Study 1 (Behavioral): Reading Out Bodily Cues to Predict Interaction[1]

3.1. Introduction

From birth, and long before we are proficient at articulating and expressing our thoughts linguistically, motor coordination of bodily movements, facial expressions, and eye gaze represent major means for learning, communicating, and achieving common goals with others. Indeed, among types of social interactions, interpersonal motor interactions are a substantial part of our daily engagement with others (Frith and Frith, 2012; Galef and Laland, 2005) and represent a primary form of social interaction widespread among animals (Duguid and Melis, 2020; Gallese, 2014; Kareklas and Oliveira, 2024; Knoblich and Sebanz, 2008; Tomasello, 2020). Importantly, during such interactions, others' bodily displays are salient stimuli which serve as powerful social cues providing information about others' intentions (Patel et al., 2012; Torricelli et al., 2023) and internal states (De Waal and Preston, 2017; Gallese, 2006) affording for adaptive interpersonal coordination. Proper decoding of such cues can drive crucial social phenomena like sensorimotor synchronization, which is important for learning (Ramsey et al., 2021) and social affiliation (Hove and Risen, 2009; Koul et al., 2023), as well as for the correct prediction of others' behavior in both cooperative or conflictual contexts (Georgiou et al., 2007; Manera et al., 2011). Notably, readouts of others' behaviour and the proper motor response preparation and execution, happen in a timescale ranging from hundreds of milliseconds to a few seconds. This means that individuals need to rapidly read and interpret their partners' actions to prepare and enact a fitting motor response. How is such an efficient action prediction during interaction achieved in daily life?

A major line of research in the last three decades has focused on understanding the processing of observed actions performed by others (Bonini et al., 2022; Torricelli et al., 2023). Watching other people's bodily displays is known to activate a broad network of brain sensorimotor areas, including motor areas related to motor control (Hardwick et al., 2018;

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[1] This study and its supplementary materials are available as preprint at the link: https://doi.org/10.31234/osf.io/kgmyn

Rizzolatti and Sinigaglia, 2016), and to impact several physiological and behavioral responses related to motor preparation (see motor resonance phenomena (Agosta et al., 2016; Amoruso and Finisguerra, 2019; Avanzini et al., 2012), suggesting a tight functional link between the perception and expression of bodily actions. This fostered early speculation that individuals' knowledge related to the contextual control of biological motion could be redeployed to aid the interpretation and prediction of others' actions (Fagg and Arbib, 1998; Jeannerod and Jacob, 2005; Kilner et al., 2007).

In this regard, long-standing research on human fine motor skills related to hand and upper limb movements has highlighted the existence of relevant statistical regularities in motor actions tied to biomechanical constraints of motor control. Among these regularities, referred to as 'kinematic invariants', are the characteristic bell-shaped velocity profile and end-effector trajectory of motion displayed by goal-oriented movements of the arm toward objects (Shadmehr and Wise, 2005; Todorov and Jordan, 2002). Proper control of hand configuration is another crucial feature of humans' manipulative skills, as reflected in preparatory phenomena for adapting the grasping configuration to the shape, texture, and size of the object of interest (Jeannerod, 1988a).

Importantly, these kinematic modulations are substantially influenced by an agent's intentions and can be used to adapt common actions such as reaching and grasping to achieve specific goals (Egmose and Køppe, 2018; Jeannerod et al., 1995). For example, specific modulations in reaching speed, grip configuration, and final positioning of the hand on the object are strongly dependent on the final use or placement of an object we need to reach for and grasp (Ansuini et al., 2008, 2015; Fogassi et al., 2005; Marteniuk et al., 1987; Rosenbaum et al., 2006). Crucially, similar modulations of movement production have been found for socially oriented actions, where detectable kinematic variations afford cues to an observer to discern an observed agent's motor intentions (Becchio et al., 2008a; Di Bono et al., 2017; Ferri et al., 2010).

Indeed, some evidence (Cavallo et al., 2016; De Marco et al., 2020; Manera et al., 2011; McEllin et al., 2018; Sartori et al., 2011) suggests that people can discriminate social intentions based on watching arm and hand movements (but see Naish et al., 2013). Moreover, studies demonstrated that viewing the same arm movement executed with different intents modulates reaction times related to motor preparation (Quesque et al., 2016; Quesque and Coello, 2015; Soriano et al., 2018) and autonomic responses (Quesque et al., 2019), suggesting early sensorimotor processing of others' movements. Neural patterns in parietal and frontal premotor areas hosting mirror neurons involved in the execution and observation of actions (Gallese et al., 1996; Rizzolatti et al., 2001) significantly modulate in response to the same motor action executed with different final intentions (Becchio et al., 2012; Bonini et al., 2012; Koul et al., 2018; Trujillo et al., 2020), highlighting the influence of perceived kinematic features on the recruitment of motor resources linked to predictive processes (cf., Amoruso and Urgesi, 2016; Cerliani et al., 2022; Chen et al., 2020; Craighero et al., 2014; Kilner et al., 2007; Schippers and Keysers, 2011; Umiltà et al., 2001).

The impact of the social context on these anticipatory processes is further testified by studies which investigated the well-known visuomotor interference effect on action preparation, in which acting is either facilitated or hindered by the observation of congruent or incongruent actions, respectively (Brass et al., 2009; Cross and Iacoboni, 2014; Era et al., 2020; Forbes and Hamilton, 2017). Importantly, this effect is either reduced or even reversed when people are in an interactive context where they have to exploit a partner's movements to prepare a complementary action (Rocca et al., 2023; Sacheli et al., 2018; Sartori et al., 2009).

Action prediction and preparation during interpersonal motor interaction also depend on the observer's reliance on multiple bodily cues. For example, the gaze direction can reveal crucial information about an action goal by providing indications of where and to what attention is being directed (Bukowski et al., 2015; Driver et al., 1999; Frischen et al., 2007), together with signalling potential interactions (Bekkali et al., 2022; Betti et al., 2019; Prinsen and Alaerts, 2019). Observing an agent simply staring at an object elicits behavioral and neural responses similar to those that occur when performing a grasping action towards the object (Castiello, 2003; Flanagan and Johansson, 2003), suggesting that observing another person's gaze in an interactive context can elicit a representation of the upcoming action (Ramsey et al., 2012). Indeed, the gaze direction of the observed agent has been found to modulate the activity of neurons in premotor areas (Coudé et al., 2016; Maranesi et al., 2013) and visual neurons selective to biological motion (Jellema et al., 2000), demonstrating that action and gaze are closely linked at the neural level.

To better understand the interplay of such bodily cues in action prediction, some studies employed spatial occlusion procedures of action stimuli to investigate the relative impact of different effectors. Sartori et al., (2011) focused on the arm and the face finding that while participants could discriminate kinematic differences in arm movements related to different intentions, occluding the face area in a video showing a reach-to-grasp action had a deleterious effect on fine social intention decoding. In another study, Vaziri-Pashkam et al. 2017) demonstrated that both the face and the arms can provide subtle preparatory cues to an observer that allow for a faster reaction to a partner's movement than to moving dots used as control.

Altogether, these data suggest that early bodily cues such as those expressed by action kinematics or gaze movements significantly influence the beholder's behaviour. However, the features of others' actions and social cues critical for signalling or decoding potential interactions remain not fully understood. Moreover, the impact on predictive abilities related to potential direct involvement in interaction has yet to be systematically investigated.

To address this, we adopted a comprehensive approach and conducted three experiments focusing on the execution and observation of a simple motor act, i.e., grasping an object, with an individualistic goal (grasp to place) vs. a social goal (grasp to pass). In the first experiment (Action Execution task), we investigated changes in spatiotemporal features of the reach-to-grasp phase of both actions by measuring hand kinematics. In line with the previous literature, we expected that the kinematics of the initial phase of the movement (which is shared) would significantly differ depending on the social nature of the action. In particular, based on previous studies (Ansuini et al., 2008; Becchio et al., 2008b; Marteniuk et al., 1987), it can be hypothesized that the major component capable of discriminating between the two conditions is that of reaching, with action executed with a social intent displaying lower speed, deceleration, and higher duration overall.

In the second experiment (Action Observation 1), we aimed to probe the perceptual potential in the kinematic features of actions recorded from the first experiment. We assessed the accuracy in decoding actions executed with a social intent from the observation of the arm movement during the reach-to-grasp phase. Stimuli were shown either in a second-person perspective or a third-person perspective, that is direct toward or away from the observer. To precisely assess how intention and action are perceived based on the kinematic characteristics of the action, we replicated the approach used by Cavallo and colleagues (Cavallo et al., 2016; Patri et al., 2020) to investigate whether there is a relevant subset of kinematic features whose thresholds correlate with perceiving an action as either socially directed or not. We expected significant parameters from Experiment 1 to be relevant for the decoding of social action.

In the third experiment (Action Observation 2), we displayed the same actions to a new cohort of participants, this time displaying not only the arm but the whole scene allowing participants to see the agents' faces. An eye-tracking approach was employed to assess which effector was most attended to and its relationship with participants' performance. In line with previous evidence (Calbi et al., 2021; Sartori et al., 2011; Vaziri-Pashkam et al., 2017), we expected the face to be highly attended and to improve participants' decoding performance.

3.2. Stimuli Production and Kinematic Analysis

The study was approved by the local ethics committee (Comitato Etico dell'Area Vasta Emilia Nord, protocol n. 20555, 2023) and was conducted following the principles expressed in the Declaration of Helsinki. All participants provided written informed consent.

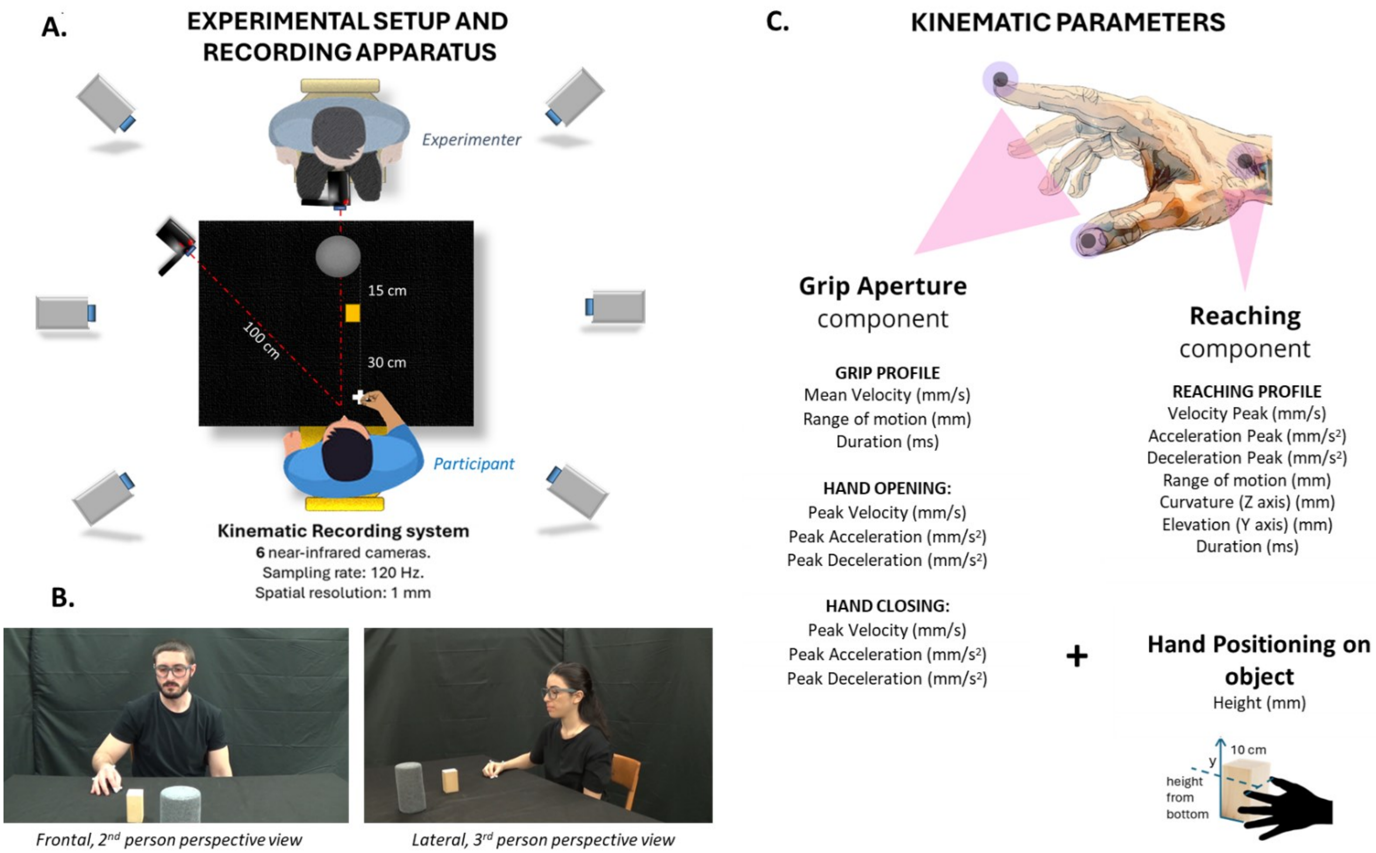
3.2.1 Participants

18 naïve volunteers (9 males and 9 females, mean age 24.8 ± 0.6 years; range 20-29) participated in Experiment 1. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). They had normal or corrected-to-normal vision and no previous diagnosis of neurological or psychiatric disorders.

3.2.2 Design and experimental procedure

The Action Execution Task comprised two sessions, balanced among participants. In one session, referred to as the PLACE session, participants were seated alone at the table without anyone else present. Experimenters remained behind a curtain, monitoring participants' behavior through the apparatus for kinematic recording. During this session, participants were instructed to perform a placing action, wherein they reached and grasped the wooden block and then placed it on top of a plastic cylinder positioned in front of them (see Figure 3.1). The PLACE session consisted of 12 consecutive trials. Before each trial, experimenters instructed participants to assume the starting position and then begin the task upon hearing a verbal cue such as 'Go'. After placing, they were instructed to leave the object and get back to the starting position. In the second session, named the PASS session, one of two experimenters (one male and one female, balanced according to participants' genders) sat across the table from the participants. Participants were tasked with either placing the wooden block on the cylinder (as in the PLACE session) or passing it to the person seated opposite them. To execute the passing action, participants held the block above the cylinder, awaiting the experimenter's reach. This session comprised 24 trials organized into 6 sets of 4 trials each. To emulate a socially realistic context for the passing action, participants were instructed to autonomously decide, trial by trial, whether to perform a passing or placing action within each set. They were further instructed to perform at least two passing actions and two placing actions within each set, without disclosing their decision to the experimenters. This approach aimed to prevent swift adaptation to the social scenario and the automatic execution of passing actions, as both experimenters and participants had no expectations regarding the forthcoming action. The trial procedure mirrored that of the PLACE session, with verbal instructions for preparation and execution.

Throughout the whole experiment, participants' performances were filmed with two cameras, one placed in front of them across the table (between the experimenter and the table during the PASS session) and one placed at a 45-degree angle on their left. Both cameras were placed 1 meter away from the participant. Recordings were used for creating video stimuli of passing actions (PASS) and placing actions (PLACE) with two visual perspectives, 2nd person perspective and 3rd person perspective, later to be used in the Action Observation experiments.



Frontal, 2nd person perspective view

Lateral, 3rd person perspective view

Figure 3.1 | Experimental setup and recording apparatus for kinematics. (A) Participants sat at a table with their right hand positioned in a ‘pinch grip’ posture. The left arm was resting straight at their side. To prevent wide torse movements, participants were asked to lean against the table with their chest, keeping their back straight and leaning against the chair. The fingertips of the right thumb and index were positioned on a tape-marked point on the table signaling the starting position, located 15 cm to the right of the participant's mid-sagittal plane and 10 cm from their chest. A small wooden block (6x4.5x11 cm) was placed on the table 40 cm from the chest and 55 cm from a cylinder (10 cm of diameter) serving as the placement base on the table. (B) Example frames from video recordings. (C) Kinematic parameters of interests.

3.2.3 Kinematic recordings: apparatus and acquisition parameters

Participants' hand kinematics were captured using the 3D-optoelectronic SMART system (BTS Bioengineering, Milano, Italy), located at the Unit of Neuroscience of the University of Parma. The system comprises six infrared cameras, which detected three passive reflective markers (spheres of 6 mm in diameter) affixed to the participant's right hand using double-sided tape: one marker at the radial styloid process of the wrist, another on the thumbnail of the thumb, and the third on the thumbnail of the index finger. Marker positions were sampled at a frequency of 120 Hz with a spatial resolution of 0.3 mm. The analysis focused on the reaching and grasping phases to measure any differences in the part of the action that is common to both the PLACE and PASS conditions (i.e., the reach-to-grasp phase), except for the differing intentional components.

The kinematics of the reaching phase were analyzed by extracting the trajectory based on time, focusing on the marker placed on the wrist. For the grasping phase, the analysis involved tracking the distance over time between the markers placed on the thumb and index finger. Consistent with previous literature (Jeannerod, 1988b) it was assumed that the grasping movement has an initial phase of finger opening, which ends when this opening reaches its peak (maximum finger opening), followed by a closing of the fingers on the object. The onset of the reaching phase was determined as the first of at least three consecutive frames during which the displacement of the marker placed on the wrist along any axis increased by more than 0.3 mm compared to the previous frame. As a criterion to determine the end of the reaching phase, 3 consecutive time frames were requested to show a wrist displacement lower than 0.3 mm. The calculation was repeated separately for the X, Y, and Z axes, and the frame nearest the end of the grasping phase. The start of the grasping phase was selected by considering the first of three consecutive frames in which the distance between the two markers placed on the fingers (thumb and index) increased by more than 0.3 mm compared to the previous frame. The end of the grasping phase was defined by considering the first of at least three consecutive frames after the start of finger closure in which the distance between the index and thumb was less than 0.3 mm compared to the previous time instant. The data were analyzed using code developed in MATLAB

(R2016b). A low-pass Gaussian smoothing filter (sigma value: 0.93) was applied to the recorded data.

In this way, we were able to reconstruct the overall spatiotemporal dynamics of several kinematic curves (see section 3.8, Supplementary Material, Supplementary Figure 1) of the reach-to-grasp movement: the Grip Aperture curve (GAc), defined as the distance between the markers placed on the fingers (mm), together with its velocity (VelGAc, mm/s) and acceleration (AccGAc, mm/s^2) profiles; the Reaching trajectory curves, defined as the movement of the marker placed on the wrist on the x (Rxc), y (Ryc), and z (Rzc) axes, reaching speed (SpeedRc) and acceleration (AccRc) curves defined as the velocity value reached by the marker placed on the wrist and its derivative.

To obtain a precise measure of the influence of different motor intentions on the reaching and grasping phases, 17 kinematic parameters were extracted from the curves and considered for the analysis (see Figure 3.1), including 9 parameters for the grip aperture component and 7 parameters for the reaching component. In addition to the spatiotemporal features of the reach-to-grasp movement, the height of the hand position on the object was measured to investigate positioning adjustment (see Figure 3.1). Hand positioning was calculated as the mean between the value on the Y axes of the thumbnail and index markers at the time of contact with the object.

3.2.4 Statistical analyses

LINEAR-MIXED EFFECT ANALYSIS. We compared placing actions executed while being alone to passing actions directed toward a partner. For the latter condition, however, we asked participants to randomly alternate between passing or placing actions (see section 3.2.2). This allowed us to measure the effect of the social context alone – being in the presence of another person – in our experimental setting, while isolating features specific to the intention to interact. A linear mixed-effect analysis was performed, with each kinematic parameter modelled through a linear-mixed model (LMM) with fixed factors Goal and Gender, and subjects (ID) as random factors. Statistical analyses were performed with R (2021), and LMMs were created using the *lme4* software package(Bates et al., 2015). Marginal (R^{2m}) and conditional (R^{2c}) coefficients of determination were calculated as a measure of effect size. Results were subjected to a chi-square test with *car* package (ref) and further corrected post-hoc applying the Bonferroni method for multiple comparisons(Fox and Weisber, 2019). We had 17 repeated tests, one for each parameter, so our significance threshold was the alpha value divided by seventeen (i.e., 0.002). We opted for a more conservative correction given the in-principle correlation of the measured variables (e.g., velocity, acceleration, amplitude etc.). Cook's distance (Cook. and Weisberg, 1982) was employed for the analysis of outliers and influential cases.

PRINCIPAL COMPONENT ANALYSIS. To further study which kinematic feature was most predictive of the overall kinematic variations, a principal component analysis (PCA) was executed on the kinematic curves for the grasping and reaching components from the whole dataset of trials. Analyses were performed using the built-in R functions ‘prcomp’.

3.2.5 Results: Kinematic correlates of social motor intentions

Our Linear Mixed Model (LMM) analysis on seventeen parameters of interest revealed that reaching and grasping in the social context, regardless of the action goal, resulted in overall slower execution and shorter spatial patterns. Grip and reaching dynamics had longer durations when the partner was present (blue rows in Table 3.1), while all others significantly modulated parameters – which regarded range of motion, peak and mean velocity, acceleration and deceleration – were higher for placing actions in the non-social context (red rows in Table 3.1). In our social condition, participants were monitored by a partner during both passing and placing actions, likely inducing heightened motor control and accuracy (cf. Mnif et al., 2022).

For the Gender factor, only one parameter held a significant result after post-hoc correction, that is the peak of acceleration in the grasp opening phase which was higher for females [Grasp Opening Peak Acceleration: M: 7013 mm/s^2 (CI: 6246-7761), 5083 (CI:4335-5831); $X^2_{(1)}$=15.78, p<0.000; R^2_m=16.23, R^2_c=30.24]. Our analysis shows no significant interaction effect between Goal and Gender.

Three main components emerged from the PCA which accounted for 83% of the variance, thus providing a good characterization of the data. The first two components accounted for 54.4% and 22.6% of the total variance, summing up 76% of the total variance. In PC1, it was the Grip aperture (GA) that held the greatest weight, while in PC2, it was the speed of reaching (SpeedR). PC3 was strongly represented by the acceleration component of the grip aperture (AccGA). A chi-squared followed by Tukey post-hoc test was conducted on the coordinates obtained for all three components with GOAL as a factor to verify if the new PCA coordinates detected the significant difference between the two actions previously observed in the LMM analysis. The results obtained show significance for PC1 [$X^2_{(1)}$= 13.9, p<0.000] and PC2 [$X^2_{(1)}$= 15.3, p <0.000], while PC3 did not result significant [$X^2_{(1)}$= 1.9, p > 0.5]. In summary, PCA analysis reveals grip aperture and reaching speed patterns as main indicators of overall kinematic variations for PASS and PLACE actions.

					Linear Mixed Models Statistics		
	Kinematic Parameters of Interest	PLACE (non-social context) (N=216)	PLACE (social context) (N=216)	PASS (social context) (N=216)	$X^2_{(1)}$	R^2_m	R^2_c
GRIP	*Mean Velocity (mm/s)*	98.4 (CI: 84.3, 112)	90.8 (CI: 76.5, 105)	91.1 (CI: 77.2, 105)	20.67	9.49	68.42
	Range of Motion (mm)	89.6 (CI: 86.4, 92.8)	85.7 (CI: 82.4, 89.0)	85.1 (CI: 81.9, 88.3)	56.43	14.52	50.23
	Duration (ms)	611 (CI: 576, 647)	657 (CI: 616, 697)	660 (CI: 625, 696)	32.87	10.23	39.23
	***Opening** Peak Velocity (mm/s)*	407 (CI: 364. 450)	375 (CI: 331, 419)	377 (CI: 334, 421)	10.84	13.44	37.89
	***Opening** Peak Acceleration (mm/s^2)*	6126 (CI: 5565, 6687)	5998 (CI: 5393, 6602)	5978 (CI: 5418, 6538)	0.5	16.94	28.69
	***Opening** Peak Deceleration (mm/s^2)*	-5371 (CI: -5769, - 4973)	-5027 (CI: -5448, -4606)	-4903 (CI: -5301, -4505)	10.92	9.21	28.77
	***Closing** Peak Velocity (mm/s)*	- 307 (CI: -341, -274)	-243 (CI: -274, -212)	-237 (CI: -271, -203)	87.52	13.44	37.89
	***Closing** Peak Acceleration (mm/s^2)*	-6364 (CI: -7120, -5609)	-5012 (CI: -5670, -4355)	-5029 (CI: 5784, -4274)	36.38	12.32	32.2
	***Closing** Peak Deceleration (mm/s^2)*	7347 (CI: 6524, 8169)	5838 (CI: 5094, 6581)	5401 (CI: 4578, 6223)	45.55	12.01	28.88
REACH	*Velocity Peak (mm/s)*	814 (CI: 772, 856)	767 (CI: 727, 808)	751 (CI: 709, 793)	25.67	9.21	60.77
	Acceleration Peak (mm/)	5144 (CI: 4899, 5389)	4842 (CI: 4615, 5068)	4934 (CI: 4689, 5179)	4.9	5.09	19.06
	Deceleration Peak (mm/s^2)	-4590 (CI: -4910, -4271)	-4357 (CI: -4684, -4030)	-4311 (CI: -4630, -3992)	19.24	9.42	36.65
	Range of Motion (mm)	250 (CI: 239, 261)	245 (CI: 234, 255)	241 (CI: 230,252)	15.52	11.23	76.22
	Curvature (Z axis) (mm)	11.5 (CI: 8.73, 14.2)	10.7 (CI: 7.86, 13.5)	11.6 (CI: 8.82, 14.3)	0.006	3.8	31.79
	Elevation (Y axis) (mm)	111 (CI: 108, 117)	111 (CI: 107, 116)	112 (CI: 106, 116)	4.08	12.04	55.76
	Duration (ms)	624 (CI: 593, 655)	663 (CI: 631, 694)	670 (CI: 638, 701)	30.56	14.52	37.23
FINAL POSITION	*Hand Position (Y axis) (mm)*	53.3 (CI: 48.7, 57.9)	52.1 (CI: 48.1, 56.1)	47.4 (CI: 42.8, 52.1)	107.83	19.23	70.24

Table 3.1 | Main results of the kinematic analysis. Table reporting main results from the LMM on kinematic parameters of interest. Means and confidence intervals (CI) for each condition of the execution task (N=3) are reported for each parameter. Chi-square value is reported along with Marginal (R2m) and conditional (R2c) coefficients of determination used as measures of effect size. Statistically significant results which passed Bonferroni correction (α/17 = 0.002) are colour-coded; non-significant results are left in white. Parameters highlighted in pink are significantly higher for at least one placing condition, while those highlighted in light blue are significantly higher for the passing condition. Darker and lighter coding highlight differences among all three conditions, indicating which ones held significantly higher values compared to the other.

3.3. Action Observation Tasks (Experiment 1 and 2)

3.3.1. Participants

40 naive volunteers (20 males and 20 females, mean age 24.8 ± 0.6 years; range 20-29) participated in Action Observation 1 while another cohort of 40 naive volunteers (20 males and 20 females, mean age 24.8 ± 0.6 years; range 20-29) participated in Action Observation 2, for a total of 80 participants. As for the Action Execution Task, all participants were right-handed according to the Edinburgh Handedness Inventory, had normal or corrected-to-normal vision, and had no previous diagnosis of neurological or psychiatric disorders.

3.3.2. Stimuli Production and Selection

Participants were presented with video clips depicting the reaching phase of the actions recorded in the first experiment. To test for observers' basic ability to detect intention from kinematics, from the whole dataset of available actions (n. 336) we selected a subset of the most representative actions that minimized the within-intention distance. As stimuli for the subsequent Action Prediction experiments, we selected a subsample of placing actions executed alone and passing actions to capture the full range of kinematic differences between these two goals. This choice was guided by the observation that the socially induced slowdown we identified aligns with previous studies on kinematic adjustments in cooperative actions, such as object passing or joint actions (Georgiou et al, 2007; Becchio et al., 2008; Gigliotti et al., 2020), as well as studies suggesting that this regulation may begin in very early developmental stages (Castiello et al., 2010). By doing so, we aimed to evaluate the extent to which different kinematic components — grasping, reaching, and hand-object interaction — are associated with potential interaction during action observation.

Most representative actions were selected based on a calculation of the proximity of their kinematic parameters to the means obtained from the kinematic analysis of Experiment 1 for passing and placing actions, respectively. To achieve this, a quantitative evaluation in two steps was conducted, wherein: 1) results from the previous PCA were used to reduce the number of parameters to consider for video selection based on proximity to the means. Kinematic parameters with the strongest correlation (either positive or negative) with the first two principal components were selected as the most representative parameters of the overall kinematic variations in passing and placing actions and then used for stimuli selection from the whole dataset; 2) once the most representative parameters were identified, actions falling within +1 and -0.5 standard deviations from global means were selected separately for the two action types (See Supplementary Figure 2). Following this procedure, the number of videos was selected to obtain 3 passing actions and 3 placing actions, both in second- and third-person perspective, per 8 participants from Experiment 1, for a total of 96 unique videos.

3.3.3. Design and Experimental Procedure

The 96 selected actions were presented to the participants in video format through the use of a HTC Vive Pro Eye head-mounted display (HMD) comfortably arranged over their heads. Participants were seated behind a table and were assisted in wearing the HMD (Figure 3.2). They were asked to keep both hands resting on the table, with the index finger of each hand standing on one of two keyboard buttons to provide a binary response. The experiment was run by employing code in Unity Software (2021.3) for both video presentation in a virtual environment and response collection. In the virtual environment, the participant was positioned in front of a screen in a pitch-black chamber. The screen size and its placement from the participant were recreated to simulate a 27-inch flat screen at ~50 cm distance from the participant's point of view. Responses, Reaction Times (RTs), and eye movement were collected for both experiments.

The design and procedure were identical for both the Action Observation tasks, differing only in how the 96 actions were presented. In Action Observation 1, videos were edited to display participants executing the actions solely from below the shoulder. In Action Observation 2, the videos depicted the entire scene, including the participant's entire upper body and face while acting.

At the beginning of the experiment, participants underwent a quick training phase. First, 8 random sample movements were shown to them in sequence, so they could see the phase where agents in the video passed the block to the experimenter or placed it on the cylinder. Subsequently, participants were trained to execute the action prediction task and presented with just the reach-to-grasp phase of 8 new videos interrupted at the moment of hand contact with the object to be grasped. For each video, participants were asked to guess the type of motor intention (i.e., passing or placing) underlying the observed action. Only in this phase, trials were followed by feedback, in which the entire video was reproduced.

In both the training and experimental session, each trial (see Figure 3) was organized as follows: first, a grey screen appeared for 1 second, followed by another screen displaying a white fixation cross (+) at the centre, also for 1 second. At 2 seconds, the first frame of one of the 96 videos (presented in random order) appeared, frozen for 0.5 seconds. Following this pause, the video began playing, concluding within 1.5 seconds. While the end of each action was synched at the time of contact with the object, the starting of each action could vary (according to its velocity, see Exp.1 results). After the video ended, a panel prompted participants to indicate the possible outcome of the observed action ("pass" or "place", using either the right or the left key, balanced among participants). Participants had a maximum of 3 seconds to respond; if they did not respond within this time frame, the trial was cancelled, and the next trial commenced. Participants were instructed to respond accurately and promptly. Unlike during the training phase, no feedback was provided after participants' responses. After selecting a response, participants were required to rate their confidence level regarding their decision on a 4-point scale ranging from 1= less confident to 4= more confident (see Figure 3) by using the computer keyboard, with no time limit for responding.

The experimental session comprised 3 blocks. Within each block, all videos (N= 96) were presented in randomized order, covering both intentions (N=48 for passing; N=48 for placing). In total, 288 trials were administered. The whole experiment had a duration of approximately 40 minutes.

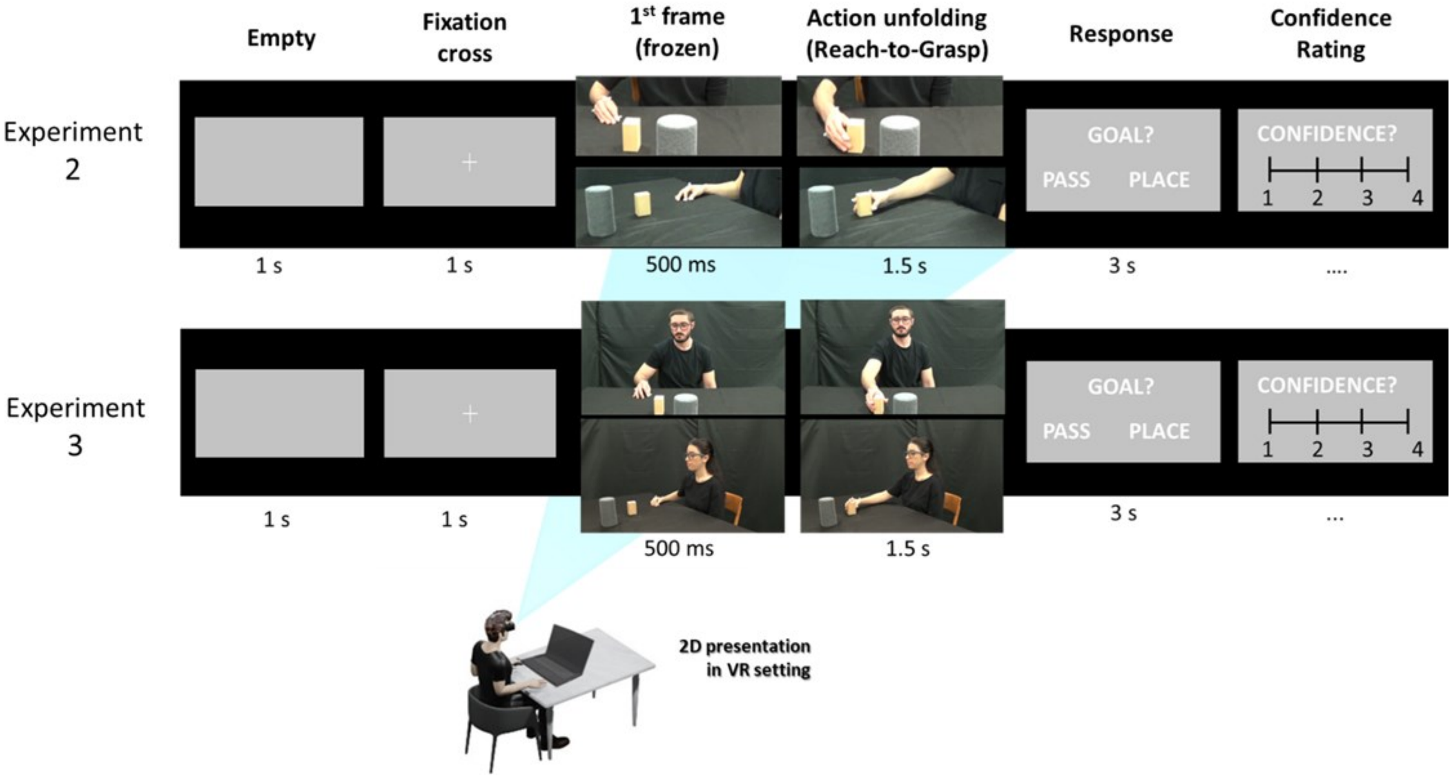


Figure 3.2 | Experiment 2 and 3 single trial structure and experimental setting.

3.3.4. Statistical Analyses

SIGNAL DETECTION ANALYSIS. To evaluate participants' ability to discriminate social intentions from kinematics in both experiments, we utilized their responses and confidence ratings to estimate the parameters of Signal Detection Theory (SDT). For each participant, we computed the proportion of hits and false alarms, using PASS actions as the signal and PLACE actions as the noise. Estimated SDT parameters were then integrated with confidence ratings to establish points on an empirical receiver operating characteristic (ROC) curve. Given that each response involved four associated ratings, there were eight potential responses per trial, resulting in seven points on the ROC curve(Stanislaw and Todorov, 1999). Subsequently, these points were plotted to determine the area under the curve (AUC) for each participant. Participants' performances were categorized based on their AUC values: those with an AUC value equal to or above 55% were labelled as 'good' decoders, participants with an AUC value between 55% and 45% were categorized as decoding by 'chance', and individuals with an AUC value below 45% were designated as 'counter' decoders.

LINEAR-MIXED EFFECT ANALYSIS. To detect differences in the behavioral response to actions executed with an individual (i.e., PLACE) or a social (i.e., PASS) intention from different viewpoints (i.e., SECOND vs. THIRD person), LMMs for participants' RTs and Accuracy were built with fixed factors Goal, Perspective, Performance (i.e., 'good', 'chance', 'counter'), and Confidence Rating, and participants (ID) as random factors. A third LMM was computed on confidence ratings with fixed factors Goal, Perspective, and Performance, and subjects as random factors. RTs were calculated on correct responses with a minimum duration of 150 ms as the threshold for physical feasibility(Harald Baayen and Milin, 2010). Statistical tests, measurements of effects, and outlier detection were executed in the same way as for the LMA in Experiment 1. Tukey's correction for multiple comparisons was applied to significant effects using the *emmeans* package(Lenth, 2022).

CLASSIFICATION TREE ANALYSIS (Action Observation Task 1). A series of classification analyses were conducted to explore the relationship between participants' responses and action features in **Experiment 2**. Specifically:

- The first set of analyses aimed to predict intention decoding from actions' kinematics. We trained and tested classification trees using significant kinematic parameters identified from the LMM analysis in Experiment 1 as predictors and participants' choices (i.e., 'place' or 'pass') as categorical outcomes. Initially, we utilized the entire dataset of trials from Experiment 2 to observe global patterns. Subsequently, we employed datasets limited to participant subgroups ('good', 'chance', and 'counter') to examine variations in the relevance of kinematic features for action prediction between subgroups.
- The second set of classification analyses aimed to determine which action features were most predictive of participants' correct responses. For this analysis, correct and incorrect

responses were used as categorical outcomes, and the classification was repeated for the entire dataset and each subgroup.

Each classification model was trained with 80% of the selected dataset and tested on the remaining 20%. Classification Trees were constructed using the *rpart* package in R(Therneau et al., 2013). The complexity of decision trees was determined based on default cost complexity pruning in the ‘rpart’ function, measured as minimization of the Gini’s index, which defined the minimum improvement in the model required at each node, in addition to cross-validation. The relative weight (i.e., importance) of each variable is calculated in the ‘rpart’ function by measuring the improvement added by variables in cost complexity minimization. The significance of classification accuracy for each classification analysis was assessed with binomial testing against chance level performance. Finally, to assess consistency in the relative weights of variables across groups and conditions, weights obtained from the classifications were compared by computing Pearson correlations in R with the function ‘cor’.

EYE-TRACKING ANALYSIS (Action Observation Task 2). To investigate participants’ attention to specific bodily features in **Experiment 3**, we analyzed the frequency and duration of their fixations on three Areas of Interest (AOIs): the FACE, the HAND, and the ARM AOIs. The dimensions of the AOIs were calculated based on the actual stimulus dimensions in the UNITY environment and were utilized as regions for fixation localization. AOIs were dynamically adjusted frame by frame by using fixed points of reference for each effector (e.g., head center, elbow, and fingertips) to be used as centers around which to build the AOIs. Analysis was performed on eye movements recorded during the reach-to-grasp epoch of the video, that is, from the onset of the reaching movement to the end of the grasping movement. Fixation identification was carried out using a detection algorithm based on two-means clustering through a MATLAB R2023a script(Hessels et al., 2017). To evaluate differences in overt attention to AOIs between conditions, LMMs were built for both the number of fixation and fixation duration. AOIs, Goal, Perspective, and Performance were used as fixed factors, while participants’ (ID) were used as random factors.

3.4. Results Experiment 1: Decoding of social action from kinematics

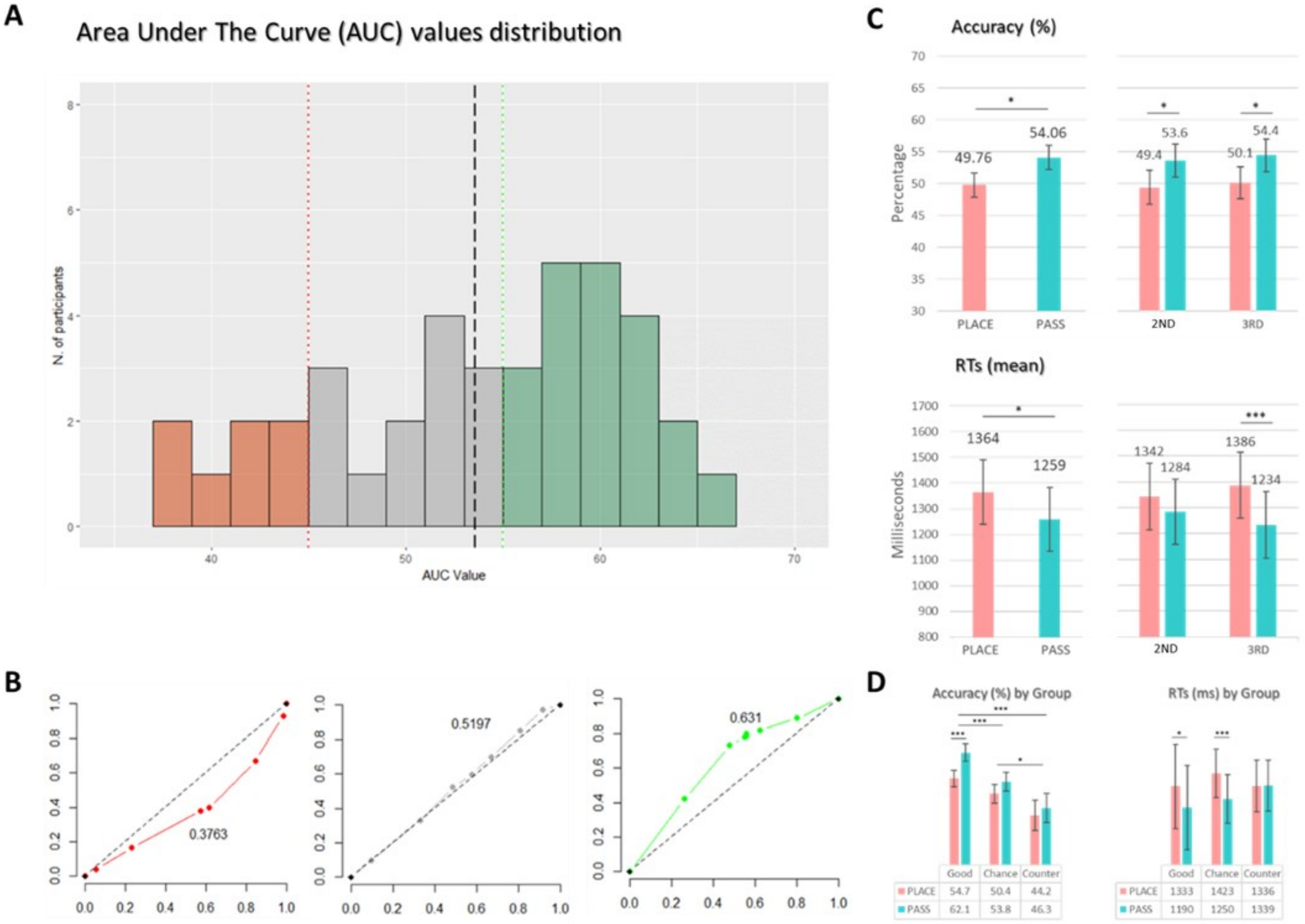


Figure 3.3 | Participants' performance from Experiment 2. (A) Histogram representing the distribution of AUCs value among participants. Categorization by performance is highlighted by color coding. Green = 'Good' subgroup (>55); Grey = 'Chance' subgroup (45-55); Red = 'Counter' subgroup (<45). (B) Examples of individual AUCs of exemplar participants from each of the three subgroups, following the same color coding as in Figure A. (C) Barplots of participants' mean Accuracy and RTs for Goal and Goal + Perspective factors. (D) Barplots of subgroup means Accuracy and RTs for the Goal factor.

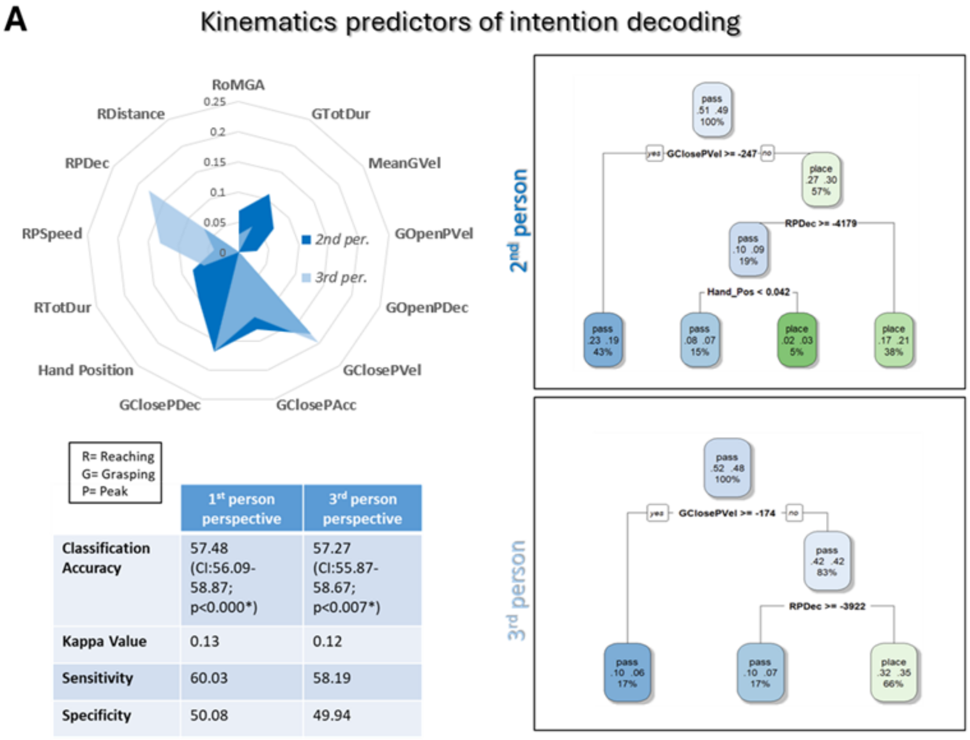
SIGNAL DETECTION ANALYSIS. Although AUC values obtained from our SDT analysis were consistently above chance level [$t_{(39)}$= 2.9758, p=0.004, CIs: 51.59-56.47], the group performance in correctly discriminating social intention from early kinematics was, on average, poor, with a mean value of 54.03. As shown in Fig. 3.3A, only 20 out of 40 participants were classified as 'good' decoders, performing fairly above the chance level (>55%). 13 participants out of 40 performed around the chance level. Lastly, 7 participants had a counter decoding performance, meaning that, differently from merely performing at chance level, they consistently misclassified one action intention for the other (in this case, PASS for PLACE, as PASS actions were taken as true values for computing the ROC; see Fig. 3.3B). Thus, while only half of the participants were good intention decoder, the majority of them (20 'good' decoders and 7 'counter' decoders) were capable of detecting differences at least at the level of movement kinematics.

LINEAR-MIXED EFFECT ANALYSIS. LMMs of participants' accuracy [R^2_m= 12.23*,* R^2_c= 40.72] and RTs [R^2_m= 30.23*,* R^2_c= 30.25] revealed a main effect for the Goal factor [Acc.: $X^2_{(1)}$= 13.9, p<0.000; RTs: $X^2_{(1)}$= 13.9, p< 0.000]. As shown in Fig. 3.3C, PASS actions were guessed significantly better [$t_{(9526)}$= 2.437, p=0.01] and faster [$t_{(4975)}$=-2.526, p=0.005] than PLACE actions. Mirroring our classification, a main effect of the Performance factor is seen for the accuracy scores [$X^2_{(2)}$= 96.84, p<0.000]. A significant interaction between the Performance and Goal factors confirmed that PASS actions were significantly better decoded by the 'Good' group [$t_{(9526)}$= 3.6, p<0.000]. On the other hand, a main effect of the Performance factor was not found for RTs [$X^2_{(2)}$= 20.38, p=0.73]. Instead, the RTs LMM showed an interaction between the Performance and Goal factors [$X^2_{(2)}$= 7.5, p=0.02]. As depicted in Fig. 3.3D, correct responses to PASS actions were faster for the 'good' [$t_{(4975)}$=-2.174, p=0.02] and 'chance' groups [$t_{(4976)}$=-4.079, p<0.000], but not for the 'counter' group [$t_{(4976)}$=0.338, p=0.69], which is coherent with their accuracy scores for PASS actions. Regarding the Perspective factor, the only effect found is for the RTs LMM, which highlighted an interaction between the Goal and Perspective factors [$X^2_{(1)}$= 9.03, p=0.002], indicating that correct PASS actions were decoded faster from the 3rd person perspective [$t_{(4976)}$=-3.55, p<0.000; see Fig.4D]. This, however, did not correlate with better accuracy from the 3rd person perspective. Overall, no other effects related to the Perspective factor were found in both models.

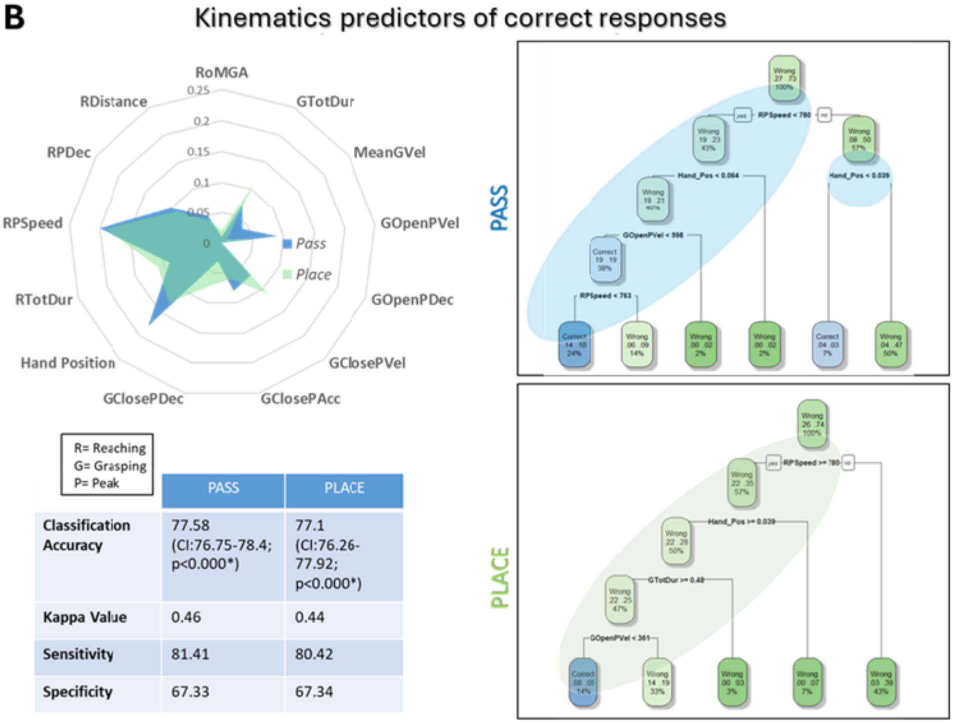
Predictably, a main effect for the Confidence Rating factor was found for RTs [$X^2_{(3)}$= 527.89, p<0.000], showing that the quicker the response the higher was the confidence rate indicated by participants [RTs for Confidence ratings: 4, M=993, CIs=1125-860; 3, M=1230, CIs=1358-1102; 2, M=1429, CIs=1558-1300; 1, M=1602, CIs=1738-1466; all ps<0.000]. On the other hand, while a main effect of Confidence Rating was initially found for accuracy [$X^2_{(3)}$= 9.48, p=0.02], this lost significance when corrected for multiple comparisons indicating that accuracy did not differ significantly among levels of confidence at the group level. Further interactions for the Confidence Rating factor are reported in the Supplementary Material (section 3.8-3) as they mostly reflect significant effects found for Accuracy and RTs.

LMMs of participants' Confidence Ratings [R^2_m= 5.23, R^2_c= 25.72] did not highlight differences in levels of confidence among subgroups, goals, or perspectives [all Ps>0.06].

CLASSIFICATION TREE ANALYSIS. Classification of participants' responses from kinematics (Fig. 3.4A) was significantly above chance level with fair although not strong accuracy (~56%), possibly reflecting the group's inconsistent performance. Indeed, greater classification scoring and stronger reliability and specificity were obtained for the 'good' and 'counter' subgroups, separately (see Supplementary Figure 3A). In contrast, accuracy for the 'chance' subgroup was at chance level (~52%), confirming greater within-subgroup coherency in decoding criteria for the former compared with the latter. As shown in the polar plot in Fig. 3.4A, hand-related parameters were the most relevant predictor of participants' responses in the second-person perspective. Interestingly, beyond global parameters like mean grasping duration, grasping range of motion, and mean velocity, a relevant cluster of parameters related to the final grasping approach emerged, formed by grasping closure parameters (GClose) and final hand placement on the object. Indeed, according to the decision tree, actions were more probably classified as social (i.e., pass) when either displaying low grasping closure deceleration (left branch of the tree) or slow reaching deceleration together with low hand placement on the object (right branch). In the third-person perspective, hand positioning did not figure as a significant predictor; instead, deceleration parameters for both reaching and grasping were the most relevant, together with the reaching mean speed.



	1st person perspective	3rd person perspective
Classification Accuracy	57.48 (CI:56.09-58.87; p<0.000*)	57.27 (CI:55.87-58.67; p<0.007*)
Kappa Value	0.13	0.12
Sensitivity	60.03	58.19
Specificity	50.08	49.94



	PASS	PLACE
Classification Accuracy	77.58 (CI:76.75-78.4; p<0.000*)	77.1 (CI:76.26-77.92; p<0.000*)
Kappa Value	0.46	0.44
Sensitivity	81.41	80.42
Specificity	67.33	67.34

Figure 3.4 | Classification analysis of participants' responses (Action Observation 1). The figure shows the main results obtained at the group level in the Action Observation 1 task, with polar plots representing the relative weight of each kinematic variable in response prediction, tables reporting parameters of classification performance, and decision trees showing the main classification process. **(A)** reports results for kinematic predictors of participants choices, while **(B)** reports results for kinematic predictors of correct responses. RoMGA= Grasp Range of Motion; GTotDur= Grasp Total Duration; MeanGVel= Mean Grasp Velocity; GOpenPVel= Grasp Open Peak Velocity; GOpenPDec= Grasp Open Peak Deceleration; GClosePVel= Grasp Close Peak Velocity; GClosePAcc= Grasp Close Peak

Acceleration; GClosePDec= Grasp Close Peak Deceleration; RTotDur= Reaching Total Duration; RPSpeed= Reaching Speed; RPDec= Reaching Peak Deceleration; Rdistance= Reaching Distance; Hand_Pos= Hand Position.

Classifications on subgroups confirmed that the ‘counter’ group decoded intentions adopting an opposite criterion compared with the other two groups. In the decision trees for the counter group (see Supplementary Figure 4B), actions were more probably decoded as social (i.e., pass) when grasp and reaching speeds were high, together with lower durations and grasping displayed a wider range of motion. Interestingly, the only parameter that was not reverted in the ‘counter’ group decoding was the hand positioning on the object: when hand position was low (Hand_Pos < 0.037 mm), the ‘counter’ group attributed a social intention to the action observed, in line with group level decoding and the ‘good’ group.

Classifications of participants’ correct responses from kinematics (Fig. 3.4B) held significance above chance level together with high accuracy (~77%), specificity (~67%), and sensitivity (~81%), highlighting high consistency in the kinematic profiles of correct responses within the group. Indeed, relative weights of the kinematic parameters were highly similar among subgroups’ (see Supplementary Figure 3B). Pearson’s correlation testing on relevance profiles for kinematic parameters held a high correlation for both correct social actions [All Rs > 0.45; All Ps <0.000] and non-social actions [All Rs > 0.53; All Ps <0.000] among subgroups. Reaching speed, Hand Position on the object and Grasping opening and closing velocities were the most relevant predictors of participants' correct responses for both social and non-social actions. However, the Hand Position parameter had a higher weight for correct social actions. As further highlighted by the decision trees, a low hand positioning alone was sufficient for a social action to be accurately decoded, whereas this was not the case for non-social actions.

3.5. Results Experiment 2: Saliency of bodily effectors

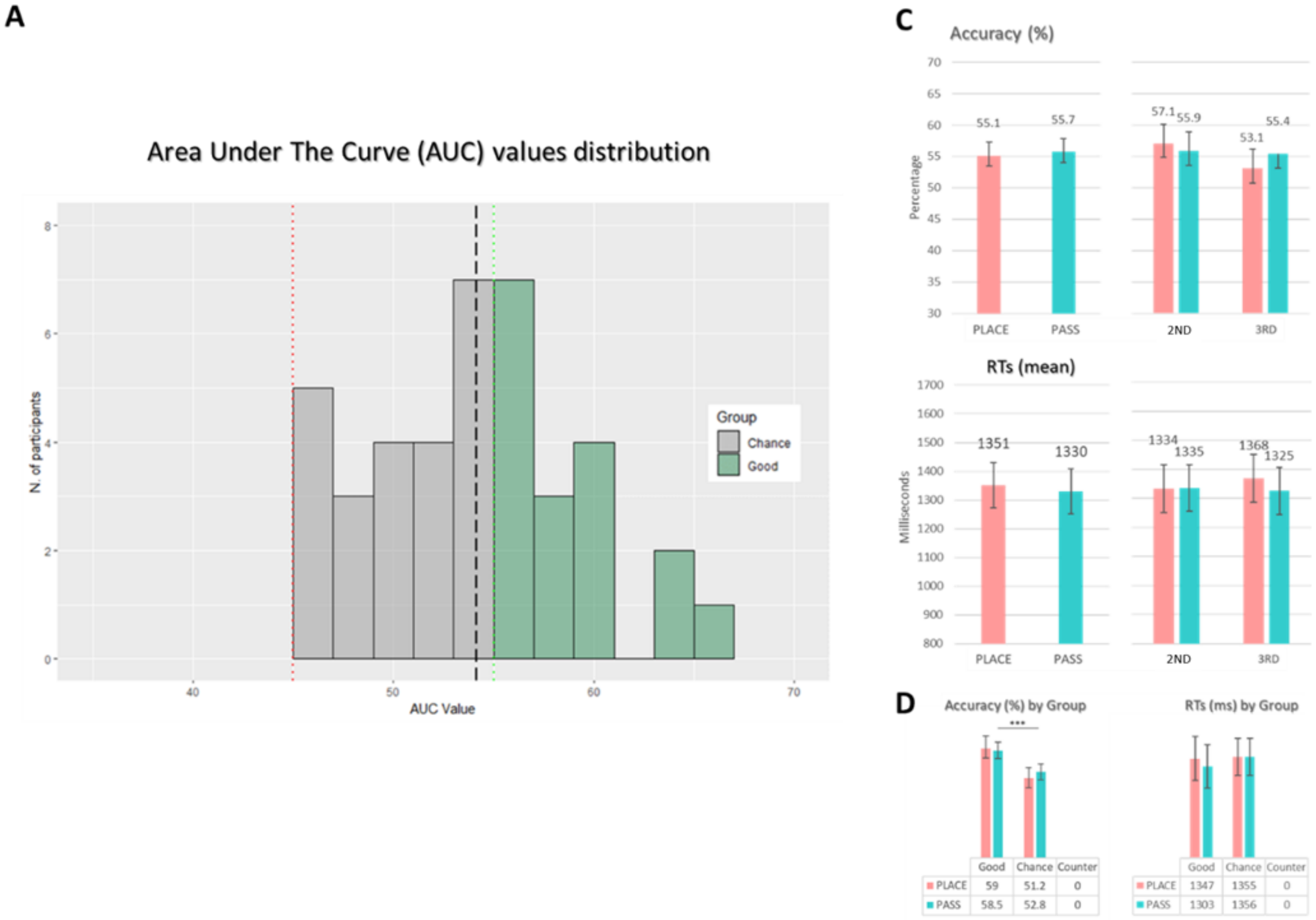


Figure 3.5 | Participants' performance from Experiment 3. (A) Histogram representing the distribution of AUCs value among participants. Categorization by performance is highlighted by color coding. Green = 'Good' subgroup (>55); Grey = 'Chance' subgroup (45-55). (B) Barplots of participants' mean Accuracy and RTs for Goal and Goal + Perspective factors. (C) Barplots of subgroup means Accuracy and RTs for the Goal factor.

SIGNAL DETECTION ANALYSIS. In terms of mean values, the group from Experiment 3 displayed a similar performance to the one in Experiment 2. The distribution of AUC values was slight, although consistently, above chance level [$t_{(39)}$= 4.94, p<0.000, M=54.4 CIs: 52.62-56.50]. However, the distribution of AUC values differed from that of Experiment 2, as no participants displayed a 'counter' performance (see Fig. 3.5A). 23 participants performed at the chance level, while the remaining 17 were good decoders.

LINEAR-MIXED EFFECT ANALYSIS. In accordance with the higher percentage of chance level performances among participants, LMMs of participants' accuracy [R^2_m= 22.28, R^2_c= 22.35] and RTs [R^2_m= 9.33, R^2_c= 28.07] were less efficient than those in Experiment 2 in representing the overall performance, as indexed by R^2 values.

As shown in Fig.3.5C, there were no significant differences in both Accuracy and RTs related to either the Goal or Perspective factors [all ps>0.20]. As for Experiment 1, the Performance factor [$X^2_{(1)}$= 29.31, p<0.000] reflected our classification, with the 'good' group being significantly more accurate than the 'chance' group [$t_{(59.7)}$=4.388, p<0.001].

Differently from Experiment 1 where no main effect on the Confidence Rate factor resulted from the Accuracy LMMs, here a main effect was found [$X^2_{(3)}$= 15.18, p=0.001] confirming that higher level of confidence ratings (i.e., 3 and 4) corresponded to higher accuracy at the group level [Accuracy for Confidence Ratings: 4, M=60.5, CIs=56.7-64.4; 3, M=56.5, CIs=54.4-58.5; 2, M=52.3, CIs=50.1-54.5; 1, M=52.3, CIs=48.7-55.8. All Ps<0.03 for Post-Hoc contrasts for 3 and 4 vs. 1 and 2]. The LMMs for accuracy also highlighted an interaction between Confidence Rate and Performance factors [$X^2_{(3)}$= 14.49, p<0.000]. The 'good' subgroup was significantly more accurate than the 'chance' subgroup at every confidence level [all Ps<0.03] except for the least confidence level [1: $t_{(919)}$=0.8, p=0.4]. Another interaction was found between Confidence Rate and Perspective [$X^2_{(3)}$= 11.17, p=0.01], showing that, when rated with the maximum level of confidence, trials in the 2nd person perspective were detected more accurately than those in the 3rd person perspective [$t_{(9662)}$=2.98, p<0.002].

LLMs on Confidence Rating values [R^2_m= 5.1, R^2_c= 15.36] highlighted the main effects of the Goal [$X^2_{(1)}$= 7.62, p=0.005] and Perspective [$X^2_{(1)}$= 13.41, p<0.000] factors. Pass trials were on average rated with more confidence than Place trials [PASS: M=2.54, CIs=0.9; PLACE: M=2.45, CIs=0.12; $t_{(9662)}$=2.83, p=0.004], while trials in the 2nd perspective were rated with more confidence than trials in the 3rd person perspective [2nd: M=2.54, CIs=0.9; 3rd: M=2.46, CIs=0.11; $t_{(9662)}$=3.33, p<0.000]. No interactions between these factors were highlighted.

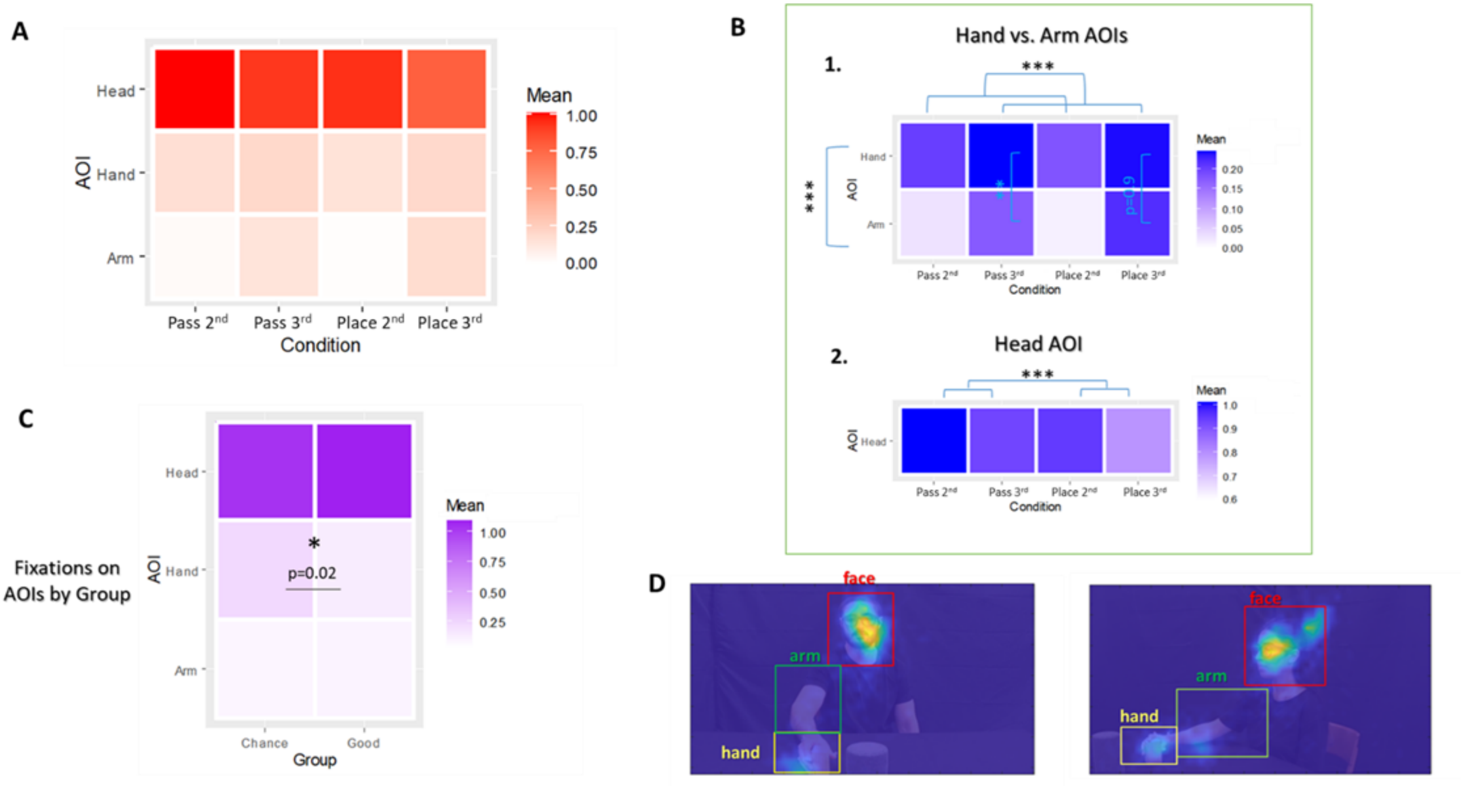


Figure 3.6 | Main results from fixation analysis in Experiment 3. Results are plotted as heatmaps of normalized mean values of the number of fixations. (A) Heatmap of the mean number of fixations per AOIs (i.e., Head, Hand, and arm) and experimental conditions (i.e., Pass 2nd, Pass 3rd, Place 2nd, and Place 3rd). (B) Heatmap of the mean number of fixations per 1) Hand and Arm AOIs per experimental condition, and 2) Head AOI per experimental condition. (C) Heatmap of mean number of fixations per AOIs and group (i.e., 'Good' and 'Chance'). (D) Areas Of Interest (AOIs) for fixation analysis. The figure displays heatmap plots calculated on the number of fixations for the second-person (left) and third-person (right) perspectives. The overlaid rectangular areas represent the adopted AOIs, that is, the Face (red); the arm (green); and the hand (yellow). AOIs were dynamically adjusted frame by frame.

Figure 3.6 shows heatmaps displaying normalised averages obtained with the LMM analysis on the number of fixations. The LMM [R^2_m= 32.97, R^2_c= 34.80] highlighted a main effect of the AOI [$X^2_{(2)}$= 10705.54, p<0.000], together with interactions between the AOI with both the Goal [$X^2_{(2)}$= 46.10, p< 0.000] and Perspective [$X^2_{(1)}$= 9.67, p< 0.001] factors and a triple interaction among them [$X^2_{(1)}$= 13.27, p< 0.000]. As shown in Fig. 3.6A, the head was by far the most attended AOI compared to both the hand [$t_{(24071)}$=83.62, p<0.001] and the arm [$t_{(24071)}$=92.95, p<0.001]. As can be seen in Fig. 7B1, the hand significantly received more fixations than the arm on average [$t_{(24071)}$=9.32, p<0.001]. This difference was stronger for 2nd person perspective trials, for both social [$t_{(24071)}$=7.96, $p<0.001$] and non-social actions [$t_{(24071)}$=7.40, $p<0.001$], than in 3rd person perspective trials, where the hand was significantly looked at more than the arm for social actions [$t_{(24071)}$=3.05, $p<0.006$] but not for non-social actions [$t_{(24071)}$=0.2, p=0.9]. Fig. 3.6B.2 also shows that the head AOI received more fixations during social actions compared to non-social actions [$t_{(24071)}$=8.02, $p<0.001$]. The LMMs also highlighted an interaction between the AOI and the Group factor [$X^2_{(2)}$= 32.40, $p<0.000$]. As shown in Fig. 3.6C, participants from the 'chance' group spent more fixations on the hand with respect to those from the 'good' group [$t_{(47.8)}$=2.28, p=0.02].

3.6. Discussion

In the last three decades, research in social cognition has witnessed a growing interest in understanding how individuals manage and process social interactions. Interpersonal motor coordination is a key form of social interaction which requires one to interpret a partner's actions quickly and respond appropriately. Research on how people process others' bodily displays has revealed numerous behavioral, physiological, and neural mechanisms involved in observing others' actions. Furthermore, studies have shown that these processes are significantly modulated by the social nature of an action, indicating that socially oriented motor actions are salient stimuli, and are possibly processed differently from other observed motor actions. Indeed, detecting and predicting potential involvement in an interaction is crucial for adapting to our social environment.

In our study, we aimed to assess the presence and relevance of early markers of social intention behind a simple motor action, i.e., grasping an object. Our goal was to test if differences in the expression of kinematic parameters between grasping with the intention to interact (i.e., to pass an object to someone else) or not (i.e., to place an object) could be effectively detected by an observer to correctly predict the outcome of the reach-to-grasp movement observed. Moreover, we wanted to test: 1) the specific weight of kinematic parameters in driving the perception of a social intention; and 2) the perceptual saliency of relevant bodily effectors like the face, the arm, and the hand during action prediction tasks.

In the **first experiment**, kinematic analysis showed that grasping with a social intention exhibited a significantly slower execution overall, together with a different hand placement on the object. The slowdown in the reaching and grasping aperture speed is in line with previous literature investigating kinematics adjustments for cooperative actions, like passing an object or joint actions (Becchio et al., 2008a; Georgiou et al., 2007; Gigliotti et al., 2020; Quesque et al., 2013; Quesque and Coello, 2014). In our experiment, participants had either to place a small wooden object on a cylindric pedestal or hand it to a partner, with both actions following very similar trajectories and covering a similar distance. Thus, the slowdown in the reach-to-grasp phase could be taken to reflect a general motor modulation related to intersubjective interactions. Interestingly, previous evidence on prenatal kinematics of twin fetuses highlighted that the slowdown of motion is a distinguishing feature of movement executed toward the other as compared to those to the self, suggesting this regulation might begin in very early developmental stages (Castiello et al., 2010). Another possible interpretation, which does not exclude the first one, is that in our study the object to be handled required a more careful approach for passing than for placing, in accordance with a speed-accuracy trade-off (Fitts, 1954). Notably, Ansuini and colleagues found a modulation in the opposite direction, that is, passing actions had a lower duration than placing actions (Ansuini et al., 2008). However, the object they employed was an 18 cm bottle affording a wider spacing of hand placement for passing it to a partner. In this regard, our finding of a lower hand placement on our object, a 11 cm wooden cube, might index socially induced end-state adjustments of the grasping action to accommodate for the other's predicted grip placement on the object.

In the **second experiment**, we tested whether the average kinematic differences in the reach-to-grasp phase from the first experiment could be used by observers to correctly predict action intentions. Participants could see only the agents' arms, with no other contextual information provided. Our results revealed an overall poor capacity for intention decoding from kinematics, with mean accuracy only slightly above the chance level (~54 AUC value). However, individual participants' performances showed variability in kinematic discrimination and intention attribution. Specifically, only 13 out of 40 participants performed at the chance level (the 'chance' group), while 20 participants decoded actions consistently above chance (>55 AUC, 'good' group). Seven participants, labelled 'counter' decoders, had AUC values significantly below the chance level (<45), meaning they consistently misattributed action intentions, interpreting passing as placing and vice versa.

This indicates that while most participants (27 out of 40) could discriminate kinematic modulations between the two types of actions, their intention attributions varied. Recent literature suggests that subjective features such as social skills and empathic abilities may influence intention attribution. Studies have shown correlations between these factors and decoding performance (Lewkowicz et al., 2015), as well as physiological responses to observed actions (Prinsen and Alaerts, 2024). Another relevant aspect may be the similarity in kinematic styles between the observer and the agent, following the hypothesis that one's motor knowledge is deployed in processing actions performed by others. A previous study using a similar experimental paradigm to ours found a positive correlation between kinematic similarities and intention decoding (De Marco et al., 2020), and evidence linked one's fine motor skills (as in sports) with better prediction skills of those same actions (Abreu et al., 2017; Aglioti et al., 2008; Makris and Urgesi, 2015; Müller and Abernethy, 2012; Paolini et al., 2023; Pedullà et al., 2020). Although we did not control for these factors, our results suggest subjective variability in how intentions are read from kinematics.

Despite this variability in our sample, analysis of participants' accuracy and reaction times showed that socially oriented actions were generally decoded with higher accuracy and speed. The 'good' group primarily drove this effect, but the 'chance' and 'counter' groups showed a similar, though non-significant, pattern. Reaction times for social actions were significantly lower for the 'good' and 'chance' groups, but not for the 'counter' group, possibly indicating they used inverted criteria for decoding actions.

But why were responses better and faster for social actions? Could this be related to the social nature of the actions, with specific discriminative features more prominently expressed by passing actions?

By employing a classification analysis to determine the kinematic components of action decoding, we found differences in the relevance of kinematic features for participants' choices and correct responses. Our results showed that parameters related to grip control in approaching the object, such as grip closing speed and deceleration, were among the most relevant predictors of participants’ choices overall. In the second-person perspective, hand positioning on the grasped object (i.e., grip height) was another significant parameter for decoding the action as socially oriented. This was not the case in the third-person perspective, where reaching speed had the major contribution, possibly due to the perceptual saliency of arm motion from that perspective.

Interestingly, hand positioning on the grasped object was a major predictor of participants correct decoding of social actions overall. A lower hand placement correlated with perceiving actions as socially directed. Analysis of subgroups confirmed this for all performance levels among participants. Notably, the 'counter' group showed a reverse pattern of decoding, where faster actions were interpreted as socially oriented. However, when the hand placement on the object was low enough, they tended to interpret the action as socially oriented regardless of other kinematic features.

Hand positioning and grip adjustment on the object are known in kinematic literature as important 'second-order' grasp parameters due to their intentional effects (Rosenbaum, 2017; Torricelli et al., 2023). Our results suggest that when potentially acting together with a partner on an object, the grasping height might be a salient feature indicating the space available for potential interaction on the object left by a partner. Our kinematic analysis further supports the relevance of this parameter. While most kinematic adjustments, such as changes in speed and spatial patterns of reaching and grasping, appeared to be driven by the social context (i.e., the presence of a partner), hand position on the object emerged as a specific marker of the intention to interact. Interestingly, the modulation of this parameter was more relevant during observation in the second-person than the third-person perspective, despite full visibility of hand placement on the object in both conditions. Recent perspectives on motor control related to social interaction have highlighted the relevance of co-adaptability as a major phenomenon in kinematic adaptation to social contexts, where inter-individual motor tuning is driven by anticipatory tendencies to adapt to another’s motor goals and patterns. The robustness of this prediction among our group might hint at a potential social marker related to the expression of anticipatory co-adaptation in motor kinematics (Casartelli et al., 2023), potentially processed as a social affordance by an observer (Orban, Lanzilotto, et al., 2021; Schilbach et al., 2013). In the last decade, much research on the neural substrates of social interaction processing has increasingly demonstrated the relevance of action goal specification in parietal-frontal nodes related to the control of manipulative actions (Bonini et al., 2022; Orban, Sepe, et al., 2021), showing the involvement of these networks in mirror mechanisms related to predicting and decoding others' actions (Di Bono et al., 2017; Patri et al., 2020). Our results show further perceivable features related to social affordance as important factors in regulating action processing along with the expression of basic kinematic features.

In our **third experiment**, a new group of participants underwent the same action prediction task, but this time the observed agent was fully visible, including the face as a source of information. On average, results replicated those in the second experiment, with the group mean performance remaining slightly above chance level (~54 AUC value). However, analysis of individual performances showed no counter-decoding performance as in the first experiment; participants either performed at chance level (n=20) or significantly above it (n=19).

While the addition of the face did not significantly improve participants' average performance, it likely impacted participants' choices by reducing the ambiguity of intention attribution seen in the previous observation task when action kinematics was the only available cue. Eye-tracking analysis confirmed the face as the most salient (i.e., primarily attended) bodily feature in the task, especially in the second-person perspective of the social condition. Moreover, participants who performed better in intention decoding (i.e., 'good' group) mostly looked at the face, while those with worse performances (i.e., 'chance' group) had significantly more fixations on the hand effector. This might indicate different strategies between the two groups or greater indecision among the 'chance' group, who may have been less effective at using facial cues to attribute intention correctly.

Overall, the lack of counter-decoder participants and the better performance of participants who looked more at the face suggest the relevance of face-related information for decoding social intentions from action observations, in line with previous studies (Bekkali et al., 2022; Betti et al., 2019; Sartori et al., 2011). Our study did not pinpoint specific features of the face or head that were relevant for determining participants' performance. Gaze movements are known to be crucial social cues, and previous studies on action observation using full grasping or pointing actions as stimuli have shown that gaze is relevant for both predicting action direction and disambiguating action intention.

It is important to note that in our study, there were no differences in gaze behavior in the video stimuli, so gaze direction alone could not explain differences in participants' performances. Nonetheless, a previous study (Vaziri-Pashkam et al., 2017) has demonstrated the relevance of subtle preparatory movements for different effectors, including the face and arm, which could help viewers integrate information from multiple effectors to predict the outcome of an action. While the face was the most attended stimulus as measured by fixations, this does not exclude participants' capacity to simultaneously gather information from peripheral cues (i.e., the whole body) or kinematic features like action execution speed or final hand positioning on the object.

3.7. Outlook and limitations

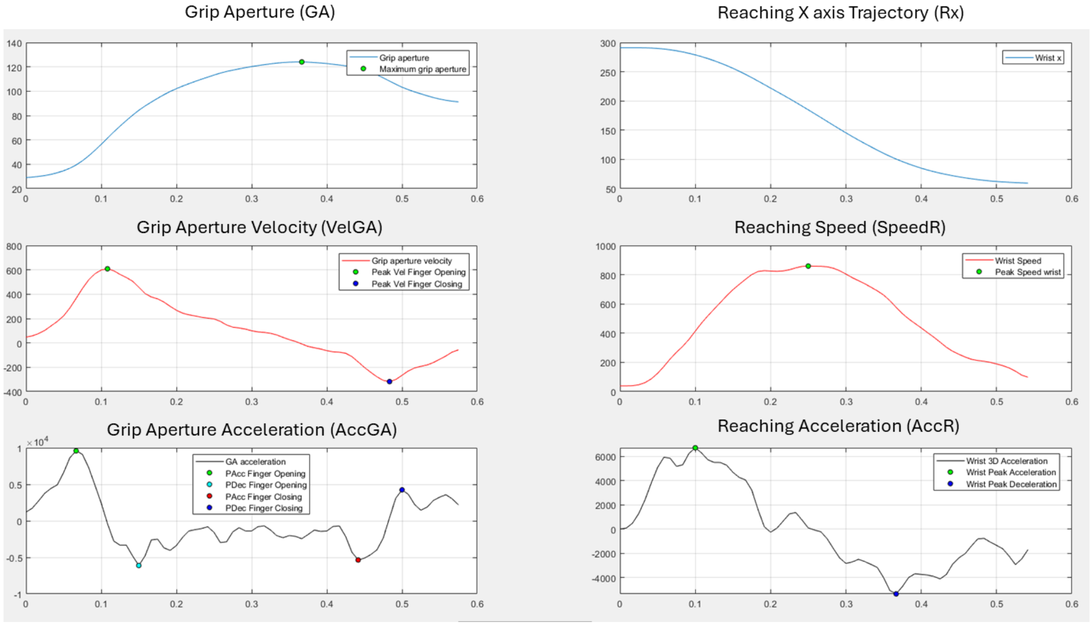
Our results call for further investigation and testing to overcome some important limitations of our study. First, it must be stressed that the Action Observation tasks were tested on a restricted set of stimuli, as done in previous studies employing similar paradigms. While the rationale behind the selection procedure is to diminish within-action kinematics variability and emphasize action differences based on measured averages, this limits the possibility of extending and generalizing our results. To our knowledge, only one study has systematically manipulated the available kinematics variability from a set of stimuli, measuring the impact on action prediction performance (Cavallo et al., 2016), demonstrating that larger sampling from executed actions significantly impacts prediction accuracy. Another limitation of our study might be related to our selection procedure of representative movements based on the kinematics principal components, which favoured reaching speed and grip aperture as the parameters for selection. This is particularly relevant considering that our classification analysis revealed the grip approach and hand position on the object as major features predicting participants' intention decoding. While this aspect supports hand positioning on the object as a potentially relevant kinematic marker of social intention in interpersonal motor coordination, we did not replicate the results through a second selection procedure based on this criterion.

Another limitation of our study is that the Action Observation tasks employed an explicit measure of action prediction (i.e., guessing the outcome of the action) with low ecological validity. First, as previously discussed, studies employing tasks where prediction processes were either inferred from physiological parameters or tied to action selection needs demonstrated the relevance of the nature of the task in modulating prediction abilities and behavioral responses. Secondly, an early criticism to the kind of paradigm employed in our study emphasized that a binary forced choice task is not strongly representative of our typical everyday interactions (Krishnan-Barman et al., 2017; Obhi, 2012). Indeed, we did not test for multiple social contexts (e.g., cooperating vs. competing) or multiple individualistic actions. Nonetheless, this was beyond our scope, as our focus was to compare two actions based on the presence or absence of a social intention and to individuate potential kinematic markers of social condition to be further explored in different experimental paradigms. A third aspect regarding ecological validity is that our stimuli were 2D videos, which are nowadays considered of low ecological value when studying social interaction (Fan et al., 2021). Adopting more engaging stimuli (e.g., 3D VR) and more naturalistic settings (e.g., real interaction in the physical space) could help to disentangle the specific interplay among bodily effectors in dynamic motor exchanges and assess the relevance of the kinematics social marker discussed so far.

A final limitation of our study is that we did not profile participants in terms of social skills, psychological traits, or motor skills assessment, which might have provided more information about their performance. Since previous studies have demonstrated a relevant correlation between subjective differences in these domains and predictive abilities, we suggest that future replication studies or studies employing similar paradigms include these measurements to provide further insights.

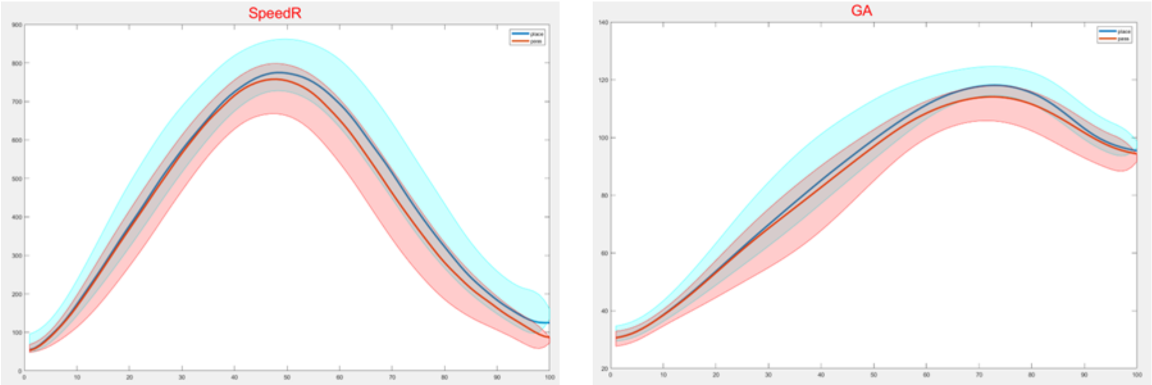
3.8. Supplementary Materials

1. Kinematics recording: apparatus and acquisition parameters



Supplementary Figure 1 *– Kinematic Curves. Screenshot of the MATLAB code output showing examples of kinematic curves. The X-axes represent time in seconds, while the Y-axes represent spatial parameters (mm), speed parameters (mm/s), and acceleration parameters (mm/s^2).*

2. Stimuli Production and Selection



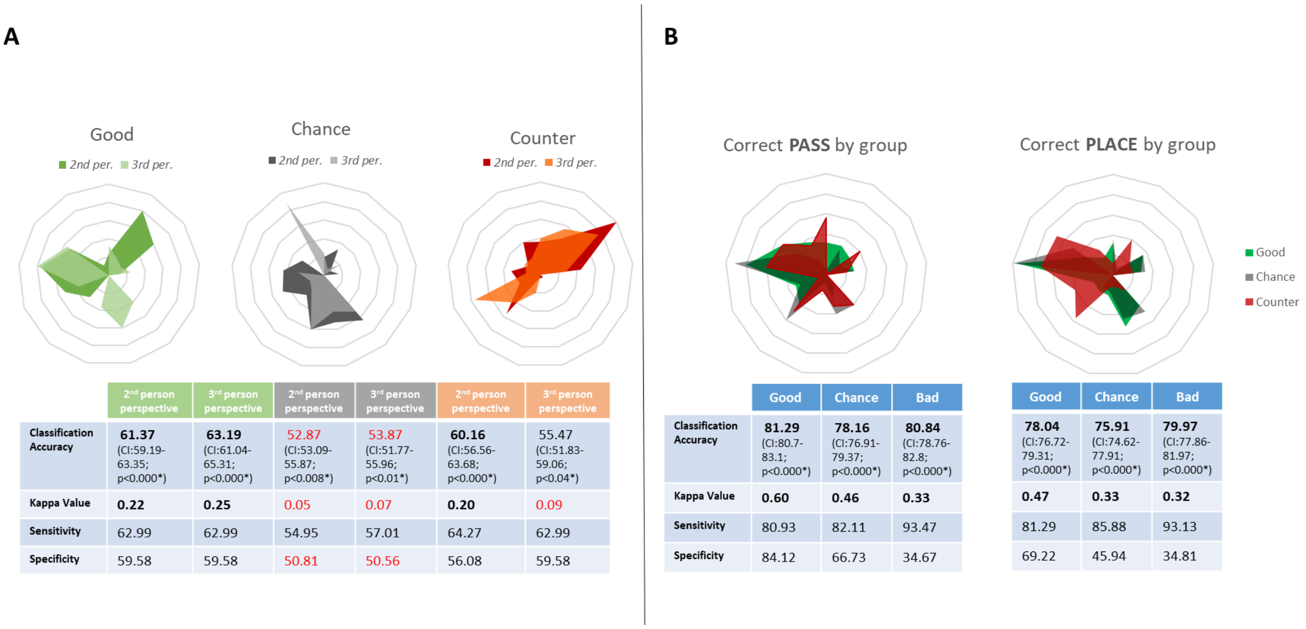
Supplementary Figure 2 *– Visualization of the ranges of interest for the selection of representative actions for Pass (light blue) and Place (pink) actions on the Reaching Speed (SpeedR) and Grip Aperture (GA) curves. Thick coloured lines indicate averages. Shaded areas represent standard deviation ranges employed for action selection (+1 to -0.5 for placing actions, +0.5 to -1 for passing actions).*

3. Results Experiment 2: Decoding of social actions from kinematics

Interactions of the Confidence Rating Factor in the Accuracy and RTs LMMs:

Confidence Rating interacted with the Goal factor [$X^2_{(3)}$= 29.76, p<0.000], as trials for PASS actions rated with the maximal confidence rating (i.e., 4 out of 4) were significantly more correct than those for PLACE actions [$t_{(9526)}$= 2.81, p=0.005]. Confidence Rating also interacted with the Performance factor [$X^2_{(6)}$= 36.72, p<0.000]. The 'good' group responses with the highest level of confidence held the most accuracy [4, M=66.9, CIs=70.45-63.35; 3, M=58.2, CIs=60.6-53.8; 2, M=55.7, CIs=58.6-52.8; 1, M=52.7, CIs=57.3-48.1; for 4 vs. 1,2, and 3, all ps<0.00], while the opposite was true for the 'counter' group [4, M=36.3, CIs=41.8-30.7; 3, M=44.2, CIs=48-40.4; 2, M=46.7, CIs=51.7-41.8; 1, M=52.2, CIs=62.6-45.1; for 4 vs. 2 and 1, all ps<0.03]. The 'chance' group did not show significant differences in accuracy throughout levels of confidence [4, M=53.8, CIs=58.7-48.9; 3, M=49.9, CIs=52.3-47.5; 2, M=51.7, CIs=54-49.3; 1, M=48.9, CIs=53.8-44; for every contrast, all ps>0.5]. Lastly, a triple interaction between Confidence Rating, Performance, and Goal factor was found [$X^2_{(6)}$= 77.93, p<0.000]. The 'good' group responses with higher confidence ratings toward PASS actions were significantly more accurate than those for PLACE actions from the same group [PASS: 4, M=79.1, CIs=83.9-74.2; 3, M=60.3, CIs=63.7-56.9; PLACE: 4, M=52.8, CIs=57.9-47.7; 3, M=54, CIs=57.5-50.5; for 4 and 3, all ps<0.000]. The 'chance' group had significantly more accurate answers for PASS actions when they indicated a moderately high level of confidence (i.e., 3 out of 4) [PASS: 3, M=55.6, CIs=59-52.3; PLACE: 3, M=44.2, CIs=47.5-40.8, p<0.000], whereas they had more accurate answers for PLACE actions when they indicated a moderately low level of confidence (i.e., 2 out of 4) [PASS: 2, M=46.7, CIs=50-43.5; PLACE: 2, M=56.6, CIs=60-53.3; p<0.000]; the opposite was true for the 'bad' group [PASS: 3, M=39.1, CIs=44.5-33.7; PLACE: 3, M=49.3, CIs=54.5-44, p=0.007; PASS: 2, M=52.3, CIs=59.3-45.2; PLACE: 2, M=41.2, CIs=48.1-34.3, p=0.02]. Overall, results from confidence rating are in accordance with effects found for interactions between Performance and Goal in accuracy and RT scores.

Classification Analysis results by Subgroup:

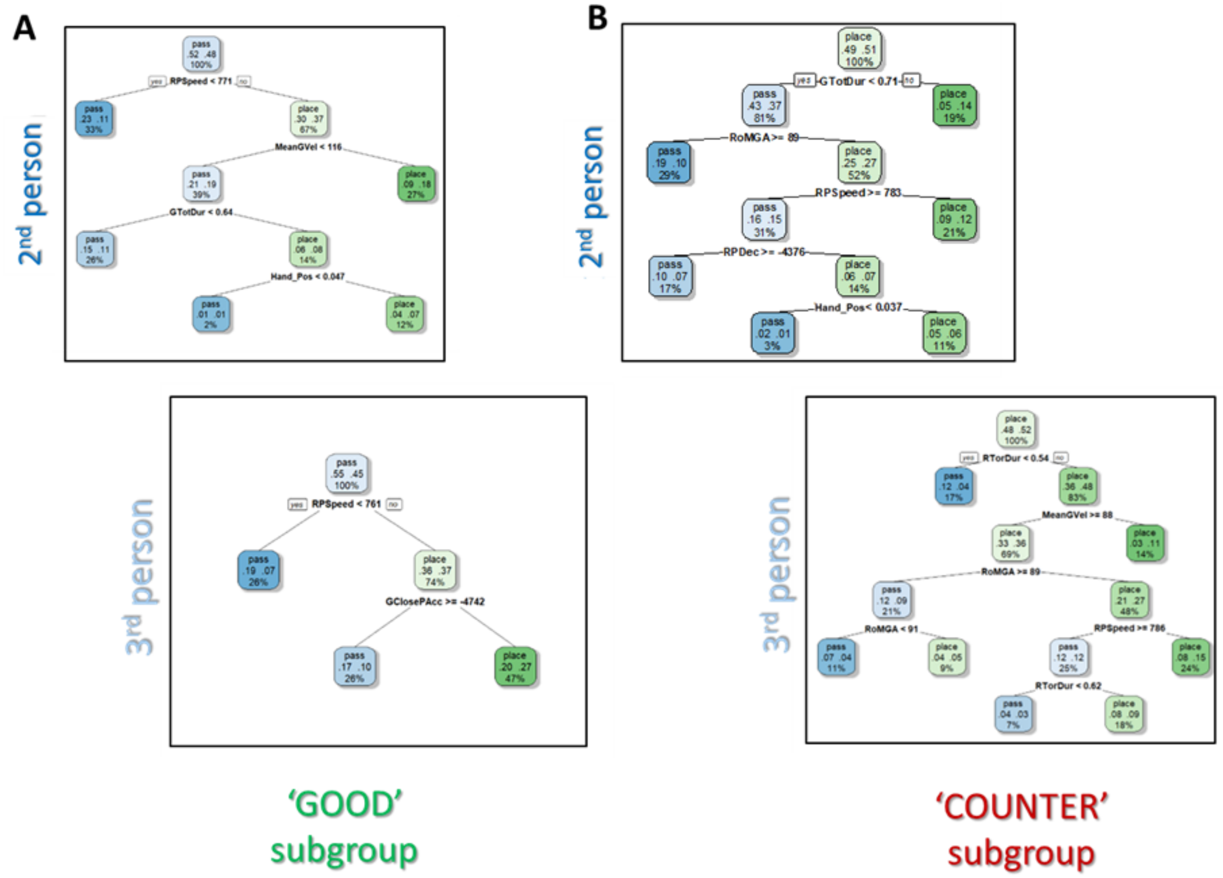


	2nd person perspective	3rd person perspective	2nd person perspective	3rd person perspective	2nd person perspective	3rd person perspective
Classification Accuracy	**61.37** (CI:59.19-63.35; p<0.000*)	**63.19** (CI:61.04-65.31; p<0.000*)	52.87 (CI:53.09-55.87; p<0.008*)	53.87 (CI:51.77-55.96; p<0.01*)	**60.16** (CI:56.56-63.68; p<0.000*)	55.47 (CI:51.83-59.06; p<0.04*)
Kappa Value	**0.22**	**0.25**	0.05	0.07	**0.20**	0.09
Sensitivity	62.99	62.99	54.95	57.01	64.27	62.99
Specificity	59.58	59.58	50.81	50.56	56.08	59.58

	Good	Chance	Bad
Classification Accuracy	**81.29** (CI:80.7-83.1; p<0.000*)	**78.16** (CI:76.91-79.37; p<0.000*)	**80.84** (CI:78.76-82.8; p<0.000*)
Kappa Value	**0.60**	**0.46**	**0.33**
Sensitivity	80.93	82.11	93.47
Specificity	84.12	66.73	34.67

Good	Chance	Bad
78.04 (CI:76.72-79.31; p<0.000*)	**75.91** (CI:74.62-77.91; p<0.000*)	**79.97** (CI:77.86-81.97; p<0.000*)
0.47	**0.33**	**0.32**
81.29	85.88	93.13
69.22	45.94	34.81

***Supplementary Figure 3** – The figure shows the main results obtained at the subgroup level in Action Prediction 1. Polar plots represent the relative weight of each kinematic variable (see Fig. 2B in the paper for list and order) in response prediction; tables report parameters of classification performance. **(A)** reports results for kinematic predictors of subgroups' choices, while **(B)** reports results for kinematic predictors of correct responses for subgroups.*



Supplementary Figure 4 *– Decision trees for the 'good' (A) and 'counter' (B) subgroups. RoMGA= Grasp Range of Motion; GTotDur= Grasp Total Duration; MeanGVel= Mean Grasp Velocity; GOpenPVel= Grasp Open Peak Velocity; GOpenPDec= Grasp Open Peak Deceleration; GClosePVel= Grasp Close Peak Velocity; GClosePAcc= Grasp Close Peak Acceleration; GClosePDec= Grasp Close Peak Deceleration; RTotDur= Reaching Total Duration; RPSpeed= Reaching Speed; RPDec= Reaching Peak Deceleration; Rdistance= Reaching Distance; Hand_Pos= Hand Position.*

4. Study 2 (fMRI): Neural substrates for the processing of potential social interactions

4.1. Introduction

Among environmental stimuli, the multifaceted and unpredictable nature of other agents' behaviour poses specific cognitive challenges to animals' cognitive systems (Humprey, 1978; Dunbar and Shultz, 2009; FieldmanHall and Shenhav, 2019). In this regard, over the last 30 years, the concept of 'Social Brain' solidly established itself as a construct in system and cognitive neuroscience referring to the existence, in the primates' brain especially, of brain networks specialised in processing information related to other agents and interactions with them, i.e., social cognition (Adolph, 2009; Lieberman, 2007; Frith and Frith, 2012). Driven by early studies showing neuronal selectivity for agents' bodily expressions in monkeys (Perrett et al., 1985; Brothers, 1990b) and by the discovery of developmental milestones in social skills in humans regarding the acquisition of 'mentalizing' skills (cf. Wimmer and Perner, 1983; Baron-Cohen, 1995), it has been influentially proposed (cf. Cacioppo et al., 2001) that brain representations of other agents' mental and bodily states are essential for accomplishing different social tasks including social inferential reasoning, prosocial behaviour, and prediction of others' actions in the environment (Brothers and Ring, 1992; Adolph, 1999).

In the human brain, two systems have attracted interest as relevant neural substrates for the processing of other agents: the parieto-frontal Mirror Neuron System (MNS), active during the observation and execution of motor actions (Gallese et al., 1996; Molenbergh et al., 2012; Rizzolatti and Sinigaglia, 2016), and the so-called 'Mentalizing' (MENTA) network , that is a set of areas, most notably the dorsomesial Prefrontal Cortex (dmPFC) and the Temporo-Parietal Junction (TPJ) (Saxe and Kanwisher, 2003; Gallagher and Frith, 2003; Kennedy and Adolphs, 2012), found to be consistently active during tasks requiring individuals to explicitly reflect on others' ideas and beliefs, i.e., Theory of Mind (ToM) tasks. These two networks are usually taken to deal with qualitatively different kinds of social information (see Wheatley et al., 2007; Spunt et al., 2011; Alcalá-López, 2019; Geiger et al., 2019), with the former specialized for processing 'low-level' sensorimotor information about others' bodily displays, like motor goals and kinematics (Cattaneo et al., 2009; Giese and Rizzolatti, 2015), while the latter primarily involved in representing 'high-level' features of others' thoughts and mental states, like intentions or affective states (Saxe, 2006; Skerry and Saxe, 2015; Thornton et al., 2019; Frith and Frith, 2021).

However, although initial meta-analysis on fMRI data provided evidence for this functional distinction (Van Overwalle and Baetes 2009; Molenbergh et al. 2016), the specific computations, functional properties, and ultimately roles of both MSN and MENTA in social cognition are far from being fully understood, being a matter of debate to date. For example, research has highlighted the involvement of both systems in very diverse mentalizing and social tasks (Schurtz et al., 2014; Thye et al., 2018; Schmidt et al., 2021, Boccadoro et al., 2021), demonstrating that the degree to which the two are involved in the processing of high or low agent's features is far from clear. Moreover, although fMRI evidence consistently reported the involvement of areas of the MENTA system during ToM tasks, decisive evidence regarding their exact functional role in ToM tasks is still lacking, as the abundant functional data is counterbalanced by contradicting (Bird et al 2004, Apperly et al., 2006; Cohen-Zimerman 2020) or poor (cf. Lieberman et al., 2019) evidence from lesion-based data and causally oriented approaches. Moreover, areas like the dmPFC and TPJ are known to be involved in a wide variety of processes beyond social cognition, ranging from semantic and autobiographical memory (Lieberman et al., 2019) to executive control (see Narayan et al., 2006; Matsuzaka et al., 2012; Kolling and O'Reilly, 2018) for the dmPFC, and from sensory integration (Blanke and Arzy, 2005; Geng and Vossel 2013) to regulation of endogenous attention (cf. Corbetta et al., 2008) and visuo-spatial processing (Pisella et al., 2011; Ionta et al., 2011) in the TPJ.

Similarly, the MNS's role in cognitive function is yet to be fully disclosed. Studies about mirror phenomena in humans have revolved around the foundational hypothesis that the premotor activity evoked by attending unfolding actions might underpin a bodily-mediated form of action understanding (Rizzolatti et al., 2001). According to the original interpretation of the mirror mechanism, this would be achieved by the automatic sensorimotor mapping of the perceived action onto the motor code for executing it, which would allow internal simulation processes to disclose the action meaning (Gallese, 2003; Kilner et al., 2007). While both functional

(Hardwick et al., 2018) and causal (Naish et al., 2014; Urgesi et al., 2014; Keysers et al., 2018) data confirm a role for nodes of the MNS in the discrimination and perception of others' bodily displays, MNS's precise role in mediating other agents' understanding is still unclear and unsettled (cf. Thompson, Bird, and Catmur 2019; Bekkali et al., 2021; Kemmerer, 2023). Furthermore, the original description of the mirror mechanism is evolving, as data from electrophysiology and fMRI in the last 30 years (Bonini et al., 2022) demonstrated that its core feature is the pragmatic coding of others' actions, including not only congruent action coding but also flexible motor response preparation (see also Sartori and Betti, 2015). In addition, expanding evidence is highlighting the relevance of mirroring outside the classic premotor MNS, with research demonstrating the involvement of mirror affective and proprioceptive responses in regulating social skills like empathy and prosocial behavior (Gallo et al., 2018; Caspar et al., 2020; Del Vecchio et al., 2024).

In light of this complex picture, many authors have expressed dissatisfaction with the traditional way of addressing computations in areas of the social brain, highlighting the methodological limits of dichotomising social tasks into action observation and reasoning about mental states (De Jaegher et al., 2010; see Tylen et al., 2012; Schilbach et al., 2013). A different approach came from the more recent 'second-person neuroscience' proposal (Schilbach, 2010; Gallese, 2016), which holds that adopting more ecological and interactive settings along with "solipsistic" tasks is a necessary effort to correctly frame brain functions and cognitive mechanisms involved in processing social information (see Shamay-Tsoory et al. 2019; Dingenmanse et al., 2023).

Indeed, evidence showed that actual or potential direct interaction with other agents leads to different involvement and functioning of social brain regions. For example, frontoparietal MNS regions respond more strongly to socially meaningful actions like intentional communicative signals (e.g. from gestures and speech) (Möttönen et al. 2016; Maffei et al. 2020) and to actions executed with a social purpose in comparison to non-social actions (Becchio et al., 2012; Tylen et al., 2012; Mainieri et al., 2013). Hyperscanning techniques highlighted interbrain synchrony in premotor areas during interactions, showing that synchronization grows with the social coordination required by the task (Tognoli et al. 2007; Saito et al. 2010; Cheng et al. 2022).

Interestingly, online monitoring of others' actions or gaze during interpersonal coordination enhances the functional connectivity of motor regions with both the dmPFC (Wang et al., 2011; Ciaramidaro et al. 2014) and the TPJ (Sperduti 2014; Miyata 2020), suggesting that together with the MNs they form an extended network for updating internal models of the ongoing interactions. Supporting this interpretation, excitatory or inhibitory stimulation of frontoparietal MNS regions is known to modulate individuals' propensity to spontaneously imitate and their overall ability to follow imitation or counterimitation instructions during motor coordination (Hogeeven et al 2015; Nobusako et al., 2017; Reader et al. 2018). Crucially, a similar influence on action control is found when trascranially stimulating regions of the TPJ, showing both enhancement and degradation of performances in tasks which require clearly distinguishing motor representations of the self from those regarding others (Uddin et al. 2006; Giardina et al. 2015; Bardi, Gheza, and Brass 2017).

Finally, neuroimaging studies have shown that MENTA regions strongly respond to social stimuli without specific mentalization tasks. For example, neuroimaging and electrophysiological data have shown the consistent involvement of the dmPFC in gaze and attention monitoring (Bristow et al., 2007; Schilbach et al., 2010; Hayashi et al., 2020; Dal Monte et al., 2022) and its activation through simple eye contact (Kampe et al., 2003; Cavallo et al., 2015). Interestingly, sub-threshold motor activity to observed actions measured by motor-evoked potential (MEPs) is amplified if eye contact is held with the person performing them (Betti et al. 2018; Prinsen and Alaerts, 2019), suggesting that information about others' gaze modulates mirror responses (also see Coudé et al. 2016, Maranesi et al., 2013). In addition, fMRI evidence in both monkeys and humans has reported that premotor and medial prefrontal cortices are more strongly activated by the same communicative facial expressions or actions when directed toward the observer (Nagel et al., 2015; Sheperd and Freiwald, 2018; Sliwa and Freiwald 2019). Interestingly, the TPJ is also found to automatically process information about self and others' visual perspectives (cf. Martin et al., 2019; Graziano et al., 2021), possibly partaking in a network for the computation of perspective-taking during interaction (see Krall et al., 2016; Lamm et al., 2016; Igelström and Graziano, 2017), rather than underpinning 'mindreading' as such.

While perceived potential first-person interaction and socially oriented bodily signals crucially modulate activity in the so-called social brain, the way these areas represent specific information about others during the encoding of potential engagement is not fully clear. To highlight differential neural activity related to second-person contexts, studies typically manipulated one of three levels: the goal of the observed actions; its orientation (e.g., away or toward the observer); and social signalling through eye contact. However, the exact way these levels interact to trigger the encoding of potential interaction and how they drive functional connectivity among social brain regions has not been thoroughly investigated.

With our study, we aimed to more precisely assess how these engagement-relevant components modulate both whole-brain and Social Brain regions' activity. To do so, we performed three different analyses employing both univariate and multivariate pattern analysis (MVPA) approaches to analyse fMRI data acquired during an observation task in which participants observed videos of grasping actions recorded from the study discussed in chapter 2 (Arcuri et al., 2024). With a first univariate contrast, we assessed how engagement-relevant features such as the social nature of the action goal, its directedness toward the observer, and the visibility of the other agent's gaze modulate whole brain activity. We expected to replicate previous studies by highlighting increased activation in premotor areas and dmPFC for actions with engagement-relevant features. With a second univariate contrast, we adopted a parametric modulation design (Wood et al., 2008) to capture a more continuous dimension of second-person encoding, using participants' ratings on the level of perceived engagement of the observed videos as predictors of BOLD modulation. We expected higher perceived engagement to correlate with the presence of engagement-relevant features and to trigger higher activity in MENTA regions. Lastly, we performed a region of interests (ROIs) based Representational Similarity Analysis (RSA) to assess the representational geometry and information specificity of activations recorded in MSN and MENTA areas. Specifically, Representational Similarity Analysis (RSA) has been employed to evaluate the hypothesis of 'representational connectivity' (see Kriegeskorte, Mur, and Bandettini 2008) between areas as the degree of interaction with the observed stimuli increases, together with the specificity of patterns for variables of interest (e.g., gaze sensitivity). Based on the literature, we hypothesized that premotor and prefrontal regions would exhibit high representational correlation, neural patterns would align with models of the social nature of observed actions, the dmPFC and temporal regions would correlate with gaze-based models, and the MNS fronto-parietal regions would show modulation based on action direction, reflecting pragmatic encoding.

4.2. Materials and Methods

The study was approved by the local ethics committee (Comitato Etico dell'Area Vasta Emilia Nord, protocol n. ID SIRER 5476 - 905/2022) and was conducted following the principles expressed in the Declaration of Helsinki. All participants provided written informed consent.

4.2.1 Participants

26 naïve volunteers (13 males and 13 females, mean age 24.3 ± 3.4 years; range 18-36) were recruited via the University of Parma mailing channels, social media, and flyers distributed across the University campuses. All the tasks in the study were administered in Italian, except for an anglophone participant whose given instructions (both verbal and written) were in English. All participants were right-handed according to the Edinburgh Handedness Inventory, had normal or corrected-to-normal vision, and had no previous diagnosis of neurological or psychiatric disorders as assessed by self-report.

4.2.2 Stimuli

The fMRI task involved an observation task using video stimuli. Participants in the scanner viewed video clips from recordings of the kinematics study described in Chapter 2 (cf. Arcuri et al., 2024). These clips featured individuals from the previous study, from now on referred to as “agents”, seated at a table and performing one of two actions on a neutral object (a wooden cube): grasping it to pass to someone (PASS actions) or grasping it to place on a cylindrical pedestal in the centre of the table (PLACE actions).

Each video was 2 seconds long and began with the agent in a starting stance (Figure 11): the right arm resting on the table, with the right hand in a pinching position, and the gaze directed at the object. Both actions shared an initial reach-to-grasp phase, during which the agent grasped the object while maintaining gaze on it. In PLACE actions, the agent lifted, then placed and released the object on the pedestal before beginning to move the arm back, though the full return was not shown as the video was cut 500 milliseconds after object release, with the arm still in motion. In PASS actions, the agent lifted the object, extended the arm fully, and made eye contact with the recipient. These videos were cut 500 milliseconds after the arm was fully extended, showing the agent holding the object mid-air and making eye contact (Figure 4.1). The recipient, though present during the recording, was not visible, as the actions were filmed from two camera angles: one directly in front of the actor and one at a 45-degree angle to the left, obscuring the receiver.

The video clips presented actions from either a third-person (facing away from the observer) or a second-person (facing the observer) perspective. Additionally, the actors wore transparent eyeglasses during filming and, for all the video clips used as stimuli, a copy was created where these were post-edited to appear as black sunglasses, obscuring the gaze. This design resulted in a 2x2x2 factorial structure with GOAL (PASS vs. PLACE actions), PERSPECTIVE (3rd vs. 2nd-person perspectives), and GAZE (visible vs. non-visible gaze) as factors. In this way, each factor is composed of an engagement-relevant feature for the observer (i.e., PASS, 2nd-person perspective, and visible gaze) and a non-engaging feature (PLACE, 3rd-person perspective, and non-visible gaze). This design allows for assessing the effect of specific engagement-relevant features during action observation. Moreover, the interaction between the several factors allowed us to create a stimulus set reflecting an increasing gradient of engagement, from the least engaging condition (“PLACE – 3rd-person – No gaze”) to the most engaging (“PASS - 2nd-person – Gaze”) (Figure 11), with intermediate levels of engagement to show the relevant weight of each feature in conveying potential engagement.

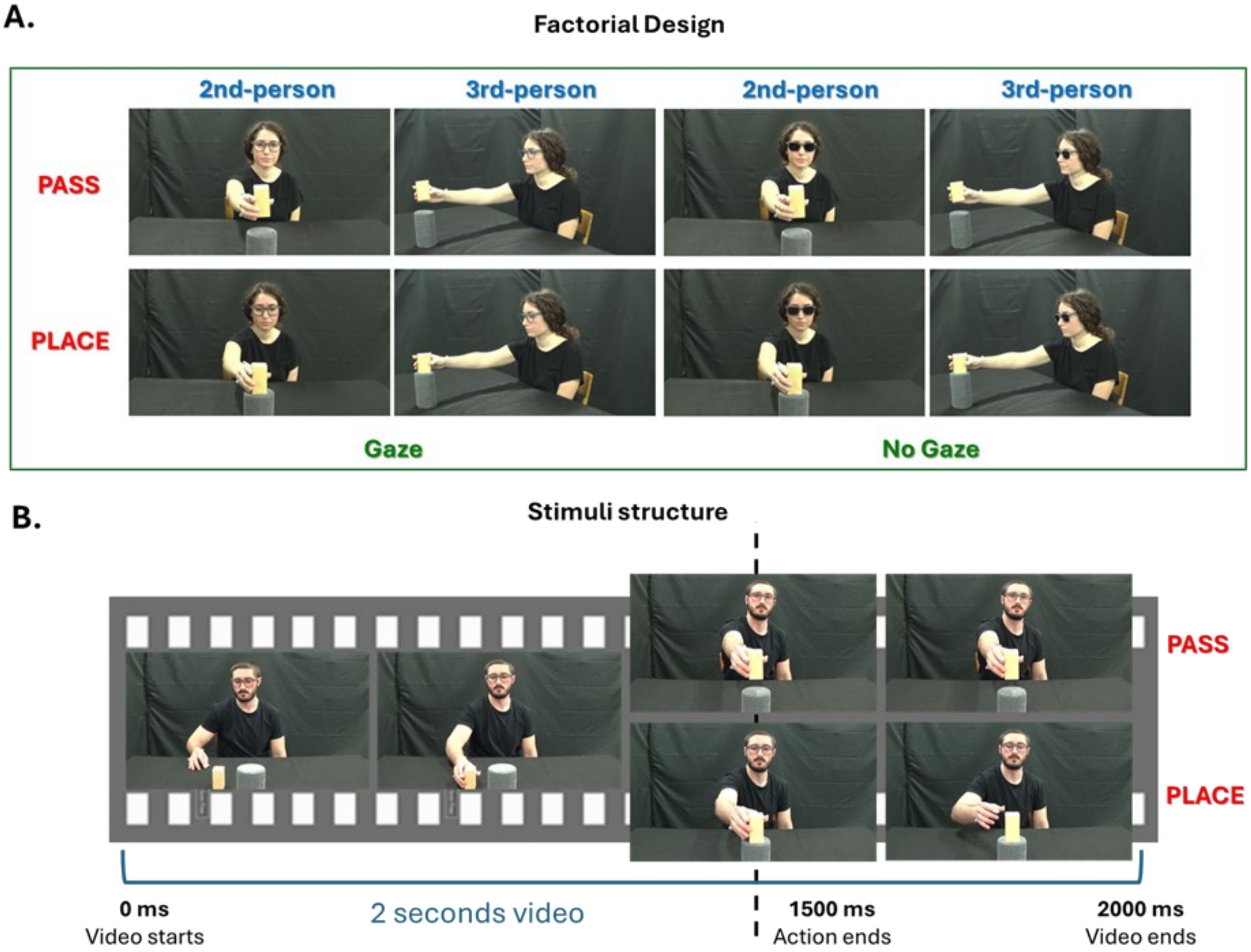


Figure 4.1 | Video stimuli used in the study. (A) Factorial design (2 x 2 x 2) of used conditions. (B) The stimuli structure, equal for all the employed stimuli.

Among the 96 available recorded actions from the action prediction study described in Chapter 2, 8 action stimuli were used to have 1 grasping action for placing and 1 grasping action for passing from 4 different actors (total: 4 unique passing actions, 4 unique placing actions), balanced for sex (i.e., 2 males and 2 females). For each unique action, both first and third-person perspective recordings were used, and each video clip underwent the editing procedure for gaze covering. In total, 32 action stimuli were created, 4 for each condition of the factorial design.

To select the 8 action stimuli among the 96 available, we verified which among the prototypical PASS and PLACE actions employed in the action prediction studies were predicted with the highest accuracy (i.e., % of correct responses), mediating by scores from both

Experiment 2 (only arm kinematic was visible) and Experiment 3 (both arm kinematic and face was visible). Following this procedure, the 2 actors among the 4 female actors available and 2 actors among the 4 male actors available showing the highest scores were selected.

Finally, an additional ninth condition was added, coded as NON-SOCIAL, consisting of 2 videos depicting the environment of the kinematics recordings without agents and only the presence of the object to be grasped, shown from the two perspectives used for actions (SECOND vs. THIRD). Thus, 34 video stimuli were eventually created and employed (32 action videos, 2 non-social videos). The inclusion of the non-social condition was dictated by both methodological necessity (i.e., having a baseline condition for quality check) and for future experimental investigations regarding differences in the coding of affordances and agent processing, which will not be discussed in the present work[2].

4.2.3 Experimental design and procedure

A) fMRI session.

The experimental session consisted of four fMRI runs, each lasting approximately 6.5 minutes, for a total session time of 30 to 32 minutes including breaks between runs. The study employed a presentation of visual stimuli in an event-related design, with a fully randomized presentation of stimuli within each run. Visual stimuli (i.e., videos) were presented to participants in the scanner using MRI-compatible, binocular Full HD OLED goggles (Nordic Neurolab, Norway)

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[2] The videos of the non-social condition present only the action context without agents. However, the object (i.e., a wooden cube) to which the grasping actions are directed is present within. Given the known role of affordance processing in ventral premotor areas (Rizzolatti et al. 1988) and the co-presence of 'canonical' neurons responding to graspable objects and mirror neurons responding to actions (as well as cells showing responses to both stimuli, see Bonini et al. 2014), it was regarded of interest to use the object of the action in both first and third person perspectives as a non-social baseline. Multivariate analysis techniques will be used to assess the representational similarity of patterns to measure the distance between an affordance (non-social) context and an action observation (mirroring and/or social affordance) context. However, it must be noted that adopting this additional factor implies the presence of a condition with a lower total number of repetitions compared to the others in the design. While this fact presents a fundamental problem for univariate analyses, in which the NON-SOCIAL videos will be employed only as regressors in the contrast against baseline (see Section 2.3.6), it does not invalidate the use for this condition in multivariate analyses such as the RSA, where the modelling of the neural pattern occurs at the level of the individual stimulus (see Popal et al. 2019).

positioned close to participants’ eyes, while the presentation and response collection through MRI-compatible Joypad (Nordic Neurolab, Norway) were programmed with the MATLAB software, version R2022b.

Each run comprised 38 trials: 34 ‘observation trials’ and 4 ‘catch trials’ (i.e., 10% of the total). The 34 ‘observation trials’ featured one of the unique videos described earlier, each shown only once per run. This was followed by a black screen with a white fixation cross during a fixed 10-second inter-trial interval (ITI), resulting in a total Stimulus-onset asynchrony (SOA) of 12 seconds (Figure 4.2). Note that the jittering procedure on ITI, usually indicated for optimizing BOLD detection in event-related design (cf. Buckner 1998; Petersen and Dubis 2012), was not adopted here, as previous studies systematically investigating the effect of jittered ITI on stimulus modelling for MVPA analysis, involving modelling at the single stimulus level, showed no significant improvement in analysis results by employing jittered designs (cf. Zeithamova et al., 2017; Popal et al. 2019). Since the action videos were shown only once per run, this resulted in 128 trials to be used for planned analyses, with 4 repetitions per condition for first-level modelling in both multivariate and univariate analyses (see Section 2.3.6). The ‘catch trials’ (16 in total) were randomly selected from the 32 action videos and distributed across the runs. Each 'catch trial' involved the presentation of an action video, followed by a 2-second response window in which participants indicated the goal of the action (i.e., pass or place). This was followed by a fixed ITI of 12 seconds, for a total SOA of 16 seconds (Figure 4.2).

Before entering the scanner, participants were informed that they would complete an observation task, organized in four sessions, involving the continuous, random presentation of brief stimuli of grasping actions with two different goals, punctuated by the appearance of a fixation cross on a black background. They were instructed to maintain focus on the cross when visible and to pay close attention to the action videos. Participants were also told that, at random points, they would be asked to indicate the goal of the observed action within a brief response window. This task helped maintain participants’ engagement and allowed us to monitor attention monitor attention through response accuracy. Participants’ responses were made using the thumb or index finger on a joystick held in their right hand throughout the scan.

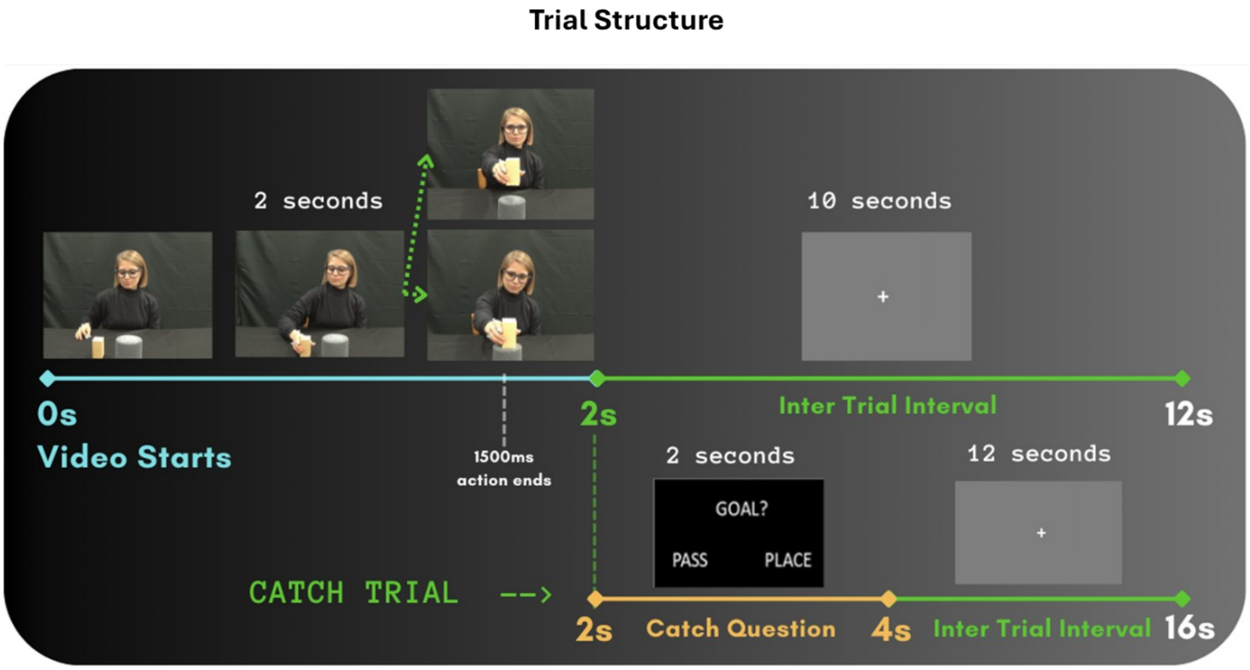

Figure 4.2 | Trial structure. Structure of single observation and catch trials used in the study.

B) Post-fMRI survey: Engagement Evaluation Questionnaire (EEQ)

Following the fMRI session, participants completed an online questionnaire created with PsychoPy (Peirce et al., 2022) and administered via Pavlovia.org. They were asked to re-evaluate the action stimuli from the experiment, rating specific parameters on a continuous scale (1 to 100; values were hidden to participants). In the questionnaire, each video was presented once, followed by a request to provide a rating ranging from “Not at all” (Italian version: “per niente”) to “A lot” (Italian version: “molto”) for the questions:

- *Question 1 (Q1)*: «How communicative does the action seem to you?» (Italian: “Quanto ti sembra comunicativa l’azione?”)

- *Question 2 (Q2):* «How potentially involved do you feel in the action observed?» (Italian: “Quanto ti senti potenzialmente coinvolto nell’azione osservata?”)

- *Question 3 (Q3):* «How much does the video make you feel observed?» (Italian: “Quanto ti fa sentire osservato il video?”)

The responses to these three questions were used to calculate an ‘Engagement Index’ (see Section 4.2.4) to assess the explicit perception of the level of involvement and potential interaction conveyed by the observed action. To assess consistency in ratings, we requested the completion of the EEQ to an independent sample of 24 participants (12 males, 12 females) contacted from the previous studies described in Chapter 2. The obtained indices were further employed at both the individual subject and group levels for the fMRI parametric modulation analysis and to create behavioural dissimilarity matrices for comparison with neural pattern matrices (see Section 4.2.6).

4.2.4 Stimuli and Behavioral analysis: Engagement Index

As mentioned above, the EEQ was submitted to both the sample of participants from the fMRI study and an independent sample to assess consistency in stimuli evaluation. To this aim, a t-test plus a Pearson correlation analysis (function '*cor*' in R 2021) was performed between the two averaged scores of each group. The results showed strongly consistent rating among groups, as the value of correlation among the two groups was 0.93 and the t-test did not evidence significant differences among means [p=0.94]. We thus decided to employ the ratings from both samples to obtain a mean EEQ score, with one value per question per video (32 videos x 3 questions).

Before proceeding to employ scores from the EEQ for further analysis, we wanted to compute an 'Engagement Index' (EI) by combining ratings from the EEQ's three questions. We wanted to evaluate if each question captured its specific, unique dimensions (e.g., communicativeness for Q1; interactiveness for Q2; feeling of being observed for Q3) or if they together pertained to a broader, common dimension related to the perceived engagement. For this reason, we performed a principal component analysis (PCA) on participants' scores from both the fMRI sample and the independent sample. The PCA was performed using the software R (2021) built-in functions '*prcomp*'.

Two main components emerged from the PCA which accounted for 94% of the variance (Figure 4.3A). The first component, PC1, accounted for most of the variance with a value of 75.71% while the second component, PC2, accounted for 19.22% of the total variance. For PC1, all three questions held similar weights and the same sign, suggesting that congruent co-variation of the three ratings represents the major dimension of the data. Thus, we take PC1 to be a global representation of perceived ‘Engagement’. On the other hand, PC2 shows a contrast between Q1 and Q2+Q3. We take this component to dissociate the ‘Communicative’ feature of our stimuli from the purely ‘Interactive’ aspects, associated in this case with the feeling of potential involvement and the feeling of being observed.

Our interpretation of the two components is further supported by looking at the distribution of values assigned to the action videos in the new dimensional space. As it can be noted (Figure 4.3B), for the PC1, EIs were distributed mostly along the GOAL factor, with ‘PASS’ having, on average, the highest positive values (which in this case correlate with higher scores on the three questions) and ‘PLACE videos’ showing the lowest values. Moreover, ‘PASS – 2nd-person – Gaze’ videos showed the highest positive values, followed by ‘2nd-person’ PLACE and PASS, ‘PASS-3rd-person’, and ‘PLACE – 3rd-person’, which yielded the lowest value. This disposition roughly matches our hypothesized gradient for perceived engagement according to the combination of engagement-relevant and non-engaging features. Interestingly, the Gaze factor seems relevant only for the PASS stimuli.

On the other hand, EIs in the PC2 showed a distribution prevalently along the PERSPECTIVE factor, with ‘2nd-person’ videos having the highest positive value and ‘3rd-person’ videos having the highest negative value. Also note that ‘PASS-3rd-person’’ videos had the highest negative scores, denoting more communicativeness with respect to ‘PLACE – 3rd-person’.

A.

Question	PC1	PC2
Q1 (Communicative)	-0.5	-0.863
Q2 (Involvement)	-0.615	0.305
Q2 (Feel observed)	-0.608	0.4
% of variance	**0.75**	**0.19**
Cumulative %	0.75	0.94

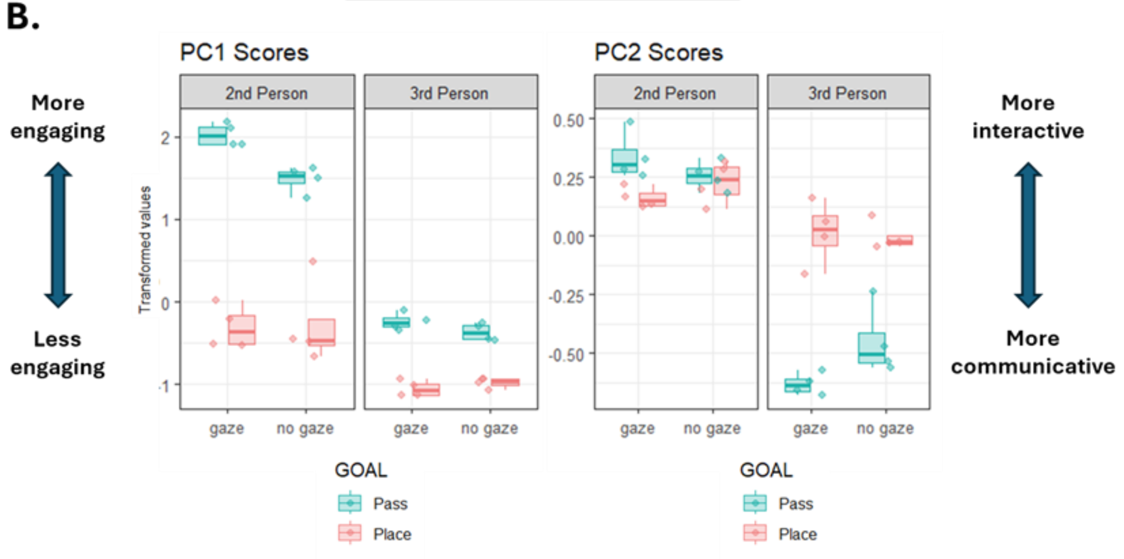

Figure 4.3 | Analysis of the Engagement Index. (A) Table reporting the outcome of the PCA on participants' scores to the EEQ. (B) Boxplots showing the distribution of values relative to PC1 and PC2 for video category.

In conclusion, according to our analysis of the EI, we take our stimuli to have efficiently captured two relevant dimensions of perceived engagement, one related to a "global" component in which the engagement-relevant features go together in conveying potential engagement, and one related to a more specific interactive-relevant aspect of our design, possibly related to the orientation of observed action: actions facing the observer are perceived as affording potential interaction, partially (but not fully) regardless of the action goal.

4.2.5 Image acquisition

Structural T1-weighted and functional T2*-weighted MR images were acquired with a 3T General Electric scanner (SIGNA Premier 3T wide-bore MRI scanner) equipped with a 48-channel head-coil. BOLD images were acquired with the following parameters: 70 axial slices of functional images covering the whole brain; slices acquisition was in an interleaved bottom-up order using gradient-echo echo-planar imaging (EPI) pulse sequence with a multiband factor of 2; in-plane resolution = 2.0 mm isotropic voxels; slice thickness = 2.0 mm, without a gap between slices; TR = 2000 ms, TE = 30 ms; FOV = 256 mm; flip angle = 90°. For 15 participants, BOLD images were acquired with an Antero-Posterior (AP) phase encoding (PE) direction, while for 11 participants BOLD images were acquired with a Postero-Anterior (PA) direction. This peculiar condition of our sample, due to a human mistake, required specific measures for distortion field correction to be further adopted in the preprocessing phase (see Section 4.2.6) in order to have comparable data for the group-level analyses.

For the structural acquisition, a high-resolution 3D T1-weighted MP-RAGE (Magnetization Prepared - RApid Gradient Echo) volume covering the whole brain was acquired for anatomical reference, with the following parameters: 256 axial slices; in-plane spatial resolution 1 mm isotropic; FOV = 256 mm; TI = 1100 ms; TE = 3.1 ms; TR = 2070 ms; flip angle 8°.

4.2.6 Functional MRI preprocessing

Functional image preprocessing was performed using FEAT (FMRI Expert Analysis Tool, Jenkinson et al., 2012) v6.00, implemented in FSL (https://fsl.fMRIb.ox.ac.uk/fsl), version 6.0.7. For structural processing, the software ANTs (Advanced Normalization Tools, https://stnava.github.io/ANTs) was used for brain extraction and intensity nonuniformity correction, while FSL's package FAST (FMRIB's Automated Segmentation Tool) was used for tissue segmentation.

All anatomical T1-weighted images underwent the following preprocessing steps: correction for radiofrequency (RF) intensity and skull-strip employing the software ANTs (bash script 'antsBrainExtraction.sh'[3] implemented on personal bash scripts); segmentation of brain tissues (cerebrospinal fluid CSF, White matter WM, and Grey matter GM) on the corrected and brain-extracted T1-weighted images using FSL's package FAST; visual check for quality evaluation.

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[3] https://github.com/ANTsX/ANTs/blob/master/Scripts/antsBrainExtraction.sh

Before proceeding with the full preprocessing pipeline for functional images, a synthetic, undistorted BOLD image for each run of each participant was generated with the tool SynBOLD-DisCo (Synthetic BOLD contrast for Distortion Correction, Yu et al. 2023). Synthetic images were produced using the preprocessed T1-weighted image and the raw 4D BOLD images as inputs[4]. The synthetic, undistorted BOLD images were used together with the original distorted BOLD images as input to the FSL's package TOPUP to perform correction of spatial distortions due to magnetic field susceptibility on the functional images. This step was regarded as necessary for two main reasons: first, obtaining an overall better quality of voxel displacement in the brain's prefrontal areas, in which one of the ROI is located (dmPFC); second, and most importantly, to uniform our sample which suffered from having two different PE direction (see Section 4.2.4). Further statistical testing has been carried out to control significant differences between the two groups in the z-map obtained by our GLM models (see section 4.2.7).

All functional images underwent the following preprocessing steps: distortion field correction (TOPUP package); motion estimation and correction through rigid body transformation with 6 degrees of freedom (DOF), MCFLIRT package (Jenkinson et al., 2002); slice timing correction using Fourier-space time-series phase-shifting; co-registration (6 DOF) of BOLD images to the standardised T1-weighted (12 DOF, FNIRT package, MNI128 template as reference) with FLIRT boundary-based registration (BBR); spatial smoothing using a 4mm FWHM Gaussian kernel; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; High pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=30.0s) for removing low frequency.

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[4] In short, the tool generates a "synthetic, undistorted" BOLD image that matches the geometry of structural T1-weighted images and matches the contrast. The tool employs a Conditional Generative Network, a deep learning technique, trained using a range of datasets, acquired on different scanners, with varying parameters (resolutions, contrasts, distortion magnitudes, etc.). For further information, see Yu et al. 2023.

4.2.7 fMRI Data Analysis

Statistical analyses of fMRI data were carried out using FSL's FEAT to obtain first-level (within-run), second-level (within-subject), and third-level (group) activation maps. The software R (2021) was used for analysing behavioral data and performing RSA on both behavioral and fMRI data.

As explained in the Introduction section, three main fMRI analyses were planned and conducted: two univariate analyses, one factorial and one parametric, and one Multivariate analysis, an RSA. For all fMRI analyses, the response amplitudes to the events of interest (described below for each analysis) were estimated using a General Linear Model (GLM). This produced voxel-wise beta maps, reflecting the estimated beta values from the GLM, which were subsequently converted to z-scores. The average response estimates across runs for each subject (i.e., second-level) were calculated using FSL's fixed-effects model by forcing the random effects variance to zero in FSL's FLAME (FMRIB's Local Analysis of Mixed Effects, cf. Woolrich, 2008). A mixed-effects model (FLAME 1+2 in FSL) was applied for group-level analyses, accounting for both within-subject and between-subject variability. A Cluster-Defining Threshold (CDT) of z = 3.1 was applied to the z-maps to perform cluster-based inference on voxel activity. A Cluster P Threshold of 0.05 was used for family-wise error rate (FWER) based correction to control for multiple comparisons at the cluster level.

As a quality check for group differences due to PE direction, second-level (within-subjects) z-maps of all the contrasts obtained from the analyses were submitted to a permuted 2-sample t-test using the function 'randomise' of the FSL software, using the default setting of 5000 permutations for non-parametric testing of imaging data.

A) Factorial Design (Univariate 1)

A whole-brain univariate approach was adopted to assess differences in brain responses between engagement-relevant features and non-engaging features in the observed actions. A GLM was built which included the following 10 main regressors of interest: the 8 experimental conditions from the 2 x 2 x 2 factorial design (cf. previous section, 4.2.3) related to the action stimuli; the catch trials condition; and the non-social condition. Each of the 10 regressors represented the onset of stimuli related to the condition, with 4 events for action stimuli and catch trials and 2 events for non-social stimuli. The estimated activity waveform for the observation conditions was modelled as a boxcar lasting 2 seconds from the video onset, covering the full video length. Catch trial events were similarly modelled, lasting 2 seconds from the participants' response. Events for each regressor were convolved with the canonical hemodynamic response function (HRF) (i.e., Gamma function, cf. Lindquist et al., 2009) to model the expected BOLD signal. ITI periods between events were considered as implicit baseline. Temporal derivatives of each main regressor were included to account for potential variations in the timing of the hemodynamic response across brain regions, as this might be particularly relevant for brief events acquired at relatively short TR (cf. Sladky et al. 2011). Six head motion parameters (3 translations and 3 rotations) derived from the realignment process were included as nuisance regressors and modelled as covariates of no interest. Lastly, FSL's pre-whitening procedure was applied to account for temporal autocorrelation in the fMRI data (cf. Woolrich et al., 2001). Contrasts between each main regressor versus baseline were calculated for sanity check.

At the first level of analysis, planned comparisons were defined to contrast engagement-relevant features with non-engaging features. For each factor (i.e., GOAL, PERSPECTIVE, and GAZE), linear contrasts were computed in both directions, e.g., for the factor GOAL, both PASS vs. PLACE and PLACE vs. PASS, to isolate the effects of both kinds of features. Note that, because regressors for action stimuli each represent one of the 8 possible combinations of the factorial design, contrasts for a single feature such as PASS were aggregated across multiple regressors. For example, for the contrast PASS vs. PLACE, positive values were assigned to all the conditions which included PASS (i.e., "PASS – 2nd-person – Gaze"; "PASS – 2nd-person – No gaze"; "PASS – 3rd-person – Gaze"; "PASS – 3rd-person – No gaze") and negative values were assigned to all the conditions which included PLACE (i.e., "PLACE – 2nd-person – Gaze"; "PLACE – 2nd-person – No gaze"; "PLACE – 3rd-person – Gaze"; "PLACE – 3rd-person – No gaze"), resulting in a [1 1 1 1 -1 -1 -1 -1 0 0] contrast design.

B) Parametric Modulation Design (Univariate 2)

To evaluate the effects on brain activity of the perceived engagement of observed actions, a whole-brain parametric univariate analysis was employed. Values from the two principal components obtained from the EI analysis were used as parametric modulators of the average response to action stimuli. The GLM comprised 5 main regressors: a regressor with all the action stimuli (n=32); one regressor with PC1 values for each video averaged among participants; one regressor with averaged PC2 values; one regressor for catch trials and one regressor for non-social stimuli. The response function of these regressors was modelled as in the GLM for the Factorial Design. As for the previous GLM, temporal derivatives of each main regressor were included, together with head motion parameters as nuisance regressors. Pre-whitening procedure was applied.

To assess activations correlated with the ‘Engagement’ dimension (PC1) and the ‘Communicative-Interactive’ dimension (PC2), two contrasts for each dimension against the baseline were planned. A “PC1-Positive” contrast [0 1 0 0 0] and a “PC1-Negative” contrast [0 -1 0 0 0] were calculated to assess activity correlated with more (“PC1-Pos”) and less (“PC1-Neg”) perceived engagement. A “PC2-Positive” contrast [0 0 1 0 0] and a “PC2-Negative” contrast [0 0 -1 0 0] were calculated to assess activity correlated with perceived interactivity (“PC2-Pos”) and communicativeness (“PC2-Neg”).

C) ROIs’ RSA (Multivariate)

To investigate the representation of engagement-related features in the MNS and MENTA ROIs, we performed an RSA. The RSA allows for representing the activity profile of an ROI in terms of similarity between neural patterns during different experimental conditions, usually referred to as ‘first-level’ representational similarity (cf. Kriegeskorte et al., 2008). Pairwise comparison of neural activity between each condition generates a matrix, called representational dissimilarity matrix (RDM), reporting similarity values for each comparison according to a given distance measure. The resulting neural RDM is thus taken as a measure of the representational structure of an ROI, described in terms of quantitative distance among neural patterns, and can be further compared for similarity to other RDMs for obtaining a ‘second-level’ representational similarity. Other RDMs can either be obtained from neural activity (e.g., from other ROIs), from behavioral data (e.g., stimuli ratings), or conceptual models regarding the hypothesized representational structure of stimuli in the experiment (cf. Popal et al., 2019).

First-level RDMs. To perform the RSA, we first computed for each subject the RDMs from fMRI data from each ROI. As parameter, we used normalized beta maps from the second level analysis of the Factorial Design GLM, which provided one regressor per condition of the factorial design. Vectors with beta values from ROIs' voxels were extracted from the beta maps per each condition. We took the 1 – *r* (Pearson correlation value) distance between all pairs of vectors (i.e., conditions), resulting in an 8 x 8 matrix (the 8 action conditions). A mean RDMs per ROI was obtained by averaging among participants' RDMs.

To investigate the representational structure of neural patterns in our ROIs, we employed three conceptual models based on our factorial design, reflecting the main features of observed actions: Goal, Perspective, and Gaze. For each model, the engaging-relevant feature of the factor was assigned a value of 1 against the value 0 for the second feature, to mark maximum dissimilarity. Thus, we obtained a GOAL-based RDM, a PERSPECTIVE-based RDM, and a GAZE-based RDMs, respectively (see Figure 4.4A).

RDMs from participants' EEQ scores were also computed to evaluate the similarity between the structure of perceived engagement and brain patterns. For each participant, we computed the Mahalanobis distance between vectors containing the scores from the two principal components previously obtained (averaged among videos of the same condition). Then, we averaged participants' RDMs to produce a mean 'Engagement' RDM. The resulting RDM is reported in Figure 4.4A, highlighted in pink. As it can be noted, in this model the 'PASS-2nd-person' conditions (regardless of gaze visibility) stand in clear contrast to all the other conditions. Thus, the 'Engagement' RDM can be taken to represent a representational structure which differentiates involvement in interaction from all other conditions.

Second-Level RSAs. In our study, we performed and compared two 'second-level' RSAs: a *Neural RSA*, where we computed the distance between all ROIs' RDMs to evaluate inter-ROI representational similarity, and a *Model RSA*, where we computed the distance between each ROIs' RDMs and the behavioral and conceptual RDMs to evaluate the ROIs' functional profiles.

For both RSAs, we computed the Pearson correlation coefficient between the lower triangular portions of the RDMs (excluding the diagonal).

To visualize the representational structure of activity patterns in the neural RSA, we first averaged RDMs across participants in each ROI. We correlated average RDMs across ROIs using Pearson's correlation and false discovery rate (FDR) correction for multiple comparisons to assess significant correlations (cf. Benjamini and Hochberg, 1995). We then used hierarchical clustering and dimensional reduction techniques to visualize representational similarities across brain regions. Unsupervised hierarchical clustering was implemented using the *hcpc* function in the FactoMineR package in R (Lê et al., 2008), which first creates a hierarchical tree based on Ward's method for hierarchical agglomerative clustering (Ward Jr., 1963), and then estimates the optimal number of clusters by calculating the partition with the higher relative loss of inertia (i.e., 'error sum of square') (Randriamihamison et al., 2021). The function then applies PCA to create a factor map with clusters labelled according to the hierarchical tree's output.

For the model RSA, each ROI was tested for similarity on 4 different models. To guarantee both the robustness of results and assess the entity of non-significant tests, we adopted a novel approach outlined by (Keysers, Gazzola, and Wagenmakers 2020). In this work, the authors argue for the relevance of using measures to assess evidence of absence when non-significant results emerge, proposing Bayesian hypothesis testing as a tool apt for this goal. Accordingly, we performed two parallel statistical tests on our participants' RSA scores: first, to assess significant RSA scores, we used a one-tailed student t-test for each model in each ROI. Statistical significance was set at .05 and we applied false discovery rate (FDR) correction for multiple comparisons following (Benjamini and Hochberg, 1995). Secondly, we applied Bayesian t-Test implemented in JASP (Love et al., 2019) to obtain Bayes Factor (BF) scores for assessing evidence in favor of both the alternative (H1) and null (H0) hypothesis. Unlike traditional p-values, Bayes Factors do not give a fixed threshold for significance (like $p < 0.05$). Instead, they provide graded evidence for or against hypotheses. The interpretation of BF values is continuous and can be expressed on a scale (in this case, a logarithmic scale adapted from Jeffreys' scale). Some points of reference for significance interpretation can be set nonetheless: a value of ≈ 0 indexes no evidence (i.e., equal support for H0 and H1); positive values (i.e., > 0) index increasing evidence for H1, with a $BF \geq 1$

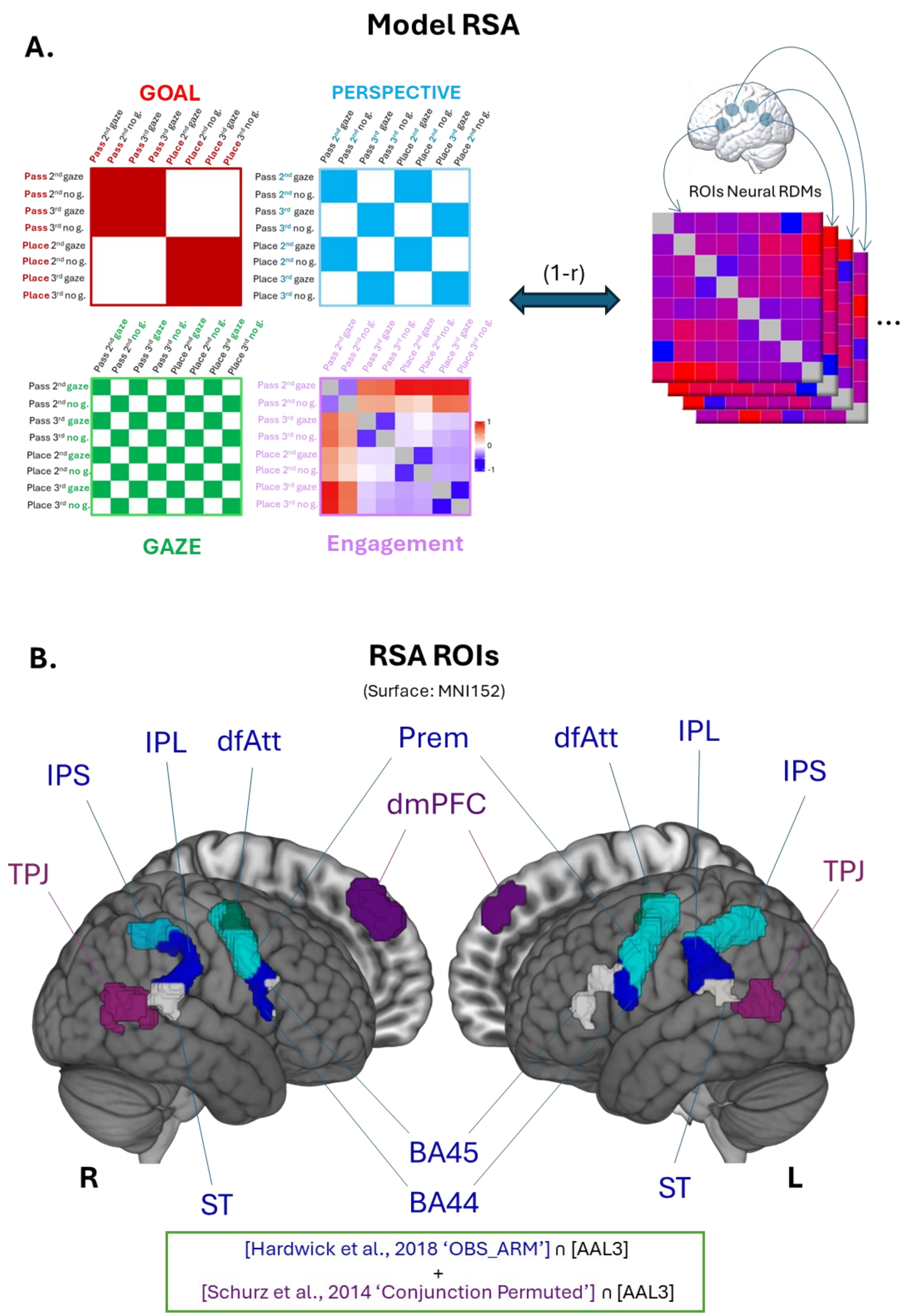


Figure 4.4 | Representational models and ROIs. (A) RDMs for the Goal model (red), Perspective model (light blue), Gaze model (green), and Engagement model (purple frame). Colored cells represent condition pairs with 0 dissimilarity, and white cells represent maximum (1) dissimilarity. The 4 models were tested for correlation with RDMs computed from BOLD activity patterns (example on the right side of the figure) from each ROI for each participant. (B) Visualization of the selected ROIs with the MNI152 template.

indicating moderate evidence (close to a $p < 0.05$), BF ≥ 2.30 strong evidence, BF ≥ 3.40 very strong evidence, BF ≥ 4.60 decisive evidence; the same scale is maintained for negative values to index evidence in favor of the null hypothesis H0 (i.e., BF ≤ -1 moderate evidence, BF ≤ - 2.30 strong evidence etc.). Results from both frequentist and bayes statistics are reported to assess the strength of significant results and trends.

ROI Selection. To define our ROIs, we combined an anatomical (i.e., atlas-defined) criterion together with a functional approach based on relevant meta-analyses aggregating data from previous fMRI studies exploring the MNS and MENTA networks. We used the Automated Anatomical Labelling atlas 3 (AAL3, cf. Rolls et al., 2020) as a reference for brain parcellation, and applied this subdivision to define voxel belonging to the same ROI in binarized functional masks.

For the MNS's functional mask, we used the aggregated activation map for the action observation of upper limb movements from Hardwick et al., 2018 (data freely available at https://osf.io/3egd5). Note that this mask includes both voxels significantly active for both action observation and execution and voxels active for observation only. We decided to adopt this broader action observation map considering the recently highlighted relevance of agent-specific responses in premotor cortices (cf. Bonini et al., 2022) along with 'classic' mirror (i.e., agent-shared) responses. We also decided to focus on lateral premotor, parietal, and temporal sectors of the mask, to focus on 'classic' MNS areas. For the MENTA's functional mask, we used the conjunction map obtained by permutation-based overlap analysis of six meta-analyses addressing six diverse categories of standard mentalizing tasks from Schurtz et al., 2014 (masks courtesy of the main author by private communication). The FSL image calculator *fslmaths* was used to generate parcelled versions of the functional masks according to the AAL3 by multiplying the AAL3 reference image ('aal_mni_v7_2mm.nii.gz', available at https://www.gin.cnrs.fr/en/tools/aal/) with the two functional binary masks.

From the application of the AAL3 to the chosen MNS mask, 18 ROIs were pre-selected using the following labels from the AAL3: Precentral Left and Right; Middle Frontal Gyrus, Left and Right; Superior Frontal Gyrus, Left and Right; IFG *pars triangularis* Left and Right; IFG *pars opercularis* Left and Right; Inferior Parietal Lobule Left and Right; Supramarginal Gyrus Left and

Right; and Superior Temporal Left and Right. We then assessed these pre-selected ROIs and labelled them according to some further anatomical and functional considerations. For example, Precentral ROIs were renamed Premotor (Prem R and Prem L) as they mostly overlapped with Brodmann Area 6 (BA6) according to the Brodmann Atlas. Dorso-frontal voxels in the Middle and Superior Frontal ROIs were rostral to area BA6, possibly overlapping with frontal areas of the dorsal parieto-frontal Attention Network (cf. Corbetta and Shulman, 2002). We employed Hardwick et al. (2018)'s action execution map and an 'attention network' map generated with NeuroSynth (http://www.neurosynth.org) to evaluate these voxels, finding that they overlapped with a cluster of the attention network. Accordingly, we merged voxels from the Middle Frontal Gyrus and Superior Frontal Gyrus ROIs to create unitary dorsofrontal Attention ROIs (dfAtt L and dfAtt R). Inferior Parietal ROIs were renamed IntraParietal Sulcus left (IPS L) and right (IPS R) as they extended adjacently somatosensory cortices and above the Supramarginal Gyri (see figure 4.4). The latter were renamed Inferior Parietal left and right (IPL L and IPL R), accordingly. Areas of the IFG's ROIs were renamed BA44 left and right and BA45 left and right, as these voxels overlapped with these Brodmann areas. Left and Right Superior Temporal ROIs were labelled ST L and ST R respectively. Eventually, 14 ROIs were obtained for the MNS mask (Figure 4.4).

From the application of the AAL to the selected MENTA mask, 4 ROIs were obtained: Superior Medial Frontal Left and Right, which we renamed dorsomesial Prefrontal left (dmPFC L) and right (dmPFC R); Temporal Medial Left and Right, which we renamed Temporo-parietal Junction left (TPJ L) and (TPJ R). In total, 14 ROIs were thus used for the RSA.

All steps for both first-level and second-level RSAs were carried out with a personal script in R.

4.3. Results.

4.3.1 Factorial analysis

Significant results are reported in Table 4.1, while activation maps are shown in Figures 4.5, 4.6, and 4.7 (see below).

Table 4.1 | Brain regions that exhibited significant activation for planned contrasts.

				(coord.)				
Hemisphere	**Region (AAL3)**	**BA**	**x**	**y**	**z**	**z-Score**	**p-Value (FWE)**	**Cluster size (voxel)**
Pass > Place								
None								
Place > Pass								
L	SupraMarginal	42	-62	-20	18	5.06	<0.001	323
L	Temporal Superior	22	-66	-20	14	4.75		
L	SupraMarginal	22	-66	-26	18	4.64		
L	Temporal Superior	42	-58	-24	16	4.32		
L	PostCentral	22	-66	-20	20	4.29		
L	Temporal Superior	42	-56	-30	14	4.09		
R	SupraMarginal	43*	62	-26	30	4.18	0.001	81
R	SupraMarginal	43*	64	-26	22	3.93		
R	SupraMarginal	43*	62	-22	26	3.88		
R	Temporal Superior	42	58	-30	18	3.7		
R	PostCentral	43*	58	-18	32	3.68		
R	SupraMarginal	2	68	-20	28	3.47		
L	Lingual	18	-16	-90	-12	4.25	0.006	67
L	Occipital Inferior	18	-20	-92	-6	4.1		
L	Lingual	18	-16	-86	-12	3.82		
L	Precentral	4	-58	-4	32	4.05	0.049	46
L	Precentral	6	-62	2	30	3.83		
2nd > 3rd								
R	Calcarine	17	12	-78	10	7.16	<0.001	5400
R	Calcarine	18	2	-80	16	6.53		
R	Lingual	17	6	-80	-4	6.51		
R	Lingual	17	4	-70	6	6.44		
L	Lingual	17	-2	-78	0	6.4		
R	Lingual	17	8	-84	-2	6.36		
R	Frontal Inferior Tri.	44	52	24	28	4.26	0.005	67
R	Frontal Inferior Op.	44*	42	18	30	4.21		
R	Frontal Inferior Op.	44	54	20	30	4.11		
R	Frontal Inferior Op.	44*	48	20	30	4.02		
3rd > 2nd								
L	Calcarine	18	-12	-76	6	7.28	<0.001	2848
L	Lingual	18	-12	-68	2	7.27		
L	Lingual	18	-18	-66	2	6.25		

L	Lingual	18	-16	-64	-6	6.17		
L	Cuneus	23*	-8	-72	24	6.16		
L	Cuneus	18	-14	-72	20	6.16		
R	Lingual	19	24	-54	2	4.93	<0.001	579
R	Calcarine	18	14	-66	20	4.83		
R	Calcarine	18	18	-70	18	4.57		
R	Calcarine	17	16	-58	18	4.56		
R	Calcarine	19	22	-60	8	4.53		
R	Calcarine	18	22	-62	20	4.44		
R	Parietal Superior	7	22	-66	60	4.78	<0.001	391
R	Parietal Superior	7	20	-68	56	4.7		
R	Parietal Superior	7	22	-60	58	4.38		
R	Precuneus	5	8	-58	60	4.31		
R	Precuneus	7	16	-70	50	4.18		
R	Occipital Superior	7	20	-64	46	4.12		
L	Occipital Middle	37	-44	-74	8	5.12	<0.001	164
L	Temporal Middle	37	-48	-70	12	4.74		
L	Occipital Middle	37*	-52	-72	6	4.7		
L	Occipital Middle	19	-44	-76	16	4.34		
L	Occipital Middle	19	-44	-74	2	4.28		
L	Occipital Middle	37	-42	-70	4	4.27		
L	Parietal Superior	7	-32	-56	62	4.37	0.001	108
L	Parietal Inferior	40	-38	-54	58	4.22		
L	Parietal Inferior	40	-34	-52	56	4.04		
L	Postcentral	2	-42	-44	62	3.8		
L	Parietal Inferior	40	-38	-46	56	3.76		
L	Precuneus	7*	-2	-54	52	4.63	0.02	53
L	Precuneus	5*	-2	-50	50	4.48		
L	Precuneus	5*	0	-50	54	4.22		
L	Precuneus	5	-6	-54	54	4.06		
R	Fusiform	37	32	-46	-8	4.36	0.04	47
R	Fusiform	37	28	-46	-8	4.2		
R	Frontal Middle	8	30	12	60	3.87	0.049	45
R	Frontal Middle	8	28	12	54	3.63		
Gaze > No Gaze None								
No Gaze > Gaze								
L	Lingual	17	-4	-72	2	3.98	0.002	77
L	Lingual	17	0	-72	6	3.68		

Contrast 1: PASS vs. PLACE. The first contrast examined the comparison between action stimuli of passing actions and placing actions. While the PASS > PLACE contrast did not hold significant results, the reverse contrast (PLACE > PASS) identified four significant activation

clusters. Two clusters highlighted bilateral activation of the Supramarginal Gyrus extending into the opercular section of the Postcentral and Superior Temporal Gyri, broader for the Left hemisphere (n. voxels = 323; MNI Z-cog coordinates: -60.4, -25, 19.8) and more delimited in the Right (n. voxels = 81; Z-cog coord.: -61.7, -25, 26.8). Occipital activation was found in a third cluster (n. voxels = 67) placed in the Left Mesial Occipital Inferior and Lingual cortices (Z-cog coord.: -18.7, -91.6, -7.9). Finally, increased activity in the Frontal Lobe was detected in a fourth, small cluster in the Left Precentral cortex (n. voxels = 46; Z-cog coord.: -59.2, -1.6, 29.5).

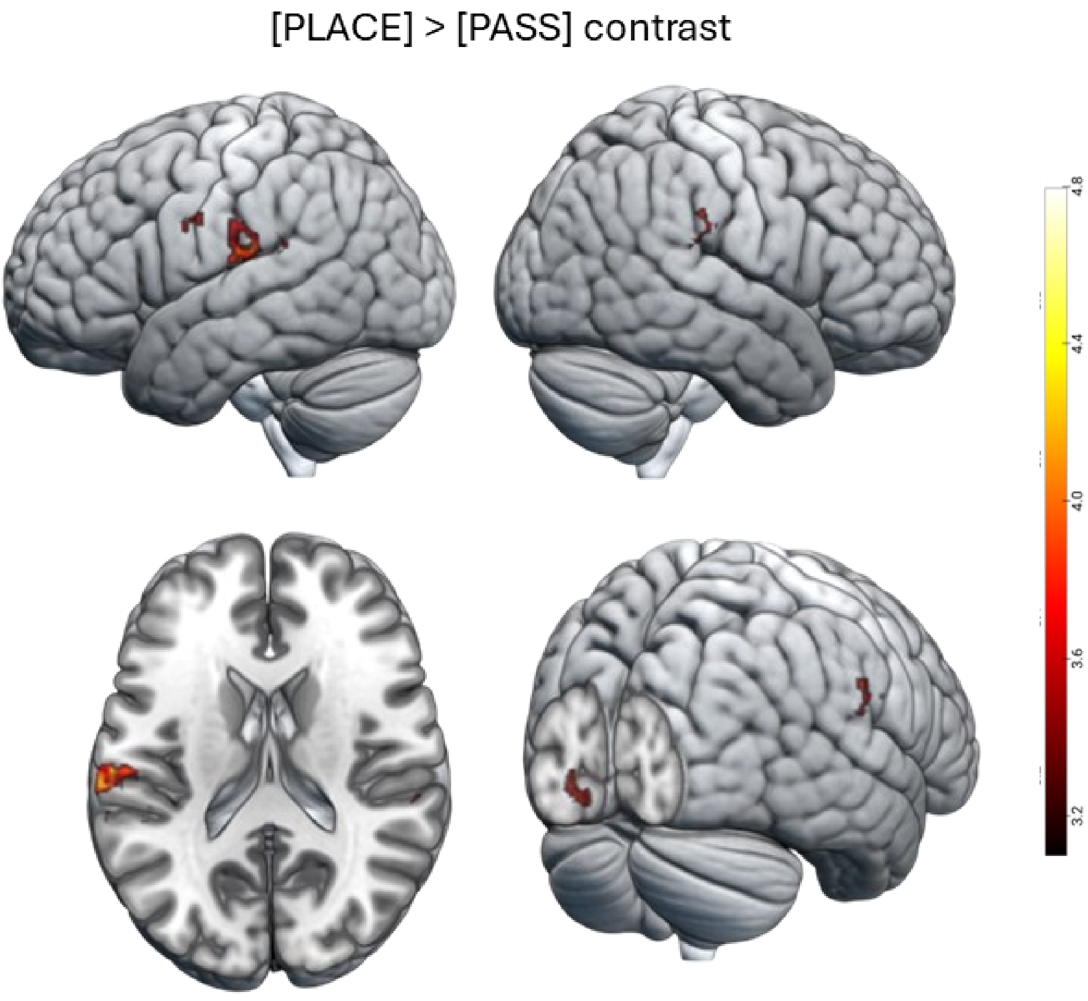


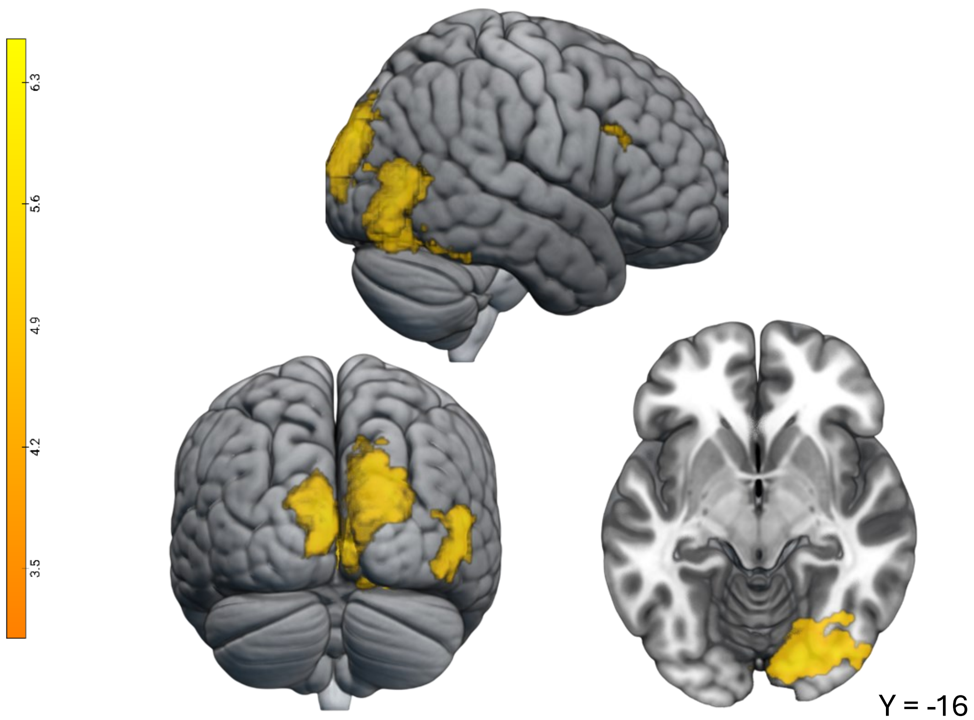
Figure 4.5 | Voxels showing significant activity for the PLACE > PASS contrast. Significant voxels are rendered on the MNI152 surface. The colorbar represents t-values (thresholded at 3.5).

Contrast 2: 2nd-person vs. 3rd-person. For the second contrast, we compared the 2nd-person with the 3rd-person perspective. Significant clusters were found for contrast in both directions in the Superior Parietal cortex, right frontal motor cortex, and Inferior Occipito-temporal cortex (mesial and lateral).

The 2nd-person > 3rd-person comparison showed significant activations all through the mesial and lateral Right Occipital cortex (n. voxels = 5400; Z-cog coord.: -18.7, -82.2, 3.21), extending from the depth of the Lingual and Calcarine gyri to the right lateral extrastriate cortex. A smaller, more compact cluster was identified in the Right Inferior Frontal Gyrus (n. voxels = 67; Z-cog coord.: -50.2, 21.8, 28.1), encompassing its Triangularis and Opercularis portions.

In the reverse contrast, 3rd-person > 2nd-person, the Mesial Occipital cortex showed a wide Left (n. voxels = 2848; Z-cog coord.: -14, -70, 10.6) and a smaller Right (n. voxels = 579; Z-cog coord.: -18.3, -61.6, 14.5) cluster. Both clusters occupy the Lingual and Calcarine cortices, with the Left one (almost 5 times bigger) extending into the Cuneus. Bilateral Occipital activity was found more laterally, with a left Occipital cluster localized at the temporo-occipital boundary (n. voxels = 164; Z-cog coord.: -46.5, -73.1, 8.5) and a right smaller cluster in the Fusiform gyrus (n. voxels = 47; Z-cog coord.: 29.3, -46.7, -6.93). Bilateral activations were also found across the Parietal cortices: a right cluster (n. voxels = 391; Z-cog coord.: 22.4, -66.8, 52.5) spanning from the Superior Parietal Lobule to the Right Precuneus; a left cluster (n. voxels = 108; Z-cog coord.: -36.1, -51.3, 59.9) occupying a more lateral area encompassing both Superior and Parietal Lobules together with part of the Postcentral gyrus. The Left Precuneus also showed a specific cluster of activity (n. voxels = 53; Z-cog coord.: -3.44, -53.2, 52). Finally, a small cluster in the Middle Frontal gyrus was identified (n. voxels = 45; Z-cog coord.: 29.7, 11.6, 58.3).

A. [2ND person > 3RD person] contrast.



B. [3RD person > 2ND person] contrast

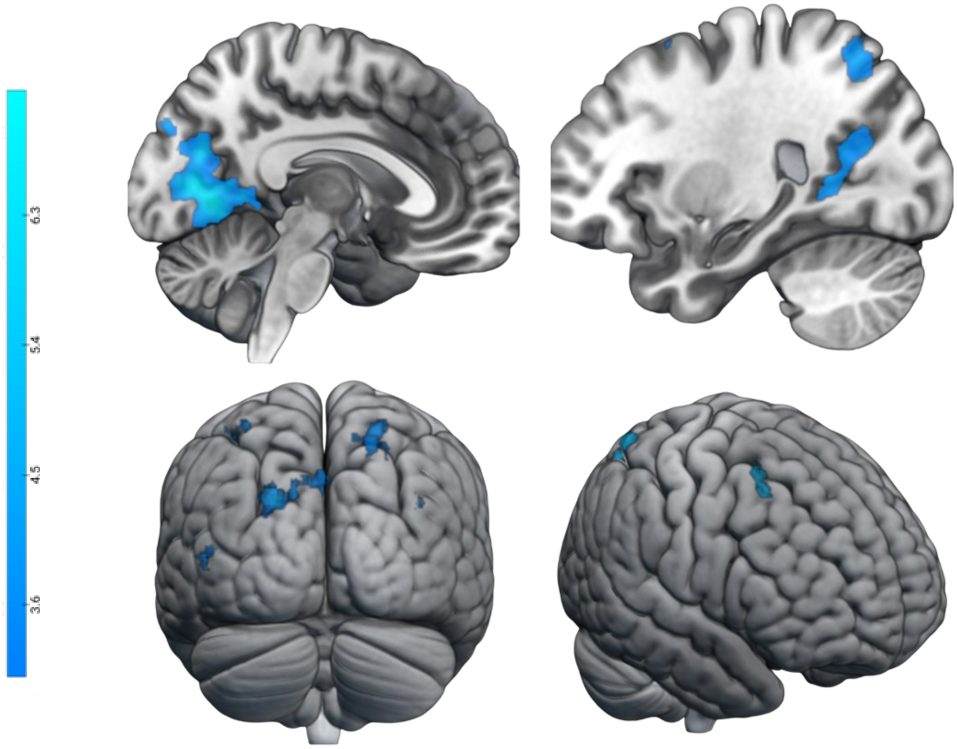
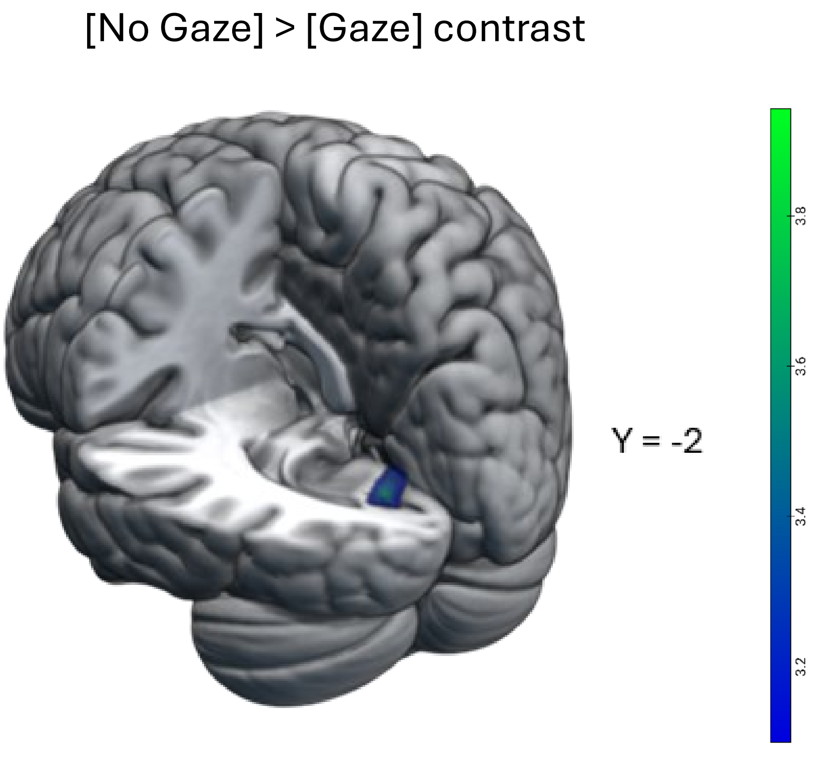


Figure 4.6 | Voxels showing significant activity for Contrast 2 (2nd vs 3rd person). Significant voxels are rendered on the MNI152 surface. The colorbar represents t-values (thresholded at 3.5).

As can be noted in the Figure 4.6, occipital activity displayed opposite lateralization between the two conditions, with predominantly left activation for the 2nd>3rd and right activation for 3rd > 2nd. This is likely due to our stimuli's nature: all actors in the video were right-handed, which located the limb movement predominantly in the left visual hemifield for the 2nd-person perspective. For the 3rd-person perspective, the camera angle was positioned on the actors' left, having the starting position of the limb movement located in the right hemifield and gradually unfolding from right to left in the video.

Contrast 3: Gaze vs. No Gaze. In the third contrast (Figure 4.7), observation of actors with visible gaze was compared with conditions of occluded gaze. Significant results were only observed for the No Gaze > Gaze comparison. In particular, a small cluster was identified in the left Lingual cortex (n. voxels = 77; Z-cog coord.: -5.68, -74.1, 115), thus highlighting increased visual processing.



[No Gaze] > [Gaze] contrast

Figure 4.7 | Voxels showing significant activity for the No Gaze > Gaze contrast. Significant voxels are rendered on the MNI152 surface. The colorbar represents t-values (thresholded at 3.5)

4.3.2 Parametric Modulation Analysis

All planned contrasts on the two parametric regressors held significant results. Peak activations are reported in Table 4.2; activation maps are shown in Figure 4.8.

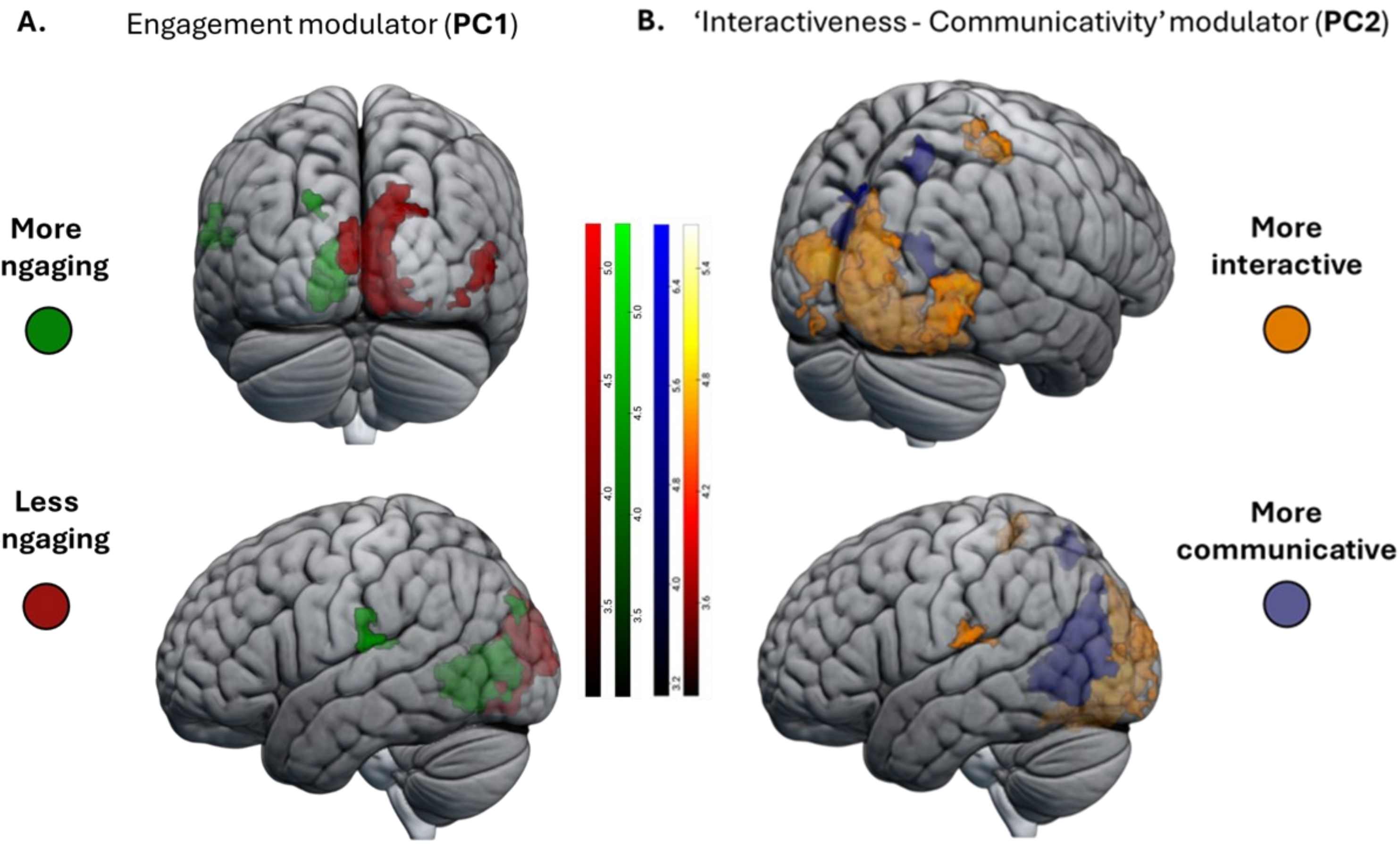


Figure 4.8 | Clusters showing significant correlation to parametric modulators. Significant correlations with the **(A)** PC1 (i.e., 'Engagement') and **(B)** PC2 (i.e., 'Interactiveness-Communicativity') modulators.

Table 4.2 | Brain regions that exhibited significant activation for planned contrasts.

				(coord.)				
Hemisphere	**Region (AAL3)**	**BA**	**x**	**y**	**z**	**z-Score**	**p-Value (FWE)**	**Cluster size (voxel)**
PC1 - Pos								
L	Lingual	18	-10	-72	-2	5.57	<0.001	932
L	Lingual	18	-10	-68	0	5.45		
L	Lingual	18	-16	-62	-2	5.32		
L	Calcarine	17	-12	-78	6	5.24		
L	Lingual	18	-14	-72	4	5.13		
L	Lingual	18	-18	-66	-10	4.95		

L	Postcentral	43	-64	-18	24	3.99	<0.001	144
L	Postcentral	22	-66	-20	16	3.98		
L	Temporal Superior	42	-58	-24	16	3.83		
L	Supramarginal	2	-64	-20	28	3.82		
L	Supramarginal	42	-56	-20	20	3.77		
L	Supramarginal	42	-62	-24	26	3.73		
L	Occipital Superior	19	-20	-88	32	4	0.049	46
L	Occipital Superior	18	-16	-88	26	3.7		
PC1 - Neg								
R	Lingual	17	6	-84	-4	7.27	<0.001	1336
R	Calcarine	18	4	-88	10	6.25		
R	Lingual	18	10	-82	-10	6.17		
R	Cuneus	18	4	-84	16	6.16		
L	Cuneus	18	-4	-96	20	6.16		
R	Cuneus	18	6	-88	24	4.93		
R	Temporal Middle	37	54	-70	2	4.83	<0.001	192
R	Temporal Middle	19	50	-74	4	4.57		
R	Occipital Inferior	19	44	-82	-12	4.56		
R	Occipital Middle	19	52	-76	0	4.53		
R	Temporal Middle	37	54	-68	12	4.44		
R	Occipital Inferior	19	42	-74	-8	4.78		
PC2 - Pos								
R	Calcarine	17	8	-80	6	5.9	<0.001	3850
R	Calcarine	17	4	-92	8	5.74		
R	Calcarine	17	10	-92	-4	5.61		
L	Calcarine	18	-2	-86	12	5.56		
R	Lingual	17	4	-78	-2	5.55		
R	Lingual	18	16	-80	-10	5.45		
R	Temporal Middle	37	44	-70	4	5.62	<0.001	608
R	Temporal Middle	37	54	-72	4	5.35		
R	Temporal Middle	37	54	-68	2	5.13		
R	Temporal Middle	37	56	-70	10	4.92		
R	Occipital Middle	19	46	-78	10	4.44		
R	Postcentral	4	38	-38	64	4.48	<0.001	169
R	Postcentral	3	28	-38	60	4.21		
R	Postcentral	2	34	-40	60	3.98		
R	Postcentral	1	34	-42	72	3.96		
R	Postcentral	2	24	-40	60	3.93		
R	Postcentral	7	34	-46	68	3.83		
L	Supramarginal	42	-62	-22	18	4.17	<0.001	117
L	Supramarginal	22	-66	-22	20	4.08		
L	Supramarginal	22	-68	-22	16	4.03		
L	Temporal Superior	42	-54	-30	16	3.8		
L	Postcentral	43	-64	-18	22	3.79		
L	Postcentral	43	-56	-22	18	3.77		
L	Occipital Middle	18	-30	-88	10	4.09	0.01	57
L	Occipital Middle	18	-26	-88	8	3.95		
L	Occipital Middle	18	-32	-84	8	3.66		

L	Occipital Middle	18	-22	-86	14	3.65		
L	Lingual	17	-12	-96	-16	4.09	0.03	50
L	Calcarine	18	-8	-98	-12	3.8		
L	Lingual	18	-8	-94	-14	3.75		
L	Occipital Inferior	18	-18	-92	-10	3.65		
PC2 - Neg								
L	Lingual	18	-12	-70	2	6.53	<0.001	1366
L	Lingual	18	-14	-68	-2	6.47		
L	Lingual	18	-10	-76	8	6.27		
L	Calcarine	18	-18	-78	10	5.51		
L	Calcarine	18	-16	-70	20	5.16		
L	Cuneus	18	-10	-76	26	4.85		
R	Lingual	19	22	-56	4	4.07	<0.001	93
R	Calcarine	18	22	-64	14	4.06		
R	Calcarine	18	6	-68	20	3.89		
R	Calcarine	17	16	-60	16	3.77		
R	Lingual	19	20	-52	2	3.51		

PC1 Modulators: Higher (PC1-Neg) and Lower (PC1-Pos) Engagement. Contrast for the higher perceived engagement modulator (PC1-Neg, green in figure 4.8A) revealed significant bilateral activation in regions associated with high-level visual and somatosensory processing. In the occipital cortex, widespread activation of the right Lingual and Calcarine cortices was detected (n. voxels = 3850; Z-cog coord.: 11.6, -84.7, 2.82). In the left occipital cortex, two smaller clusters in the left for the mesial (n. voxels = 50; Z-cog coord.: -12.2, -95, -12.8) and the lateral (n. voxels = 57; Z-cog coord.: -28.4, -87.8, 10.5) visual cortex were found. Temporo-occipital (n. voxels = 608; Z-cog coord.: 48.2, -72.7, 2.53) and superior parietal (n. voxels = 169; Z-cog coord.: 34.7, -39.5, 63.3) activations were identified in the right hemisphere, while a significant Supramarginal cluster was found in the left hemisphere (n. voxels = 117; Z-cog coord.: -62.1, -21.2, 18.1).

Contrast for the lower perceived engagement modulator (PC1-Pos, red in figure 4.8B) revealed three main clusters of activity, all in the left hemisphere, encompassing a mesial occipital cluster (n. voxels = 932; Z-cog coord.: -12.9, -71.1, 1.05), a lateral superior occipital cluster (n. voxels = 46; Z-cog coord.: -62.3, -21.8, 19.9), and a Postcentral cluster (n. voxels = 144; Z-cog coord.: -20.2, -87.3, 31.5) partially overlapping with the Supramarginal cluster from the PC1-Neg modulator.

PC2 Modulators: Interactiveness (PC2-Pos) and Communicativiness (PC2-Neg) modulators. Contrasts from the PC2 revealed bilateral activity of the mesial occipital cortex for both modulators: a more posterior cluster for the PC2-Pos modulator (n. voxels = 1336; Z-cog coord.: -6.88, -86.6, 8.28) and a deeper (anterior) cluster for the PC2-Neg (n. voxels = 1366; Z-cog coord.: -12.8, -69.7, 9.91). The modulator related to perceived Communicativiness highlighted a further cluster of activity in the temporo-occipital cortex (n. voxels = 192; Z-cog coord.: 50, -75, 0.23), while the modulator related to interactiveness showed a cluster of activity in the superior parietal lobule (n. voxels = 192; Z-cog coord.: -28.4, -87.8, 10.5).

4.3.3 RSA

Neural RSA. Figure 4.9 presents the patterns of correlations between neural RDMs, displayed both as a correlation matrix (Figure 4.9A) and as topological connectivity (Figure 4.9C), along with the clustering of similarity patterns among ROIs (Figure 4.9B).

The neural RDM correlation patterns highlight three key features of neural similarity across social brain ROIs during action observation: 1) Frontoparietal ROIs and the TPJ show extensive representational similarity; 2) the dmPFC displays the greatest representational distance from other ROIs, with significant correlations limited to its contralateral counterpart; 3) representational similarity is stronger within each hemisphere, especially for right-lateralized ROIs. Notably, some inter-hemispheric correlations emerged among midline and dorsal ROIs, such as the bilateral IPS, dorsofrontal Attention ROI, and the left Premotor cortex.

Among frontal areas, the **left Premotor** ROI demonstrated the broadest representational connectivity, showing similarities both within and between hemispheres. It displayed the highest representational similarity with the bilateral IPS, forming a representational cluster that also included the right dorsofrontal Attention ROI. In contrast, the **right Premotor** cortex exhibited a primarily lateralized similarity pattern, with only moderate correlation to its contralateral counterpart. It showed significant correlations with all frontoparietal and temporal ROIs and the strongest similarity to the BA44/45 ROIs, as well as the TPJ. Regions in the **inferior frontal gyrus** (BA44 and BA45) exhibited the strongest similarity with neighbouring and ipsilateral Premotor

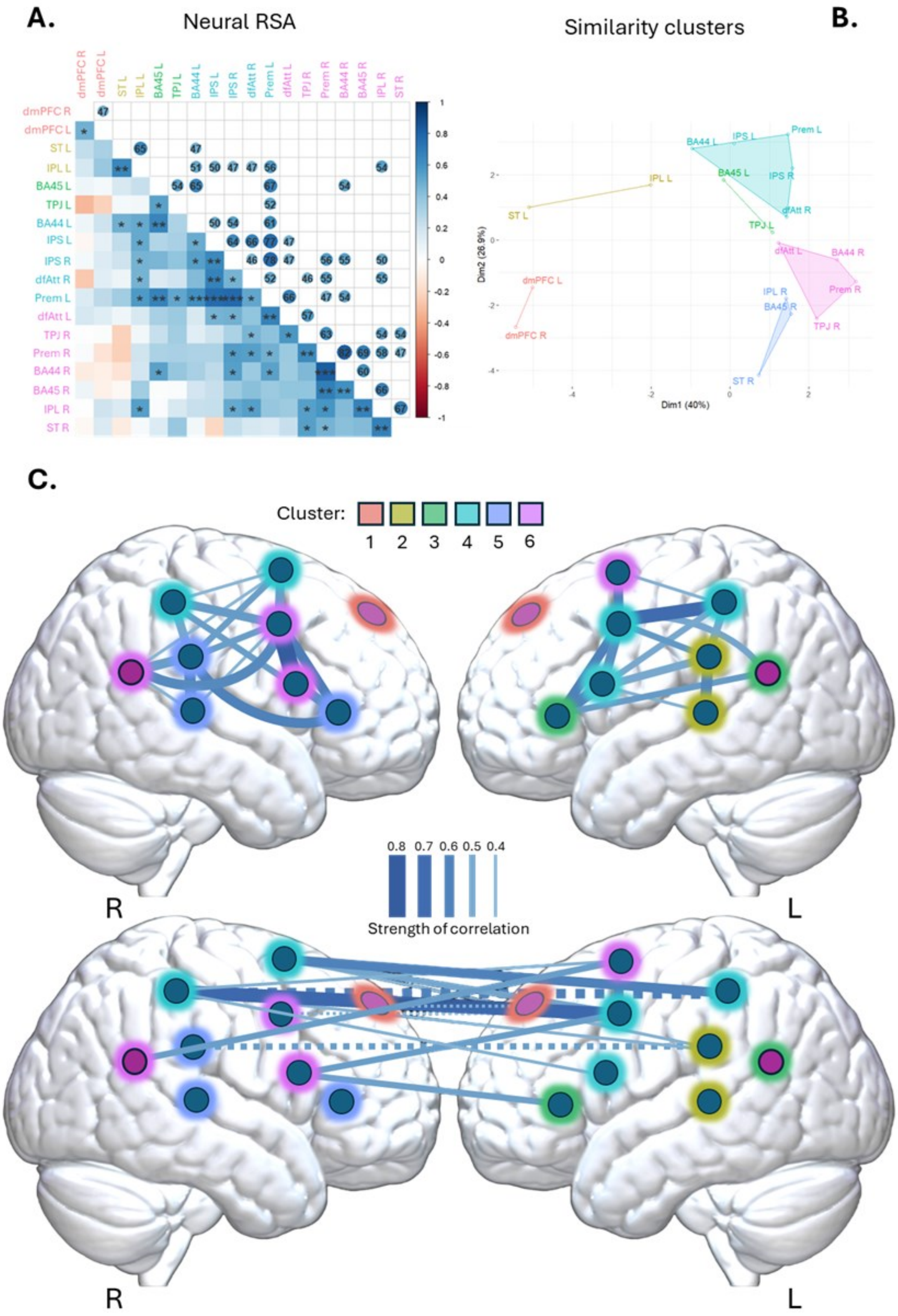


Figure 4.9| Neural RSA. (A) Dissimilarity matrix representing distance among ROIs' RDMs. The lower triangle highlights significant correlations (*, **, and ***), while the upper triangle reports the strength of significant correlations. (B) Plot of the dimensionality reduction analysis with clusters obtained by the Unsupervised Hierarchical Clustering on the neural RSA. (C) Correlations among ROI's RDMs are represented as topological connectivity plots: the upper one reporting intra-hemisphere significant correlations; the lower one reporting inter-hemisphere

significant correlations. Significant correlation between homologue contralateral areas are represented with dashed lines. The colour of the glows around the circles indicates the ROI's cluster.

ROIs. BA44 similarity patterns were primarily confined to ipsilateral frontoparietal MNS regions, while BA45 showed hemispheric differences: left BA45, but not right BA45, showed representational similarity with the ipsilateral TPJ.

The **dorsofrontal Attention ROIs** showed significant correlations both within and across hemispheres, particularly with the ipsilateral Premotor ROI and contralateral IPS. Notably, the left dfAtt was significantly similar to the right TPJ, forming a representational cluster with right premotor ROIs (i.e., right Premotor and right BA44).

In the temporal areas, the Superior Temporal ROIs and the TPJs exhibited distinct patterns: the **Superior Temporal** ROIs displayed a more localized pattern of similarity, forming lateralized networks with significant similarity to at least one premotor ROI (i.e., left BA44 or right Premotor) and the highest similarity to the ipsilateral IPL. Similarly, IPLs displayed predominantly lateralized similarity, with limited or absent inter-hemispheric correlations. In contrast, the TPJ displayed a more widespread pattern of representational similarity, with notable differences between the left and right TPJ. The left TPJ exhibited similarity only with ipsilateral frontal areas, that is the ipsilateral Premotor ROI and BA45, forming a cluster with the latter. On the other hand, the right TPJ showed the highest similarity with the ipsilateral Premotor ROI, followed by the right IPL, and the left dfAtt.

As noted, the dmPFC showed no significant correlations to any other ROI except their contralateral counterpart, with which they formed a highly isolated cluster.

The hierarchical cluster analysis (Figure 4.9B) further emphasized intra-hemispheric neural similarity, with left ROIs mostly occupying the upper part and the right ROIs mostly occupying the lower part of the factor map. The STs were the most distant nodes for each hemisphere, reflecting their strongly proximal pattern of representational similarity. Interestingly, the dorsofrontal Attention ROIs both belonged to a contralateral representational cluster, possibly due to their widespread inter-hemispheric connectivity and coherently with their role in integrating information to drive action selection (cf. Coudè, Maranesi).

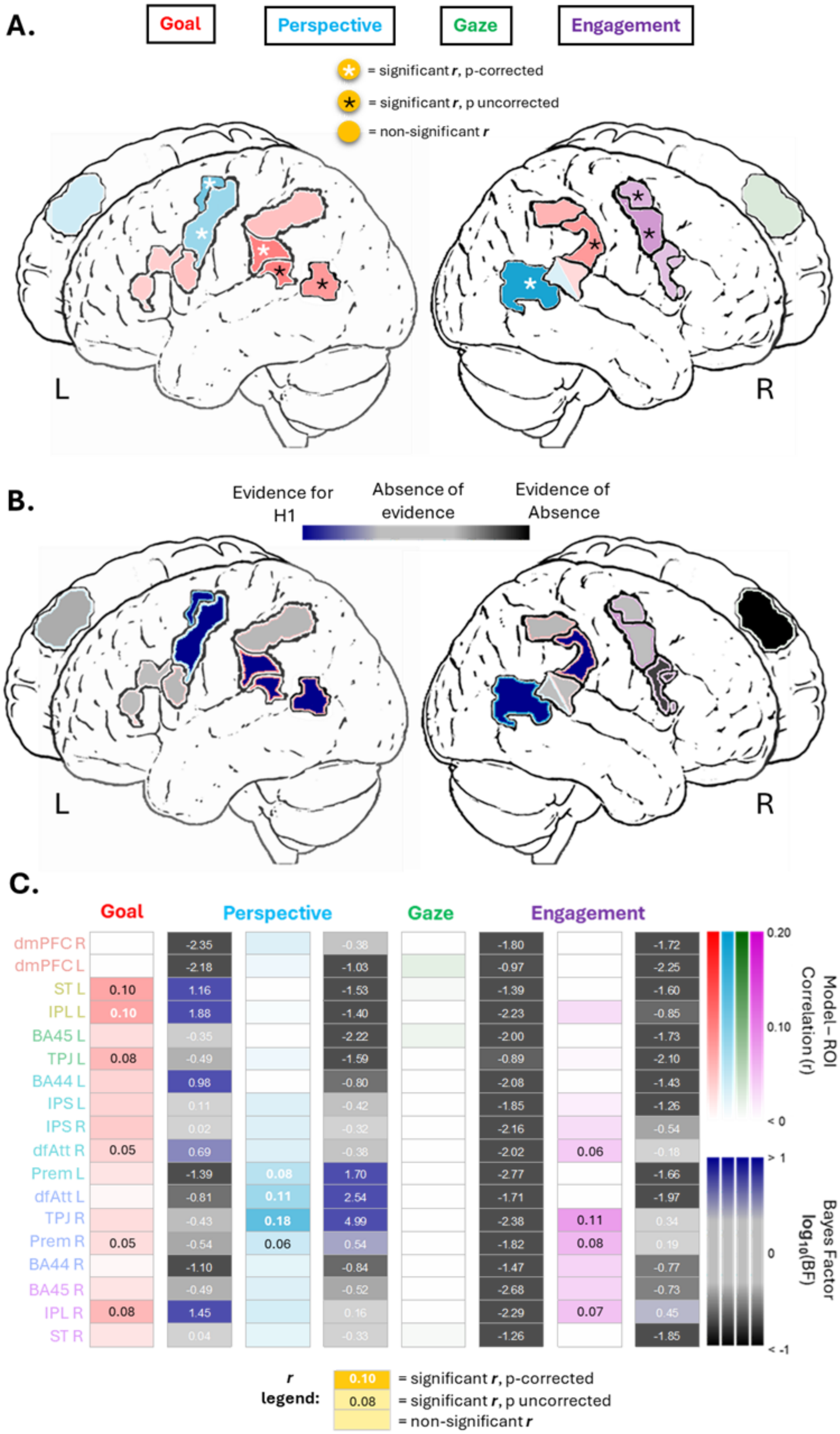
Model RSA. Figure 4.10 shows two brain maps with ROIs coloured according to the model which yielded the highest correlation (fig. 4.10A) and the strength of evidence for the correlation (fig. 4.10B). Heatmaps reporting the statistical results of the model RSA is displayed beneath, with ROIs (rows) sorted following clusters obtained from the neural RSA.

The ‘Perspective’ model yielded the strongest significant correlations and scored highest evidence, as measured with Bayesian testing, in both MENTA and MNS areas. In particular, the right TPJ, the left Premotor area, and the left dorsofrontal Attention ROI showed the most robust correlation with these models.

The ’Goal’ model showed the strongest correlations and trends with left-lateralized, posterior ROIs, that is the left IPL, TPJ, and the Superior Temporal area. Bayesian analysis also highlighted evidence for a significant correlation between the ‘Goal’ model and the right IPL.

The ‘Gaze’ models yielded no significant results, indicating that gaze visibility was not a major factor affecting neural patterns in social brain ROIs. Weak correlations were observed in the left dmPFC and left Superior Temporal area; however, Bayesian testing showed strong evidence of absence for these correlations, as indexed by the BF.

Finally, the ‘Engagement’ model also had no significant results. However, differently from the ‘Gaze’ models, it yielded high correlation values in a right-lateralized cluster of areas which included the right TPJ, right IPL, right Premotor ROI, and the right dfAtt. Given the neural proximity among these areas highlighted by the neural RSA, this suggests the existence of a potential right-lateralized network sensitive to the first-person engagement in the observed action (see Figure). However, this result requires further investigation due to the low overall statistical scores and lack of strong probability as evidenced by the BF for these correlations (see heatmap scores for Prem M, TPJ R, IPL R, and dfAtt R).



	Goal		Perspective		Gaze		Engagement	
dmPFC R		-2.35		-0.38		-1.80		-1.72
dmPFC L		-2.18		-1.03		-0.97		-2.25
ST L	0.10	1.16		-1.53		-1.39		-1.60
IPL L	0.10	1.88		-1.40		-2.23		-0.85
BA45 L		-0.35		-2.22		-2.00		-1.73
TPJ L	0.08	-0.49		-1.59		-0.89		-2.10
BA44 L		0.98		-0.80		-2.08		-1.43
IPS L		0.11		-0.42		-1.85		-1.26
IPS R		0.02		-0.32		-2.16		-0.54
dfAtt R	0.05	0.69		-0.38		-2.02	0.06	-0.18
Prem L		-1.39	0.08	1.70		-2.77		-1.66
dfAtt L		-0.81	0.11	2.54		-1.71		-1.97
TPJ R		-0.43	0.18	4.99		-2.38	0.11	0.34
Prem R	0.05	-0.54	0.06	0.54		-1.82	0.08	0.19
BA44 R		-1.10		-0.84		-1.47		-0.77
BA45 R		-0.49		-0.52		-2.68		-0.73
IPL R	0.08	1.45		0.16		-2.29	0.07	0.45
ST R		0.04		-0.33		-1.26		-1.85

Figure 4.10 | Model RSA results. (A) Brain map with ROIs coloured according to the model which yielded the highest correlation score for that area. (B) Brain map with ROIs coloured based on the degree of evidence as measured by the Bayesian Factor. representing dissimilarity scores for the Model RSA. (C) Heatbars color-

coded according to the strength of correlation (red, blue, green, and purple heatbars) and strength of evidence (black-blue heatbars) of each model per ROI. Clusters from the neural RSA were employed to sort the ROIs to display how the neural similarity was predictive of functional similarity as indexed by the model RSA.

Figure 4.11 recaps results from both RSAs by displaying the neural cluster map with overlapped strongest correlations to models for each ROI. The distribution of models on the neural map emphasizes prominently Goal-based neural representation in the left hemisphere (upper part of the map) and a potential Engagement-based neural representation in the right hemisphere. Notably, both regions of the map have ROIs significantly related to Perspective-based neural patterns (i.e., the right TPJ, the left Premotor, and the left dorsofrontal Attention ROIs).

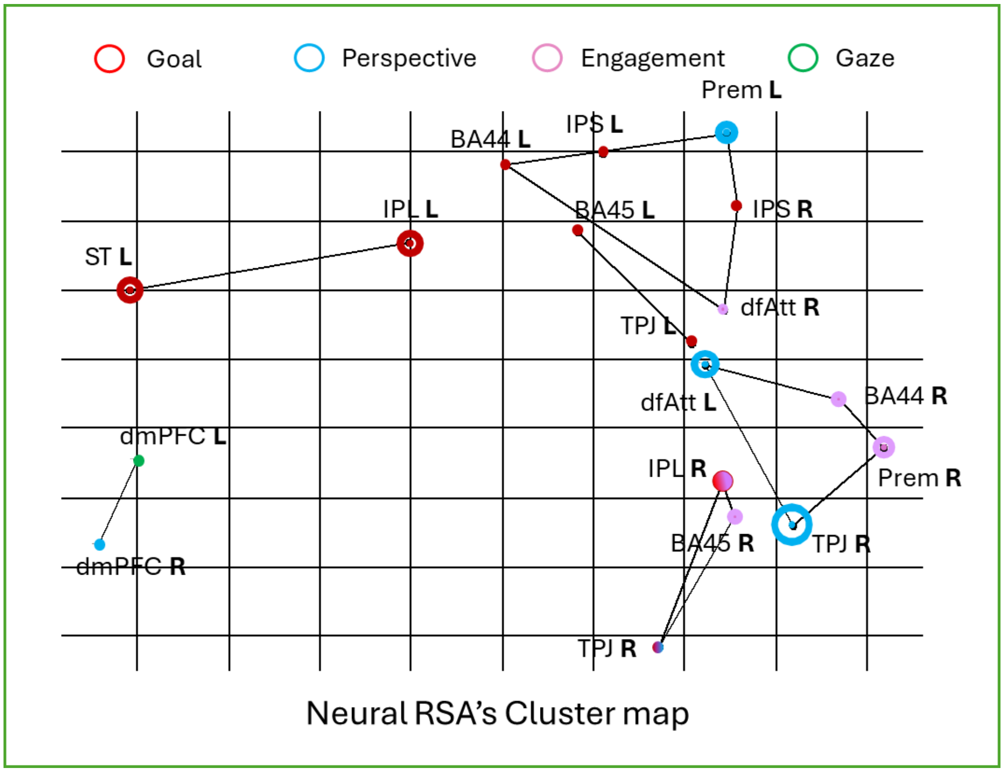


Figure 4.11 | Distribution of ROIs' highest correlations to models on the neural RSA's cluster map. The circles' dimension correlates with the strength of the correlation (cf. fig MODEL.C).

4.4. Discussion

The neuroscience of social cognition has witnessed a gradual shift in focus from the study of abstract reasoning about others' minds to that of behavioral control in online and reciprocal social interactions. While much has been debated and explored in terms of how the brain represents specific features of others' behavior, less attention has been traditionally given to a crucial dimension of social stimuli: their engaging nature for the individual. In this fMRI study, we wanted to compare cerebral patterns in response to observed actions which afford or do not afford interaction, led by previous research that demonstrated how direct (or potential) engagement in interpersonal interaction changes how social information is processed in the brain.

To this aim, we employed a traditional action observation task while adopting a novel experimental design in which action stimuli were created to reproduce a gradient of progressively increased engagement for the observer, manipulating different engagement-relevant features such as the action goal, the perspective, and the visibility of the agent's gaze. We performed two whole-brain univariate analyses to see where in the brain activity was more responsive to individual engagement-related features and to shifts in the overall perceived engagement level. Then, we had specific hypotheses as to how regions of the 'Social Brain' such as the MNS and the MENTA system would process social engagement and its related features, and we performed a multivariate RSA on neural patterns to assess similarities and differences in the representational structure of observed actions in these areas.

4.4.1 Engagement perception and sensorimotor simulation.

In the factorial analysis, we contrasted brain responses to engagement-relevant features against non-engaging features for the factors GOAL, PERSPECTIVE, and GAZE.

For the GOAL contrasts, the comparison of passing vs. placing actions yielded no significant differences in the PASS > PLACE direction, but significant activations were observed in the reverse (PLACE > PASS) contrast. The lack of significant differences in the processing of passing actions contradicts our expectations based on previous literature showing that socially oriented action differentially activates regions involved in social perception. However, different reasons related to our design and the stimuli's nature could have determined this result. A first, methodological reason might regard the relatively low number of repetitions and stimuli per run; furthermore, our design was optimized for studying gradients of activity and patterns, rather than eliciting peak activations, making this contrast not effective in detecting differences. Indeed, previous studies with similar paradigms adopted block designs (cf. Ciaramidaro et al., 2014; Begliomini et al., 2017) and a wider variety of stimuli (Becchio et al., 2012; Trujillo et al., 2020), more suited for response estimation to specific stimuli's features (Friston et al., 1998; Birn et al., 2002). However, this is partially contradicted by the significant results we obtained for placing actions, showing that the two actions are processed differently. Thus, a second explanation for the lack of results might be related to the very nature of the task: passively observing the action limits actual involvement in the observed action, a major factor impacting activity in social brain areas (cf. Sperduti et al., 2014; for comparative evidence, see Roumazeilles et al., 2021; Ninomiya et al., 2021). Indeed, some fMRI studies adopting passive viewing paradigms during the observation of third-party interactions failed to show strong involvement of areas such as the dmPFC (cf. Otti et al., 2014; Masson and Isiki, 2021). The passive condition possibly dampens the saliency of the social nature of the action and, together with the repetitiveness of the task and the high similarity of our stimuli, could have contributed to the lack of significant differences in BOLD signal.

This was not the case for placing actions, however, which showed increased activity in the left precentral gyrus, the bilateral supramarginal and postcentral gyri (especially the opercular sectors), and the left visual cortex. One salient feature of placing actions was the physical interaction between the agent and the cylinder at the time of placement. The involvement of somatosensory cortices in the processing of goal-oriented actions, especially the opercular SII, has been highlighted by in fMRI studies in humans (Keysers et al., 2004; Ebisch et al., 2008) and monkeys (Raos, Evangeliou, and Savaki, 2007). Indeed, witnessing people or objects being touched drives vicarious somatomotor activity related to tactile manipulation (Schaefer et al., 2009; Aberbach-Goodman and Mukamel, 2023; Bellard et al., 2023). Moreover, sensorimotor cortices have been shown to consistently encode more abstract features of physical causality

(Albertini et al., 2021, Karakose-Akbiyik et al., 2023). Thus, our results further highlight the saliency of physical interaction during action observation.

Visible physical interactions were not part of our social stimuli, likely contributing to our results for the GOAL contrasts. If this is the case, this could suggest that observed or potential physical interactions in a social context, both from a 2nd and a 3rd-person perspective, might be a relevant driver of changes in neural activity in sensorimotor areas. Indeed, results from our parametric analysis showed that a somatosensory cluster similar to that found for the Place > Pass contrast significantly correlated with higher perceived engagement (PC1-pos), where high scores related to passing actions, and higher interactiveness (PC2-pos), associated with the 2nd person perspective. Moreover, higher perceived engagement correlated with a further somatosensory region in the contralateral superior parietal lobule. Interestingly, we did not find activity in these regions to correlate with communicativeness alone (PC2-neg), underscoring the interaction-driven nature of somatosensory activity. This result highlights the contextual recruitment of sensorimotor resources involving the observers' body control system when witnessing others' bodily displays. In particular, it highlights the involvement of multimodal sectors integrating motor, tactile, and visual information for somatosensory processing and haptic control in the encoding of a social and pragmatic dimension of perceived engagement. The involvement of the opercular postcentral in the processing of the level of engagement adds further evidence to the relevance of somatosensation in the control of social interaction. Both first and secondary somatosensory cortices are known to be involved in the vicarious processing of observed touch (see Keysers et al., 2010 for an overview), with expanding evidence relating these proprioceptive responses in the regulation of social skills like empathy and prosocial behavior (Gallo et al., 2018; Caspar et al., 2020). However, our results demonstrate that proprioceptive processing is involved even in the absence of visible physical contact. A possibility is that higher perceived engagement enhances immersiveness and, thus, simulation of actual engagement (see Gallese 2007; Bastiaansen et al., 2009). According to such an interpretation, the involvement of the opercular postcentral region in the continuous processing of the level of engagement might be related to action-oriented predictive processes (Franklin and Wolpert, 2011; Friston, 2011), functional to sensory prediction and interaction control (Ostry and Gribble, 2016; Kilteni et al., 2018). A recent study employing transcranial magnetic stimulation (TMS) (Guidali et al., 2023) measured corticospinal excitability related to hand control during the observation of non-social grasping (grasping a bottle) and social grasping (grasping another person's hand) and found that motor activity is significantly higher right before the contact with the other hand. This heightened 'motor resonance' (see Finisguerra et al., 2015) for social touch suggests that bodily-related representations are contextually and continuously updated to map one's potential interactions with the environment, among which social ones represent a salient and complex kind.

4.4.2 Pragmatic encoding of action stimuli in sensorimotor regions.

A further contrast analysis regarded differences for the PERSPECTIVE factor. For both perspectives, significant activations were found in different loci of the bilateral mesial and lateral occipital cortex, bilateral superior parietal areas, and right premotor regions. The activation differences observed in the perspective condition can partly be explained by the low-level features of the conditions, as the widespread activations detected in both primary and higher-level visual cortices are most likely due to the unbalanced lateralization of stimuli discussed in the result section. Indeed, activation for both perspectives reveals a specular pattern which spreads from the primary visual cortex to known visual regions involved in the analysis of biological motion and bodily displays in the lateral occipitotemporal cortex (LOTC) (see de Gelder and Poyo-Solanas, 2021, for an overview).

However, some noticeable differences regard the entity of activations in the lateral and ventral visual streams, more extended for the 2nd-person perspective including the fusiform gyrus (Peelen and Downing, 2005), and the clusters found in dorsolateral (SPL) and mesial (Precuneus) parietal areas for the 3rd-person perspective, suggesting stronger involvement of dorsal streams. According to classic views of the visual streams (cf. Milner and Goodale, 2006; Cloutman, 2013), this might suggest that the 2nd-person perspective elicits stronger recruitment of neural resources for efficient discrimination and categorization of action goals, while the 3rd-Person Perspective recruits processes related to spatial cognition and attention control (cf. Corbetta and Shulman, 2011; Szczepanski et al., 2013). In our parametric analysis, higher engagement (PC1-pos) correlated with right lateral and ventral visual activations overlapping with those found for the 2nd-person perspective. Moreover, the parametric modulator for communicativeness (PC2-neg) revealed a right dorsal parietal cluster overlapping with a cluster in the SPL for the 3rd-person condition, suggesting that perceived communicativeness correlates with increased attentional saliency.

Interestingly, our results also showed that two perspectives activated distinct sectors of the premotor cortex: the opercular IFG, involved in hand action control and high-level action processing (Borra et al., 2017; Papitto et al., 2020), was more active for the 2nd-person perspective, while the BA8 in the middle frontal gyrus, a dorsal region involved in control of eye movements (cf. Curtis, 2006; Dadario et al., 2023), was more active for the 3rd-person. Following the more current literature on the subdivision of parieto-frontal circuits for effector-related motor control (Cisek and Kalaska, 2010; Caminiti et al., 2017), the two visual perspectives may recruit different action-control systems to manage different social affordances (Lanzilotto et al., 2021; Bonini et al., 2023). Stronger activity in the IFG, part of the MNS, speaks in favour of the pragmatic relevance of the direction of the observed action in modulating premotor responses, as demonstrated for actions involving the observer's peripersonal space (Jackson et al., 2006; Bonini et al., 2014; Maranesi et al., 2017; Angelini et al., 2018). Accordingly, higher activity in the ventral and lateral occipito-temporal regions for the 2nd-perspective could be related to increased extraction of sensory features (e.g., kinematics) relevant to action prediction and preparation, while dorsal activations for the 3rd-person perspective could be mostly due to eye movement control for scanning the scene and in the monitoring of other's attention and perspective, as further suggested by activation of the Precuneus, a region strongly related to visual perspective-taking (cf. Petrini et al., 2014). This would be in line with our initial assumption that an action directed toward the observer, which we categorised as engagement-relevant, enhances the processing of action stimuli to guide the control of the potential interactions with the action observed (cf. Orban et al., 2021).

Lastly, for the GAZE factor, only the No Gaze > Gaze contrast yielded significant activation, specifically in the left lingual cortex. We did not find activation for the dmPFC as initially hypothesized. This might be for similar reasons to the lack of activation for social actions in the

GOAL contrasts, that is the overall low engaging nature of the task and the high similarity of the stimuli which makes it difficult to detect slight neural changes. However, we also did not detect activations in other gaze monitoring areas (e.g., the SPL, the Frontal Eye Fields, the STS), which might mean that gaze processing was similar in the two conditions, rather than absent. Higher visual activity might point to enhanced visual processing when the gaze was occluded, compensating for the lack of sensory information for trials in which the actors' gaze was not visible.

4.4.3 Representational connectivity links frontal MNS regions and the TPJ

With our RSA we wanted to assess neural similarity among key nodes of the MNS and MENTA system, based on previous findings showing enhanced functional connectivity among these regions during the processing of social interactions. In this regard, our study revealed highly divergent representational structures and correlation patterns for TPJ and dmPFC. Contrary to our initial hypothesis, the neural patterns in dmPFC showed no significant correlations with other social brain ROIs, while the TPJ exhibited robust representational similarity with the frontal Premotor Cortex bilaterally. Lateralization was observed, as patterns in the lTPJ correlated only with the frontal ipsilateral Premotor cortex and BA45, while the rTPJ showed neural similarity with a broader network of areas which included the ipsilateral Premotor cortex, IPL, and ST areas, and the bilateral dorsofrontal Attention ROIs.

In contrast to the TPJ, clustering and dimensionality reduction analyses underscored the dmPFC's isolated representational geometry, with no significant correlations outside of its contralateral part. Dimensionality reduction suggested a modest proximity between patterns in the left ST area and left dmPFC, which our model RSA posits may be related to gaze processing — a function associated with both the dmPFC and STS (Hoffman and Haxby 2000; Marquardt et al., 2017). However, this correlation for the left dmPFC was non-significant, and Bayesian testing further confirmed the absence of a meaningful relationship. Additionally, the left ST region's functional profile aligned more closely with a Goal-encoding cluster, which also included the IPL, reinforcing the dmPFC's distinctiveness.

While MENTA regions showed vastly different similarity profiles, our RSA confirmed the widespread intra-network neural similarity of frontoparietal regions of the MNS like the Premotor cortex, the BA44, the IPL, and the IPS, as predicted by their well-known anatomo-functional profile (Mendoza and Merchant, 2014; Bruni et al., 2018). However, the RSAs showed that together with the Superior Temporal Areas, the TPJs, and dorsofrontal Attention regions they partake in neural clusters showing different functional trends.

The bilateral IPL showed neural proximity to the ipsilateral STs and a significant Goal-based representational structure. This result is coherent with the known functional profiles and the connectivity of these two regions for the processing of observed actions and motor goals (cf. Perret et al., 1989; Borra et al., 2008; Evangeliou et al., 2008; Kilintari et al., 2014). The Goal-based profile was particularly strong for the left IPL-ST cluster and, notably, the adjacent lTPJ. Instead, the representational structure of the rIPL also showed a trend for Engagement-based coding. Interestingly, the Engagement model scored the highest correlations in a right-lateralized network of areas including the rTPJ, the rIPL, the right Premotor Cortex, and the right dorsofrontal Attention region, possibly hinting at a lateralized network in the right hemisphere for the encoding of social engagement during action observation.

For frontal areas, the strongest and most significant correlations were between the left Premotor and dorsofrontal Attention regions with the Perspective-based representational model. The rTPJ also showed a strongly Perspective-based representational structure and displayed moderate neural similarity with the left dorsofrontal Attention region, but not the left Premotor region. For the latter, neural patterns were instead more similar to the IPS (bilateral) and the ipsilateral inferior frontal gyrus, which both showed trends toward Goal-based encoding. This possibly indicates that, while action orientation is a key modulator of neural activity of both MENTA and MNS ROIs, the Perspective-encoding function in the rTPJ and the left Premotor cortex might be involved in different computations, as evidenced by their neural distance and their belonging to differen networks.

These results add several novel insights regarding the functional profile of key areas of the social brain. First, while previous fMRI studies employing univariate analyses highlighted differential activation of premotor regions in response to action directed toward the observer compared to action seen in a 3rd-person perspective, our study is the first to demonstrate that this effect is specifically tied to action directedness, rather than to the action goal or other communicative features. Instead, goal-based coding was localized in parietal nodes of the MNS, in line with evidence showing action classes categorization in inferior parietal regions (Patri et al., 2020; Lanzilotto et al., 2020; Aflalo et al., 2020; Urgen and Orban, 2022). Our results for a Perspective-based representational structure in the premotor cortex adds further, although indirect, evidence to the pragmatic coding view of premotor processing of observed actions (cf. Bonini et al., 2023; Maranesi et al., 2024), suggesting that modulations of motor responses to spatial and directional features of the observed actions might be related to the encoding of social motor affordances (Schilbach et al., 2013; Orban et al., 2021; Bonini et al., 2023).

Secondly, our study is the first to highlight the neural similarity between the TPJ and premotor regions during action observation without explicit mentalizing tasks, suggesting that activity in TPJ is fundamentally tight to sensorimotor processes. Several possible interpretations based on the previous literature might explain our results. First, the rTPJ Perspective-based representational geometry supports the perspective-taking coding account of TPJ (Schurz et al., 2013; Martin et al., 2021). However, sensitivity to first-person engagement in rTPJ and to the action goal in lTPJ suggests that this area partakes in coding either more abstract action features or sensorimotor information (see Baichen Li et al., 2023) relevant to interaction control. While one possibility does not exclude the other, the similarity of rTPJ with perspective and engagement-based models in our experiment suggests the latter, that is, a pragmatic coding of the observed action. Indeed, while previous studies employing RSA focused on abstract goals and mental state representation in the rTPJ during mentalizing tasks (Corradi et al., 2014, Koster-Hale et al., 2017, Golec-Staśkiewicz et al., 2022), others have demonstrated that the TPJ does contain self-related motor representation, as evidenced by studies showing shared activation in this region for action execution, observation, and motor imagery (cf. Simos et al., 2018). Moreover, studies employing transcranial stimulation demonstrated the causal role of TPJ in modulating executed motor responses to observed actions during diverse tasks, including motor imitation and joint action (Giardina et al., 2011; Rauchbauer et al., 2015, Hogeveerd et al., 2015). Finally, evidence for causal interaction between the TPJ and primary motor and premotor cortices has been demonstrated for the regulation of motor response to aversive stimuli (Sagliano et al., 2019) and suppression of interference motor effect due to action observation (Bardi et al., 2017), demonstrating TPJ's involvement in motor control.

Our study does not address, however, the exact mechanism through which TPJ exerts synergistic motor regulations with parieto-frontal networks. While TPJ's precise role in sensorimotor transformation is still a matter of debate, its established role in embodiment processes (Berlucchi and Aglioti, 1998; Blanke et al., 2005) and multimodal integration suggest that potential motor interaction might trigger stronger involvement of the TPJ in managing internal models of the self and the other actions, as evidenced by TPJ role in managing conflicting self-other representations (cf. Quesque and Brass 2019; Arioli et al., 2023). Indeed, a study employing MVPA decoding demonstrated that activity in the TPJ could discriminate between self and other actions during a working memory task (Woniak et al., 2022). Our results add indirect evidence to this hypothesis.

While strong similarity and significant functional profiles were evidenced for TPJ and premotor-motor regions, our RSA did not confirm our hypothesized IFG-dmPFC similarity. Instead, activity in the left and right IFG regions correlated with the left-lateralized Goal-oriented network and a right-lateralized engagement-oriented network, respectively. However, correlations of IFG regions such as the BA44 and BA45 with our models were overall not significant, indicating that activity in the IFG was only weakly modulated during action observation. Similarly, the dmPFC did not show any significant similarity with our conceptual models, contradicting our hypothesis for a strong involvement of this area in engagement and gaze processing. Moreover, differently from IFG, its activity did not correlate with any functional network. Thus, our results speak against a conjunct role for these areas during the observation of action affording potential interactions. However, a different interpretation, more in line with the accrued evidence discussed in the introduction, is that the very nature of the task is relevant for driving activity in the IFG and crucial for the involvement of dmPFC during action observation. In light of the previous literature, our negative result might be a piece of further evidence for dmPFC playing an eminently executive control structure within the social brain, particularly sensitive to the on-demand management of multifaceted social information in social tasks ranging from online motor interactions (cf.Ninomiya et al., 2018; Baéz-Mendoza et al., 2021) to self-other comparison (Wittmann et al., 2016, 2021).

4.5. Outlook and limitations

By combining univariate and multivariate analyses, we were able to capture both main neural activations and finer-grained representational profiles, offering a more comprehensive understanding of the neural mechanisms underlying the perception of socially oriented actions. Indeed, our results confirm the relevance of integrating both approaches, as the two analyses pinpointed both common trends and specific results.

Both analyses highlighted the relevance of action perspective as a major modulator of neural activity during action observation: the univariate analyses emphasized the involvement of occipito-temporal activity and specific premotor foci, while our neural RSA uncovered significant modulations of the right TPJ and the left premotor cortex. This convergence strengthens our findings and adds further evidence to the relevance of the potential space of interaction as a key feature of the sensorimotor processing of observed actions.

On the other hand, the two analyses provided specific information. Our whole-brain univariate approach highlighted the strong involvement of somatosensory cortices in the processing of social engagement, adding a novel piece to the second-person literature. The RSA captured lateralized functional networks for goal and engagement processing, suggesting the need for future investigations on the role of hemisphere specialization in action observation and social cognition.

As underscored in the previous section, the task appears to be crucial in modulating neural activation within the social brain. A limitation of our study resides in its attempt to study the implicit processing of potential motor interaction with a task which does not require responding to the observed stimuli. As thoroughly discussed in the introduction, the brain processes stimuli differently in interactive contexts, and our study was not in a second-person setting after all. Thus, our results, especially the negative ones, need to be complemented by further investigation of engagement employing diverse tasks. Future work could investigate how the representational patterns we found change during action execution or imagery as opposed to observation, providing insights into the dynamic coding of social information.

Another limitation related to the task is that we asked our participants to focus on the goal of the action, that is to be ready at any time to provide a response regarding the goal of the action observed. By changing the focus on the other factors (e.g., the perspective or gaze), we might have obtained different results and correlational patterns. Moreover, the relatively restricted number of stimuli and the very repetitive nature of contents might have quickly dampened stimuli saliency and brought rapid adaptation, possibly penalizing the sensitivity to BOLD increase in areas like the IFG and the dmPFC. While this problem is generally shared among fMRI approaches, it is particularly relevant in the context of studying responses to potential motor actions, given their scattered and on-demand nature in naturalistic contexts. Incorporating dynamic connectivity analyses alongside multivariate RSA could further elucidate how neural representations of action features evolve over time and across brain networks

5. Conclusions

Interpersonal motor interactions make up a substantial part of daily social experiences and are a primary form of intersubjective interactions in animals. These interactions demand complex, skilful control and rapid processing of multiple information streams regarding one's own body movements and those of others. Over the last 30 years, social neuroscience research has revealed that these processes are not distinct at the neural level. Instead, information about the self and others interweave in various brain regions involved in bodily control and goal-directed motor actions, creating a 'we-centric' neural space (Gallese, 2006; Gallotti and Frith, 2013).

Insights into motor control at neural and behavioral levels suggest that, in interactive contexts, individuals rely on rapid, predictive processing of others' actions. Observing the initial phase of a complex, goal-directed action activates neurophysiological processes for action prediction and preparation. Moreover, socially oriented actions seem to constitute a distinct class of motor actions, processed differently from those aimed at individual goals. The social nature of action goes beyond communicative content or third-party observation; rather, the engaging nature of another's actions — directed toward us and allowing for responses — gives them pragmatic relevance for the observer.

Our findings provide evidence in favor of the biological relevance and saliency of second-person interactions in the study of social cognition. With our behavioral measurements, we showed that reaching to grasp an object with a social intention exhibits a slower and more accurate execution of the action, showing that actions towards others are more finely controlled. Moreover, these social actions were better decoded overall than individualistic actions by observers, especially from a second-person perspective, and our analysis revealed that this was due to the expression of specific kinematic parameters like movement speed and hand positioning on the object. This aspect, overlooked in previous studies, may be linked to social affordance processing, where agents prepare and execute grasping actions to create space for others' interactions. In turn, observers might interpret this as a cue for social intention detection in naturalistic coordination.

This novel finding opens avenues to future studies exploring the relevance of such interactive ‘attunement’ for adaptive interpersonal coordination and the underlying motor representations. Social affordances, as those we identified, could result from multiple factors including sensitivity to social cues, the ability to interpret others’ movements, and the individual’s motor and social skills. Replicating these findings in clinical populations with impairments in perceiving or responding to social cues could further illuminate the role of social motor behaviors in connecting individuals to their environments. Additionally, social affordances may play a crucial role in perceptions of social affiliation or, conversely, hostility and competition. Investigating these dynamics in contexts of varying uncertainty could provide insight into how bodies in interaction influence one another through action alignment or misalignment.

Importantly, we also highlighted that when observing an action to predict its intention individuals are highly attentive to information from the face of the observed agent. This adds to previous research underscoring the importance of gaze and head orientation in anticipating action intentions. Gaze serves as a key indicator of attention and, ultimately, the next likely action or intention. We observed that in cases of greater uncertainty, attention shifted to other body cues, like the hands. Future studies might explore the extent to which gaze and body movements are interlinked for the observer. Are they complementary? Do they imply different interpretations or actions? Do they form a unified representation? Addressing these questions by manipulating the relevance of gaze and body movements across various interaction contexts would further clarify these relationships.

To investigate how the perception of a social versus nonsocial action affects neural processing, we examined how this information is represented in brain areas associated with social cognition. Results from our univariate analyses confirm and expand the latest knowledge on how representations of others’ bodily displays are processed and remapped across sensorimotor and associative networks. We demonstrated that visual streams related to action control are differentially involved depending on the direction of the observed action (toward or away from the observer). Moreover, we identified that activity in the high-level somatosensory cortex predicts the perceived engagement of an observed action.

These results suggest a fusion of two prominent frameworks used for interpreting social perception in sensorimotor networks: the 'affordance competition hypothesis' (Cisek, 2007), which emphasizes sensorimotor transformations for action selection, and the 'Embodied simulation' theory (Gallese, 2003) which underscores the implicit activations of motor and sensory bodily representation when observing others. Modulation of activity in the somatosensory cortex correlating to the level of perceived engagement indexes differential employment of vicarious proprioceptive representations driven by the pragmatically relevant condition of being the recipient of a motor action. Causal approaches, such as transcranial stimulation of the secondary somatosensory cortex during tasks requiring rapid social responses, could clarify how internal simulation supports physical interaction readiness. Further questions remain about the nature of this sensorimotor simulation: is somatosensory activity a preparation for physical interaction? If so, what is its relationship to motor responses? Does this modulation merely signal potential action preparation, or is it a finer simulation that involves monitoring both one's own and another's bodily states for precision and regulation?

Lastly, our RSA revealed the strong complementarity of sensorimotor networks of the MNS and the TPJ — a complex and multifaceted region — in processing interaction-relevant features during action observation. We showed that together with frontoparietal networks, the TPJ formed lateralized representational clusters sensitive to Goal-coding, in the left hemisphere, and to interaction coding, in the right hemisphere. We also showed that the right TPJ and the left premotor cortex, key areas of the MENTA and MNS system, share a representational structure based on the perceived orientation of the observed action. These results add new evidence in favour of the hypothesis, outlined in the introduction, that involvement in interaction triggers a broad network for representing features relevant to interaction management. However, our experimental paradigm did not allow us to assess, at a fine-grained level, the interplay between self and other representations and their distributions among key sensorimotor regions. Moreover, further analyses might be performed to understand the flow of information among our ROIs, assessing functional and effective connectivity alongside representational connectivity. It might be hypothesized that the hemispheric laterality reflects a partially separated processing of features of the observed action, integrated at a higher level by specific inter-hemispheric partners.

Understanding the integration of diverse features could be crucial for addressing the limited involvement of the dmPFC in our RSA, a key area for social cognition. If, as suggested, the dmPFC manages motor interactions, our passive task may have failed to engage this region. Alternatively, the dmPFC might serve a broader integrative role not captured by our models, which focused on specific action features (e.g., goal, perspective, gaze). Should the dmPFC and other social brain areas simulate ongoing interaction sequences, they may form complex representations that may be better captured by allocentric or third-person models involving action sequences or abstract embodied representations.

In conclusion, these findings suggest that although the TPJ and dmPFC are traditionally regarded as core MENTA areas, they serve fundamentally different functions within social cognition networks. Together with prior studies linking the mirror mechanism to dmPFC computations in interactive contexts, our results support revising the framework of social brain computations. Contrary to the dichotomy between abstract mentalization and sensorimotor encoding of others' behavior, our analysis suggests that so-called Theory of Mind regions and sensorimotor networks function within a distributed sensorimotor processing, in which Other-to-Self remapping processes and Self-Other distinction might constitute two fundamental functional axes. This would represent a novel way to approach and frame social behavior for future research. This approach is based primarily on the study of embodied, (inter)action-oriented features of behavior, shedding new light on the reconstructive mapping processes of others' social behaviors in the brain.

6. References

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