

Review Article

Social Cognition through the Lens of Cognitive and Clinical Neuroscience

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Social cognition refers to a set of processes, ranging from perception to decision-making, underlying the ability to decode others' intentions and behaviors to plan actions fitting with social and moral, besides individual and economic considerations. Its centrality in everyday life reflects the neural complexity of social processing and the ubiquity of social cognitive deficits in different pathological conditions. Social cognitive processes can be clustered in three domains associated with (a) perceptual processing of social information such as faces and emotional expressions (social perception), (b) grasping others' cognitive or affective states (social understanding), and (c) planning behaviors taking into consideration others', in addition to one's own, goals (social decision-making). We review these domains from the lens of cognitive neuroscience, i.e., in terms of the brain areas mediating the role of such processes in the ability to make sense of others' behavior and plan socially appropriate actions. The increasing evidence on the "social brain" obtained from healthy young individuals nowadays constitutes the baseline for detecting changes in social cognitive skills associated with physiological aging or pathological conditions. In the latter case, impairments in one or more of the abovementioned domains represent a prominent concern, or even a core facet, of neurological (e.g., acquired brain injury or neurodegenerative diseases), psychiatric (e.g., schizophrenia), and developmental (e.g., autism) disorders. To pave the way for the other papers of this issue, addressing the social cognitive deficits associated with severe acquired brain injury, we will briefly discuss the available evidence on the status of social cognition in normal aging and its breakdown in neurodegenerative disorders. Although the assessment and treatment of such impairments is a relatively novel sector in neurorehabilitation, the evidence summarized here strongly suggests that the development of remediation procedures for social cognitive skills will represent a future field of translational research in clinical neuroscience.

1. Making Sense of Others' Behavior with Social Cognition

Social cognition refers to a set of neurocognitive processes underlying the individuals' ability to "*make sense of others' behavior*" as a crucial prerequisite of social interaction [1]. Such a complex ability entails a variety of skills, ranging from decoding social information (e.g., faces and emotional expressions) and drawing inferences on others' mental or affective states to making decisions consistent with social norms and others' welfare.

Social abilities emerge as early as 14 months [2], also in nonhuman species [3], and remain crucial for the lifespan [4]. Their centrality in everyday life is clearly shown by those conditions in which a social cognitive impairment

results in a variety of adverse outcomes, e.g., mental [5] and physical [6] deficits, functional disability [7], unemployment [5], and more generally poor quality of life [8]. The last edition of the American Psychiatric Association's Diagnostic and Statistical Manual for Mental Disorders (DSM-5) has indeed introduced social cognition as one of the six main factors of neurocognitive functioning, impaired in different pathological conditions.

Social cognitive impairments are a prominent concern, or even a core facet, of several neurodegenerative (e.g., behavioral variant of frontotemporal dementia), neuropsychiatric (e.g., schizophrenia, major depressive disorder, and bipolar disorder), and neurodevelopmental (e.g., autism spectrum disorder and attention deficit hyperactivity disorder) conditions, and often occur after acute brain damage (e.g.,

traumatic brain injury and stroke) [9]. Moreover, such deficits are critical predictors of functional outcomes because they affect the ability to create and maintain interpersonal relationships, thereby removing their benefits in everyday life [7]. In this respect, the rewarding and healthy value of social interaction [10] is shown by growing evidence on the negative consequences of isolation in terms of morbidity and mortality [11–13]. Interestingly, *perceived* social isolation (i.e., loneliness) is a major risk factor for several diseases, including dementia, independent of objective social isolation [14].

In order to pave the way for other articles of this special issue on the social cognitive deficits associated with acquired brain injury, this review aims at providing an overview of the social brain and its main functions. We will pursue this goal by summarizing the main findings obtained within the research field popularly known as “social cognitive neuroscience” [15]. For explanatory purposes, the complexity of social cognition will be addressed in terms of its three main domains, i.e., social perception, social understanding, and decision-making in the social context. Each of these subjects, representing distinct—although strictly intertwined—sectors of social neuroscience, will be first addressed in terms of cognitive processes and their modulating variables and then with regard to the available *f*MRI evidence on their neural correlates. Since the consequences of brain damage on social cognitive performance might be confounded by aging effects, in the last section we will briefly summarize the main findings of a fast-growing literature concerned with age-related changes in different facets of social cognition. To complement the evidence on the effects of acquired brain injury presented in other articles of this issue, this section will also review few selected findings from a lively interdisciplinary research sector exploring social cognitive deficits in neurodegenerative disorders. To introduce the potential translational implications of research in social cognitive neuroscience, we conclude by discussing selected examples of social cognitive treatment protocols assessed in previous studies and the available meta-analytic evidence about their effectiveness.

2. Three Main Domains of Social Cognition

The ability to establish appropriate social interactions entails several distinct processes. First, the social agent must recognize the others as “living persons,” via the analysis of complex perceptual information including facial expressions, gestures, postures and body language, and voice, [16]. Once integrated, this information will represent the input for higher-level processes underlying a direct resonance to others’ affective states (i.e., “empathy”) and/or the interpretation of their observable behaviors in terms of mental states and dispositions (i.e., “mentalizing” or “theory of mind” [17]). By modulating decision-making, the outcome of these processes will likely lead the observer to adapt her/his own social behavior [18]. This framework highlights the three key domains of social cognition which will be discussed in the next sections, i.e., social perception, social understanding, and social decision-making.

2.1.

2.1.1. Social Perception. A basic prerequisite of social cognition is the ability to distinguish between objects (whose behavior is completely explained by physical forces) and persons (characterized by inner experiences, such as motivations, reasons, and intentions, which make their behavior not completely predictable) (Fiske and Taylor, 2013) [19].

A related question in social cognitive neuroscience is whether social stimuli represent a qualitatively different perceptual category or rather the specificity of their neural processing can be reduced to “low-level” perceptual dimensions such as vividness, salience or familiarity (Fiske & Taylor, 2013). The former hypothesis fits with the centrality of social stimuli in human life, with their different functions being expressed at various levels of complexity: survival for the single individual, communication in dyads, social coordination in groups, and, finally, culture in institutions [20]. The prototypical example, in this respect, is represented by the neural processing of human faces [21], providing multifaceted information on both others’ changeable characteristics such as emotions and intentions, and invariant features such as identity. The unique salience of human faces [22] is indeed considered to reflect their predictive power with respect to others’ intentions and thus their potential consequence in social terms [23]. In line with this view, different experimental paradigms suggest that faces and objects undergo different styles of cognitive processing, i.e., holistic vs. part-based coding, respectively, with parts being integrated into a whole in upright but not inverted faces [24]. This evidence for the unique status of faces fits with the existence of a dedicated neural circuitry for this category of social stimuli, additionally showing stronger responses to upright than inverted faces [25].

In particular, the eyes represent the most dynamic and informative social stimulus, capturing our attention more than head/body movements and postures [26]. Gaze direction reveals overt attention shifts, and the informative value of another’s eye-movement patterns with respect to her/his mental states explains why gaze perception is considered a crucial prerequisite of mentalizing [27]. Alongside gaze, also the emotional expressions produced by the contractions of facial muscles provide crucial social information [28, 29]. In addition to the obvious communicative valence of emotions (“*A radar and rapid response system, constructing and carrying meaning across the flow of experience*” [30]), it is important to stress their adaptive value for appraising experience and preparing to act in response to external stimuli. The popular Ekman and Friesen’s (2003) facial action coding scheme (FACS) describes facial expressions as combinations of the action units characterizing different emotions. This model is based on the notion of a set of six basic universal emotions (happiness, anger, sadness, fear, disgust, and surprise) which all humans can express and recognize regardless of sociocultural effects [31]. It is worth mentioning that more recently, a similar proposal has been made for specific social emotions such as shame and embarrassment (Cordaro et al., 2017). On the other hand, available evidence on the role played by cultural rules on the processing of facial expression

and interpretation of emotions strengthens an “interactionist perspective” taking into consideration both biological and social/cultural factors [32].

While facial expressions represent the most effective means for emotional communication, the latter can involve also the body [33] and the voice [34]. In the first case, bodily changes are related to the role of emotions in preparing to act in response to external stimuli. If different emotions involve specific patterns of body movement and posture, this information could support emotional decoding based on visuomotor analyses of body language. Evidence based on point-light displays indeed shows high accuracy in relating such a minimal information to the emotion expressed by a moving body [35]. In addition, voices reveal our feelings as well, through nonverbal vocalizations (e.g., laugh) and prosody. However, available evidence suggests that the voice conveys mostly unspecific facets of affective states, such as physiological arousal [36], but no clear cue to specific emotions. On the other hand, the combination of different features could contribute to distinguish emotions in spoken sentences [37], and there is evidence for intersubject reliability in emotional judgments based on vocalizations [38]. Moreover, although most studies have addressed the information provided by face, body, and voice in isolation, the typical co-occurrence of multiple input channels improves emotional decoding (Martinez et al., 2015).

According to the “Feedback hypothesis”, faces, voices, and bodies not only express but also influence emotional experiences, because the production of facial expressions, sounds, and postures results in related sensory feedback which in turn modulates the intensity of feelings [39]. The latter would be thus enhanced by the expression of a congruent emotion and decreased either by the inhibition of a congruent emotion or by the expression of an incongruent emotion [40]. This hypothesis suggests a tight relationship between the perceptual and “private” facets of emotional processing, which fits with recent evidence on emotion perception. Several theoretical speculations and empirical investigations on this subject revolve around the notion of “embodied simulation.” That is, a mirror-like mechanism [41] is considered to provide a direct link between the first- and third-person experiences and thus access to the meaning of others’ actions and emotions [42]. In this perspective, mirroring the others’ facial emotional expressions, via the engagement of the corresponding motor circuits and muscular contractions (i.e., mimicry; [43, 44]), underpins a direct and experiential grasp of their meaning [45].

The notion of embodiment, however, has been also proposed to underlie even cognitive phenomena exceeding perception and action. According to the “embodied cognition” framework [46], all cognitive representations and operations would be fundamentally grounded in their physical sensory-motor context [47]. Even our semantic knowledge would be ultimately represented, at the neural level, in the sensory-motor systems underlying our direct experience with the world (Niedenthal, 2007), so that semantic representations of objects or events involve (some of) the brain sensory-motor states associated with their direct experience (Barsalou, 2008). This approach strongly departs from associative

network models, considering memory as a web of semantic concepts that describe objects and events [48] in terms of basic units represented by propositions [49]. In the latter framework, any object would be represented in memory by a set of descriptive propositions, interconnected by associative links made through experience. The engagement of an emotion unit would spread activity in this interconnected web [50], thus increasing the accessibility to words and memories associated with the target emotion [51]. In the embodied cognition framework, instead, even the somehow “abstract” facets of emotional processing, such as those representing the affective value of an object brought to memory, involves reactivating the motor programs and feelings associated with its direct sensorimotor experience [52]. The latter would then provide an experiential access to the meaning of concepts, including their affective features.

2.1.2. Neural Correlates of Social Perception. The fast growth of social cognitive neuroscience is providing increasing evidence on the brain networks subserving the different domains previously described, and the available data nowadays allow to fractionate the social brain in distinct sets of areas associated with relatively specific functions. We will focus on the neural processing of visual stimuli, representing the richest source of information in everyday social life as well as in the available literature.

The first nodes of the neural pathways underlying the processing of visual social stimuli involve the occipitotemporal cortex, where distinct brain regions have been associated with a preliminary decomposition of the visual scene into different categories and particularly faces (Occipital Face Area (OFA) in the inferior occipital gyrus and Fusiform Face Area (FFA) in the fusiform gyrus; [53]) and bodies or body-parts (Extrastriate Body Area (EBA) in the lateral occipito-temporal cortex and Fusiform Body Area (FBA) in the fusiform gyrus [54]). The activation of these areas has been interpreted as reflecting a dedicated neural circuitry for faces (“*face-selective hypothesis*” [21]), or a greater expertise in discriminating faces compared with other kinds of stimuli (“*expertise hypothesis*” [55]). The latter hypothesis found support in the FFA activation in participants trained to identify novel artificial objects sharing some typical constraints of faces (i.e., greebles; [56]), but subsequent studies reinterpreted this evidence in terms of subjects coding these stimuli as face-related [57].

While the OFA and EBA appear to underpin the neural representation of parts of faces and bodies, respectively, the FFA and FBA seem to reflect more holistic representations of these stimuli, i.e., processing the configurations of face- and body-parts into wholes [58]. Alongside the proximity of FFA and FBA in the posterior fusiform gyrus, the latter evidence raises the possibility that their functional integration underpins the ability to identify other individuals based on cues from both faces and bodies, particularly when a single cue-type is not sufficient for recognition [54]. This proposal fits with the notion that, among distinct neural pathways originating from these areas, a “ventral” pathway, running along the temporal cortex, underpins the semantic representation of specific concepts, i.e., the *identity* of familiar

or unique stimuli. In particular, the polar sectors of the temporal and medial temporal cortex seem to be associated with the processing of unique houses or persons (e.g., the White House or President Obama) [59]. Along this pathway, single-cell recordings during awake-surgery have highlighted, in the human temporal and hippocampal cortex, neurons showing invariant responses to single persons, landmarks, and object [60]. The fact that these neurons are activated by different pictures of a same stimulus and some of them even by letter strings reporting its name strongly suggests their role in coding an abstract representation of specific concepts.

Another neural pathway of social perception involves the posterior portion of the lateral temporal cortex, where a hierarchical organization includes brain areas responding to pure motion (area MT/V5 in the inferior/middle temporal cortex), the typical motion of objects (middle temporal cortex), and biological motion (posterior portion of superior temporal sulcus; pSTS) [61] (Figure 2(a)). The pSTS represents a crucial hub of the brain network of social perception, processing the changeable features of biological stimuli and particularly their action-related motion patterns [62]. Neurophysiological studies have highlighted, in this region, single neurons responding to the observation of movements performed by different biological effectors, including eye-gaze [63]. Some of these neurons respond to complex visual patterns, such as the interaction between effector and objects, or a reaching action but only if the agent's gaze is directed to the target object [64]. Overall, the available evidence suggests that the pSTS plays a key role in the sensory binding of different features of biological motion, likely generating a superordinate representation of perceived actions [65]. Since pSTS neurons do not discharge during active movements, this region of the monkey brain does not display a "mirror-like" response. However, both neurophysiological data from the monkey [62] and neuroimaging evidence in human subjects [66, 67] suggest that the pSTS sends higher-level perceptual inputs to the frontoparietal mirror system associated with the analysis of the meaning of others' actions (see Section 2.2.1 and Figure 2(b)).

The pSTS is also part of another network, including the amygdala and orbitofrontal cortex (Amaral et al., 1992), associated with the processing of the affective value of observed stimuli. The amygdala is a key node of the social brain (Brothers, 1990), in which neuroimaging studies are associated with the emotional facets of social perception, such as the processing of facial expressions (Todorov et al., 2012) and judgments of trustworthiness [68]. This correlational evidence found support in lesional data showing the consequences of its damage, or abnormal functioning, on social cognitive processing [69] and real social interactions [70].

In line with the recent emphasis on the notion of "connectome" [71], diffusion imaging studies have started to address the structural connections underpinning the different facets of social cognition [72]. In the case of face processing, converging evidence shows the involvement of the inferior longitudinal fasciculus (IFL) and inferior frontooccipital fasciculus (IFOF), projecting from the occipital cortex to the anterior temporal and frontal cortex, respectively [73]. Their crucial role in connecting the nodes of the network

subserving face processing is shown by studies relating distinct metrics of structural connectivity to face perception skills in normal conditions [74], physiological aging (disruption of the right IFL [75]), and in association with face blindness in developmental prosopagnosia (disruption of both the right IFL and IFOF [76]). Preliminary evidence additionally shows the involvement of the superior longitudinal fasciculus (SLF), connecting temporal, parietal, and frontal regions [77] and particularly face-responsive portions of the STS with orbitofrontal and inferior frontal cortex ([78, 79].

2.2.

2.2.1. Social Understanding: Representing Others' Behavior.

Since others' behavior is not completely predictable, the success of social interactions depends on the ability to decode their mental and, particularly, intentional states [80]. Interpreting others' behavior in terms of mental states, such as beliefs, desires, intentions, goals, experiences, sensations, and emotions, is thus a critical step for predicting their future actions [81]. This natural disposition to mentalizing entails the development of a "Theory of Mind" (ToM) based on the awareness that people have mental states, information, and motivations that may differ from one's own (Frith and Frith, 2006) [82]. On this assumption, mentalizing performance is typically measured with tasks assessing whether an individual is able to represent mental states, attributes them to oneself vs. other persons, and then, based on such attribution, correctly understands and/or predicts others' behavior [83–85].

Far from being a unique process, mentalizing involves several components and the integration of different facets of social understanding [86, 87]. Neuroimaging studies are providing increasing knowledge on the neural correlates of such components. A first crucial distinction regards the ability to attribute mental states vs. affective states, i.e., *cold* or *cognitive ToM* vs. *hot* or *affective ToM*, respectively [88]. Moreover, representing others' thoughts, desires, feelings, and traits, i.e., mentalizing, differs from grasping and automatically sharing affective states, i.e., empathy [89]. On the other hand, these constructs are partially overlapping [90], and an influential model considers cognitive ToM a prerequisite for affective ToM, which additionally requires empathic skills ([91] see Figure 1).

In addition, a dissociation has been proposed between implicit and explicit mentalizing [80]: while the former would be present even in infants, who can ascribe false beliefs to agents from nonverbal behavior [2], explicit mentalizing represents a cognitively demanding sociocultural skill acquired by verbal instructions. Considerable evidence nowadays shows that explicit mentalizing develops slowly in the childhood [87]. Finally, based on computational complexity it is common to distinguish between first and higher-order Theory of Mind processing. First-order ToM, involving the representation of another individual's mental states (inclusive of both its affective and cognitive components) [92], develops between the age of 4 and 5 [93]. Second-order ToM, i.e., mentalizing what someone else is thinking or feeling about a third person's mental states [94], typically develops at the age of 6.

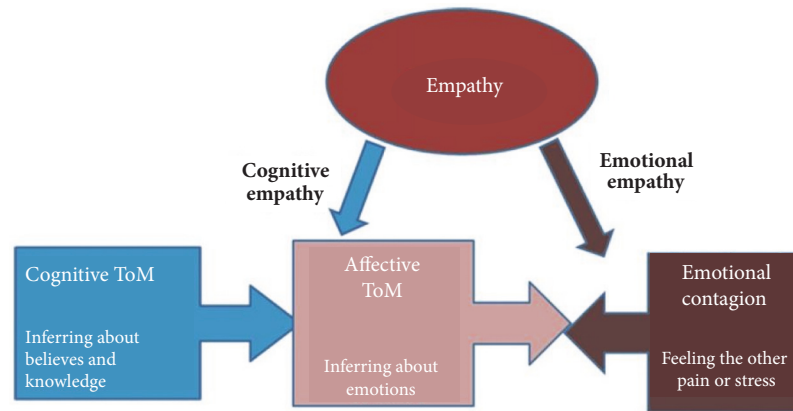


FIGURE 1: Empathy and mentalizing. The figure depicts Shamay-Tsoori et al.'s [91] model of the relationship between the key processes of social understanding, i.e., empathy and mentalizing. According to the model, cognitive mentalizing is a prerequisite for affective mentalizing, which however interacts with emotional empathy. Reproduced with permission from Shamay-Tsoori, Harari, Aharon-Peretz, and Levkovitz, [91].

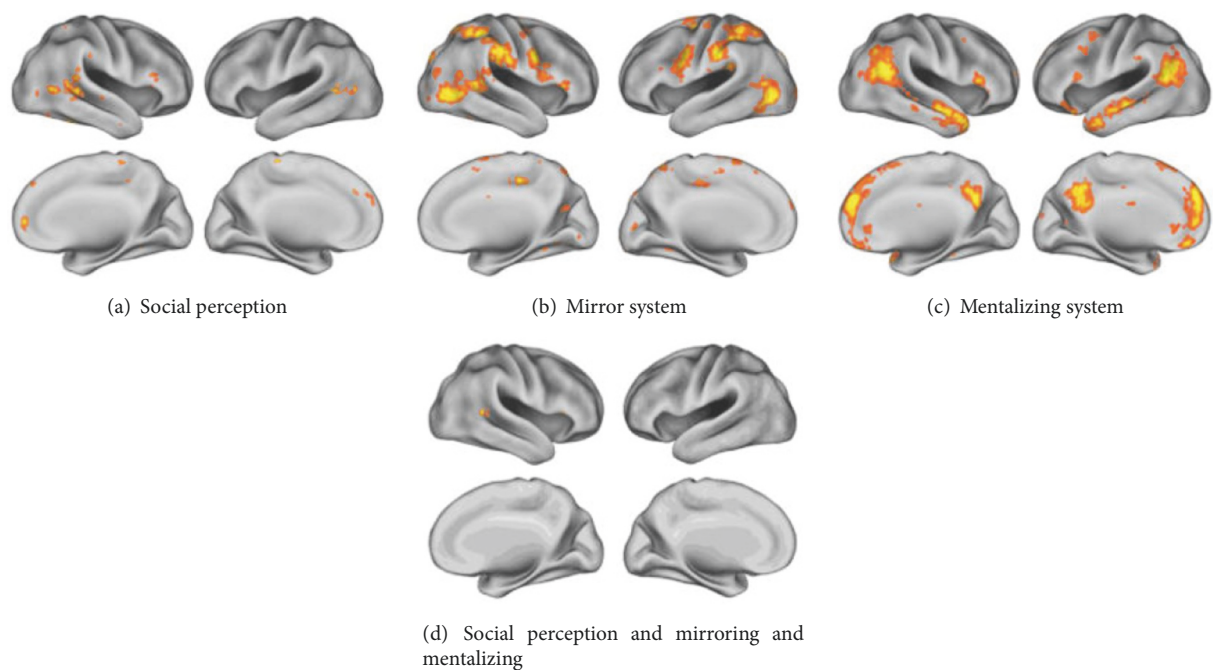


FIGURE 2: Brain networks of social cognition. Meta-analytic evidence for the neural networks underlying social perception (a), action observation (mirror system) (b), and mentalizing (Theory of Mind system) (c). As shown in the bottom sector of the figure, these three networks overlap in the STS, a crucial hub of the social brain providing inputs to both the mirror and mentalizing systems [66]. Reproduced with permission from Yang, Rosenblau, Keifer, and Pelphrey, *An Integrative Neural Model of Social Perception, Action Observation, and Theory of Mind*, Neuroscience and Biobehavioral Reviews, 51 (2015) 263–275, doi:10.1016/j.neubiorev.2015.01.020.

Social perception and in particular emotion decoding are considered to precede mentalizing [85]. The former stage would indeed reflect low-level perceptual processes providing inputs to the higher-level integrative and inferential processes associated with mentalizing [95]. On the other hand, mentalizing can influence social perception via top-down mechanisms mediated by long-term knowledge. This bidirectional relationship represents a core element of the influential Mindreading model [96], in which social perception and mentalizing represent different components of a

larger system subserving the ability to perceive and respond appropriately to others' emotions and intentions [97]. This model entails three key perceptual detectors for mental states, gaze, and affective states, alongside a shared attention mechanism supporting the ability to selectively focus on specific stimuli and integrating the outcome of detector-specific basic perceptual processes. On top of this hierarchy, an advanced mentalizing ability allows us to perceive and respond appropriately to others' emotions, beliefs, and behaviors.

The kind of processes underpinning the mentalizing ability is, however, strongly debated (Goldman and Sripada, 2005). According to so-called “Theory-theory”, people act as naïve social scientists, developing psychological theories to infer others’ mental states [98]. Based on the aforementioned mirroring process, “Simulation theory” rather states that we attribute mental states to others by simulating them in our own mind [45, 99]. A considerable literature, mostly based on neuroimaging data, suggests that different processes, revolving around simulative mechanisms vs. inferential routines, are recruited depending on the type of stimuli (visual vs. verbal) and instructions (implicit vs. explicit) ([66, 100] see [101]).

An alternative to both these approaches is represented by so-called “interaction theory” [102], stressing the role played by embodiment and direct perception when experiencing real social interactions (Froese and Gallagher, 2012). Based on the uniqueness of social interaction, in terms of the richness of incoming information and complexity of the responses, the advocates of this perspective aim to address social cognition from an interactor’s point of view [103], also with innovative experimental designs grounded in virtual reality [104, 105], to investigate the mechanisms whereby individuals modulate their actions online [106]. This change of perspective involves shifting from “open-loop” to “closed-loop” scenarios where interactors influence one another dynamically, reciprocally, and continuously [107]. Neuroimaging studies based on this approach have shown that compared with the mere observation of social stimuli, being actively engaged in a social interaction activates a more extensive network of areas associated with perception-action coupling and affective evaluations, promoting motor responses coherent with the social stimulus [107]. These results highlight the potential implications of such an ecological approach not only for studying the neural bases of social cognition in normal individuals, but also for characterizing related disorders in pathological populations and for rehabilitation after brain damage. For example, recent evidence based on human-avatar online interactions shows that apraxics’ motor impairments in a social reach-to-grasp task are abolished when patients are asked to interact with a virtual partner rather than performing actions on their own [108].

2.2.2. Neural Correlates of Social Understanding. Distinct research lines, within social cognitive neuroscience, have addressed the neural bases of the ability to understand others’ behaviors and decode their intentions and feelings. Most of the related evidence revolves around the mirror and mentalizing brain networks which, based on inputs from the pSTS (see Section 2.1.2), appear to underpin distinct levels of the hierarchy of social understanding [66, 109].

The mirror system includes inferior frontal, premotor, and parietal regions which are activated both when performing an action and when observing the same action performed by someone else [41] (Figure 2(b)). This network is considered to underpin a variety of action-related social functions, from action recognition [110] and imitation learning (Vogt et al., 2007) to the context-based decoding of so-called “private goals,” e.g., grasping a cup to drink vs. to clean the table

(Iacoboni et al., 2005). The mirror system is anatomically and functionally distinct from the mentalizing system, which includes the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), medial precuneus/posterior cingulate cortex, and temporal poles [86, 111, 112] (Figure 2(c)). This network of areas is typically engaged when others’ intentions cannot be automatically derived from visual cues and must thus be inferred in terms of thoughts and beliefs [101, 109].

Therefore, a superordinate dimension eliciting the specific recruitment of the mirror vs. mentalizing systems is represented by the aim to identify, respectively, *how* (executed movements associated with a behavioral state) vs. *why* (beliefs and intentions associated with a mental state) an action is performed [113–115]. The mirror and mentalizing systems seem thus to play complementary roles in processing others’ intentions, driven by the presence of, respectively, biological actions vs. abstract information (e.g., observing real scenes vs. reading stories) or implicit vs. explicit instructions (e.g., to passively observe vs. to infer characters’ intentions) [101], and by identifying *how* vs. *why* the character is expressing a feeling (i.e., explicit identification vs. attribution [114]).

While the evidence reviewed above involves the attribution of intentions and cognitive states, other research lines have addressed the neural bases of empathy, i.e., grasping others’ feelings through their direct resonance in the observer’s brain. This process seems to recruit a mirror-like mechanism specific for different kinds of empathic responses, involving the same brain regions associated with their first-person experience rather than the frontoparietal mirror network. This is the main finding of a series of studies which have reported the involvement of (a subset of) the same brain regions when directly experiencing, and when attending in someone else, specific affective or sensory stimulations. Such a mechanism has been described for the direct and vicarious experience of pain (anterior insula and anterior cingulate cortex, i.e., the affective sector of the so-called pain matrix [116, 117]), disgust (anterior insula [118]), tactile sensations (secondary somatosensory cortex SII [119]), and even regret for the outcomes of choices (orbitofrontal cortex and anterior cingulate cortex [120, 121]). In keeping with the notion of “mirroring,” these results suggest that the observation, or even the mere awareness [116, 117], of another person in a particular emotional state may automatically activate the neural representation of the same state in the observer. Such representation includes its associated autonomic and somatic responses, neurally associated with the activation of the anterior insula and dorsal anterior cingulate cortex [122, 123], which provides support to the concept of a mirroring, sensorimotor, and nature of empathy [124]. This notion is strengthened by recent evidence on the neurophysiological correlates of facial mimicry, i.e., the unconscious and unintentional automatic response to the facial expressions of others [125]. The simultaneous recording of facial muscular reactivity (via electromyography, EMG) and brain activity (via fMRI) highlighted a correlation between spontaneous facial muscle reactions to facial expressions and brain activity in the frontoinsula and inferior parietal “mirror” sectors associated with their motor simulation. Overall, considerable evidence indicates that such a limbic, visceromotor, mirroring system

for shared sensory and emotional experience provides the neural framework for emotional insights into other minds.

Both mirroring and mentalizing have been associated with structural connections between temporal, parietal, and frontal lobes underpinned by the superior longitudinal fasciculus [72]. The latter has been indeed associated with individual differences in abilities such as emotion recognition [126, 127], empathy [128], and imitation [129]. Other facets of embodied cognition have been ascribed to further limbic tracts, i.e., the uncinate fasciculus linking medial temporal and orbitofrontal cortex [130], involved in socioemotional processing [131], and the anterior thalamic radiation connecting the hypothalamus and limbic structures to prefrontal and anterior cingulate cortex [132], associated with affective processing and emotional regulation [133]. In keeping with their role in face processing, the inferior longitudinal fasciculus (ILF) and inferior frontooccipital fasciculus (IFOF) have been also associated with emotion recognition and empathy skills both in healthy [128, 134] and brain-lesioned [135, 136] individuals. In addition to the SLF, mentalizing seems to be supported also by the cingulum (linking medial prefrontal, posterior cingulate and medial temporal cortex [130]) and arcuate fasciculus (connecting the temporoparietal junction with prefrontal cortex [137]). Mentalizing abilities have been related to the degree of axonal injury in the left cingulum in brain-lesioned children [138] and in the arcuate fasciculus, near the temporoparietal junction, in high-functioning autistic individuals [139]. Strong evidence for this association comes also from direct electrical stimulation during neurosurgery, showing that the virtual disconnection of these tracts results in a marked decrease of mentalizing performance [140, 141].

2.3.

2.3.1. Social Decision-Making. Understanding others' behaviors in terms of dispositions and intentions is often critical for making appropriate decisions in a variety of social contexts. Most choices are made within direct or indirect social interactions within complex and dynamic environments. They will thus depend either on the choices already made by others (if they are known) or on our prediction of the choices they will make (if concurrent with our own ones) and more generally on the awareness of their consequences for both ourselves and others [142]. From the economic standpoint, studying decisions made in different types of social context, or even within social interactions, is aimed at identifying the optimal choice among the available ones. On the other hand, psychological studies have shown several examples of preferences which seem to reflect prosocial and/or affective considerations even more than economic utilities. Researchers have thus begun to investigate the social and cognitive variables modulating social decision-making using tasks originally developed in distinct research fields within the economic sciences.

One typical example is represented by studies modeling agents' choices with the tools of Game Theory. The latter is based on rigorous models aiming to identify the optimal choice for interacting agents, in different possible situations

in which they know the respective outcomes of each possible choice and they can, or cannot, make agreements before choosing. As anticipated, however, real human choices often deviate from the predictions of such models. For instance, classical Game Theory predicts that a group of rational players will make decisions to reach outcomes, known as Nash equilibria [143], from which no player can increase his/her own payoff unilaterally. Still, considerable evidence shows that people introduce psychological and prosocial considerations in their strategies, which appear to be less selfish and more fairness-oriented than predicted by economic models [144]. Typical examples of such prosocial attitude are represented by the usual response patterns observed in three tasks entailing two interacting players, popularly known as Ultimatum, Dictator, and Trust games (Fehr and Fischbacher, 2006).

In the *Ultimatum Game* [145], the proposer is asked how much of a financial endowment she/he is willing to send to an unknown responder. The latter can accept or reject the offer: in the first case, the sum is divided as proposed; in case of rejection, instead, no one receives anything. Against the economic prescription, i.e., to accept any offer as a responder and thus to offer as less as possible as a proposer [146], people usually propose "fair" offers [147] and reject unfair offers [148], although with some cultural differences [149], rejection-rates increase substantially as offers decrease in magnitude. A similar trend is found in the *Dictator game*, although the responder can only accept the proposer's offer.

In the *Trust Game*, two players receive the same initial endowment. Then, the "trustor" player decides how much of this sum to send to a trustee. Both players know that the transferred amount will be multiplied by a factor >1 . The trustee must then decide whether to return some of her/his payoff to the trustor. If she/he honors trust, both players end up with a net monetary increase. If instead the trustee keeps the entire amount, the trustor ends up with a loss. In the case of a single interaction (i.e., "one-shot"), a rational and selfish trustee would not be expected to honor the first player's trust. Therefore, the latter should never trust the other player. Against this prediction, instead, in most studies the first player sends some money to the second one, with trust being typically reciprocated [150].

Both in their "one-shot" and iterated versions, these tasks typically highlight the willingness to punish, at own expenses, defectors who will never be met again [144, 151]. Considerable evidence seems indeed to show the role played, in real human interactions, by an *expectation of reciprocity*. The latter is the basis of the "tit-for-tat" strategy, i.e., trusting the partner at the first move and then replicating her/his next moves, in which both informatic simulations and psychological studies highlight as the natural strategy in social interactions (Axelrod and Hamilton, 1981). Importantly, this strategy requires the identification and punishment of defectors, even when this is not directly beneficial to the punisher. Since the simple presence vs. absence of the possibility to punish has been shown to increase vs. reduce cooperation in social interaction [151], this behavior has been called "altruistic punishment" because its costs will benefit individuals other than the punisher. While representing another puzzling

behavior for economic theories, real interaction-games have shown that altruistic punishment is a key prerequisite for cooperative behavior to spread in a society [151]. There must exist, then, some incentive to behaviors which are socially advantageous, but individually expensive. A possible incentive for altruistic punishment by single individuals has been found in the strong negative emotions associated with unfairness, defection, and abuse of one's own trust, eliciting a "desire of revenge" [151]. In simpler words, anticipating the pleasure inherent in satisfying such desire would represent the incentive to punishment behaviors which, although irrational in purely economic terms for the single individual, exert prosocial consequences at the society level.

While classical economic models had largely ignored the influence of emotions on decision-making, growing evidence at the crossroad between cognitive neuroscience and economics is showing the effect of affective processing on actual choices [152]. It is now widely acknowledged that decision-making is driven by anticipated outcome-related feelings and particularly by the attempt to experience positive feelings associated with gains and prosociality and to avoid negative feelings such as disappointment for a loss, regret for a foregone outcome, or guilt for the adverse consequences of one's choices for another [153]. The neural bases of these processes constitute the subject of neuroeconomics, a lively research field at the crossroad among neural, psychological, and social sciences.

2.3.2. Neural Correlates of Social Decision-Making. Understanding others' affective and cognitive states and particularly intentions is often a crucial step for different facets of social decision-making. These might include anticipating others' choices in a strategic context, or planning the reaction to another's defection, e.g., an unfair proposal in the Ultimatum Game, or unreciprocated trust in the Trust Game. While the aforementioned psychological studies have highlighted actual behaviors inconsistent with "rational" economic predictions, neuroscientific data suggest that the typical human prosocial attitude might largely reflect motivational drives associated with brain regions underlying affective and hedonic evaluations. This research field is indeed grounded in the notion that the weight of affective drives, largely acknowledged in individual decision-making (e.g., [120, 121, 154, 155]), is even enhanced when making choices in a social context [156, 157].

A fast-growing literature is unveiling a mosaic of brain regions underlying the different facets of this process. First, the activation of the anterior insula in association with the receipt and rejection of unequal offers by another human subject [158] might reflect the negative affective reactions elicited by unfairness. Interestingly, accepting unfair offers reflects in increased activity of the dorsolateral prefrontal cortex, a key node of the executive network associated with cognitive control and response inhibition. The latter evidence has been initially interpreted in terms of the role played by this region in inhibiting the negative affects prompting the rejection of unfair offers [158]. However, against this hypothesis further studies have shown an increase of acceptance rate after its deactivation with transcranial magnetic stimulation

(TMS) [159, 160]. The dorsolateral prefrontal cortex might thus underpin the selfish drive to accept every offer, rather than the prosocial aptitude toward altruistic punishment. On the other hand, the fact that punishing defectors reflects in the activation of the ventral striatum [161], the key node of the brain reward network (Schultz et al., 2006), suggests that altruistic punishment might be also stimulated by the rewarding experience implicit in satisfying the desire for revenge against nonreciprocators. Due to its costs, such behavior requires to weigh economic and hedonic outcomes, a tradeoff involving the ventromedial prefrontal cortex [161]. Overall, the activation of the striatum in association with "tit-for-tat" behaviors and particularly with reciprocated cooperation [162] highlights a neurobiological interpretation of the, economically irrational, tendency to prefer prosocial behaviors over individual gratifications [163]: the subjective utility associated with mutual cooperation would represent a short-term social reward outweighing that resulting from unilateral defection (which, in contrast, might additionally reflect in negative feelings such as shame and guilt).

While these data seem to highlight a natural human disposition to prosocial behavior and sharing of resources, less optimistic evidence comes from studies investigating the neural bases of altruism and charity, i.e., costly behaviors providing benefits only to other people. On the one hand, the activation of the ventral striatal hub of the reward network [164, 165] might suggest that altruistic behavior is rewarding in itself, which could be interpreted as an evidence against the existence of "pure" altruism. Moreover, other studies have shown, in the same subjects, overlapping ventral striatal activations when deciding to donate money while knowing to be observed and when deciding to keep the money while knowing that no one was observing them [166]. These results suggest the opportunity to reframe the theoretical speculations and empirical analyses of the putative human prosocial, or even altruistic, disposition in a broader perspective merging economic, psychological and neuroscientific evidence.

3. Age-Related Changes in Social Cognition

A growing literature on age-related changes in cognitive proficiency reveals that physiological aging entails both losses and gains of functions (Kensinger et al., 2017) [167]. Despite a global decrease of cognitive efficiency, some facets of social cognitive and affective processing remain stable or even improve with age [168], bringing potential benefits to everyday functioning [169].

Such changes involve the interaction of multiple processes, i.e., disruption of functions, resource limitations, and reallocation, as well as compensative mechanisms (Kensinger et al., 2017). In turn, these processes are modulated by a wide range of factors including, among others, individual differences in education [170], level of fluid cognition [171], and resource availability [172]. Within this complex scenario, two variables are considered to provide the strongest contribution to age-related changes in social cognition [173].

The first variable concerns the cooperation vs. competition between automatic and controlled processes. Since

aging mainly impacts executive control (von Hippel and Henry 2012), a significant reduction of the ability to inhibit automatic responses can result in socially disinhibited and inappropriate behaviors [174]. The same mechanism appears to facilitate stereotypical thoughts, which are automatically activated in the presence of stereotyped group members, making older adults more inclined to show prejudices than younger adults (von Hippel and Henry 2012).

Secondly, changes in social cognition seem to depend on whether and to what extent tasks rely on novel information processing vs. accumulated experience [175]. Despite a global decrease of cognitive efficiency (in terms of speed processing, memory, complex reasoning, attention, and inhibitory control), as well as physical [176] and perceptual [177] functioning, several studies reported smaller age-related effects in domains related to past experience, including vocabulary and general knowledge [175]. This is a crucial notion, since these skills might contribute to specific facets of social cognitive and affective processing and thus partially compensate the overall cognitive decline.

For instance, although older adults perform worse than young adults on memory recall tasks, even when presented with social and affective stimuli [178], they show equally, or even more, effective emotion regulation skills [171]. While the latter evidence may appear at odds with an executive decline, emotion regulation may require less resources in older than young adults due to the improved procedural knowledge accumulated throughout life [168]. In addition, older adults may allocate a greater proportion of resources to emotion regulation compared to younger adults [179], due both to the possible prioritization of arousing and to self-relevant information (Kensinger et al., 2017), and to age-related motivational changes toward the maximization of the emotional satisfaction in the “here and now” [168].

Overall, these findings highlight the complexity of age-related changes in social cognition, which are deeply intertwined with both the physiological decrease of cognitive functioning and the shifts in life goals. We will briefly review the available evidence on the changes reported in the three domains of social cognition previously described.

3.1. Age-Related Changes in Social Perception. As discussed in Section 2.1.1, faces represent a crucial source of social signals, and emotion recognition from facial expressions is a critical prerequisite for appropriate interpersonal communication and social functioning [180] (von Hippel and Henry, 2012).

While aging is associated with significantly decreased performance in recognizing negative emotions such as fear, sadness, and anger [180], older adults perform better than younger ones in the case of positive emotions (i.e., happiness and surprise) and disgust. This evidence has been ascribed to the *top-bottom bias*, indicating age-related changes in face-processing strategies: older, compared with younger, adults are more likely to focus on the bottom half of the face (mouth or nose), which provides information concerning the muscular contractions specifically associated with happiness and disgust [181], rather than on the eyes [182]. This pattern might reflect functional and/or structural age-related changes within the face-processing brain network—including the

STS, medial PFC and amygdala—associated with eye-gaze perception and decoding [167].

On the other hand, the decline in recognizing negative emotions from faces might be also attributed to the “*age-related positivity effect*” [183], indicating the older adults’ tendency to focus more on positive than negative stimuli compared with younger adults. This effect, consistently described also in attention and memory domains [184], has been linked to age-related changes in emotion regulation mechanisms, helping elders to preserve a better mood [185]. These changes might reflect the fact that, in the elderly, only negative stimuli are associated with the activation of the medial prefrontal cortex (PFC), possibly supporting top-down emotion regulation processes aimed to inhibit negative emotions [186].

3.2. Age-Related Changes in Social Understanding. The preservation of functions underlying social understanding, such as emotional sharing and the attribution of cognitive or affective states to others, predicts successful outcomes in aging [187]. In the attempt to disentangle specific changes in the different facets of social understanding, several studies have shown a prominent age-related decline in its *cognitive* components (i.e., mentalizing and social metacognition), with a relative conservation, or even an enhancement, of the *affective* ones (i.e., empathy and compassion) [167, 173, 188]. Also in this case, the former evidence may reflect an overall decline in executive control and fluid intelligence [189], associated with reduced activity of the dorsolateral PFC [167]. Additionally, older adults seem to shift their motivations: according to the *socioemotional selectivity theory* they disengage their focus from future-oriented goals and prioritize social and emotional meaningful activities by selectively allocating more resources on emotional processing and emotion regulation strategies [190]. This view is supported by a study reporting age-related neurostructural changes in 883 healthy individuals. While cortical thickness decreased with age in brain regions related to executive functioning, such as the dorsal ACC alongside the superior and lateral sectors of the PFC, no age effect was found in regions typically engaged in emotion regulation, such as the ventromedial PFC and ventral ACC [191].

3.3. Age-Related Changes in Social Decision-Making. Alongside an enhancement of affective processing skills, different facets of social behavior and decision-making, like generativity and prosociality, undergo substantial changes with age.

Generativity, i.e., the tendency to expand the individual focus of concern beyond oneself [192], becomes a prominent challenge in late life, prompting the desire of cooperation between generations and the need for older adults to offer emotional support and mediate conflicts, which are perceived as essential goals for survival (Gurven and Kaplan, 2009). Compared with young people, older adults endorse more generative goals and other-focused problem solving [193]. Moreover, both the feeling of pity and the willingness to help others seem to progressively increase with age [194].

Closely related to social affective skills, also the tendency to prosociality seems to increase in late life [195].

In line with the *socioemotional selectivity theory*, contexts relevant to social and affective goals might motivate older adults, even more than younger ones, to help others, since empathy and/or compassion represent powerful skills capable of promoting prosocial behaviors [195]. This is the core of “empathic concern” [196], whereby acting to benefit needy others can mitigate the negative emotional arousal induced by experiencing their needs. The enhancement of emotion regulation skills might thus mediate the higher prosociality displayed by older adults, ultimately increasing their well-being, satisfaction and emotional fulfillment [193].

4. Altered Social Cognition in Neurodegenerative Diseases

Increasing evidence highlights a variety of social cognitive impairments in different neurological (e.g., neurodegenerative diseases, traumatic brain injuries, and brain tumors) and psychiatric (e.g., mood disorders, autism, and schizophrenia) conditions [197–200]. These alterations are mainly associated with the functional consequences of neuropathological processes or brain lesions affecting regions and networks underlying social cognition skills.

Within the realm of neurodegenerative diseases, pathological changes in social cognition and behavior are a major hallmark of the frontotemporal dementia (FTD) disease spectrum, including the primary progressive aphasia (i.e., semantic, nonfluent, and logopenic variants) [201] and the behavioral variant (bvFTD) [202]. Due to the progressive degeneration of frontobasal and limbic networks associated with the processing of emotional and social cues [203–207], bvFTD represents a prototypical example of the breakdown of social cognition. A marked neurocognitive impairment has been reported, in this disease, in all the domains previously discussed, from emotion recognition and social understanding to judgment involving social dilemmas and violations (Elamin et al., 2013). Despite similar deficits in emotion recognition and social understanding [208, 209], bvFTD and both the semantic and the nonfluent FTD variants have been associated with different patterns of structural damage within a frontoinsula-temporal network which is also known as “social context network” [210]. This model is based on the notion that different social cognitive processes are encapsulated into specific context circumstances, having an intrinsic social meaning. Specific patterns of social cognitive impairment, typical of neurological and psychiatric diseases, might thus arise from selective dysfunctions within a distributed network causing a global impairment in the processing of social context information. This network is considered to include three main hubs with specific functions, i.e., (1) frontal areas, supporting the updating of context cues to make predictions; (2) temporal cortex, underlying the consolidation of value-based learning of contextual associations; (3) insular cortex, managing the convergence between emotional and cognitive states related to the coordination between external and internal milieus and thus facilitating frontotemporal interactions in processing social contexts.

Further cues into the abnormal social brain come from the literature revolving around the FTD-Amyotrophic Lateral

Sclerosis (ALS) continuum hypothesis [211]. The growing evidence on the neuropathological, genetic, neuroimaging, and clinical commonalities between the two conditions [212–217] now includes social cognitive deficits, which have been revealed also in ALS patient without dementia [218].

Social cognitive impairments have been described also in other neurodegenerative disorders. Although these symptoms are not considered central or typical expressions of these diseases, the impairment can involve one or more of the domains reviewed before. As discussed in the next paragraphs, social perception and social understanding are, to date, the most frequently investigated domains in neurodegenerative disorders.

4.1. Altered Social Perception in Neurodegenerative Diseases.

With respect to social perception, evidence exists for abnormal visual and/or auditory (i.e., based on prosodic cues) recognition of basic emotions, especially involving negative emotions, in bvFTD [219–222]. Interestingly, emotion recognition from faces discriminates bvFTD from other neurodegenerative, as well as psychiatric, diseases [207]. However, abnormal affective processing and emotion recognition (particularly for negative emotions) have been found also in other disorders (Elamin et al., 2013) [223], such as ALS [126, 224], Parkinson's disease [225], corticobasal syndrome and progressive supranuclear palsy [226], and Huntington's disease [223, 227], as well as Alzheimer's disease (AD) and mild cognitive impairment, particularly when subtle or static emotional stimuli are presented [8, 228].

4.2. Altered Social Understanding in Neurodegenerative Diseases.

The studies addressing social understanding in neurodegenerative diseases are contributing to unveil a complex scenario, with different disorders reflecting in distinct patterns of functional impairment. Defective mentalizing skills have been reported in bvFTD and AD [229]. However, while in AD this deficit likely reflects a global cognitive breakdown, bvFTD patients display a relatively selective impairment in affective mentalizing [229], likely reflecting their marked difficulties with empathic abilities [230]. In line with the continuum hypothesis, this pattern has been also described in a subset of ALS patients displaying a prominent impairment in the processing of emotional cues (Cerami et al., 2013) [127]. In Parkinson's disease, early mentalizing deficits are accompanied by decreased empathic skills in the later disease stages, reflecting the progression of the pathology from the dorsolateral prefrontal to orbitofrontal circuits (Elamin et al., 2013). In Huntington's disease, the impairment of both cognitive and affective components of social understanding is often associated with the severity of executive decline and motor symptoms [223].

4.3. Altered Social Decision-Making in Neurodegenerative Diseases.

Abnormal performance in tasks assessing individual decision-making has been described in different neurodegenerative diseases, such as FTD, AD, Parkinson's disease, and Huntington disease (see [231] for a review). Instead, the evidence on social decision-making in neurodegenerative diseases is still limited and mainly related to bvFTD and

AD [223]. In particular, bvFTD patients display a significant reduction in the tendency to prosociality [232] and cooperative behavior [233] (O'Callagan et al., 2015). In line with the “social context network” model described above [210], such changes might reflect the damage in frontostriatal areas supporting the generation and update of predictions based on social contextual information.

5. Conclusions

The data reviewed here summarize the main results of social cognitive neuroscience in the attempt to unveil the brain networks underlying the humans' automatic disposition to make sense of others' behavior. While most of the initial efforts within this lively research field dealt with the “social brain” in healthy individuals, its most recent developments are concerned with identifying the changes associated with physiological aging or different pathological conditions. A growing literature shows that the multilevel approach of social cognitive neuroscience, connecting seemingly distinct drivers of human behavior such as hormones or prosocial motivations [234], constitutes a platform providing experimental paradigms for targeting specific social cognitive processes, as well as objective metrics for assessing their impairment, or the effectiveness of remediation procedures, in different neuropsychiatric diseases [7].

The advancements in parcellating social cognitive processes and their neural bases nowadays allow design interventions based on robust evidence at the level of the construct of interest (e.g., face processing), or of deeper neurobiological mechanisms such as the modulation of amygdala activity by oxytocin (Ebert and Brune, 2017). The complexity of social cognition and its multifaceted nature indeed reflect in the variety of different remediation procedures which have been already proposed to improve social skills and to assess their impact beyond the trained process. Different approaches aim to improve either basic cognitive skills, to increase relational competence via training strategies underlying the analysis of social context and emotional information (i.e., “wide interventions; Peyroux and Frank, 2014), or specific components of social cognition such as emotion recognition [235], mentalizing [236], or empathy (Klimecki et al., 2013) (i.e., “targeted interventions”), particularly in schizophrenia [237] and autism [238, 239]. Meta-analytic results highlight moderate training effects on emotion recognition and mentalizing, with such improvements being transferred to daily social life [240], but also limited success in remediating more complex, higher-order social cognitive functions [241]. Possible explanations for this negative evidence might include the lack of consideration of basic cognitive impairments and of real-world social situations characterized by a basic property of social cognition such as the mutual interdependence between agents. As previously discussed (Section 2.2.1), the potential implications of novel paradigms entailing real or virtual social interactions represent one of the most promising challenges for social neuroscience [106], already supported by positive outcomes in neurological patients [108].

More generally, the available evidence suggests that the effectiveness of social cognitive remediation depends on

“baseline” skills and that successful programs require adapting management strategies based on individual profiles. A detailed description of social cognitive processes and their neural correlates is thus critical to tailor remediation protocols to target specific brain networks and their associated cognitive functions. By summarizing the extensive available evidence on the neural bases of social cognition, the present review highlights specific domains which should be evaluated in pathological populations, taken into consideration when designing novel tests [242, 243] or rehabilitation procedures [244], and addressed in original studies. As in all areas of empirical research, the quality of the answers depends on the quality of the questions. This is one of the main reasons why the increasing interaction among social and clinical as well as basic and translational research areas represents one of the most exciting developments within cognitive neuroscience.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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