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Effective connectivity gateways to the Theory of Mind network in processing communicative intention

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ABSTRACT

An Intention Processing Network (IPN), involving the medial prefrontal cortex, precuneus, bilateral posterior superior temporal sulcus, and temporoparietal junctions, plays a fundamental role in comprehending intentions underlying action goals. In a previous fMRI study, we showed that, depending on the linguistic or extralinguistic (gestural) modality used to convey the intention, the IPN is complemented by activation of additional brain areas, reflecting distinct modality-specific input gateways to the IPN. These areas involve, for the linguistic modality, the left inferior frontal gyrus (LIFG), and for the extralinguistic modality, the right inferior frontal gyrus (RIFG). Here, we tested the modality-specific gateway hypothesis, by using DCM to measure inter-regional functional integration dynamics between the IPN and LIFG/RIFG gateways. We found strong evidence of a well-defined effective connectivity architecture mediating the functional integration between the IPN and the inferior frontal cortices. The connectivity dynamics indicate a modality-specific propagation of stimulus information from LIFG to IPN for the linguistic modality, and from RIFG to IPN for the extralinguistic modality. Thus, we suggest a functional model in which the modality-specific gateways mediate the structural and semantic decoding of the stimuli, and allow for the modality-specific communicative information to be integrated in Theory of Mind inferences elaborated through the IPN.

Introduction

Human communicative competence is based on the ability to process a specific class of mental states, namely, communicative intention (Bara, 2010). According to the cognitive pragmatics approach, communicative intention is defined as the intention to communicate a meaning to someone else, plus the intention that the former intention should be recognized by the addressee (Grice, 1975). The process involved in understanding this form of intention is independent of the communicative modality (linguistic or gestural) through which it is conveyed, and connects human communication with a more general type of social competence, such as Theory of Mind (ToM), i.e., the ability to explain and predict other people's communicative and non-communicative behavior by attributing independent mental states to them (Baron-Cohen, 1995; Premack and Woodruff, 1978).

In previous studies we proposed the Intention Processing Network (IPN) model, according to which a set of brain areas are differentially involved in comprehending different types of intentions, such as private or social intentions. Whereas a private intention involves the representation of a private goal, i.e. a goal involving only a single actor, a social intention involves the representation of a social goal, i.e. a goal that necessitates at least another person to achieve the goal (Adenzato et al., 2017; Bara et al., 2011). In three functional Magnetic Resonance Imaging (fMRI) studies (Ciaramidaro et al., 2007; Walter et al., 2004; Walter et al., 2009), we used a story completion task presented in a comic strip form to show the differential recruitment of the ToM network according to private versus social intentions. The brain areas associated to the IPN include the medial prefrontal cortex (MPFC), the

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precuneus (PREC), the bilateral posterior superior temporal sulcus (pSTS), and the temporoparietal junctions (TPJ). During the comprehension of a social (communicative) intention, all four areas of the IPN are recruited. In contrast, the comprehension of a private intention involved only the PREC and the right TPJ/pSTS. As a whole, the four IPN brain regions constitute a subset of the ToM system that is specifically recruited when people try to infer the intentions of others. This occurs even in the absence of detailed information on biological motion (Van Overwalle and Baetens, 2009). Thus, the IPN shows no complete anatomo-functional overlap, neither with the mirror system, nor with the brain regions of the ToM system specifically implicated in inferring other's affective mental states such as emotions (Corradi-Dell'Acqua et al., 2014).

Previous work extensively clarified the specific role of individual brain areas constituting the IPN in communicative intention recognition and comprehension. For example, the anterior (in particular the MPFC) and posterior (in particular the right TPJ) cortices have a key role for verbal irony comprehension (Spotorno et al., 2012), for metaphors comprehension (Prat et al., 2012), and in indirect replies in spoken dialogue (Bašnáková et al., 2014), as shown by studies entailing the comprehension of pragmatic phenomena in which literal and intended meaning dissociate. Meta-analysis studies (Van Overwalle 2009; Van Overwalle and Baetens, 2009) suggested the implication of the PREC for elaboration of contextual information and identification of situational structure. In contrast, the role of the TPJ was generally associated with the identification of end state behaviors. Specifically, according to Van Overwalle (2009), the TPJ along with the PREC and MPFC takes part in the broader process of goal identification in a social context. Strong empirical evidence demonstrates MPFC engagement in social inferences, in particular in understanding social scripts that do not only concern a single actor, but that describe adequate social actions for all of several actors involved in a particular context (for reviews, see Van Overwalle 2009; 2011).

Converging evidence for the role of the IPN in communicative intention processing comes from lesion studies. Deficits in inferring speaker intentions were found in people with MPFC lesions (Lee et al., 2010). Impaired comprehension of non-literal language, such as sarcasm, metaphor, and indirect requests was found in people with brain diseases that affect the functioning of the medial frontal cortex, such as frontotemporal dementia (Shany-Ur et al., 2012), Tourette syndrome (Eddy et al., 2010), and progressive supranuclear palsy (Ghosh et al., 2012), even when controlling for the possible confounding effect of executive function deficits (see however Aboulafia-Brakha et al., 2011, for the complex relationship between executive functions and ToM in patients with acquired neurological pathology). Conversely, extensive damage to the perisylvian fronto-temporal language network resulting in aphasia and characterized by lexical-semantic impairments, does not cause specific deficits in intention recognition (see Willems and Varley, 2010, for a review), nor does it compromise the ability to express intended communicative meanings *per se*. Indeed, using alternative communicative resources, such as drawing, facial expression, and gesture, these patients are able to convey meaningful messages (Siegal and Varley, 2006; Varley and Siegal, 2006). As shown by Willems et al. (2011), aphasic patients are able to process communicative intention (both comprehension and production) and to exhibit communication strategies comparable to those adopted by the healthy population, when using a novel non-verbal communication paradigm.

In a more recent study by our group (Enrici et al., 2011), we specifically asked whether the verbal versus the non-verbal communication modalities are processed by distinct neural networks, and whether these neural networks do overlap or are rather independent from the IPN network implicated in communicative intention processing. We used a story completion task, whose distinguishing feature was that the stories represented the social communicative intention in either a verbal (linguistic) or a gestural, (extralinguistic) modality. We showed that the IPN was recruited for the comprehension of communicative intention, independently of the linguistic or extralinguistic modality through which it was conveyed. Additional brain areas, outside those involved in intention processing, were specifically engaged according to the particular communicative modality. Specifically, the linguistic modality additionally recruited the perisylvian language network, including the pars opercularis of the left inferior frontal gyrus (LIFG). In contrast, the extralinguistic modality additionally recruited a sensorimotor network, including the pars opercularis of the right inferior frontal gyrus (RIFG). Based on these activation results, we hypothesized that the LIFG and RIFG reflect modality-specific input gateways, conveying stimulus and associated high-order information to the IPN.

The importance of the IFG as an interface node to the IPN is suggested by the presence of structural inter-connection pathways. In particular, the frontal aslant white matter tract links the IFG directly to the MPFC and is part of the core neural network underlying communicative intention processing (Catani and Bambini, 2014). In addition, the IFG is a crucial integration hub for communication comprehension (Kemmerer, 2015), and is thus a likely candidate region to exchange high-order information with the IPN for the purpose of communicative intention decoding. In the context of modality-specific parsing of communicative signals, the LIFG and RIFG present a relative hemispheric specialization for, respectively, sentences and gestures (Straube et al., 2012).

While these observations altogether provide a plausible premise, the precise functional relationship between IPN and the inferior frontal gyri in the two hemispheres has not been investigated yet. In the present study, we tested the modality-specific gateway hypothesis, by focusing on inter-regional functional integration between the IPN and LIFG/RIFG. To this aim, we further analyzed the data collected in the Enrici et al. (2011) study, by measuring effective connectivity with Dynamic Causal Modeling (DCM). More specifically, we employed DCM network discovery (Friston and Penny, 2011; Friston et al., 2011), as an approach that enables one to test the connectivity between a priori specified brain regions, and to discover, over a large number of possible models, the one with the greatest evidence to have generated the observed fMRI data. Based on the body of knowledge reviewed above, we specified our models as including four brain regions of the IPN – i.e., MPFC, left TPJ (LTPJ), right TPJ (RTPJ) and PREC – together with LIFG and RIFG as modality-specific input gateways. We expected that the model with greatest evidence would be consistent with the modality-specific propagation of stimulus information from the LIFG to IPN for the linguistic modality, and from the RIFG to IPN for the extralinguistic modality.

Materials and methods

A full description of fMRI data acquisition and preprocessing procedures can be found in Enrici et al. (2011). Details relevant for the present study are reported in what follows.

Participants

Twenty-four right-handed Italian native speakers (13 females, mean age 24.45 years, SD 5.71) with no history of neurological or psychiatric diseases participated in the imaging study. The Ethics Committee of the San Raffaele Scientific Institute approved the study. All participants gave their written informed consent prior to scanning.

Stimuli and task

The experiment conformed to a 2 × 2 factorial design, with factors *Intention* (communicative intention versus non-intentional physical causality) and *Modality* (linguistic versus extralinguistic). The four resulting experimental conditions were: 1) Linguistic Communicative Intention (LCInt); 2) Extralinguistic Communicative Intention