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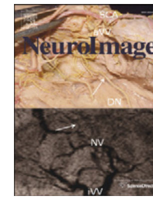

Dynamic causal modelling of effective connectivity during perspective taking in a communicative task

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ABSTRACT

Previous studies have shown that taking into account another person's perspective to guide decisions is more difficult when their perspective is incongruent from one's own compared to when it is congruent. Here we used dynamic causal modelling (DCM) for functional magnetic resonance imaging (fMRI) to investigate effective connectivity between prefrontal and posterior brain regions in a task that requires participants to take into account another person's perspective in order to guide the selection of an action. Using a new procedure to score model evidence without computationally costly estimation, we conducted an exhaustive search for the best of all possible models. The results elucidate how the activity in the areas from our previously reported analysis (Dumontheil et al., 2010) are causally linked and how the connections are modulated by both the social as well as executive task demands of the task. We find that the social demands modulate the backward connections from the medial prefrontal cortex (MPFC) more strongly than the forward connections from the superior occipital gyrus (SOG) and the medial temporal gyrus (MTG) to the MPFC. This was also the case for the backward connection from the MTG to the SOG. Conversely, the executive task demands modulated the forward connections of the SOG and the MTG to the MPFC more strongly than the backward connections. We interpret the results in terms of hierarchical predictive coding.

Introduction

Verbal and non-verbal social interactions both rely on an understanding of other people's mental states, also called theory of mind (ToM) or mentalising (Frith and Frith, 2007, 2012; for an excellent review of the extensive research in theory of mind literature we refer the reader to Apperly, 2011). During social interactions, in a complex real-world environment, ToM enables individuals to take decisions and choose actions that are appropriate to the present situation and the inferred mental states of the other people involved. Recent research suggests that it is important to investigate not only ToM development but also how individuals are able to efficiently use ToM information during decision making and reasoning (Samson and Apperly, 2010), and the distinction between ToM-specific processes and executive control (e.g. Dumontheil et al., 2012; Meyer et al., 2012; Saxe et al., 2006; Scholz et al., 2009; Van Overwalle, 2009, 2011).

Studying the neural mechanisms of social cognition with the "Director" task

Keysar and colleagues designed a paradigm to investigate real-world social decision-making, in which participants are faced with a real set of shelves containing objects that are either visible or not visible from the viewpoint of a "director" (a confederate; Keysar et al., 2000, 2003; Lin et al., 2010). The director asks participants to move objects in the shelves and critical instructions require the participant to use information about the director's viewpoint to interpret his instructions correctly. In this Director task, around 50% of the time adult participants fail to use information about the director's perspective and instead erroneously use their own (egocentric) viewpoint when trying to follow instructions (Keysar et al., 2000, 2003). These results were replicated using a computerised version of the task (Apperly et al., 2010; Dumontheil et al., 2010). The Director task differs from other ToM tasks in that it requires participants both to have a functioning ToM to compute the perspective and intentions of another person (the director), and to use this ToM information in concert with other cognitive processes such as attentional and inhibitory control to overcome their egocentric bias and select the appropriate response quickly and accurately (Apperly et al., 2010).

In a previous fMRI study, we employed an adapted version of this Director task (Dumontheil et al., 2010), which in contrast to previous studies that were designed to assess error rates, included extensive task instructions such that participants performed at high levels of accuracy. As in the behavioural version of the task (Keysar et al., 2000), participants followed auditory instructions to move objects in a set of shelves. Using this modified paradigm for fMRI, we found that: (1) selection of an appropriate action when faced with alternatives (Object factor) was associated with domain-general bilateral brain

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activations located primarily in the frontal and parietal cortices, with additional activations in the inferior temporal cortex; (2) the processing of social information vs. symbolic cues (Director factor) was associated with specific activations in the dorsal medial prefrontal cortex (MPFC) and superior temporal sulcus; (3) the use of social cues as opposed to symbolic cues for the selection of the appropriate action from the alternative options (interaction) was associated with further recruitment of dorsal MPFC and middle temporal gyri, extending into the left temporal pole (Dumontheil et al., 2010, 2012).

Thus, part of the network of brain regions implicated in social cognition, specifically the MPFC and temporal cortex (Brothers, 1990; Frith and Frith, 2007; Van Overwalle, 2009), was recruited when the guiding information was of a social nature compared to more arbitrary symbolic stimuli. Research using visual search paradigms suggests that the prefrontal cortex (PFC) supports the integration of information from the current environment and internal representations, thereby providing a "top-down" influence (i.e. intentionally driven by knowledge, expectations and goals) on attentional orientation and action selection appropriate with current goals (Burgess et al., 2007; Fuster, 2000, 2008; Koechlin and Summerfield, 2007), in contrast with stimulus-driven "bottom-up" mechanisms (Beck and Kastner, 2009; Hahn et al., 2006). Therefore one interpretation of these findings is that the dorsal MPFC, similarly to lateral parts of the PFC, may play a role in providing a top-down influence for the selection of the correct target among distractors when the relevant guiding information is in the social domain. To test this hypothesis we examined the top-down and bottom-up influences of social and executive manipulations on network coupling during the Director task, using Dynamic Causal Modelling (DCM: Friston et al., 2003).

The current study: dynamic causal modelling

DCM estimates the experimental modulation of forward and backward connections between regions that are active during a particular task in a directional manner, and thus makes it possible to infer whether experimental manipulations affect top-down or bottom-up influences. We refer to forward and backward connections in the framework of hierarchical predictive coding, in which sensory input is passed forward and processed in the brain hierarchically, from primary sensory to secondary sensory areas, then on to association areas and finally to higher (frontal) areas (Clark, 2012; Friston, 2005, 2010). We used DCM to investigate coupling between frontal, temporal and occipital brain regions (which represented the aforementioned hierarchy in descending order) involved in the Director task, and its modulation by social cues, using fMRI data from a group of adults (Dumontheil et al., 2010).

An important methodological advance in our analysis is the use of a new post hoc model selection procedure (Rosa et al., 2012) to find (1) the best model out of all possible connection architectures with Bayesian model selection (BMS), (2) posterior probabilities resulting from family level inferences testing whether a parameter exists or not, and (3) Bayesian parameter averages (BPA) over all possible models showing how strong fixed connections were and how much they were modulated. Until recently, DCM required very specific hypotheses about the structure of the model (e.g. which connections are modulated by the experimental manipulations). This is because the estimation of each different model takes a few seconds and with increasing number of nodes in each model the combinatorial explosion of possible models that makes it prohibitively expensive in computational terms to estimate all possible models in model space. Instead, we used a new method to find the model evidence for all possible models without estimating them (Friston and Penny, 2011; Friston et al., 2011; Rosa et al., 2012). This approach permits the selection of the winning model as well as family level inferences (Penny et al., 2010) over all possible models to find (1) the probability of certain connections existing and (2) whether these connections are modulated by the experimental manipulations.

We hypothesized that, while occipital and temporal cortex regions process the social aspects of the stimuli in a bottom-up manner (faces and bodies of the directors), the MPFC is involved in the computation, maintenance, and use of perspective information to guide the selection of an appropriate action. These processes are recruited in the Director present vs. Director absent conditions, where the role of the MPFC may be particularly important in the 3-object condition, which requires, on half of the trials, the inhibition of the prepotent bottom-up responses related to one's own perspective.

Material and methods

Participants

Fourteen adult (mean age 24.9 years, standard deviation (SD) 3.0, range 21.3–30.6) right-handed female volunteers included in Dumontheil et al. (2010) were considered for DCM analysis, of which 11 were included in the final analysis (see Volume of interest extraction section). All participants spoke English fluently and had no history of psychiatric or neurological disorders. Participants gave written informed consent and the study was approved by the University College London ethics committee.

Experimental design

Our paradigm includes two manipulations embedded in a 2 × 2 factorial design with the factors Director ("Director present" vs. "Director absent") and Object ("3-object" vs. "1-object"). In the Director present conditions, two directors are shown, one female and one male. This enabled the participant to identify easily which director was speaking by the sound of their voice. One director stands behind the shelves, facing the participant, while the other stands on the same side of the shelves as the participant. The position of the male and female directors changed within blocks and was counterbalanced between conditions and within and between participants. Therefore the gender of the directors was not confounded with the different experimental conditions. In the 3-object conditions, the instructions refer to an object that is one of three exemplars in the shelves; the correct object to move depends on which director is speaking and whose perspective to take (see Fig. 1A). Thus in the Director present 3-object trials, participants need to use the social cues, i.e. the position of the speaking director, to select and move the appropriate object. On half of the Director present 3-object trials the perspective of the director issuing the instruction is different from that of the participant; on the other half the director's and participant's perspectives are the same. This is varied on a trial-by-trial basis, and thus participants need to consider the director's perspective on every trial. Note that this is not an experimental factor (our analyses collapsed across these trial types) but a manipulation that ensures participants integrate trial-specific cues. In Director present 1-object trials, there is no need to take into account the director's perspective to identify the correct object (e.g. "Move the turtle left"), as there are no distractors or other referents; this resembles a bottom-up, visual pop-out as opposed to an effortful top-down visual search (Buschman and Miller, 2007). The Director absent conditions were logically equivalent to the Director present conditions, but the directors were replaced by symbolic cues (see Fig. 1B).

Stimuli consisted of sets of 4 × 4 shelves with objects located in half of the shelves. Five of the shelves had a grey background (Fig. 1; see Dumontheil et al., 2010 for details). On each trial, participants were given instructions via headphones, by either a male or a female voice, to move one of the eight objects in the shelves to a different slot, either up, down, left or right (note that this was the participant's left or right). A 2 × 2 factorial within-subject design was used with the factors Director (present vs. absent) and Object (1-object vs. 3-object) varying between blocks.