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Individual differences in response of dorsomedial prefrontal cortex predict daily social behavior

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Abstract

The capacity to accurately infer the thoughts and intentions of other people is critical for effective social interaction, and neural activity in dorsomedial prefrontal cortex (dmPFC) has long been linked with the extent to which people engage in mental state attribution. In this study, we combined functional neuroimaging and experience sampling methodologies to test the predictive value of this neural response for daily social behaviors. We found that individuals who displayed greater activity in dmPFC when viewing social scenes spent more time around other people on a daily basis. These findings suggest a specific role for the neural mechanisms that support the capacity to mentalize in guiding individuals toward situations containing valuable social outcomes.

Key words: fMRI; mentalizing; theory of mind; social interaction; experience sampling

Introduction

The complex nature of human social interaction necessitates the ability to recognize and infer the contents of other minds. This sophisticated capability, also referred to as having theory of mind or mentalizing, allows people to empathize with others, to cooperate with others and to predict future behaviors (Frith and Frith, 2001; Mitchell and Heatherton, 2009). In this way, the capacity to represent others' thoughts and intentions facilitates the development and maintenance of harmonious social interactions (Heatherton, 2011), which is critical for survival (Baumeister and Leary, 1995).

Functional neuroimaging research has reliably shown activity in the dorsomedial prefrontal cortex (dmPFC) when people make social judgments and inferences about the minds of other people (Mitchell *et al.*, 2002, 2004, 2006; for review, see Gallagher and Frith, 2003). Indeed, a recent meta-analysis of 107 studies revealed that dmPFC activation is consistently observed in studies investigating the mental representation of knowledge about other people (Denny *et al.*, 2012). Although the dmPFC has been broadly implicated in the neural representation

of others (Wagner *et al.*, 2012), much of the work in the literature has focused on the role of this brain region in mental state attribution or 'mentalizing'. Along these lines, the meta-analysis by Denny *et al.* (2012) showed that the activity in dmPFC is greater when thinking about other people relative to thinking about one's self, further underscoring the role of this particular brain region in social cognition specifically (see also Mitchell, 2008; Van Overwalle and Baetens, 2009).

Although the majority of research on the neural basis of mentalizing has examined how people infer thoughts and intentions when explicitly instructed to do so, everyday social inferences often occur spontaneously as we encounter other people in our social world. Recent neuroimaging studies have shown that dmPFC is similarly recruited when people watch video clips (Iacoboni *et al.*, 2004) or simply view images (Wagner *et al.*, 2011) depicting social interactions, suggesting a role for dmPFC in spontaneous social cognition. Indeed, in more direct investigations of the neural bases of spontaneous mentalizing, Spiers and Maguire (2006) found that the dmPFC was reliably engaged when participants were thinking about other people they encountered in a virtual reality environment, according to

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retrospective reports. Other studies directly comparing dmPFC activity during spontaneous (e.g. 'read this statement') and intentional (e.g. 'infer this person's trait') judgments found that both types of mentalizing judgments produce robust activity in dmPFC and, critically, that the dmPFC response evoked by spontaneous inferences closely parallels that evoked by explicit inferences in both magnitude (Ma et al., 2010) and neural timing as measured by event-related potentials (Van Duynslaeger et al., 2007). Taken together, this work supports the proposition that spontaneous and explicit mentalizing processes are subserved by a common neural network centered on the dmPFC (Van Overwalle and Vandekerckhove, 2013). By showing that dmPFC activity is associated with spontaneous social cognition, these findings suggest that this neural response may reflect an attempt to understand the minds and intentions of others.

From an evolutionary perspective, the capacity to mentalize allows people to understand that they are the targets of social evaluation and to adaptively react when social bonds are threatened (Heatherton, 2011). Consistent with this interpretation, we recently provided evidence that experiencing threats to social relationships modulates neural activity in dmPFC (Powers et al., 2013). Specifically, we found that dmPFC subsequently exhibits more activity when viewed positive compared with negative social cues, suggesting that social exclusion motivates people to mentalize about the positive aspects of their social worlds, which may ultimately be important for re-establishing social connections. Other studies have found that dmPFC activity tracks cues of social status (Muscatell et al., 2012) and is associated with changes in self-esteem following social evaluation (Eisenberger et al., 2011) thought to underlie the sociometer aspect of self-esteem (Leary et al., 1995). This work collectively demonstrates that dmPFC activity is influenced by momentary assessments of social relationship status and reflects differential motivations for future social interactions. Taken together, these findings point to a critical role of the dmPFC in underlying cognitive processes aimed at forming social connections.

However, the extent to which this neural response in dmPFC directly contributes to real-world behavioral tendencies to seek out social contact and forge social bonds has not been empirically tested. A number of recent studies have demonstrated the clear utility of functional magnetic resonance imaging (fMRI) in predicting real-world outcomes, such as reductions in smoking (Falk et al., 2011), consumer choices (Levy et al., 2011) and monetary donations (Ma et al., 2011). This growing trend to establish links between neural markers and meaningful behavioral outcomes occurring outside of experimental sessions has important implications for understanding complex behaviors in everyday situations that are distinct from those that can be achieved through traditional laboratory tasks and self-report measures (Berkman and Falk, 2013). In particular, experience sampling methods afford the opportunity to capture especially rich behavioral profiles of individuals over extended periods of time (e.g. weeks), and researchers have successfully paired this technology with fMRI to uncover unique, ecologically valid brain-behavior relationships (Berkman et al., 2011; Lopez et al., 2014).

In this study, we employed a similar approach integrating fMRI and experience sampling methods to explicitly test the predictive value of dmPFC activity for affiliative social behaviors. Specifically, we tested the hypothesis that the degree to which individuals recruited this brain region when considering other people would predict the degree to which they spent time with other people on a daily basis.

Materials and methods

Participants

Forty Dartmouth College undergraduates were recruited for this study. Six participants were dropped from the final analyses due to poor task compliance during the scanning session (64% response rate, $n=1$) or the weeklong experience sampling period (37% response rate, $n=2$); inability to participate in the experience sampling portion of the experiment due to smartphone compatibility issues ($n=1$) or poor fMRI signal quality as indicated by signal to noise ratio ($n=2$). Examination of individual neural responses in dmPFC sensitive to social scenes (see 'fMRI parameters and analysis' for specific contrast description) revealed the presence of one statistical outlier (defined as ± 2 s.d. from the mean), so data from this participant was also discarded. This resulted in a final sample of 33 participants (23 female, age range 18–21 years). All participants were right handed, native English speakers and had normal or corrected-to-normal visual acuity. They were paid for their participation and gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

Experimental design and procedure

The study consisted of one initial fMRI scanning session followed by a 1 week period of experience sampling of participants' daily social behaviors.

fMRI session. Upon arrival for the fMRI scanning session, participants were told that this study was investigating the influence of ecological perception on environmental situations and behavior. Participants then underwent fMRI scanning while viewing a series of pictures selected from the International Affective Picture System (Lang et al., 2008) and categorizing each as an indoor or outdoor scene, a task chosen for its consistency with the experimental cover story and to ensure that participants were alert and attending to the stimuli. Critically, pictures varied on the dimension of sociality, in that they either contained people (i.e. social scenes) or did not (i.e. non-social scenes; images depicting food, landscapes and common objects). A total of 180 pictures were presented for 2.5 s each. The order of the pictures was pseudo-randomized and counterbalanced across participants. In order to accurately estimate the hemodynamic response function, pictures were intermixed with passive fixation trials of variable duration (0–10 s).

Following fMRI scanning, participants generated an estimate of the size of their social network. Specifically, participants were asked to list the number of individuals they regularly spoke to (i.e. at least once every 2 weeks) either in person, on the phone, online or via text (Brissette et al., 2000).

Experience sampling session. Following the fMRI scanning session, the experimenter set up participants' smart phones for the subsequent weeklong experience sampling portion of the experiment and provided participants with detailed instructions on accessing and completing the surveys. The experience sampling protocol was administered via participants' smart phones using SurveySignal (<http://www.surveysignal.com>). Participants were signaled seven times per day for seven consecutive days, beginning the day after the fMRI session. Within each day, signals were distributed across a 14 h time period (9 am to 11 pm), with each signal scheduled to occur randomly within consecutive 2 h blocks (Hektner et al., 2007; Lopez et al., 2014).

A restriction was set so that any two signals could not occur within 30 min of each other. If participants did not respond within 10 min, a reminder would be sent for that particular signal. If the signal went unanswered for 30 min, the response was logged as missing.

Responses to all answered signals were averaged across the week-long period and an average score for each of the following questions assessing frequency of social engagement was computed for each participant: 'Are other people around you?' (yes/no) and 'Are you interacting with other people?' (yes/no). These questions were part of a larger study examining everyday emotional and self-evaluative experiences and to maintain focus on daily interpersonal social behavior; responses to the other questions administered are not reported here.

fMRI parameters and analysis

Structural and functional imaging was conducted at Dartmouth College on a Philips Inera Achieva 3T scanner using a 32-channel phased array coil. Structural images were acquired using a T1-weighted MP-RAGE protocol (160 sagittal slices, Repetition Time (TR) = 9.9 ms, Echo Time (TE) = 4.6 ms, 8° flip angle, $1 \times 1 \times 1$ mm voxels). Functional images were acquired in an event-related design using a T2*-weighted echo-planar sequence (TR = 2500 ms, TE = 35 ms, 90° flip angle, field of view = 24 cm). Data were collected in 2 functional runs (36 axial slices per volume, 3 mm thick, 0.5 mm gap, 3×3 mm in-plane resolution), each consisting of 140 whole-brain volumes. An Epson ELP-7000 LCD projector was used to project stimuli onto a screen at the end of the magnet bore that participants viewed via an angled mirror mounted on the head coil.

Neuroimaging data were preprocessed and analyzed using SPM8. First, functional data were preprocessed using a standard routine that corrected for differences in slice acquisition time, realigned data within and across functional runs to correct for head movement and unwarped to reduce residual movement-related image distortions not corrected by realignment. Functional data were then normalized into standard space (3 mm isotropic voxels) based on the SPM8 EPI template that conforms to the ICBM 152 brain template. Finally, normalized data were spatially smoothed using a 6 mm full-width-at-half-maximum Gaussian kernel.

To isolate neural responses specific to social scenes, a general linear model incorporating task effects and covariates of non-interest was specified for each participant. Each regressor was convolved with a canonical hemodynamic response function and used to generate contrast images (weighted parameter estimates) for each participant comparing neural responses to social scenes with neural responses to non-social scenes. These contrast images were then entered into a second-level random effects analysis (False Discovery Rate (FDR) corrected, $p < 0.05$, $k > 25$).

Given our prespecified hypothesis involving dmPFC, our primary analysis interrogated regional hemodynamic responses specifically within the region of dmPFC identified from this contrast. To do this, a region-of-interest (ROI) analysis was performed on parameter estimates (β) extracted by centering a 6 mm sphere on the voxels of peak dmPFC activation identified by the social > non-social contrast described above (MNI coordinates 9, 54, 18). We note the close spatial similarity of this particular location with results from prior work implicating dmPFC in spontaneous mentalizing (Wagner et al., 2011; Powers et al., 2013). These parameter estimates were submitted to offline correlations testing the relationship with daily assessments of social behavior obtained via experience sampling. To test the

specificity of this relationship, we also examined correlations of activity within other brain regions demonstrating sensitivity to social scenes by extracting parameter estimates from 6 mm spherical ROIs centered on the peak voxels of the other clusters that emerged from the social > non-social contrast. Importantly, as all ROIs were defined based on task-sensitive regions demonstrating a preference for social scenes, the correlations with daily assessments of social behavior obtained via experience sampling are independent of the ROI selection criteria.

Results

Brain regions sensitive to social scenes

A whole-brain analysis comparing regions that displayed a greater response for social scenes compared with non-social scenes for all participants revealed a system of brain regions sensitive to social information, including the medial prefrontal cortex, posterior cingulate/precuneus extending to the medial occipital gyrus and temporal poles (Figure 1A and Table 1). Activity in these particular regions has been consistently and robustly observed when participants view social scenes (Iacoboni et al., 2004; Wagner et al., 2011; Powers et al., 2013).

Experience sampling descriptives

Overall, compliance was high as participants responded to 75.9% of the signals sent over the 7 day experience sampling period. On average, participants reported being around other people 67.5% of the time (s.d. = 9.1%, range 41.5–88.4%) and interacting with people 44.6% of the time (s.d. = 10.6%, range 23.3–68.8%). These two measures were significantly correlated ($r = 0.45$, $p = 0.009$).

Predicting daily social behavior

As predicted, activity in dmPFC in response to viewing social scenes correlated positively with social behavior, such that individuals who displayed greater activity in this region when viewing social scenes reported spending more time around other people on a daily basis, $r(33) = 0.43$, $p = 0.012$, 95% confidence interval (10 000 bootstrap samples) = [.16–.64] (Figure 1B). Although dmPFC activity did not significantly predict reports of social interaction, the same positive relationship between the two variables was observed ($r = 0.11$, $p = 0.56$).

To further clarify the observed significant relationship between dmPFC activity and time spent around other people, we performed a few additional analyses. First, to argue that dmPFC occupies a central role in determining the degree to which individuals spend time with other people, this relationship should show specificity to dmPFC at the exclusion of other brain regions sensitive to social scenes. Indeed, additional ROI analyses confirmed that no other regions that emerged from the contrast identifying brain regions sensitive to social scenes in this study demonstrated a significant correlation with time spent around other people (all $ps > 0.23$).

We also tested whether the observed relationship between dmPFC and daily social behavior could be explained by the size of an individual's social network. Estimates of the size of each participant's social network were marginally correlated with time spent around other people ($r = 0.33$, $p = 0.06$), providing confirmation that participants with large social networks do indeed tend to spend more time around other people on a daily basis. However, there was no relationship between the size of

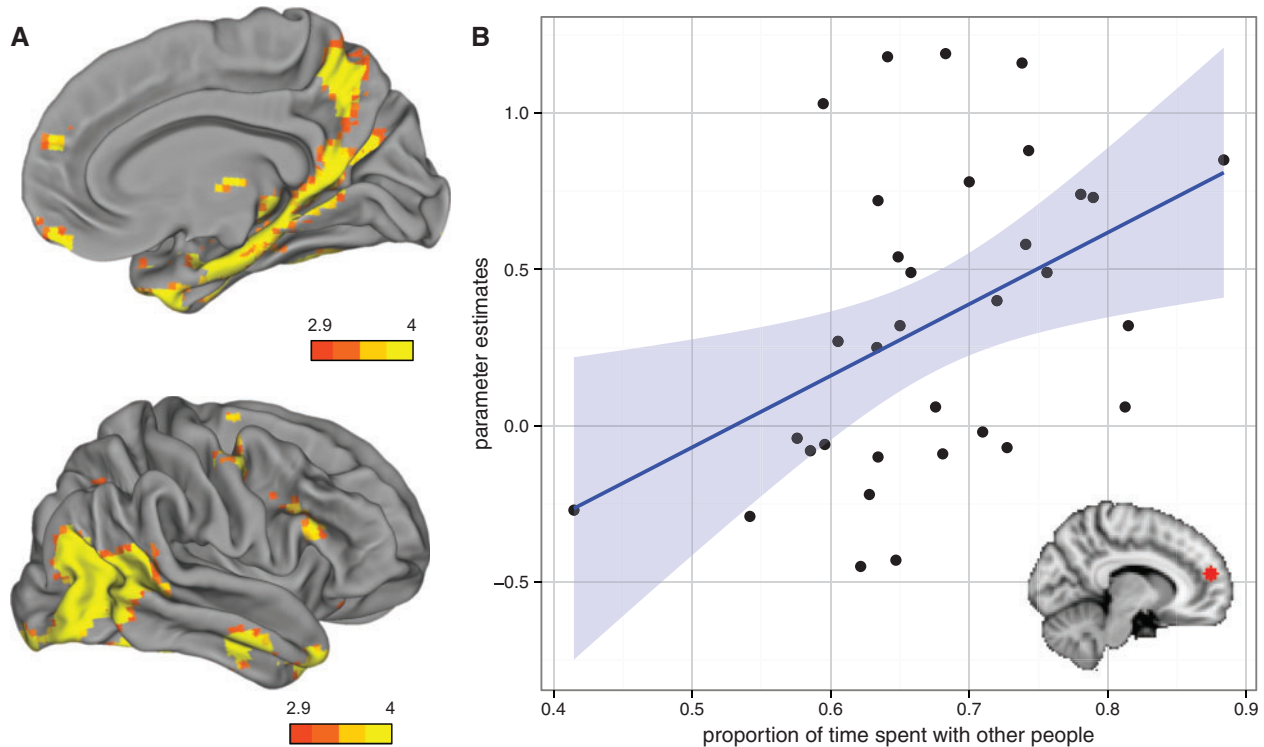


Fig. 1. (A) Results from a whole-brain, random-effects analysis of all participants contrasting social scenes to non-social scenes (FDR corrected, $p < 0.05$). Statistical maps of right medial hemisphere and right lateral hemisphere are overlaid onto inflated cortical renderings. Results reveal a network of regions, including the dorso-medial prefrontal cortex, that have been shown to consistently and reliably respond when participants view social scenes. (B) Results of a correlational analysis revealing that dmPFC response to social scenes significantly predicts the amount of time spent with other people, indexed via experience sampling ($r = 0.43$, $p = 0.012$). The shaded area represents 95% confidence interval.

Table 1. Results of a whole-brain contrast identifying brain regions sensitive to social scenes vs non-social scenes

Region	Coordinates			t-value
	x	y	z	
dmPFC	9	54	18	5.11
Temporal pole	-66	-3	-24	4.70
Orbitofrontal cortex	3	51	-21	4.83
Middle occipital gyrus	51	-72	3	14.01
Middle occipital gyrus	-51	-78	9	11.54
Middle frontal gyrus	45	0	45	5.39
Middle frontal gyrus	-33	-6	45	4.67
Inferior frontal gyrus	45	24	15	4.42
Cerebellum	-3	-78	-27	5.88

Notes: Coordinates are reported in Montreal Neurological Institute stereotaxic space. FDR corrected, $p < 0.05$, $k > 25$.

social network and dmPFC activity ($r = 0.03$, $p = 0.86$), suggesting that the size of social network does not account for the brain-behavior relationship we report here.

Discussion

As social beings, humans have an intrinsic motivation to affiliate and bond with one another (Bowlby, 1969; Baumeister and Leary, 1995). In this study, we combined experience sampling and neuroimaging methodologies to examine whether there is a specific role for the neural mechanisms that support

mentalizing in guiding individuals toward situations containing potentially valuable social outcomes.

Effective social behavior requires the ability to understand the intentions and thoughts of those in our surrounding social worlds. The involvement of dmPFC in tasks that explicitly require mentalizing about social knowledge has been well established (Gallagher and Frith, 2003; Mitchell et al., 2002, 2004, 2005, 2006; Gobbini et al., 2007; Spreng et al., 2009), and recent work has provided converging empirical support for the conclusion that simply encountering social information similarly recruits dmPFC in order to spontaneously extract person knowledge and make sense of the minds of others (Spiers and Maguire, 2006; Ma et al., 2011; Wagner et al., 2011; Van Overwalle and Vandekerckhove, 2013). Here, we extend the functional role of this brain region by demonstrating that individual differences in the reflexive engagement of this brain region when viewing social information reliably predict time spent in social situations. That is, the magnitude of the response in dmPFC when considering other people determined the degree to which these individuals sought out social contact on a daily basis. Critically, this predictive relationship was uniquely specific to dmPFC; that is, no other brain regions that demonstrated sensitivity to social scenes exhibited a significant relationship with daily social behavior. As increased attempts to accurately understand what other people are thinking and feeling could facilitate attempts at social reconnection (Heatherton, 2011), the ability to use these inferences to inform the implementation of goal-directed behavior may be particularly critical when social relationships have been threatened. Consistent with this perspective, our prior work (Powers et al., 2013) shows recruitment of dmPFC in response to motivationally relevant social cues

following social exclusion, suggesting that these individuals are drawing on this neural mechanism as they work to recover broken social ties.

These findings demonstrate the importance of individual differences in how people process and respond to social cues in their everyday lives. More broadly, these results contribute to a growing body of research linking dmPFC activity with real-world social outcomes. Heightened dmPFC responsivity has also been shown to predict altruistic behavior (Waytz et al., 2012), accuracy in empathic inferences (Zaki et al., 2009), decisions to pursue romantic relationships (Cooper et al., 2012) and written gestures of empathic concern (Masten et al., 2011). More recently, Spunt et al. (2015) identified a relationship between activity in dmPFC at rest to higher reported levels of social expertise, suggesting that baseline functioning of this brain region contributes to the ability to navigate daily social life. Taken together with this study, these findings collectively highlight the specific functional role of this brain region in understanding complex social situations and responding in flexible and adaptive ways.

Although the relationship between dmPFC activity and reports of social interaction did not reach significance, the behavior indexed by this question nevertheless showed a consistent relationship with dmPFC response. It is noteworthy that, on average, participants reported low to moderate levels of social interaction. Thus, it is possible that the failure to capture high levels of social interaction dampened the strength of this particular effect. It is also possible that the phrasing of this question produced confusing results in this sample of participants. A clear direction for future research is to examine the specifics of social dynamics (e.g. precise nature of social interaction) as well as the influence of key personality variables (e.g. extraversion/introversion) on the findings we report here.

Although our interpretation of dmPFC activity as an index of social cognition is rooted in an extensive literature bridging explicit and implicit mentalizing tasks, we note that dmPFC activity has been linked with a number of cognitive processes other than inferring the mental states of other people (for review, see Mitchell, 2009). In addition to carefully constraining task design, future work may benefit from including measures used in prior studies to successfully capture the cognitive processes related to spontaneous mentalizing to strengthen inferences regarding dmPFC function. Examples of such measures include retrospective reports (Spiers and Maguire, 2006) and individual assessments of trait empathizing (Wagner et al., 2011).

Our ability to forge and maintain social bonds is a fundamental aspect of the human experience. In this study, we showed that individual differences in the reflexive engagement of dmPFC possess predictive value for subsequent social behavior. From an evolutionary perspective, the sensitivity of this neural system to social needs is adaptively beneficial, as it enables individuals to effectively navigate complex social environments and maximizes power to predict socially profitable outcomes.

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Conflict of interest. None declared.

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