

The Default Mode of Human Brain Function Primes the Intentional Stance

Robert P. Spunt¹, Meghan L. Meyer², and Matthew D. Lieberman²

Abstract

■ Humans readily adopt an intentional stance to other people, comprehending their behavior as guided by unobservable mental states such as belief, desire, and intention. We used fMRI in healthy adults to test the hypothesis that this stance is primed by the default mode of human brain function present when the mind is at rest. We report three findings that support this hypothesis. First, brain regions activated by actively adopting an intentional rather than nonintentional stance to a social stimulus were anatomically similar to those demonstrating default responses to fixation baseline in the same task. Second, moment-to-moment variation in

default activity during fixation in the dorsomedial PFC was related to the ease with which participants applied an intentional—but not nonintentional—stance to a social stimulus presented moments later. Finally, individuals who showed stronger dorsomedial PFC activity at baseline in a separate task were generally more efficient when adopting the intentional stance and reported having greater social skills. These results identify a biological basis for the human tendency to adopt the intentional stance. More broadly, they suggest that the brain's default mode of function may have evolved, in part, as a response to life in a social world. ■

INTRODUCTION

Humans have a seemingly irresistible tendency to conceive the actions of others as intentional and guided by beliefs and desires (Rosset, 2008; Uleman, Adil Saribay, & Gonzalez, 2008; Mesoudi, Whiten, & Dunbar, 2006; Dennett, 1989; Vallacher & Wegner, 1987; Heider & Simmel, 1944). This intentional stance toward other humans is already apparent in the first year of life (Kovacs, Teglas, & Endress, 2010) and eventually becomes so automatized that it is effortlessly adopted to understand the behavior of not just other humans but also pets and iPhones (Epley, Waytz, & Cacioppo, 2007). The importance of the intentional stance is highlighted by the enormous difficulties faced by those who are not predisposed to it, such as individuals with an autism spectrum disorder (Senju, 2012). Although the tendency to engage the intentional stance is regarded as essential to human sociality, the neurobiological basis of this preparedness remains a mystery.

Numerous functional neuroimaging studies in humans have demonstrated that a psychological process at the core of the intentional stance—mental state inference—is reliably associated with a set of cortical regions commonly referred to as the theory-of-mind or mentalizing network (Amodio & Frith, 2006; Saxe, Carey, & Kanwisher, 2004; Gallagher & Frith, 2003; Happé et al., 1996; Fletcher et al., 1995; Goel, Grafman, Sadato, & Hallett, 1995). For instance, our own work has shown that regions of this net-

work, namely dorsomedial PFC (dmPFC), precuneus, TPJ, and anterior superior temporal sulcus (STS), show a supramodal association with the use of mental state concepts to produce and evaluate explanations of others' actions and emotional behavior (Spunt & Adolphs, 2014; Spunt & Lieberman, 2012a, 2012b; Spunt, Satpute, & Lieberman, 2011). Although these studies outline the functional neuroanatomy of experimentally induced mental state inference, it remains unknown why the human mind seems naturally primed to adopt the intentional stance in the first place.

The explanation considered here is motivated by two empirical facts about the human brain. The first is that most of the brain's energy budget is consumed not by activity evoked by specific cognitive tasks (e.g., mental arithmetic) but by spontaneous ongoing activity that is most notable when the brain is at rest (Raichle, 2010). This spontaneous activity is most prominent in a distributed cortical network commonly referred to as the default-mode network (DMN; Greicius, Krasnow, Reiss, & Menon, 2003; Mazoyer et al., 2001; Raichle et al., 2001; Binder et al., 1999; Shulman et al., 1997). Given that the brain consumes a disproportionate amount of the energy available to the body (Attwell & Laughlin, 2001), it is likely that the persistent activity of the DMN during periods of rest serves important adaptive functions (Andrews-Hanna, Smallwood, & Spreng, 2014).

Here, we consider a function of the DMN that is suggested by a second fact about the human brain: The anatomical boundaries of the DMN largely correspond with the neuroanatomy associated with adopting the intentional stance (Mars et al., 2012; Schilbach et al., 2012; Spreng, Mar, & Kim, 2009; Schilbach, Eickhoff,

¹California Institute of Technology, ²University of California, Los Angeles

Rotarska-Jagiela, Fink, & Vogeley, 2008). Importantly, this anatomical coincidence does not permit the conclusion that spontaneous DMN at rest is functionally relevant for adopting the intentional stance in response to social stimuli. This is because regional brain activity observed under different conditions (e.g., resting vs. inferring a mental state) may reflect different underlying processes (Poldrack, 2006). Hence, this anatomical coincidence raises an important yet unanswered question: Does spontaneous activity in the DMN during periods of mental rest prime the intentional stance, preparing us to conceive others as minds and not merely bodies?

A handful of neuroimaging studies already illustrate that intraindividual variability in the neural (Fox, Snyder, Zacks, & Raichle, 2006; Arieli, Sterkin, Grinvald, & Aertsen, 1996) and behavioral (Callard & Margulies, 2014; Hsieh, Colas, & Kanwisher, 2012; Fox, Snyder, Vincent, & Raichle, 2007) response to a nonsocial stimuli can be partially explained by spontaneous brain activity occurring in the resting periods before stimulus onset. Building on this logic, we designed a novel fMRI task to test the hypothesis that default activity in the DMN functions to prepare the mind to adopt the intentional stance to social stimuli. This hypothesis also has strong theoretical ties to large body of research on priming and accessibility in social and cognitive psychology (Tulving & Schacter, 1990; Higgins, 1989; Neely, 1977), which reliably observes that the efficiency of evaluating a target stimulus (e.g., the word “DOCTOR”) is increased by recent exposure to a conceptually related priming stimulus (e.g., the word “NURSE”). Hence, our hypothesis can be elaborated as follows: If spontaneous activity in the DMN between stimulus events involves mental operations that are similar to those involved when adopting the intentional stance, then spontaneous DMN activity before encountering a social stimulus may make

it easier to adopt an intentional (rather than nonintentional) stance to that stimulus. If this is true, then sustained activity in the DMN during periods of rest might serve as an endogenous prime that makes an intentional stance the default strategy for making sense of the social world.

METHODS

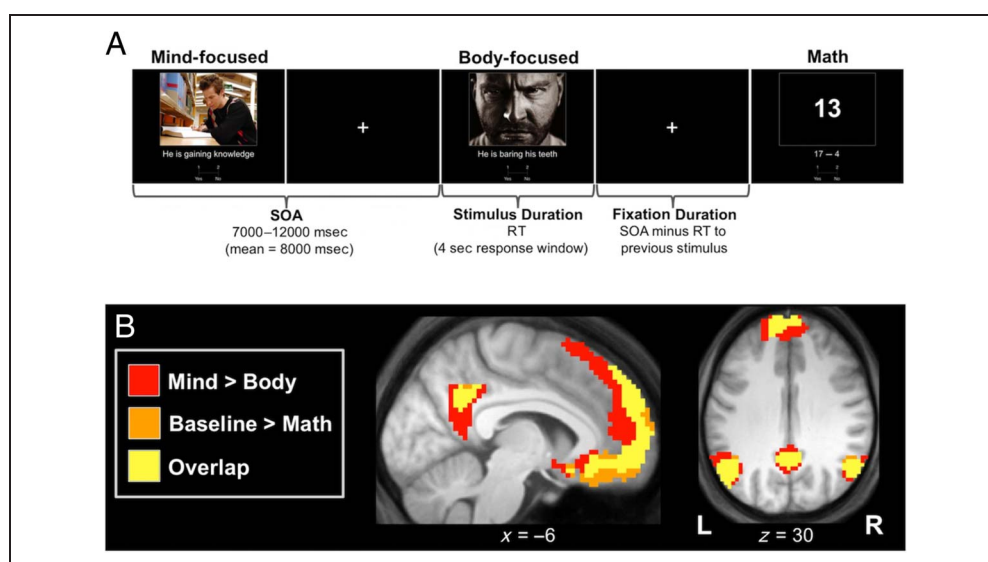
Participants

Twenty-one right-handed participants (10 men, 11 women; mean age = 22.86 years, age range = 18–31 years) were recruited from the University of California, Los Angeles (UCLA) participant pool and provided written informed consent according to the procedures of the UCLA institutional review board. All participants were native English speakers and were not taking psychotropic medications at the time of the study.

Judgment Task

The primary experimental task (Figure 1A) involved making speeded yes/no judgments under three conditions. Mind-focused judgments evoked the intentional stance by asking participants to evaluate the appropriateness of a sentence describing the mental state of a person in a photograph. Body-focused judgments featured the same photographs but evoked a nonintentional stance by asking participants to evaluate a sentence providing a physical description of the person who is performing an action. In numerous published studies, we have shown that conceptually similar manipulations robustly and selectively modulate activity in the regions of the brain associated with mental state reasoning (Spunt & Adolphs, 2014; Spunt & Lieberman, 2012a, 2012b; Spunt

Figure 1. (A) Schematic of the event-related design used to manipulate social judgments focused on either a person’s mind or body. To isolate spontaneous DMN activity related to the fixation baseline periods dividing each trial, structurally similar mathematical judgments were interleaved with these social judgments. Although the examples used to illustrate the mind-focused and body-focused judgments feature different photographs, all photographs were the object of one mind-focused judgment and one body-focused judgment. (B) Anatomical overlap of brain networks associated with mind-focused judgments and the default mode. Individual contrasts of interest were first thresholded so that all remaining clusters were significant at an FWE rate of 0.05. These maps were then binarized, as shown as a color as indicated, and overlaid on the group mean anatomical image. See Table 2 for regions surviving a test of these contrasts against the conjunction null. L = left; R = right.



et al., 2011). Finally, math judgments were entirely non-social and asked participants to evaluate arithmetical expressions. Mental arithmetic is a cognitive task known to reliably suppress activity in the DMN (Mazoyer et al., 2001) and would thus provide a method for independently defining regions demonstrating high activity during the fixation baseline period that preceded each judgment.

The mind-focused and body-focused conditions featured 40 naturalistic photographs of people performing goal-directed actions and/or displaying expressions of emotion. Each photograph was paired with two sentences, one that described an inference about the person's state of mind and one that described a physical feature of their behavior. For both conditions, 70% of the sentences were intended to provide an accurate or plausible description, whereas the remaining 30% were intended to provide an inaccurate or implausible description. The sentences featured in the two conditions were matched on length (mean number of characters: descriptive statements = 23.58, inferential statements = 23.23). To create the stimuli used in the experiment, each sentence was paired with its corresponding photograph in a single image (image size = 800×600 pixels, photograph size = 509×382 pixels, font height = 33 pixels, black background with white foreground). In addition, a 2-point yes/no scale was added to the bottom of each image. Finally, the arithmetic condition featured the 20 integers from 10 to 29, each of which was paired with two arithmetical expressions (70/30 correct/incorrect), one performing addition (e.g., $14 + 2$) and one performing subtraction (e.g., $20 - 4$). The formatting for the final arithmetic stimuli was the same as that used for the social stimuli, with the target integers (font height = 96 pixels) printed in the center of a rectangular white line with the same dimensions as the photographs used in the social conditions.

In a separate laboratory-based study, 72 undergraduates (30 men, 42 women; mean age = 20.64 years, $SD = 3.64$ years) from the UCLA performed the judgment task while seated at a computer station. When examining normative data on the individual stimuli, all stimuli elicited an accuracy rate of at least 79.5%. Indeed, the accuracy ranges for the individual stimuli across the three conditions were very similar (why = 80.7–100.0%, how = 79.5–100.0%, math = 79.5–100.0%). Importantly, a repeated-measures ANOVA revealed no significant effect of Judgment type on accuracy rates, $F(2, 142) = 0.754, p = .47$.

During functional MRI scanning, the 120 trials (40 mind-focused, 40 body-focused, 40 math) were presented to participants in an event-related design (Figure 1A). Each trial was presented for a maximum duration of 4 sec, and RT to trial onset was recorded at participant response. If the participant responded before 4 sec elapsing, the experimental stimulus was replaced with a fixation crosshair stimulus, which remained onscreen until the onset of the next trial. The order and onset of trials were optimized for estimation efficiency using custom MATLAB software (The MathWorks, Natick, MA). Trial order was constrained so

that the maximum number of consecutive trials from the same condition was 2. Onsets were constrained so that the SOA had a mean of 7.5 sec (min = 6.5 sec, max = 9.5 sec).

The following procedures were used to prepare all participants for task performance. Before entering the scanner, participants were told they would perform a task requiring them to make judgments about people and numbers. They were then shown two trials from each of the three conditions. For people trials, they were told to indicate whether the bottom statement is a good description of what they see happening in the photograph. For number trials, they were told to indicate whether the bottom statement equals the number in the box. For both trial types, participants were told to respond quickly and accurately. Immediately before starting the task in the scanner, participants were shown a screen with the same instructions and were given the opportunity to ask questions before beginning.

Match-to-Sample Task

After performance of the judgment task described above, participants performed a blocked visual match-to-sample task that would allow us to independently assess DMN activation levels in each participant. For each trial, participants judged which of two shapes matched a target shape in both shape and orientation (see Figure 2A for an example trial; image size = 800×600 pixels, shape height = 94 pixels, black background with white foreground). Participants had 2 sec to respond to each trial, and trials were presented in blocks of nine. The onset and offset of each block featured brief cues (1 sec) instructing participants to “Get Ready!” or “Relax!”, respectively. Each block was preceded and followed by a 20-sec rest period featuring a fixation cross centered onscreen.

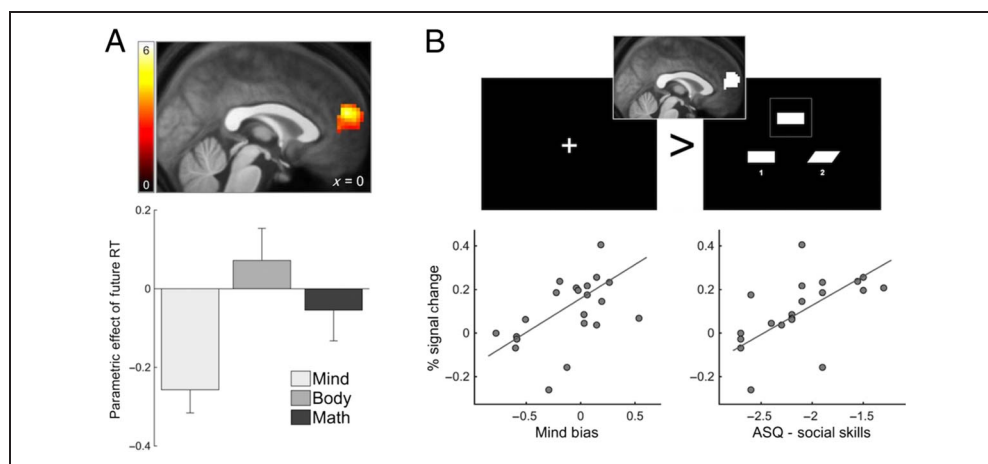
Stimulus Presentation and Response Recording

For both tasks, stimuli were presented using the MATLAB Psychophysics Toolbox (version 3.0.9; Brainard, 1997). Participants viewed the stimuli through LCD goggles (800×600 pixels) and made their responses with a button box using their right-hand index and middle fingers.

Personality Measures

Before their scanning session, all participants were asked to complete an online survey that included two personality questionnaires that were examined for this study. This study was not specifically designed to examine individual differences and indeed is underpowered in this respect (Button et al., 2013; Yarkoni, 2009). Hence, we clarify that these analyses were conducted only to provide additional constraint on interpreting the effects observed in our primary within-subject analysis.

Figure 2. (A) The region of dmPFC whose response to the fixation period preceding accurate mind-focused judgments was negatively associated with RT to those judgments (initially identified with a cluster-level FWE rate of 0.05 and shown at $p < .01$ uncorrected to show extent). Plotted is the region's mean parametric effect for the three conditions. (B) Sample screens from blocks of the match-to-sample task that participants performed after the primary judgment task. Data from this task were used to



independently estimate the magnitude of spontaneous resting activity in the dmPFC region (inset) that was found to prime mind-focused judgments previously. Individual variation in the rest-related response of this region in the match-to-sample task was predicted by two individual measures tied to the intentional stance: mind bias, a general bias to respond more efficiently to mind-focused compared with body-focused judgments, and social skills, measured with the ASQ.

First, the autism spectrum quotient (ASQ) is a 50-item scale designed to measure behaviors and preferences associated with autism spectrum disorders (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). Although this study's participants completed the full scale, our interest was only in the two 10-item subscales directly relevant to social cognition: social skills ($\alpha = .70$; e.g., "I find it difficult to work out people's intentions") and communication ($\alpha = .24$; e.g., "I am often the last to understand the point of a joke"). Given that responses to the communication subscale demonstrated poor reliability, they were not retained for further analysis. Second, participants completed the 12-Item Daydream Frequency Scale (DFS) from the Imaginal Process Inventory (Singer & Antrobus, 1972; $\alpha = .83$; e.g., "I am the kind of person whose thoughts often wander"), which has been used in previous neuroimaging studies to establish the relationship between DMN function and mind wandering (Mason et al., 2007). Because of participant noncompliance, ASQ data were available for only 20 participants, whereas DFS data were available for only 19 participants.

Behavior Analysis

MATLAB was used to compute performance on both tasks. For the judgment task, response accuracy was near ceiling for both the mind-focused and body-focused conditions (results presented below). Therefore, our behavioral analysis focused on RT to accurate trials as a measure of processing efficiency. To eliminate the influence of outliers, we removed trials to which RT deviated from the mean by 3 *SDs* (the cutoff was computed for each trial separately using a leave-one-out procedure). Then, for each participant, we computed a measure of the difference in processing efficiency for mind-focused compared with body-focused trials, which we term mind

bias (Figure 2). This was achieved by subtracting the mean RT for accurate body-focused trials from the mean RT to accurate mind-focused trials and normalizing the result by their pooled standard deviation. Hence, a positive mind bias indicates more efficient performance on mind-focused relative to body-focused trials.

The mean mind bias in the group was -0.11 ($SD = 0.34$), indicating that, on average, accurate body-focused RTs were faster than mind-focused RTs. However, there was considerable interindividual variability (scores ranged from -0.78 to 0.54), which we capitalized on in the individual difference analyses. Importantly, this variability is unlikely because of a general speed-accuracy tradeoff, as mind bias showed a nonsignificant positive association with accuracy to mind-focused judgments ($r = .33$) and a nonsignificant negative association with accuracy to body-focused judgments ($r = -.20$; to address negative skewness, accuracy scores were Box-Cox transformed for this analysis). This supports the validity of using this as a measure of individual differences in the relative ease of adopting an intentional rather than nonintentional stance to other human beings.

Image Acquisition

Imaging data were acquired using a Siemens Trio 3.0-T MRI scanner (Erlangen, Germany) at the UCLA Ahmanson-Lovelace Brainmapping Center. For each participant, we acquired 590 functional T2*-weighted EPI volumes (slice thickness = 3 mm, gap = 1 mm, 36 slices, repetition time [TR] = 2000 msec, echo time [TE] = 25 msec, flip angle = 90° , matrix = 64×64 , field of view = 200 mm). The judgment task was performed in two runs (each acquiring 230 volumes). The match-to-sample task was performed in a single run (130 volumes). We also acquired a T2-weighted matched-bandwidth anatomical scan (same

parameters as EPIs, except TR = 5000 msec, TE = 34 msec, flip angle = 90°, matrix = 128 × 128) and a T1-weighted magnetization-prepared rapid-acquisition gradient echo anatomical scan (slice thickness = 1 mm, 176 slices, TR = 2530 msec, TE = 3.31 msec, flip angle = 7°, matrix = 256 × 256, field of view = 256 mm).

Image Analysis

Functional data were analyzed using SPM (SPM8; Wellcome Department of Cognitive Neurology, London, U.K.) operating in MATLAB. Before statistical analysis, each participant's EPI volumes were subjected to the following preprocessing steps: (1) EPI volumes were corrected for slice-timing differences; (2) within each run, each EPI volume was realigned to the first EPI volume of the run; (3) the T1 structural volume was coregistered to the EPI time series by initially registering the T2 structural volume to the mean EPI and then registering the T1 to the T2; (4) the group-wise DARTEL registration method included in SPM8 (Ashburner, 2007) was used to normalize the T1 structural volume to a common group-specific space (with subsequent affine registration to Montreal Neurological Institute [MNI] space); and (5) normalization of all EPI volumes to MNI space using the deformation flow fields generated in the previous step, which simultaneously resampled volumes (3 mm isotropic) and applied spatial smoothing (Gaussian kernel of 8 mm, FWHM).

Single-participant Contrast Estimation

A general linear model was used to estimate the effects of interest for each task. We defined three such models, one for the match-to-sample task and two for the judgment task. All models used the canonical (double-gamma) hemodynamic response function for convolution and modeled serial correlations as an AR(1) process. Moreover, as covariates of no interest, all models included the six motion parameters from image realignment as well as regressors modeling time points where in-brain global signal change exceeded 2.5 *SDs* of the mean global signal change or where estimated motion exceeded 0.5-mm translation or 0.5° rotation (cutoffs were computed for each time point separately after excluding the time point from the distribution). Finally, high-pass filtering was applied using a cutoff period of 100 sec.

The match-to-sample task was modeled using a single fixed-epoch regressor modeling shape matching blocks. The first judgment task model was set up to allow the simple comparison of the task-evoked activity when participants responded accurately to each of the three judgment conditions. For each condition, a variable epoch model was used (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008) with the epoch for each trial spanning stimulus onset to participant response. Additional covariates of no interest included regressors modeling inaccurate and no-response trials.

The second judgment task model was set up to test the hypothesis that, during the course of task performance, DMN activation to the resting period preceding each trial is predictive of the ease with which participants make accurate mind-focused (but not body-focused) judgments about people. In the description to follow, the term pre-trial response (PTR) will be used to refer to the evoked response to the offset of the trial that precedes a given trial. In other words, the PTR models the brain's response to the onset of the fixation baseline period that divided the offset and onset of sequential trials. We modeled the PTR for each condition separately using an impulse function placed at the onset of the fixation period. Next, we modulated the amplitude of the evoked PTR by RT to the next trial. We omitted PTRs for trials featuring outlier RTs (criteria described above) and removed variance in the RT parameter explained by a binary variable coding whether the accurate response to each trial was to accept or reject the statement paired with the photograph. To constrain interpretation of the PTR × RT parametric regressors, multiple regressors of no interest were included in the model: (1) the unmodulated (i.e., time-invariant) response to the PTR for each condition, (2) the PTR for each condition modulated by the duration of the pre-trial interval, (3) the PTR for each condition modulated by a binary variable indexing whether the preceding trial was from the same condition, and (4) the variable epoch response to the trials themselves (modeled separately for each condition). To additionally minimize the influence of task-evoked effects, we estimated this model on the residuals from the first judgment task model (described above).¹

Group-level Analysis

Except for the ROI analysis described below, all group-level effects were investigated by subjecting participants' contrast images for the effects of interest into one-sample *t* tests. To test the conjunction null, a minimum statistic image (Nichols, Brett, Andersson, Wager, & Poline, 2005) was computed from the mind-focused > body-focused and rest > math statistical images produced by these one-sample *t* tests.

All analyses were interrogated using a cluster-level family-wise error (FWE) rate of 0.05 with a cluster-forming voxel-level *p* value of .001 (uncorrected). Regions of activation were labeled based on a combination of visual comparison to functional regions identified in existing meta-analyses (Denny, Kober, Wager, & Ochsner, 2012; Mar, 2011; Caspers, Zilles, Laird, & Eickhoff, 2010; Lieberman, 2010; Carrington & Bailey, 2009; Van Overwalle & Baetens, 2009) and by reference to probabilistic cytoarchitectonic maps of the human brain using the SPM anatomy toolbox (Eickhoff et al., 2005). For visual presentation, thresholded *t* statistic maps were overlaid on the average of the participants' T1-weighted anatomical images.

Definition of dmPFC ROI

The dmPFC ROI used in the individual difference analyses was defined using the cluster observed in the group-level parametric effect of pretrial activity on RTs to correct mind-focused judgments (Figure 2B; peak $t = 5.707$; $x = 3, y = 51, z = 21$). Given that this analysis was conducted within a mask of regions showing the conjunction effect in the first neuroimaging analysis, this ROI necessarily overlaps with both the task-negative effect observed in the rest > math contrast and the task-positive effect observed in the mind-focused > body-focused contrast. To account for interindividual variability in the anatomical locus of the estimated dmPFC response, the ROI was defined using an uncorrected threshold of $p < .01$. The resulting 136-voxel ROI was used to extract data from the match-to-sample task in all participants.

RESULTS

Performance Results

Mean accuracy and RT for each condition are shown in Table 1. For the two conditions demanding social judgments, response accuracy was high (mind-focused: $M = 96.79\%$, $SD = 5.25\%$; body-focused: $M = 96.19\%$, $SD = 3.32\%$) and did not significantly differ by condition, $t(20) = 0.446$, $p = .66$. Similarly, RT to correct trials (mind-focused: $M = 2.02$ sec, $SD = 0.30$ sec; body-focused: $M = 1.96$ sec, $SD = 0.27$ sec) did not significantly differ by condition, $t(20) = 1.479$, $p = .16$.

Within-subject Neuroimaging Results

To confirm that the brain regions associated with the intentional stance were also associated with the DMN, we tested the conjunction (minimum statistic) of two whole-brain contrasts: mind-focused compared with body-focused judgments and fixation baseline (i.e., rest) compared with math trials. Consistent with published meta-analyses (Schilbach et al., 2012; Spreng et al., 2009), this revealed common functional responses in the dmPFC and ventromedial PFC, the TPJ bilaterally, the anterior STS, and the precuneus/posterior cingulate cortex (Table 2). The medial and transverse slices in Figure 1B show widespread, distributed correspondence between these two ostensibly unrelated contrasts. The overlap spans the major nodes of

Table 1. Performance Results for the Three Conditions in the Primary Judgment Task ($N = 21$)

Measure	Judgment Condition					
	Mind-focused		Body-focused		Math	
	Mean	SD	Mean	SD	Mean	SD
Accuracy (%)	96.79	5.25	96.19	3.32	94.05	4.90
RT (sec)	2.02	0.31	1.96	0.27	1.85	0.32

Table 2. Peak Coordinates from Significant Clusters Observed When Testing against the Conjunction Null for the Contrasts Mind-focused > Body-focused and Rest > Math ($N = 21$, Whole-brain Search with a Cluster-level FWE Rate of 0.05)

Region Name	L/R	Extent	t	MNI Coordinates		
				x	y	z
Dorsomedial PFC	L	750	7.041	-9	57	30
	R	-	5.460	18	42	48
Ventromedial PFC	L	-	5.243	-3	54	-12
TPJ	L	168	7.408	-51	-66	30
	R	96	6.175	54	-63	33
Anterior STS	L	102	6.095	-60	-6	-18
Precuneus/PCC	L	120	5.328	-6	-51	36

Coordinates are all local maxima observed, which were separated by at least 20 mm. $x, y,$ and z are MNI coordinates in the left-right, anterior-posterior, and inferior-superior dimensions, respectively. PCC = posterior cingulate cortex.

both networks in the medial frontoparietal, temporoparietal, and anterior temporal cortices.

The anatomical correspondence of the two cognitive states suggests that DMN activity during rest may prime the intentional stance to social stimuli. If the DMN activity during rest primes the intentional stance, we should observe that, as the magnitude of its pretrial response increases, the time it takes to produce a correct response on subsequent mind-focused trials should decrease. When restricting the search to the regions of overlap identified in the previous analysis, we observed such an effect in one area of the DMN, the dmPFC (Figure 2A; peak: $t = 5.71$, $x = 3, y = 51, z = 21$; extent = 50 voxels).² The region of dmPFC identified is anatomically similar to those observed in numerous neuroimaging studies highlighting the importance of the dmPFC to mental state inference (Amodio & Frith, 2006; Gallagher & Frith, 2003; Happé et al., 1996; Fletcher et al., 1995; Goel et al., 1995). As is evident in the plot shown in Figure 2A, this priming effect is specific to mind-focused trials in our study. In fact, the priming effect for mind-focused judgments was significantly stronger than the same effect estimated for body-focused judgments, which featured the same set of social stimuli (peak: $t = 5.91, x = 3, y = 54, z = 21$; extent = 34 voxels). Finally, no regions within the overlap were found to exhibit a significant priming effect on RTs to either body-focused or math-focused trials, and in all three conditions, there were no regions that showed an antipriming effect, that is, pretrial activity that positively correlated with RTs.

Between-subject Neuroimaging Results

The evidence so far demonstrates that, within the same individual, transient changes in spontaneous dmPFC activity over time prime more efficient responses to

judgments requiring the intentional stance. To corroborate this transient priming effect, we examined the extent to which individual differences in rest-related responses during the match-to-sample scan can be predicted by individual differences in our measure of mind bias, that is, the relative speed with which participants executed accurate mind-focused and body-focused judgments, averaged across trials. We examined the extent to which this measure could predict individual variation in the amplitude of the rest-related activity in dmPFC ROI defined based on the priming effect observed above.

In line with the results presented so far, variation in baseline activity in dmPFC was positively predicted by variation in mind bias ($r_{19} = .50, p = .021, 95\% \text{ CI}_{\text{bootstrapped}} [0.21, 0.70]$; Figure 2D). Moreover, this relationship is robust when controlling for individual differences in both performance on the match-to-sample task and self-reported mind wandering as measured using the DFS ($r_{\text{partial}} = .51, p = .039$). In addition, the same individuals who exhibited greater dmPFC activity during rest also scored higher on a self-report measure of the social skills that are commonly impaired in individuals with an autism spectrum disorder ($r_{18} = .57, p = .009, 95\% \text{ CI}_{\text{bootstrapped}} [0.15, 0.78]$; Figure 2D), and this relationship also remains after controlling for match-to-sample task performance and DFS scores ($r_{\text{partial}} = .52, p = .032$). Thus, individuals who exhibited greater activity in dmPFC while at rest (compared with while performing a speeded match-to-sample task) showed a general processing advantage for adopting an intentional (rather than nonintentional) stance to people and reported having higher levels of everyday social expertise.

DISCUSSION

Taken together, the findings reported here suggest that the default mode of human brain function, perhaps centralized to the dmPFC, primes the intentional stance to social stimuli. Just as the word “face” primes people to initially see the Ruben’s illusion as faces rather than a vase, spontaneous DMN activity before a social interaction may prime the mind to treat others as minds rather than simply bodies extended in space. Drawing on a psychological theory and method on priming, we reasoned that, if spontaneous DMN activity features mental operations that are utilized when adopting the intentional stance, DMN activity should make it easier to adopt the intentional stance in the event that another person is encountered. We found evidence that variability in spontaneous dmPFC activity both within and across participants has a priming-like effect that is selective for mind-focused judgments of other people. We offer this as strong evidence that DMN activity in between moments of cognitive activity is the biological basis for the powerful human tendency to adopt the intentional stance.

This study was motivated by an observation that has now been made many times before in the literature:

The functional neuroanatomy of mental-state reasoning and the resting state are remarkably similar (Mars et al., 2012; Spreng et al., 2009; Schilbach et al., 2008; Buckner & Carroll, 2007). Yet, to our knowledge, this is the first study to identify the widespread neuroanatomical overlap of the two networks in the same set of participants and using the time series of brain activity measured in a single behavioral task. This allowed us to demonstrate that the very same voxels that show a task-negative effect (deactivation to math judgments) can also show a task-positive effect (activation to mind-focused judgments). This compellingly highlights the fallacy implied by labeling the DMN a “task-negative” network (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012; Spreng, 2012). Whether regions of the DMN show “task-negative” or “task-positive” effects depends on cognitive requirements of the task at hand.

Most importantly, this is the first study to provide direct evidence that stimulus-independent activity in DMN regions is functionally consequential for the execution of stimulus-dependent mental state inferences. This establishes the mechanism by which individual differences in resting baseline activation (Kennedy, Redcay, & Courchesne, 2006) and connectivity (Li, Mai, & Liu, 2014) would be associated with variability in both typical and atypical social functioning. Moreover, it suggests that the early maturation of the DMN may be functionally critical in early development, providing children with a “jump start” on acquiring the psychological skills necessary for understanding a complex and heterogeneous social world.

Of course, these findings should not be taken to imply that social cognition is the only domain in which the DMN makes a functional contribution. In fact, the DMN can be functionally divided into at least two subsystems (Andrews-Hanna et al., 2014; Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). The first subsystem is primarily localized to medial temporal lobe (MTL) structures, whereas the second, termed the dmPFC subsystem, includes the TPJ, lateral and polar temporal cortex, and an area of the dmPFC that is anatomically consistent with the region of dmPFC highlighted by this study. The MTL subsystem is not reliably observed in studies of mental state reasoning; hence, we had no strong reason to hypothesize either an anatomical or functional relationship of this system with mind-focused judgments. Of course, default activity in the MTL subsystem likely does serve adaptive functions, for instance, in the consolidation of long-term memories (Wig et al., 2008).

Given that the DMN activity is metabolically costly, widely distributed in the cortex, and highly sensitive to both the presence and type of task demand, it should be no surprise that this network would have functional consequences in multiple domains. A related but wholly separate question regards the reasons why the DMN evolved in the first place. Evidence suggests that the DMN is a basic and phylogenetically old feature of human cortical function: The basic elements of the DMN can be observed in human neonates (Fransson et al., 2007), and

similar default networks have been observed in chimpanzees (Rilling et al., 2007) and monkeys (Vincent et al., 2007). In light of these observations, we suggest our results converge with theories proposing that primate intelligence evolved as a response to the enormous demands imposed on the brain by living in increasingly large and complex social groups (Sallet et al., 2011; Cheney & Seyfarth, 2008; Dunbar, 1998). The data we present here suggest that the DMN and its activity in between moments of directed thought may be evolution's solution to the problem of other minds. Evolution seems to have made a "bet" that the best thing to do with any spare moment is to get ready to see the world in terms of other minds. This bet has allowed human beings to get together in groups and achieve far more than ever would have been possible separately.

Acknowledgments

We acknowledge Catherine Mulvenna for help with data collection, and Uta Frith, Nathan Spreng, Lucina Uddin, and Jamil Zaki for helpful comments on an earlier version of the paper.

Reprint requests should be sent to Matthew D. Lieberman, Department of Psychology, 1285 Franz Hall, UCLA, Los Angeles, CA 90095-1563, or via e-mail: lieber@ucla.edu.

Notes

1. We note that the PTR effects reported in the main text are also observed when estimating them on the nonresidualized time series with a model including the task-related effects.
2. This region is also observed in the whole-brain analysis (peak: $t = 6.34$, $x = 6$, $y = 48$, $z = 21$; extent = 83 voxels). However, given that our analysis was specifically designed to investigate the functional implications of the neuroanatomical overlap of the resting state and the intentional stance, all remaining analyses restrict the search to the mask of regions showing evidence of such overlap in this study (see Methods for further details).

REFERENCES

- Amodio, D., & Frith, C. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*, 268–277.
- Andrews-Hanna, J., Reidler, J., Sepulcre, J., Poulin, R., & Buckner, R. (2010). Functional-anatomic fractionation of the brain's default network. *Neuron*, *65*, 550–562.
- Andrews-Hanna, J., Smallwood, J., & Spreng, R. (2014). The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, *1316*, 29–52.
- Arieli, A., Sterkin, A., Grinvald, A., & Aertsen, A. (1996). Dynamics of ongoing activity: Explanation of the large variability in evoked cortical responses. *Science*, *273*, 1868–1871.
- Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage*, *38*, 95–113.
- Attwell, D., & Laughlin, S. B. (2001). An energy budget for signaling in the grey matter of the brain. *Journal of Cerebral Blood Flow & Metabolism*, *21*, 1133–1145.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism Developmental Disorders*, *31*, 5–17.
- Binder, J., Frost, J., Hammeke, T., Bellgowan, P., Rao, S., & Cox, R. (1999). Conceptual processing during the conscious resting state. A functional MRI study. *Journal of Cognitive Neuroscience*, *11*, 80–95.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Buckner, R., & Carroll, D. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, *11*, 49–57.
- Button, K., Ioannidis, J., Mokrysz, C., Nosek, B., Flint, J., Robinson, E., et al. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *14*, 365–376.
- Callard, F., & Margulies, D. S. (2014). What we talk about when we talk about the default mode network. *Frontiers in Human Neuroscience*, *8*, 619.
- Carrington, S., & Bailey, A. (2009). Are there theory of mind regions in the brain? A review of the neuroimaging literature. *Human Brain Mapping*, *30*, 2313–2335.
- Caspers, S., Zilles, K., Laird, A., & Eickhoff, S. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*, *50*, 1148–1167.
- Cheney, D. L., & Seyfarth, R. M. (2008). *Baboon metaphysics: The evolution of a social mind* (1st ed.). Chicago: University of Chicago Press.
- Dennett, D. C. (1989). *The intentional stance*. Cambridge, MA: MIT Press.
- Denny, B., Kober, H., Wager, T., & Ochsner, K. (2012). A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience*, *24*, 1742–1752.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, *9*, 178–190.
- Eickhoff, S., Stephan, K., Mohlberg, H., Grefkes, C., Fink, G., Amunts, K., et al. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*, *25*, 1325–1335.
- Epley, N., Waytz, A., & Cacioppo, J. (2007). On seeing human: A three-factor theory of anthropomorphism. *Psychological Review*, *114*, 864–886.
- Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S. J., et al. (1995). Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition*, *57*, 109–128.
- Fox, M., Snyder, A., Vincent, J., & Raichle, M. (2007). Intrinsic fluctuations within cortical systems account for intertrial variability in human behavior. *Neuron*, *56*, 171–184.
- Fox, M., Snyder, A., Zacks, J., & Raichle, M. (2006). Coherent spontaneous activity accounts for trial-to-trial variability in human evoked brain responses. *Nature Neuroscience*, *9*, 23–25.
- Fransson, P., Skiold, B., Horsch, S., Nordell, A., Blennow, M., Lagercrantz, H., et al. (2007). Resting-state networks in the infant brain. *Proceedings of the National Academy of Sciences, U.S.A.*, *104*, 15531–15536.
- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of "theory of mind." *Trends in Cognitive Sciences*, *7*, 77–83.
- Goel, V., Grafman, J., Sadato, N., & Hallett, M. (1995). Modeling other minds. *NeuroReport*, *6*, 1741–1746.
- Greicius, M., Krasnow, B., Reiss, A., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences, U.S.A.*, *100*, 253–258.
- Grinband, J., Wager, T., Lindquist, M., Ferrera, V., & Hirsch, J. (2008). Detection of time-varying signals in event-related fMRI designs. *Neuroimage*, *43*, 509–520.

- Happé, F., Ehlers, S., Fletcher, P., Frith, U., Johansson, M., Gillberg, C., et al. (1996). "Theory of mind" in the brain. Evidence from a PET scan study of Asperger syndrome. *NeuroReport*, 8, 197–201.
- Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *The American Journal of Psychology*, 57, 243.
- Higgins, E. T. (1989). Knowledge accessibility and activation: Subjectivity and suffering from unconscious sources. In J. S. Uleman & J. A. Bargh (Eds.), *Unintended thought* (Vol. 3, pp. 75–123). New York: Guilford Press.
- Hsieh, P., Colas, J., & Kanwisher, N. (2012). Pre-stimulus pattern of activity in the fusiform face area predicts face percepts during binocular rivalry. *Neuropsychologia*, 50, 522–529.
- Kennedy, D., Redcay, E., & Courchesne, E. (2006). Failing to deactivate: Resting functional abnormalities in autism. *Proceedings of the National Academy of Sciences, U.S.A.*, 103, 8275–8280.
- Kovacs, A., Teglas, E., & Endress, A. (2010). The social sense: Susceptibility to others' beliefs in human infants and adults. *Science*, 330, 1830–1834.
- Li, W., Mai, X., & Liu, C. (2014). The default mode network and social understanding of others: What do brain connectivity studies tell us. *Frontiers in Human Neuroscience*, 8, 74.
- Lieberman, M. (2010). Social cognitive neuroscience. In S. T. Fiske, D. T. Gilbert, & G. Lindzey (Eds.), *Handbook of social psychology* (5th ed., pp. 143–193). New York: McGraw-Hill.
- Mar, R. (2011). The neural bases of social cognition and story comprehension. *Annual Review of Psychology*, 62, 103–134.
- Mars, R., Neubert, F., Noonan, M., Sallet, J., Toni, I., & Rushworth, M. (2012). On the relationship between the "default mode network" and the "social brain". *Frontiers in Human Neuroscience*, 6, 189.
- Mason, M., Norton, M., Van Horn, J., Wegner, D., Grafton, S., & Macrae, C. (2007). Wandering minds: The default network and stimulus-independent thought. *Science*, 315, 393–395.
- Mazoyer, B., Zago, L., Mellet, E., Bricogne, S., Etard, O., Houde, O., et al. (2001). Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Research Bulletin*, 54, 287–298.
- Mesoudi, A., Whiten, A., & Dunbar, R. (2006). A bias for social information in human cultural transmission. *British Journal of Psychology*, 97, 405–423.
- Meyer, M. L., Spunt, R. P., Berkman, E. T., Taylor, S. E., & Lieberman, M. D. (2012). Social working memory: An fMRI study of parametric increases in social cognitive effort. *Proceedings of the National Academy of Sciences*, 109, 1883–1888.
- Neely, J. H. (1977). Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited-capacity attention. *Journal of Experimental Psychology: General*, 106, 226–254.
- Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J. (2005). Valid conjunction inference with the minimum statistic. *Neuroimage*, 25, 653–660.
- Poldrack, R. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, 10, 59–63.
- Raichle, M. (2010). Two views of brain function. *Trends in Cognitive Sciences*, 14, 180–190.
- Raichle, M., Macleod, A., Snyder, A., Powers, W., Gusnard, D., & Shulman, G. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences, U.S.A.*, 98, 676–682.
- Rilling, J., Barks, S., Parr, L., Preuss, T., Faber, T., Pagnoni, G., et al. (2007). A comparison of resting-state brain activity in humans and chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.*, 104, 17146–17151.
- Rosset, E. (2008). It's no accident: Our bias for intentional explanations. *Cognition*, 108, 771–780.
- Sallet, J., Mars, R., Noonan, M., Andersson, J., O'Reilly, J., Jbabdi, S., et al. (2011). Social network size affects neural circuits in macaques. *Science*, 334, 697–700.
- Saxe, R., Carey, S., & Kanwisher, N. (2004). Understanding other minds: Linking developmental psychology and functional neuroimaging. *Annual Review of Psychology*, 55, 87–124.
- Schilbach, L., Bzdok, D., Timmermans, B., Fox, P., Laird, A., Vogeley, K., et al. (2012). Introspective minds: Using ALE meta-analyses to study commonalities in the neural correlates of emotional processing, social & unconstrained cognition. *PLoS One*, 7, e30920.
- Schilbach, L., Eickhoff, S., Rotarska-Jagiela, A., Fink, G., & Vogeley, K. (2008). Minds at rest? Social cognition as the default mode of cognition and its putative relationship to the "default system" of the brain. *Consciousness and Cognition*, 17, 457–467.
- Senju, A. (2012). Spontaneous theory of mind and its absence in autism spectrum disorders. *Neuroscientist*, 18, 108–113.
- Shulman, G., Fiez, J., Corbetta, M., Buckner, R., Miezin, F., Raichle, M., et al. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, 9, 648–663.
- Singer, J., & Antrobus, J. (1972). Daydreaming, imaginal processes, and personality: A normative study. In P. Sheehan (Ed.), *The function and nature of imagery* (1st ed., pp. 175–202). New York: Academic Press.
- Speng, R. (2012). The fallacy of a "task-negative" network. *Frontiers in Psychology*, 3, 145.
- Speng, R., Mar, R., & Kim, A. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, 21, 489–510.
- Spunt, R., & Adolphs, R. (2014). Validating the why/how contrast for functional MRI studies of theory of mind. *Neuroimage*, 99, 301–311.
- Spunt, R., & Lieberman, M. (2012a). An integrative model of the neural systems supporting the comprehension of observed emotional behavior. *Neuroimage*, 59, 3050–3059.
- Spunt, R., & Lieberman, M. (2012b). Dissociating modality-specific and supramodal neural systems for action understanding. *Journal of Neuroscience*, 32, 3575–3583.
- Spunt, R., Satpute, A., & Lieberman, M. (2011). Identifying the what, why, and how of an observed action: An fMRI study of mentalizing and mechanizing during action observation. *Journal of Cognitive Neuroscience*, 23, 63–74.
- Tulving, E., & Schacter, D. (1990). Priming and human memory systems. *Science*, 247, 301–306.
- Uleman, J., Adil Saribay, S., & Gonzalez, C. (2008). Spontaneous inferences, implicit impressions, and implicit theories. *Annual Review of Psychology*, 59, 329–360.
- Vallacher, R. R., & Wegner, D. M. (1987). What do people think they're doing? Action identification and human behavior. *Psychological Review*, 94, 3–15.
- Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *Neuroimage*, 48, 564–584.
- Vincent, J., Patel, G., Fox, M., Snyder, A., Baker, J., Van Essen, D., et al. (2007). Intrinsic functional architecture in the anaesthetized monkey brain. *Nature*, 447, 83–86.
- Wig, G., Grafton, S., Demos, K., Wolford, G., Petersen, S., & Kelley, W. (2008). Medial temporal lobe bold activity at rest predicts individual differences in memory ability in healthy young adults. *Proceedings of the National Academy of Sciences, U.S.A.*, 105, 18555–18560.
- Yarkoni, T. (2009). Big correlations in little studies: Inflated fMRI correlations reflect low statistical power-commentary on Vul et al. (2009). *Perspectives on Psychological Science*, 4, 294–298.