

Repetition suppression of ventromedial prefrontal activity during judgments of self and others

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One useful strategy for inferring others' mental states (i.e., mentalizing) may be to use one's own thoughts, feelings, and desires as a proxy for those of other people. Such self-referential accounts of social cognition are supported by recent neuroimaging observations that a single brain region, ventromedial prefrontal cortex (vMPFC), is engaged both by tasks that require introspections about self and by tasks that require inferences about the minds of others perceived to be similar to self. To test whether people automatically refer to their own mental states when considering those of a similar other, we examined repetition-related suppression of vMPFC response during self-reflections that followed either an initial reflection about self or a judgment of another person. Consistent with the hypothesis that perceivers spontaneously engage in self-referential processing when mentalizing about particular individuals, vMPFC response was suppressed when self-reflections followed either an initial reflection about self or a judgment of a similar, but not a dissimilar, other. These results suggest that thinking about the mind of another person may rely importantly on reference to one's own mental characteristics.

functional neuroimaging | mentalizing | self-reference | social cognition

Humans consistently explain the behavior of those around them by appealing to others' mental states; that is, their thoughts and feelings, likes and dislikes, current goals and intentions, and enduring dispositions and personality traits (1). Although this understanding of others depends critically on a capacity for rapidly inferring the internal states of those around us (2–4), little is known about how exactly one successfully gains insight into the inner workings of another's mind. After all, no one has ever directly observed the thoughts or feelings of another individual, yet we routinely infer such mental content quickly and easily (5).

One possible solution to the problem of mentalizing may be found in the use of one's own thoughts and feelings as a basis for understanding those of others (6–9). Although the mental states of other people are inherently imperceptible, perceivers do enjoy immediate access to a highly similar system: their own minds. As such, one may infer another person's internal states by spontaneously imagining one's own thoughts, feelings, or desires under similar circumstances and then assuming that the other person would experience comparable mental states, a view alternately described as “simulationist,” “projectionist,” or “self-referential” accounts of social cognition.

Importantly, introspection can only provide insight about another's feelings, beliefs, and preferences to the extent that one's own mind serves as a reasonable proxy for that of the other person. If two people tend to experience very different mental states in the same situations, neither would be well advised to attempt to mentalize about the other on the basis of her own introspection. Thus, the strategy of using one's own mental states as a basis for understanding those of others should be limited to situations in which one can assume that another person generally thinks and feels similarly to oneself. Perceivers may less readily use their own mental states as a guide to the thoughts and

feelings of people perceived to be substantially dissimilar from self.

Recently, researchers have used functional neuroimaging to illuminate a specific link between introspection about self and mentalizing about those people perceived to be similar (10, 11). Across several studies, mentalizing about similar versus dissimilar others has been associated with a distinct division of labor in the medial prefrontal cortex, a region ubiquitously identified in neuroimaging studies of mental state inference (12–14). Specifically, a dorsal aspect of the medial prefrontal cortex has been associated with mentalizing about people perceived to be dissimilar from oneself, whereas a more ventral aspect of medial prefrontal cortex (vMPFC) has been linked to mentalizing about those perceived to be similar. Critically, this vMPFC region also has been observed repeatedly during tasks that require participants to introspect about their own mental experiences (15–18), suggesting a connection between tasks that require self-referential thought and those that require inferences about the mental states of similar others.

That the same brain region appears to subserve introspection about oneself and mental state inferences about similar others suggests that an overlapping set of cognitive processes carries out these two otherwise disparate tasks and is consistent with suggestions that perceivers may spontaneously refer to their own mental states to infer those of other people. However, although colocalization of function provides positive evidence that two tasks draw on the same set of mental operations, the limited spatial resolution of hemodynamic imaging techniques, such as fMRI, prevents researchers from using shared functional neuroanatomy as the basis for strong conclusions about the overlap of cognitive process. Because such techniques integrate neural activity across hundreds of thousands of neurons, activation of the same brain voxel by different tasks might occur because each activates distinct, but neighboring or interdigitated, neuronal populations. In this way, two tasks could possibly coactivate the same brain voxel despite engaging different sets of neurons that subserve disparate cognitive processes.

Fortunately, such technical limits can now be circumvented by recently developed paradigms that support stronger conclusions regarding the coactivation of the same neurons by different stimuli or different tasks. These techniques rely on an effect known as “repetition suppression,” the observation that neural activity in stimulus-sensitive brain regions is typically reduced when a stimulus is repeated (19). Repetition suppression was initially reported during single-cell recordings in monkeys (20–

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22) and has since been observed consistently across a number of studies that measured the fMRI BOLD response in humans (23–29), where it has been used to characterize the response profiles of brain regions involved in a variety of cognitive processes, such as those subserving visual processing, memory, semantics, syntax, number, and motor execution (for reviews, see refs. 19, 30–33).

Although the precise physiological basis of repetition suppression has yet to be fully elucidated, researchers generally agree that the suppressed fMRI BOLD response to repeated stimuli must reflect changes in the firing properties of neurons that subserve the processing of a stimulus, and that suppression across two stimuli indicates that the same (or at least a largely overlapping) population of neurons is engaged by both stimuli (19, 30–33). For example, a demonstration of repetition suppression for the number “3” when it follows “4” but not when it follows “40” might suggest that a relatively high proportion of the neurons that code for the number “3” also participate in representations of similar numerosities (such as “4”), but not in representations of more distant numerosities.

These characteristics of repetition suppression render it well suited for examining the hypothesis that mentalizing about like-minded individuals draws on the same cognitive processes as introspecting about one’s own mental characteristics. If (i) repeatedly considering one’s own mental states produces repetition suppression in self-sensitive regions such as vMPFC, and (ii) one engages in self-referential processing when considering the minds of similar others, then (iii) repetition suppression also should be observed when perceivers first mentalize about a similar other and then introspect about self. To test these hypotheses, participants in the current study underwent fMRI scanning while answering a series of questions that required introspection about their opinions or preferences (e.g., “How frustrated do you get sitting in traffic?”; see *Methods*). Immediately before each of these self-reflections, participants performed one of three different types of judgments: (i) an initial self-reflection; (ii) a judgment of the opinions/preferences of a person manipulated to be perceived as similar to self; or (iii) a judgment of the opinions/preferences of a person manipulated to be dissimilar from self (participants considered the identical opinion question across phases on half the trials and two different opinion questions for across phases on the other half of trials). Of critical interest was the vMPFC response during self-reflection as a function of the target of the immediately preceding judgment. We expected to observe substantially reduced activity in this region for self-reflections immediately preceded by a prior self-reflection (self-after-self), that is, a significant suppression of the BOLD response when processing the same stimulus category twice consecutively. More important, to the extent that self-referential processing spontaneously accompanies mentalizing about similar others, we expected similar suppression of vMPFC response during self-reflections preceded by judgments of similar others (self-after-similar). In contrast, because referring to one’s own mental states should not be an appropriate strategy for mentalizing about dissimilar others, no suppression should be observed when self-reflections follow judgments of dissimilar others (self-after-dissimilar).

Results

Behavioral Data. Postscanning questionnaires confirmed that participants generally held liberal attitudes and perceived themselves to be more similar to the liberal than to the conservative target. On average, participants reported their sociopolitical attitudes as 3.03 on a 7-point scale (1 = very liberal, 4 = neither liberal nor conservative, and 7 = very conservative). Likewise, participants rated the liberal target to be more similar to self ($M = 4.80$ on a 7-point scale) than the conservative target ($M = 3.00$; $P < 0.02$). Moreover, no participant rated the conservative

target to be more similar to self than the liberal target. Accordingly, the liberal target was treated as the similar other and the conservative target as the dissimilar other for subsequent fMRI analyses.

Confirming the appropriateness of these target assignments, participants judged the preferences of similar targets to be more closely in line with their own self-reflections than were the preferences of dissimilar targets. For each opinion question, we calculated the mean absolute difference between the participant’s self-reported opinion and (i) that of the similar other and (ii) that of the dissimilar other. Consistent with the notion that one’s own preferences may more strongly inform judgments of those perceived to be similar to oneself, judgments of similar others were significantly closer to one’s self-reported opinions than were judgments of dissimilar others [$M_s = 0.73$ vs. 1.12 , respectively; $t(12) = 3.25$, $P < 0.01$].

fMRI Data. Regions of interest (ROIs) in vMPFC were identified through two independent analyses. We first examined results from the explicit self-reference task, during which participants judged how well an adjective described either their own personality or that of a familiar, but not personally known, other. Consistent with earlier studies (15–18), a single region was obtained from the random effects contrast of self > other trials located in vMPFC (Fig. 1). The response in this region both to self-singletons ($M = 0.06$) and to similar singletons ($M = -0.05$) was significantly greater than the vMPFC response to dissimilar singletons ($M = -0.11$; both $P_s < 0.04$). Consistent with extant literature suggesting that the vMPFC responds preferentially during judgments about self, the response to similar singletons was intermediate between dissimilar singletons and self-singletons.

This vMPFC ROI was then interrogated for differences among trials on the opinion-judging task, during which participants reported their own opinions/preferences immediately after an initial judgment of self or one of the two other targets. We expected to observe suppression of activity in this vMPFC region for trials on which participants introspected about self immediately after introspecting a first time (i.e., self-after-self) because on these trials participants would be performing the very same task (i.e., reflecting on their own opinion/preference) twice consecutively. Consistent with this prediction, self-after-self judgments were associated with a robust suppression of activity in vMPFC. Indeed, as displayed in Fig. 1, although vMPFC response to self-reflections was typically greater than baseline when participants self-reflecting in isolation (i.e., for self-singleton trials), activity in this region was significantly reduced during self-reflections that followed an initial self report. That is, although this vMPFC ROI responded preferentially during self-reflection, its response was substantially suppressed when participants self-reported their opinions twice in a row. Importantly, no difference was observed in the level of repetition suppression during self-after-self trials as a function of whether participants responded to the identical or a different opinion question on the second phase of the trial [$t(12) = 0.50$, $P > 0.62$]. Likewise, identical and different judgment pairs both differed significantly from self-singletons (both $P_s < 0.05$).

In contrast, we expected to observe robust vMPFC activation for self-reflections that immediately followed judgments of dissimilar others (self-after-dissimilar) because perceivers should not spontaneously engage in self-referential thought when mentalizing about those perceived to be different from self, and thus less initial vMPFC processing should occur before the initial self-reflection. Indeed, self-after-dissimilar judgments were associated with a significant increase in vMPFC response over baseline [$t(12) = 4.75$, $P < 0.0005$]. This response also was significantly greater than for self-after-self and self-after-similar trials for both identical and different trials (all P values < 0.008),

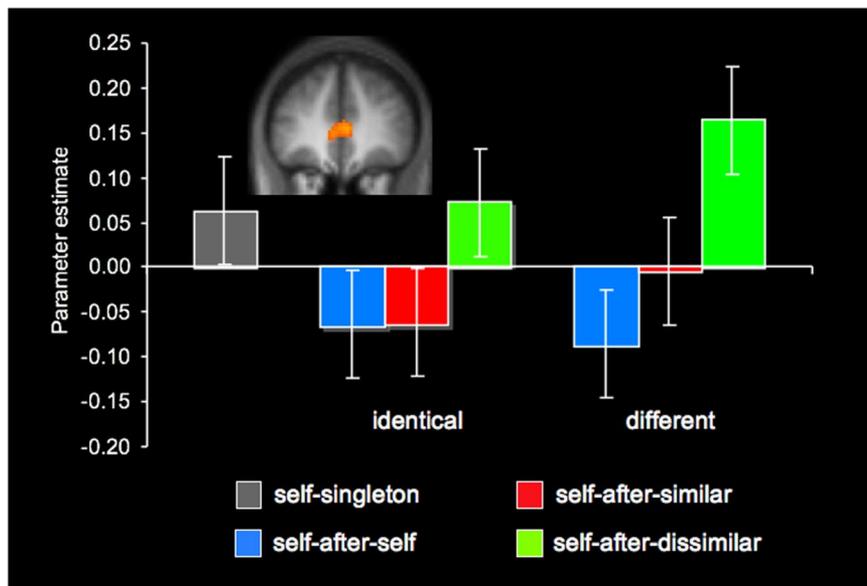


Fig. 1. A region of vMPFC ($-6, 45, 3$; 47 voxels in extent) was defined from an explicit self-reference task in which judgments of one's own personality characteristics were compared with judgments of another person (i.e., self > other). On a separate task, participants completed a series of paired judgments, in which they introspected about their own preferences and opinions immediately after one of three types of judgments: (i) an initial report about self (self-after-self), (ii) a judgment of a person with the same sociopolitical attitudes as oneself (self-after-similar), or (iii) a judgment of a person with opposing attitudes (self-after-dissimilar). On an equal number of trials, participants considered the identical question for prime and self or a different question across the two phases. The bar graph depicts the BOLD response associated with these self-reports after subtracting out the response associated with the initial judgment (see *Methods*); values therefore represent the additional BOLD response specifically associated with subsequent judgments of self. For comparison purposes, the figure includes the response in this region to self-reports made in isolation (gray bar). Significant repetition suppression was observed for self-reports that followed either an initial self-report (blue bars) or a judgment of a similar other (red bars), but not judgments of a dissimilar other (green bars). Error bars represent the 95% confidence interval for within-subject designs (43).

indicating that the response of vMPFC during self-reflection was not suppressed when participants first mentalized about a dissimilar other.

Of critical interest was whether activity in vMPFC would demonstrate repetition suppression for trials on which participants introspected about self immediately after making a judgment about a person perceived to be similar (self-after-similar). If the same neural processing accompanies both introspection and mentalizing about similar others, the response of vMPFC should fail to distinguish between introspection about self and judgments of similar others. Consistent with this prediction, just as for self-after-self judgments, vMPFC response to self-reflections was substantially suppressed when participants reported their opinion immediately after judging a similar other. For identical judgments, self-after-similar trials were associated with nearly indistinguishable levels of repetition suppression as for self-after-self judgments [$t(12) = 0.06, P > 0.95$; for different judgments, $P > 0.11$]. As for self-after-self trials, the response to self-after-similar judgments was negative-going and did not differ significantly from baseline activity (repeated, $P > 0.19$; novel, $P > 0.93$). Together these results suggest that activity in vMPFC, a brain region widely acknowledged to subserve self-referential thought, can be suppressed either by repeatedly introspecting about the self or by introspecting about self immediately after judging a similar, but not a dissimilar, other.

In addition, a second vMPFC ROI was defined from trials within the opinion-judging task by contrasting self-singleton trials to both similar- and dissimilar-singleton trials (i.e., self > other). Random effects analysis identified a region of vMPFC that was preferentially engaged by judgments of self [see [supporting information \(SI\) Fig. 2](#)]. Importantly, the pattern of repetition suppression within this alternative vMPFC ROI was indistinguishable from that in the region defined by the explicit self-reference task (with the exception of self-after-similar-

different trials, as detailed below). These results serve to confirm the pattern of findings observed in the vMPFC ROI defined independently by the explicit self-reference task and confirm that vMPFC activity was suppressed for self-reflections that either followed an initial self-reflection or a judgment of a similar, but not dissimilar, other.

Secondary Data and Analyses. In both vMPFC regions, the predicted pattern of repetition suppression was observed across both identical judgments (when participants judged the same opinion question twice within the same trial) and different judgments (when participants judged a different question in the second phase than in the first phase of the trial). The 3×2 interaction of pair type (self-after-self, self-after-similar, and self-after-dissimilar) \times question repetition (identical or different) did not approach significance in either vMPFC region (both $P_s > 0.18$), suggesting that the pattern of repetition suppression was similar across identical and different trials. Likewise, when restricted to self-after-similar and self-after-dissimilar trials, the 2×2 interaction of trial type \times question repetition failed to approach significance in either region (both $P_s > 0.55$), suggesting that vMPFC activity was similarly suppressed for self-reflections after judgments of similar others, relative to judgments of dissimilar others. Most critically, the same pattern of differences was observed between self-after-similar trials in both regions regardless of whether questions were identical or different. Specifically, vMPFC activity did not differentiate between self-after-similar and self-after-self trials for either identical (both $P_s > 0.56$) or for different (both $P_s > 0.20$) trials, but was consistently lower for self-after-similar than self-after-dissimilar (all $P_s < 0.05$). Finally, pairwise t tests conducted between all trials across repetition (e.g., self-after-self-identical vs. self-after-self-different) revealed a significant difference only for self-after-similar trials in the vMPFC region defined from the explicit

self-reference task ($P < 0.03$) (Fig. 1). Because this effect was not replicated in the alternate vMPFC region identified from self > other from within the judgment task (SI Fig. 2), it remains unclear whether less repetition suppression occurs when a different question is asked about self and a similar other.

Unsurprisingly, participants gave the identical behavioral response for self and other (e.g., responding 3 to both other and self) more often for self-after-similar than self-after-dissimilar targets (37% vs. 29% of trials, respectively; $P < 0.05$). That participants more often made the same behavioral response consecutively for self-after-similar than self-after-dissimilar trials opens the possibility that vMPFC suppression associated with self-after-similar trials could result from repeated motor output, rather than shared cognitive operations between thinking about self and similar others. However, further analysis of the fMRI data belied this possibility. In a secondary analysis of the fMRI data, trials were subconditionalized as a function of whether the same behavioral response was made twice in a row, resulting in four trial types: self-after-similar, same response; self-after-similar, different response; self-after-dissimilar, same response; and self-after-dissimilar, different response (the creation of subconditions was not possible for self-after-self trials, for which prohibitively few different responses were obtained). When analysis was restricted to those trials on which participants made the same behavioral response twice in a row (e.g., pressing 3 for both other and self), we continued to observe repetition suppression for self-after-similar, but not for self-after-dissimilar, judgments, although the difference between the two trial types only reached marginal significance ($P < 0.07$), most likely owing to the reduced power inherent in reducing the number of trials per condition (e.g., as few as 10 trials in a condition for some participants).

In addition, we conducted a secondary analysis restricted only to identical trials, segregating trials on which participants made the same response twice in a row (e.g., 3 to the prime and to self) from those on which participants made two different responses across the two phases of the trial. Critically, the pattern of repetition suppression did not differ as a function of whether participants made the same behavioral response twice in a row to the identical question. First, the difference in the amount of repetition suppression for self-after-similar versus self-after-dissimilar trials did not differ as a function of whether participants made the same behavioral response: the pair type (self-after-similar, self-after-dissimilar) \times response overlap (same response, different response) interaction did not approach significance ($F = 1.07$, $P > 0.32$). Second, no simple effect was observed between same versus different responses for either self-after-similar or self-after-dissimilar trials (both P s > 0.26), suggesting that repetition suppression was not significantly affected by whether participants made the same behavioral response twice in a row. Although these findings are consistent with the interpretation that the pattern of repetition suppression did not differ as a function of making the same behavioral response, results must be interpreted cautiously because these analyses are based on a small subset of the data with reduced power to detect any differences inherent in making the same response or not.

Finally, an accompanying behavioral study reinforced the observation that the facilitation of self-after-similar trials did not result from making a repeated behavioral response. In this data collection, we made use of a behavioral analogue of repetition suppression, wherein repeated processing results in speeded performance on subsequent trials of the same kind (i.e., repetition priming) (33). Specifically, the primary dependent measure in this supporting study was the speed with which a separate group of participants reported their introspection about self after judgments of a similar or dissimilar other. Consistent with the fMRI data, participants ($n = 14$) were significantly faster to

self-reflect after a judgment of a similar ($M = 1,990$ ms) than a dissimilar ($M = 2,079$ ms) target [$t(13) = 2.84$, $P < 0.02$]. (The parallel analysis of response time in the fMRI experiment was precluded by the abbreviated length of trials necessitated by rapid event-related scanning, such that participants were typically near the ceiling allowed by the response window.) Consistent with the secondary analysis of fMRI data, the significant difference in reaction time between self-after-similar versus self-after-dissimilar was observed even when analysis was restricted to those trials on which participants made the same behavioral response for both self and the other person (M diff = 299 ms; $P < 0.02$). In other words, introspections about one's own attitudes were significantly more facilitated by first mentalizing about a similar than a dissimilar target, even when controlling for participants' tendency to make the same response for self and similar others.

Discussion

These results underscore the tight link between thinking about oneself and thinking about other people, suggesting that self-referential processing may be triggered spontaneously when considering the mental states of others. Using two different sets of contrasts, we identified ROIs in vMPFC that, consistent with earlier studies of self-reference (15–18), responded preferentially during trials that required introspection about one's own mental characteristics. We then examined the pattern of response in these ROIs during an opinion-judging task in which participants reported their preferences and opinions immediately after a prior self-reflection, a judgment of a similar other, or a judgment of a dissimilar other. Extending earlier observations that repeatedly processing the same stimulus leads to the suppression of the activity in task-sensitive brain regions, the response of vMPFC was attenuated for self-reflections that immediately followed a preceding introspection about self. Critically, this same repetition suppression was observed for self-reflections that followed judgments of similar, but not dissimilar, targets. That is, whereas self-reflections were associated with a significant activation of vMPFC after judgments of a dissimilar other, the response of this region was equivalently suppressed during self-reflections that followed judgments of a similar other as during those that followed initial self-reflections, suggesting that vMPFC failed to discriminate between self-referential thought and mentalizing about a similar other.

The use of repetition suppression provides particularly strong support for the conclusion that mentalizing about similar others draws on the same cognitive processes as introspecting about oneself. Most proposals regarding the physiological basis of repetition suppression conclude that the likely basis of the effect is that the same, or largely overlapping, population of neurons subserves the processing of two distinct stimuli. These changes may include neurons "fatiguing" upon repeated firings, briefer neuronal firing durations, or the recruitment of fewer total neurons to process stimuli a second time (19, 33, 34). Regardless of the precise nature of the neuronal change, observing repetition suppression in a brain region across two seemingly distinct stimuli provides evidence that the neurons in that region are insensitive to any difference between the stimuli. This interpretation of repetition suppression suggests the intriguing possibility that the population of vMPFC neurons subserving introspections about self serve double-duty by also participating in representing the minds of similar others. Accordingly, these results contribute additional support for simulationist views of social cognition, which have suggested that one important mechanism for understanding the thoughts and feelings of others is reference to one's own mental states.

The observed dissociation between the functional neuroanatomy associated with mentalizing about similar and dissimilar others joins several other recent observations that likewise

suggest that the cognitive processes deployed during mentalizing will vary as a function of exactly whose mental states one is attempting to infer (10, 11). When another person is assumed to be sufficiently similar to self, perceivers appear to make use of the same processes deployed for introspecting about their own mental characteristics, but decline to do so for others assumed to be dissimilar from self. Such findings reinforce the emerging view that social cognition, rather than being composed of a single, all-purpose module for mentalizing (35), relies on a number of different strategies for mentalizing that vary with the particulars of the social environment (36–39). Of course, exactly how perceivers determine whether a particular individual is sufficiently similar to justify the use of self-referential mentalizing remains an open question, as does characterization of the cognitive processes that subserve mentalizing about dissimilar others.

Putting introspection to use in mentalizing undoubtedly provides a rich starting point for contemplating the minds of others, allowing perceivers to bring to bear the full complement of their own attitudes, feelings, and beliefs in inferring those of another person. Somewhat ironically, however, because one's own mental states may serve as an appropriate proxy only for those whom we assume think and feel like we do, human social cognition may possess an intrinsic bias to discriminate between those perceived to be similar, like-minded members of one's ingroup and those perceived to be dissimilar, exotic others. Indeed, that our minds naturally segregate dissimilar from similar others and then mentalize in a distinct way about those perceived to be different from self may be one of the factors that gives rise to aspects of outgroup prejudice, such as stereotypes about members of various racial, ethnic, or cultural backgrounds. Accordingly, one strategy for successfully counteracting such biases may be to augment the degree to which perceivers engage in self-referential mentalizing about otherwise dissimilar others, for example, by consciously taking the perspective of another person (44). Like many of the cognitive heuristics that typically serve us well, but periodically lead to undesirable or maladaptive behavior (40), the use of self-reference in mentalizing may be a double-edged sword: a useful strategy for providing rich and accurate insights into the minds of similar individuals, but rife with the potential to exclude those minds assumed at first glance to be different from our own.

Methods

Participants. Participants were 13 (8 male) right-handed, native English speakers with no history of neurological problems (mean age 20.7 years, range 19–23). One additional participant, who was being treated for depression at the time of the study, was excluded from analysis. All participants were undergraduate or graduate students at universities in the Boston area, and all provided informed consent in a manner approved by the Human Studies Committee of the Massachusetts General Hospital.

Stimuli and Behavioral Procedure. Participants were told that the experiment investigated the ability to make inferences about others on the basis of minimal information. Before scanning, participants read a short paragraph about each of two unfamiliar target individuals depicted by face photographs. Following Mitchell *et al.* (11), one target was described as a college student in the Northeast who maintained liberal social and political attitudes similar to those of our typical student participant. In contrast, the other target was described as a conservative, fundamentalist Republican attending a large university in the Midwest (i.e., as fairly dissimilar from our typical participant). Targets were always the same sex as the participant, and both the pairing of particular faces to descriptions and the order of presentation (liberal target first, conservative target first) were randomized across participants. Participants were given as much time as needed to read about each of the two targets.

During scanning, participants performed a modified version of the opinion-judging task used by Mitchell *et al.* (11) Trials were divided into prime and self phases. Each trial began with the presentation of one of three primes: (i) the photograph of the liberal target, (ii) the photograph of the conservative

target, or (iii) a chalk outline of a head with the word "me" written inside, used to represent the participant her or himself. This prime image appeared above a four-point response scale (1 = not at all and 4 = definitely). Simultaneously, an opinion question appeared between the prime and the response scale, and participants were asked to use the scale either to estimate how likely the target would be to endorse the opinion or, for the chalk outline, to report their own response to the question. Opinion questions referred to a range of personal issues that were pretested to be unrelated to political orientation (e.g., "dislike mushrooms on pizza?"; "enjoy crossword puzzles?"; "like to be the center of attention?"; "generally see things from many perspectives?"; "enjoy helping friends with problems?"; and "like impressionist artwork?"). The prime image, question, and scale remained onscreen together for 3,600 ms.

The self phase of each trial began after a 400-ms interval and was identical to the chalk outline prime described above, in which participants reported their own response to an opinion question. Self-judgments were conditionalized as a function of the preceding target, resulting in three trial types: self-after-similar, self-after-dissimilar, and self-after-self. Because participants were identified as having liberal sociopolitical attitudes, the liberal target was designated "similar" and the conservative target was designated "dissimilar"; the validity of these target assignments was confirmed by postscan questionnaires that asked participants to rate how similar they perceived each of the two targets to be relative to self.

For half the trials, the same opinion question was asked in both the prime and self phases of the trial (identical trials). In the remaining half of the trials, a different question was asked in the two phases (different trials). However, participants were instructed to consider each question individually. Although none of the primary analyses was qualified by whether the identical or different question was asked across the two phases, we report data separately for these two trial types for the sake of completeness.

Participants completed 240 such paired prime-self trials. In addition, the experimental design included 90 singleton trials, on which participants saw only the prime phase (30 each of self, similar, and dissimilar) without a subsequent self phase. These singletons were included as catch trials used to facilitate deconvolution of the hemodynamic response specifically associated with the self phase (see below).

After the opinion-judging task, participants completed an explicit self-reference task that has been used previously to identify a region of vMPFC that responds preferentially during self-referential judgments (15, 16). On each of 100 trials, participants saw a single trait adjective that could be used to describe a person's personality or dispositional traits (e.g., curious, intelligent, or neurotic). Each trait adjective was accompanied by the name of one of two targets: self or Bush. For self-trials, participants were asked to use a 4-point scale to indicate how well the trait adjective described themselves. For Bush trials, participants were asked to use the scale to indicate how well the adjective described the current U.S. president, George W. Bush. This choice of other was guided by earlier studies of self-referential processing, which have typically used the current head of state (a familiar, but not personally known, other) as a comparison to self-judgments (15, 16, 41). To optimize estimation of the event-related fMRI response, on both the opinion-judging and explicit self-reference tasks, trials were intermixed in a pseudorandom order and separated by a variable interstimulus interval (400–8,000 ms) (42), during which participants passively viewed a fixation crosshair.

After scanning, participants answered two questions about their own sociopolitical attitudes in random order ("How politically liberal or conservative are you?" and "How socially liberal or conservative are you?") by using a 7-point scale (1 = very liberal, 4 = neither liberal nor conservative, and 7 = very conservative). Finally, participants reported how similar they perceived each of the two targets to be to themselves (1 = most dissimilar to 7 = most similar).

Imaging Procedure. fMRI data were collected by using a 3 Tesla Siemens Trio scanner. The opinion-judging task comprised five functional runs of 296 volume acquisitions, and the explicit self-reference task comprised two functional runs of 130 volume acquisitions (26 axial slices, 5 mm thick; 1 mm skip). Functional imaging used a gradient-echo echo-planar pulse sequence (TR = 2 s; TE = 35 ms; 3.75 × 3.75 in-plane resolution). After the functional scans, we collected a high-resolution T1-weighted structural scan (MP-RAGE). PsyScope software for Mac OS X (L. Bonatti, International School of Advanced Studies, Trieste, Italy) was used to project stimuli onto a screen at the end of the magnet bore, which participants viewed via a mirror mounted on the head coil. A pillow and foam cushions were placed inside the coil to minimize head movement.

fMRI data were preprocessed and analyzed by using SPM99 (Wellcome Department of Cognitive Neurology, London, United Kingdom). First, functional data were time-corrected for differences in acquisition time between

slices for each whole-brain volume and realigned to correct for head movement. Functional data were then transformed into a standard anatomical space (3-mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute). Normalized data were then spatially smoothed [8 mm full-width-at-half-maximum (FWHM)] by using a Gaussian kernel.

Statistical analyses were performed by using the general linear model in which the event-related design was modeled by using a canonical hemodynamic response function, its temporal derivative, and additional covariates of no interest (a session mean and a linear trend). This analysis was performed individually for each participant, and contrast images for each participant were subsequently entered into a second-level analysis, treating participants as a random effect.

First, a region of vmPFC was identified from the comparison of self > other (i.e., self trials vs. Bush trials). In addition, a second vmPFC ROI was defined from within the opinion-judging task from the comparison of self > other by using singleton trials only (i.e., self-singletons > similar singletons plus dissimilar singletons). Peak coordinates were identified by using a statistical criterion of 25 or more contiguous voxels at a voxel-wise threshold of $P < 0.001$. This cluster size was selected on the basis of a Monte Carlo simulation (S. Slotnick, Boston College, Boston) of our brain volume, which indicated that this cluster extent cutoff provided an experiment-wise threshold of $P < 0.05$, corrected for multiple comparisons.

For the opinion-judging task, trials were conditionalized as a function of (*i*)

whether they were paired or singleton, and (*ii*) the identity of the prime, resulting in six trial types: self-after-self, self-after-similar (i.e., judgment of the liberal target, then self), self-after-dissimilar, self-singleton, similar singleton, and dissimilar singleton. The parameter estimates associated with each of these six trial types were extracted from the two vmPFC ROIs identified after the above procedure. Of critical interest was the extent to which brain activity associated with the self phase was suppressed as a function of the identity of the preceding prime (self, similar, and dissimilar). Because the self phase was always preceded by a prime (i.e., self and prime were intrinsically confounded), we obtained such a measure of repetition suppression by subtracting the response to singleton trials from the corresponding paired prime-self trials. For example, the response that was associated with the self phase of self-after-similar trials was indexed as the difference of self-after-similar trials minus similar-singleton trials. The resulting scores represent activity that is specifically associated with the self portion of trials as a function of whether this judgment was made immediately after an initial judgment of self, of a similar other, or a dissimilar other.

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- Dennett DC (1987) *The Intentional Stance* (MIT Press, Cambridge, MA).
- Tomasello M (1999) *The Cultural Origins of Human Cognition* (Harvard Univ Press, Cambridge, MA).
- Gilbert DT (1998) in *Handbook of Social Psychology*, eds Gilbert DT, Fiske ST, Lindzey G (McGraw-Hill, New York), pp 89–150.
- Frith CD, Frith U (1999) *Science* 286:1692–1695.
- Apperly IA, Riggs KJ, Simpson A, Chiavarino C, Samson D (2006) *Psychol Sci* 17:841–844.
- Gordon RM (1992) *Mind and Language* 1:158–171.
- Heal J (1986) in *Language, Mind and Logic*, ed Butterfield J (Cambridge Univ Press, Cambridge, UK), pp 135–150.
- Davies M, Stone T, eds (1995) *Mental Simulation: Evaluations and Applications* (Blackwell, Oxford).
- Nickerson R (1999) *Psychol Bull* 125:737–759.
- Mitchell JP, Banaji MR, Macrae CN (2005) *J Cogn Neurosci* 17:1306–1315.
- Mitchell JP, Macrae CN, Banaji MR (2006) *Neuron* 50:655–663.
- Blakemore SJ, Winston J, Frith U (2004) *Trends Cogn Sci* 8:216–222.
- Frith C, Frith U (2001) *Curr Dir Psychol Sci* 10:151–155.
- Mitchell JP (2006) *Brain Res* 1079:66–75.
- Kelley WM, Macrae CN, Wyland CL, Caglar S, Inati S, Heatherton TF (2002) *J Cogn Neurosci* 14:785–794.
- Macrae CN, Moran JM, Heatherton TF, Banfield JF, Kelley WM (2004) *Cereb Cortex* 14:647–654.
- Zysset S, Huber O, Ferstl E, von Cramon DY (2002) *NeuroImage* 15:983–991.
- Johnson SC, Baxter LC, Wilder LS, Pipe JG, Heiserman JE, Prigatano GP (2002) *Brain* 125:1808–1814.
- Grill-Spector K, Henson R, Martin A (2006) *Trends Cogn Sci* 10:14–23.
- Li L, Miller EK, Desimone R (1993) *J Neurophysiol* 69:1918–1929.
- Miller EK, Desimone R (1994) *Science* 263:520–522.
- Sobotka S, Ringo JL (1996) *J Neurosci* 16:4222–4230.
- Demb JB, Desmond JE, Wagner AD, Vaidya CJ, Glover GH, Gabrieli JD (1995) *J Neurosci* 15:5870–5878.
- Stern CE, Corkin S, Gonzalez RG, Guimaraes AR, Baker JR, Jennings PJ, Carr CA, Sugiura RM, Vedantham V, Rosen BR (1996) *Proc Natl Acad Sci USA* 93:8660–8665.
- Henson R, Shallice T, Dolan R (2000) *Science* 287:1269–1272.
- Buckner RL, Petersen SE, Ojemann JG, Miezin FM, Squire LR, Raichle ME (1995) *J Neurosci* 15:12–29.
- Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzhak Y, Malach R (1999) *Neuron* 24:187–203.
- Jiang Y, Haxby JV, Martin A, Ungerleider LG, Parasuraman R (2000) *Science* 287:643–646.
- Vuilleumier P, Henson RN, Driver J, Dolan RJ (2002) *Nat Neuro* 5:491–499.
- Grafton ST, Hamilton AFdC (2007) *Hum Mov Sci* 26:590–616.
- Grill-Spector K, Malach R (2001) *Acta Psychol (Amst)* 107:293–321.
- Sawamura H, Orban GA, Vogels R (2006) *Neuron* 49:307–318.
- Wiggs CL, Martin A (1998) *Curr Opin Neurobiol* 8:227–233.
- Henson RN, Goshen-Gottstein Y, Ganel T, Otten LJ, Quayle A, Rugg MD (2003) *Cereb Cortex* 13:793–805.
- Leslie AM, Friedman O, German TP (2004) *Trends Cogn Sci* 8:528–533.
- Ames DR (2004) *J Pers Soc Psychol* 87:340–353.
- Ames DR (2004) *J Pers Soc Psychol* 87:573–585.
- Macrae CN, Bodenhausen GV, Milne AB (1994) *J Pers Soc Psychol* 66:37–47.
- Malle BF (2005) in *Other Minds: How Humans Bridge The Divide Between Self and Other*, eds Malle BF, Hodges SD (Guilford, New York), pp 26–43.
- Tversky A, Kahneman D (1974) *Science* 27:1124–1131.
- Rogers TB, Kuiper NA, Kirker WS (1977) *J Pers Soc Psychol* 35:677–688.
- Dale AM (1999) *Hum Brain Mapp* 8:109–114.
- Loftus GR, Masson MEJ (1994) *Psychonomic Bull Rev* 1:476–490.
- Ames DL, Jenkins AC, Banaji MR, Mitchell JP (2008) *Psychol Sci*, in press.