

Neuromodulation of group prejudice and religious belief

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Abstract

People cleave to ideological convictions with greater intensity in the aftermath of threat. The posterior medial frontal cortex (pmFC) plays a key role in both detecting discrepancies between desired and current conditions and adjusting subsequent behavior to resolve such conflicts. Building on prior literature examining the role of the pmFC in shifts in relatively low-level decision processes, we demonstrate that the pmFC mediates adjustments in adherence to political and religious ideologies. We presented participants with a reminder of death and a critique of their in-group ostensibly written by a member of an out-group, then experimentally decreased both avowed belief in God and out-group derogation by downregulating pmFC activity via transcranial magnetic stimulation. The results provide the first evidence that group prejudice and religious belief are susceptible to targeted neuromodulation, and point to a shared cognitive mechanism underlying concrete and abstract decision processes. We discuss the implications of these findings for further research characterizing the cognitive and affective mechanisms at play.

Key words: ethnocentrism; religiosity; transcranial magnetic stimulation; posterior medial frontal cortex

Introduction

Parochial ideologies motivate numerous aspects of human social life, from art movements to wars. Moralistic ideologies involving group chauvinism and religion are arguably the most socially impactful—and, at times, the most perniciously divisive. The extent of commitment to political and religious ideologies shifts across contexts, with cues of threat eliciting particularly sharp increases in adherence (McGregor *et al.*, 2013; Jonas *et al.*, 2014; Holbrook, 2016). Although social scientists have attended for some time to the manner in which threats moderate commitment to political and religious values, only recently have psychologists turned their attention to the neurobiological mechanisms at play (Inzlicht *et al.*, 2009; Proulx *et al.*, 2012; Tritt *et al.*, 2012; Klackl *et al.*, 2014; Luo *et al.*, 2014). Here, we experimentally demonstrate that a region of the brain previously shown to enable problem solving

with respect to low-level conflicts, such as switching motor behavior to achieve a reward, plays a central role in investment in ideological beliefs.

The posterior medial frontal cortex (pmFC) is a plausible mediator of shifts in ideological commitment. The pmFC complex includes the dorsal anterior cingulate cortex (dACC) and the dorsomedial prefrontal area anterior to the supplementary motor cortex (dmPFC), and has been linked to a wide variety of reactions to negative emotional stimuli (Etkin *et al.*, 2011; Maier *et al.*, 2012; Rushworth *et al.*, 2007). The pmFC plays a key role in detecting discrepancies between desired and current conditions, and adjusting subsequent behavior during decision-making tasks (Shima and Tanji, 1998; Bush *et al.*, 2002; Ridderinkhof *et al.*, 2004). In humans, the dACC component of the pmFC has been proposed to induce a compensatory increase

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in moral or cultural values following exposure to threats (e.g. reminders of death, uncertainty or meaninglessness) (Proulx et al., 2012; Tritt et al., 2012). Reminders of death trigger activity in the dmPFC (Han et al., 2010; Shi and Han, 2013), and have been shown to increase ideological investment in a range of topics, including national identification and punishment of norm-violators (Jonas et al., 2014). Likewise, cues of social isolation both activate the dACC (Eisenberger, 2012) and elicit heightened ethnocentrism (Navarrete et al., 2004). Interestingly, ACC activation elicited by low-level Stroop-like conflicts can be attenuated by priming religious participants with reminders of their religious beliefs (Inzlicht and Tullett, 2010). Conversely, just as reactivity to low-level (e.g. Stroop) conflicts appears susceptible to moderation by high-level (e.g. religious) beliefs, relatively high-level conflicts, such as asking participants to contemplate their future non-existence, can polarize evaluations of low-level target stimuli (e.g. aversive noise blasts; Holbrook et al., 2011). These findings suggest that, because different conflict response systems efficiently share certain components, activation of one system (e.g. for managing physical pain) can influence the operation of other systems (e.g. for managing social isolation).

Noting the evident degree of shared structure uniting diverse sorts of reactions to diverse sorts of threats, proponents of the Reactive Approach Motivation (RAM) model argue that threatening goal conflicts (of any kind) are detected within the ACC, triggering feelings of anxiety which are subsequently palliated by activating approach-motivated states (Nash et al., 2011; McGregor et al., 2013). Consonant with the RAM model, activity in the anterior cingulate region is associated with anxiety, and the act of imagining cherished ideological convictions has been found to activate brain states associated with approach motivation and subsequent reductions in anxiety (Harmon-Jones, 2004; Urry et al., 2004). Importantly, these reactive approach-motivated responses are theorized to include ideological reactions such as out-group derogation and religious extremism. Thus, the RAM theory (and similar accounts such as ‘the Meaning Maintenance Model’; Heine et al., 2006) predicts that the dACC is involved in exaggerating ideological responses in the aftermath of any poignant threat. Importantly, according to the RAM and related perspectives, the function of ideological reactions to threat is to reduce intrapsychic threat anxiety—not to address the eliciting threat itself in any strategic, domain-specific way (Holbrook and Fessler, 2015).

In contrast to the RAM model’s emphasis on the interchangeability of threats and the heightened ideological reactions that they elicit, convergent lines of evidence generated independently of the RAM literature indicate that the dmPFC/dACC complex functions as an interface relating threat detection with the coordination of targeted solutions relevant to resolving particular threats. The pMFC has been observed to consistently react to various sorts of discrepancies within the social domain, and pMFC activity correlates positively with social behavioral shifts that reduce the given discrepancy (Izuma, 2013). For example, pMFC activity is associated with preference changes to reduce cognitive dissonance (van Veen et al., 2009; Izuma et al., 2010, 2015) and with increases in social conformity upon detecting divergences between one’s stated opinions and group consensus (Klucharev et al., 2009; Izuma and Adolphs, 2013). Klucharev et al. (2011) further demonstrated that experimental downregulation of activity in the pMFC using transcranial magnetic stimulation (TMS) decreases social conformity. Thus, upon detection of concrete physical problems such as receiving a negative outcome in a motor task (Shima and Tanji, 1998), or relatively abstract problems such as realizing that one is out of step with social consensus, processes associated with pMFC activity appear to coordinate relevant

responses (Rushworth et al., 2004; Ullsperger et al., 2004; Izuma and Adolphs, 2013), such as switching motor behavior to achieve a reward or changing one’s opinion to conform with others.¹ These results indicate that the pMFC is part of a neurocognitive architecture that is co-opted into distinct, domain-specific networks that manage both concrete and abstract challenges of various types. Note that this problem-solving account of the role of pMFC structures focuses on the production of responses that are relevant to the eliciting problem, whereas approaches such as the RAM model emphasize the reduction of anxiety as a functional benefit which may stem from problem-irrelevant responses (Holbrook, 2016).

Building on these findings, we hypothesize that when problems involve conflicting ideological values or insoluble dilemmas such as the inevitability of death, pMFC mechanisms may invoke relevant belief systems. Specifically, we predict that participants confronted with their own mortality will ‘solve the problem’ via pMFC mechanisms that facilitate amplifying their belief in God; likewise, participants confronted by an out-group member’s critique of their group’s values will more intensely derogate out-group critics. Participants whose pMFC has been experimentally downregulated via TMS should therefore display less religiosity following a reminder of their own mortality and less derogation of critical out-group members. Ours is an admittedly ambitious hypothesis, as both the problems and the solutions at issue are more abstract than those previously shown to be addressed by the pMFC. In addition, it is important to note that the RAM model, which highlights the production of ‘any’ anxiety-reducing approach-motivated response to threat rather than the problem-focused interpretation that we have emphasized, produces the same predictions. Accordingly, this study should be regarded as an initial investigation of whether ethnocentrism or religiosity can be experimentally neuromodulated by targeting the pMFC—a hypothesis that accords with multiple theoretical perspectives—and not as a test of the problem-specific vs generically palliative nature of the process.

Overview of the study

To test the causal role of the pMFC in adherence to group and religious ideologies, we applied TMS or sham stimulation followed by a 10-min filler task to ensure that downregulation of the pMFC took effect. We then primed all participants with thoughts of death using a brief writing task, followed by a self-report affect schedule to assess potential effects of TMS on conscious emotion. Next, participants were asked to read essays (one critical of the USA, one complimentary) ostensibly written by immigrants to the USA, then evaluate the authors’ personalities and attitudes, a dependent measure frequently used to assess ethnocentrism. Given that the pMFC reacts to aversive cues, including social disagreement (Klucharev et al., 2009) and rejection (Eisenberger, 2012), sharp criticism of participants’ national in-group appears likely to elicit a pMFC conflict response reaction, in addition to that elicited by the prior reminder of death. We therefore predicted that TMS of the pMFC would particularly increase the favorability of ratings of the critical immigrant (as the complimentary immigrant poses no evident

1 Following others (Binder et al., 2005; Jost and Amodio, 2012; Jonas et al., 2014), we use the terms concrete and abstract in the straightforward sense of poles defining a spectrum from the immediately physical (e.g. hand movements in a motor task) to the intangibly conceptual (e.g. shifting one’s views on social welfare policies to accord with a newly adopted moral schema).

challenge aside from out-group status). Religious belief was then measured using two self-report scales targeting parallel 'negative' beliefs in the Devil, demons and Hell, and 'positive' beliefs in God, angels and Heaven, respectively. We predicted that the TMS manipulation would particularly decrease the endorsement of positive religious beliefs (as the negative beliefs do not offer as appealing an alternative to non-existence following death). Thus, both ethnocentrism and religiosity were assessed using matched positive and negative affective targets, enabling an assessment of whether effects of TMS might be explained by a simple positivity or negativity bias.

Methods

Participants

Undergraduates were recruited for a study, ostensibly consisting of a series of unrelated measures, in exchange for \$25. Participants were pre-screened by telephone for history of neurological disorders and other contraindications to TMS, as well as for political orientation, ethnicity and US citizenship. As has been done in similar ways in prior studies employing this measure of intergroup bias (McGregor et al., 1998; Greenberg et al., 2001; Navarrete et al., 2004; Holbrook et al., 2011), to ensure that participants would respond aversively to a Latino immigrant's criticisms of the USA, those who identified as 'extremely liberal' or as non-US citizens were excluded from participating, and four individuals who self-identified as 'Hispanic/Latino' after participating were dropped prior to analysis.² The final sample consisted of 38 participants (58% female, $M_{\text{age}} = 20.9$ years, $s.d. = 2.67$). About 36.8% of the participants identified as White, 36.8% as East Asian, 13.2% as South Asian, 7.9% as Middle Eastern and 5.3% as Other. As intended, the sample was politically moderate ($M = 4.68$, $s.d. = 1.51$; 1 = 'Extremely Liberal'; 5 = 'Moderate'; 9 = 'Extremely Conservative').

The Magstim Rapid 2 device used for this experiment can only perform the TMS protocol adopted here at up to 44% of the equipment's maximum stimulator output. Four participants, however, had high active motor thresholds that would have exceeded this limit, and hence these four participants were assigned to the sham group. All other participants were randomly assigned to the TMS condition (19 participants) or the sham control condition (19 participants). The sample size was based on Klucharev et al.'s (2011) demonstration of the effects of TMS of the pMFC on a social judgment. The study was approved by the University of California, Los Angeles, Institutional Review Board, and written informed consent was obtained from all participants.

² Follow-up analyses were later conducted including these four excluded individuals. Consistent with the theoretically grounded methodological concerns regarding the inclusion of self-identified Hispanic/Latino participants in a study assessing ideological responses to Latino immigrant targets intended to be regarded as out-group members, the effect of TMS on ratings of the anti-US immigrant author was no longer significant [sham: $M = 3.11$, $s.d. = 1.34$; TMS: $M = 3.94$, $s.d. = 1.64$; $F(1, 39) = 3.67$, $P = 0.063$, $\eta_p^2 = 0.09$, 95% CI -1.71 to 0.05]. The effect of the TMS manipulation on ratings of the pro-US author also remained non-significant [sham: $M = 5.44$, $s.d. = 1.35$; TMS: $M = 5.98$, $s.d. = 0.87$; $F(1, 39) = 3.03$, $P = 0.09$, $\eta_p^2 = .07$, 95% CI -1.18 to 0.09]. The effect of the TMS manipulation on religiosity was unchanged. Avowed conviction in positive religious beliefs remained significantly lower in the TMS condition [sham: $M = 4.68$, $s.d. = 2.21$; TMS: $M = 3.29$, $s.d. = 1.96$; $F(1, 39) = 4.67$, $P = 0.037$, $\eta_p^2 = 0.11$, 95% CI 0.09 – 2.71], with no effect on negative religious beliefs [sham: $M = 3.91$, $s.d. = 2.38$; TMS: $M = 2.92$, $s.d. = 1.89$; $F(1, 39) = 2.18$, $P = 0.147$, $\eta_p^2 = 0.05$, 95% CI -0.36 to 2.33].

TMS manipulation

We stimulated the right pMFC: rostral cingulate zone, Brodmann areas 24, 32, 6 and 9; center of mass at MNI coordinates (x, y, z) [8, 16, 52] mm (Klucharev et al., 2011). At the beginning of the experiment, we localized the motor cortex using single pulse TMS. As the tibia representation and the pMFC are located at the same depth within the medial cortex, the pMFC location was ascertained by moving the coil anteriorly to the motor cortex. The distance of the pMFC from the motor cortex was calculated for each participant according to the size of their head, using the international 10–20 system (Klem et al., 1999), as has been done in prior TMS studies (Knoch et al., 2009; Klucharev et al., 2011). During stimulation, the TMS coil was placed at an average distance of 3.75 cm to the motor cortex. We used continuous theta-burst stimulation, in which 600 pulses were applied in bursts of three pulses at 50 Hz, repeated at 5 Hz for a total of 40 s (see the Supplementary Online Materials for details). This technique has been demonstrated to reduce neural activity for at least 1 h (Huang et al., 2005). Participants in the TMS condition were stimulated at 80% of their active motor thresholds; those in the sham condition were stimulated at 10% of their active motor thresholds. Following actual or sham stimulation, participants performed the experimental tasks at a computer station in the same room. The entire protocol, following TMS or sham stimulation, required ~40 min.

Measures

Motor and visual distracter tasks. Immediately following stimulation, participants completed filler motor and visual estimation tasks to ensure that downregulation of the pMFC took effect (Huang et al., 2005) and to defray suspicion about the target hypothesis regarding ideological affirmation (see the Supplementary Online Materials for details).

Reminder of death. Next, participants were asked to write brief responses on the subject of their own death, a threat induction that was selected because of the evident link between the prospect of death and palliative thoughts of God and the afterlife (Rosenblatt et al., 1989; see the Supplementary Online Materials).

Self-reported affect. Following the death writing task, participants completed the Positive and Negative Affect Schedule—Expanded Form (PANAS-X; D. Watson and L.A. Clark, unpublished data; see the Supplementary Online Materials).

Group prejudice. Participants were next asked to read two essays (presented in counterbalanced order) that were ostensibly written by immigrants to the United States from Latin America (see the Supplementary Online Materials). The text for these essays was taken directly from previous research in which being reminded of death intensified ethnocentric bias as measured by evaluations of the immigrant authors (Greenberg et al., 1994). After reading each essay, participants rated their agreement with six statements using an 8-point Likert scale (1 = 'Strongly Disagree'; 8 = 'Strongly Agree'): (i) 'I like the person who wrote this', (ii) 'I think this person is intelligent', (iii) 'This is the kind of person I would like to work with', (iv) 'I think this person is honest', (v) 'I agree with this person's views' and (vi) 'I think this person's opinions of America are true' (complimentary essay: $\alpha = 0.79$; critical essay: $\alpha = 0.92$).

Religious belief. Next, religious belief was measured using a version of the Supernatural Belief Scale (Jong et al., 2013) modified

to create two scales which mirror positive and negative aspects of Western religious belief, comparable with the positive and negative immigrant authors in the ethnocentrism measure. The items were presented in random order and rated according to the same scale employed in the immigrant ratings. The positive scale consisted of the following: (i) 'There exists an all-powerful, all-knowing, loving God'; (ii) 'There exist good personal spiritual beings, whom we might call angels' and (iii) 'Some people will go to Heaven when they die' ($\alpha = 0.90$). The negative scale consisted of the following: (i) 'There exists an evil personal spiritual being, whom we might call the Devil'; (ii) 'There exist evil, personal spiritual beings, whom we might call demons' and (iii) 'Some people will go to Hell when they die' ($\alpha = 0.93$). An overall religiosity variable combining both scales was calculated by averaging all six items ($\alpha = 0.95$).

Results

Self-reported affect

A Multivariate analysis of variance (MANOVA) revealed no significant effects of condition on any of the subscales comprising the PANAS-X ($P_s = 0.09\text{--}0.92$) (see Supplementary Online Material Table 1 for detailed results). Participants in both conditions reported feeling relatively low levels of negative affect (TMS: $M = 1.22$, $s.d. = 0.27$; Sham: $M = 1.43$, $s.d. = 0.51$) or fear (TMS: $M = 1.32$, $s.d. = 0.38$; Sham: $M = 1.52$, $s.d. = 0.57$). Likewise, the participants reported feelings of moderately positive affect (TMS: $M = 2.44$, $s.d. = 0.61$; Sham: $M = 2.37$, $s.d. = 0.75$). This pattern indicates that participants experienced low levels of conscious anxiety despite having been recently reminded of death.

Group prejudice

Preliminary tests detected a significant effect of the order of essay presentation on ratings of the 'anti-US' immigrant [presented first: $M = 2.94$, $s.d. = 1.46$; presented second: $M = 4.03$, $s.d. = 1.47$; $F(1, 36) = 5.30$, $P = 0.027$, $\eta_p^2 = 0.13$, 95% confidence interval (CI) -2.07 to -0.13], with no order effect observed for ratings of the 'pro-US' immigrant ($P = 0.74$). Essay order was therefore controlled for in subsequent analyses of the effects of condition on ratings of the immigrant who was critical of the United States. As predicted, participants in the TMS condition rated the critical immigrant 28.5% more positively ($M = 4.10$, $s.d. = 1.66$) than did participants in the sham condition [$M = 2.93$, $s.d. = 1.22$; $F(1, 35) = 7.01$, $P = 0.012$, $\eta_p^2 = 0.17$, 95% CI -2.06 to -0.27]. In contrast, overall ratings of the laudatory, pro-US immigrant were an average of 8.2% higher ($M = 5.90$, $s.d. = 0.87$) in the TMS condition than in the sham condition ($M = 5.42$, $s.d. = 1.17$), and this difference did not attain statistical significance [$F(1, 36) = 2.09$, $P = 0.157$, $\eta_p^2 = 0.06$, 95% CI -1.16 to 0.20] (Figure 1). Follow-up tests confirmed that there was no interaction between condition and order of presentation on the ratings of either essay ($P_s > 0.17$) and that controlling for essay order does not alter the significance or approximate magnitude of the effects of condition.

Religious belief

We next tested the effects of TMS on endorsement of religious beliefs following a reminder of death. In a marginal trend, overall avowed religious belief (including both positive and negative beliefs) was reduced in the TMS condition ($M = 2.95$, $s.d. = 1.85$) relative to the sham condition [$M = 4.26$, $s.d. = 2.32$; $F(1, 36) = 3.74$, $P = 0.061$, $\eta_p^2 = 0.09$, 95% CI -0.06 to 2.70]. As predicted,

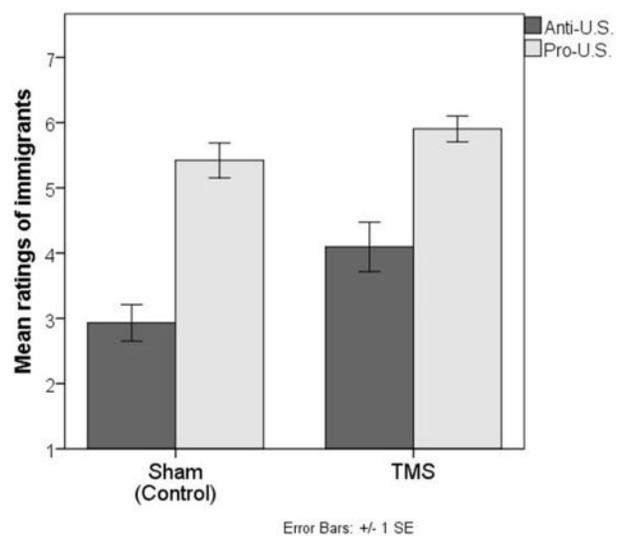


Fig. 1. Effects of TMS on US citizens' ratings of pro-US and anti-US immigrants.

this shift was driven by a significant reduction in expressed belief in positive religious ideas. Participants in the TMS condition reported an average of 32.8% less conviction in positive religious beliefs ($M = 3.05$, $s.d. = 1.92$) than did sham participants [$M = 4.54$, $s.d. = 2.26$; $F(1, 36) = 4.80$, $P = 0.035$, $\eta_p^2 = 0.12$, 95% CI 0.11 to 2.87]. Participants in the TMS condition also reported less conviction in negative religious beliefs ($M = 2.84$, $s.d. = 1.89$) relative to sham participants ($M = 3.98$, $s.d. = 2.50$), but this difference was not statistically significant [$F(1, 36) = 2.52$, $P = .122$, $\eta_p^2 = 0.07$, 95% CI -0.32 to 2.60] (Figure 2).

Discussion

Downregulating the pmFC via TMS significantly decreased both derogation of an anti-US out-group member and avowed belief in God, angels and Heaven following a reminder of death, supporting the hypothesis that the pmFC plays an important role in ideological responses to threat. These neuromodulated shifts in expressions of group bias and religious belief cannot be taken as indiscriminate positive or negative bias, as ratings of an out-group member expressing strikingly negative views increased, yet ratings of traditionally positive religious beliefs (e.g. belief in a benevolent God) decreased. Rather, the pmFC seems to mediate changes in abstract beliefs to address contextually shifting problems, such that, for example, reminders of the inevitability of death bolster beliefs in God and Heaven. However, this study did not include problem-irrelevant modes of ideological endorsement, leaving open the possibility that, consistent with the RAM model, participants in the sham condition would have expressed more exaggerated ideological responses that were incidental to the problems of death or scathing criticism of one's group values.

Given the prior evidence that downregulation of the pmFC decreases social conformity (Klucharev et al., 2011), the diminished expressions of group prejudice and religious belief observed here may stem from a mechanism sensitive to affirming consensus attitudes, insofar as out-group derogation and belief in God are considered normative (Navarrete et al., 2004). However, although some of our results are consistent with this interpretation, a narrow social conformity account would not clearly explain the lack of significant shifts in ratings of the

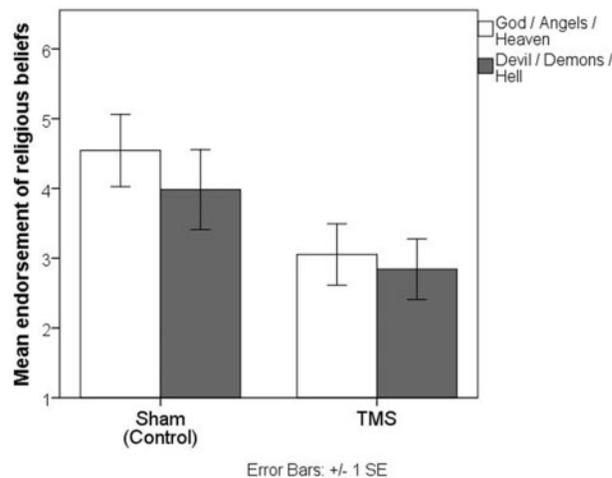


Fig. 2. Effects of TMS on endorsement of positive vs negative religious beliefs.

pro-US immigrant or of negative religious beliefs. Instead, the results are more consistent with a portrait of the pMFC as detecting poignant conflicts (including ideological conflicts), and recruiting responses relevant to addressing those conflicts (including ideological representations). According to this approach, the pro-US immigrant posed no ideological conflict and hence did not elicit a significantly enhanced affirmation of group values, whereas the problem of death is not as effectively ameliorated by negative religious beliefs (i.e. relative to Heaven, continued existence in Hell presents a poor alternative to annihilation), and hence negative religious beliefs were not bolstered following reminders of mortality to the extent that positive beliefs were.

Future directions

This study provides a 'proof-of-concept' that adherence to high-level abstract beliefs can be experimentally neuromodulated. However, the present design does not address several key questions that should be pursued in further research. Most notably, in order to create a context in which ideological adherence could be expected to be relatively intense, particularly with regard to religious ideas, we reminded all of our participants of death. Our data therefore do not reveal whether downregulation of the pMFC via TMS would reduce either group bias or religious belief in the absence of a recent threat prime. Relatedly, we have conceptualized the present design as involving two sorts of problems (i.e. mortality and criticism of group values) that may each be addressed by custom-tailored solutions (i.e. religiosity, and derogation of the critical out-group member, respectively). This framing is consistent with the finding that TMS influenced evaluation of the critical author, but not the complimentary author. However, death primes have been found to exaggerate derogation of individuals who criticize in-group values in numerous studies, such that encountering an attack on group values in the aftermath of a reminder of death may constitute a double-shot threat. Thus, the reduction in out-group derogation observed in the TMS condition may reflect a diminution in the impact of the death prime rather than—or in addition to—a diminution in the response to the challenge posed by the out-group critic. Future research incorporating a non-threat control condition will be essential to ascertain whether downregulation of the pMFC reduces out-group derogation, or avowed religious belief, in the absence of a background threat.

The present design is also limited inasmuch as it focuses on the threat posed by death, whereas a diverse array of threats have been shown to exacerbate various forms of ideological adherence (Jonas et al., 2014; Holbrook, 2016). Future research should assess the relative fit vs interchangeability of threats and subsequent expressions of forms of ideological investment. For instance, a special relationship likely obtains between the problem of death and the apparent solution afforded by Western concepts of the afterlife (Holbrook and Sousa, 2013), such that reminders of death exert unique effects on the role of the pMFC in adherence to religious beliefs in comparison with threats that are unrelated to the desirability of a pleasant afterlife. Accordingly, more investigation is needed to assess the effects of the neuromodulation of the pMFC on ideological investment following both alternate threats and alternate forms of ideology (e.g. related to environmentalism or human rights). Future research is also required to address the potential role of individual differences in political orientation, personality, emotion and other potentially relevant dimensions in moderating the relationship between the pMFC and ideological investment.

Ideological responses are abstract in that they invoke ideas regarding intangibles such as group values or religious convictions rather than the concretely physical. This distinction between 'abstract' and 'concrete' should not be conflated with the distinction employed in Construal Level Theory research on abstract (i.e. broad, superordinate, decontextualized) vs concrete (i.e. specific, subordinate, contextualized) modes of representation with which one may construe the same stimulus (Liberman and Trope, 2008). Note, for example, that participants might conceptualize the ideologically relevant stimuli utilized in our study (e.g. God, or the out-group critic) at varying levels of hazy generality or vivid detail. However, although these senses of abstractness are conceptually distinct, there are grounds to speculate that ideological responses—particularly those related to group bias—sometimes involve shifts toward a more superordinate, schematic mode of categorization (Fiske and Neuberg, 1990). For example, manipulating participants to engage a superordinate mode of categorization via unrelated tasks has been reported to increase stereotype-based attributions of qualities both to other people and to the self (McCrea et al., 2012). It is therefore possible that downregulating the pMFC in this study increased ratings of the critical out-group author in part because participants placed into a less ideological mindset conceptualized the target as a unique individual rather than as a homogeneous out-group member invested with negative stereotypical traits. Future research might explore whether pMFC increases use of group stereotypes and related superordinate modes of categorization in contexts of threat, and, if so, whether this shift toward abstraction mediates some ideological responses.

Interestingly, the pMFC appears to marshal ideological shifts in the absence of increased conscious anxiety. We observed no significant differences between the TMS and sham conditions in any of the 13 subscales comprising our self-report affect measure, and the participants reported feeling low levels of negative affect and moderate levels of positive affect. This pattern of apparent sanguinity despite being reminded of death is consistent with prior research showing that implicit, but not explicit, anxiety increases following the death writing task used here (for a review, see Jonas et al., 2014). Accordingly, our TMS manipulation may have reduced ideological responses by (i) reducing the extent to which the threatening stimuli were cognitively categorized as threats, (ii) reducing the implicit anxiety typically associated with the detection of threats, (iii) reducing

the capacity to coordinate enhanced ideological adherence following threat-detection or (iv) some combination of the above. Follow-up investigations might employ measures targeting implicit anxiety to clarify which of the above possibilities applies.

We utilized a sham control (TMS at 10% of the maximum stimulator output) rather than equivalently intense TMS of a neural control region. Although we acknowledge that follow-up research should include tests of neural control regions, it does not appear likely that TMS of any brain region would equivalently neuromodulate ideological cognition. In addition to the considerable evidence for a special relationship between ideological reactions and pmFC, Klucharev *et al.* (2011) observed comparable judgment shifts in both sham TMS and control TMS (of the medial parietal cortex) relative to TMS of the same pmFC area manipulated here. In addition, because the present design did not include an active TMS control condition, we cannot rule out the possibility that the experience of TMS in general is responsible for the observed effects. For example, TMS is associated with mild discomfort, whereas sham TMS is not, and this difference in experience might account for our findings. However, for multiple reasons, we think this unlikely. First, the equivalence of self-reported affective states between conditions makes it unlikely that the observed effects owe to differences in the subjective experience of receiving TMS vs sham TMS. Second, religious belief has a demonstrable analgesic effect (Wiech *et al.*, 2008), hence we might expect that any physical discomfort associated with TMS would enhance, rather than diminish, endorsement of positive religious ideas. Nonetheless, future designs incorporating TMS of neural control areas could importantly confirm the unique contribution of the pmFC and experimentally circumscribe the precise component(s) of the pmFC complex that direct ideological responses to threat. Neuroimaging would also be particularly valuable in clarifying the effect of the TMS manipulation used here on the subregions of the pmFC, as, at present, it is unclear whether the effects that we obtained are due to downregulation of the dmPFC, downregulation of the underlying dACC or downregulation of both.

Crucially, the brain areas mediating shifts in ideological adherence should not be construed as modularly confined to the pmFC, as TMS may be expected to affect regions that are interconnected with the target region (Driver *et al.*, 2009), and as the pmFC is itself a large complex directing diverse aspects of cognition and behavior (Ridderinkhof *et al.*, 2004; Amodio and Frith, 2006). Perhaps the greatest challenge for future research will be mapping the precise neural mechanisms that undergird threat-related uptakes in ideological modes of processing.

Conclusion

History teaches that investment in cherished group and religious values can bring forth acts of both heroic valor and horrific injustice. Understanding the psychological and biological determinants of increases in ideological commitment may ultimately help us to identify the situational triggers of, and individuals most susceptible to, this phenomenon, and thereby gain some leverage over the zealous acts that follow. The present findings suggest that the pmFC integrates processing distributed across interconnected brain regions to augment adherence to high-level ideals upon detection of relevant conflicts (e.g. criticisms of group values trigger strengthening of investment in group values; reminders of death motivate enhanced belief in a pleasant afterlife). The results provide evidence that relatively abstract personal and social attitudes are susceptible to targeted

neuromodulation, opening the way for researchers to not only describe the biological mechanisms undergirding high-level attitudes and beliefs, but also to establish causality via experimental intervention. Finally, these findings illustrate the economical manner with which the brain utilizes common conflict resolution mechanisms to achieve shifts in both concrete behavior and adherence to abstract beliefs.

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Supplementary data

Supplementary data are available at SCAN online.

References

- Amodio, D.M., Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*, 268–77.
- Binder, J.R., Westbury, C.F., McKiernan, K.A., Possing, E.T., Medler, D.A. (2005). Distinct brain systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience*, *17*, 905–17.
- Bush, G., Vogt, B.A., Holmes, J., *et al.* (2002). Dorsal anterior cingulate cortex: a role in reward-based decision making. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 523–8.
- Driver, J., Blankenburg, F., Bestmann, S., Vanduffel, W., Ruff, C.C. (2009). Concurrent brain-stimulation and neuroimaging for studies of cognition. *Trends in Cognitive Sciences*, *13*, 319–27.
- Eisenberger, N.I. (2012) Broken hearts and broken bones: a neural perspective on the similarities between social and physical pain. *Current Directions in Psychological Science*, *21*, 42–7.
- Etkin, A., Egner, T., Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Science*, *15*, 85–93.
- Fiske, S.T., Neuberg, S.L. (1990). A continuum model of impression formation: from category-based to individuating processes as a function of information, motivation, and attention. In: Zanna, M.P., editor. *Advances in Experimental Social Psychology*, Vol. 23, New York: Academic Press, 1–74.
- Greenberg, J., Arndt, J., Schimel, J., Pyszczynski, T., Solomon, S. (2001). Clarifying the function of mortality-salience induced worldview defense: renewed suppression or reduced accessibility of death-related thoughts? *Journal of Experimental Social Psychology*, *37*, 70–6.

- Greenberg, J., Pyszczynski, T., Solomon, S., Simon, L., Breus, M. (1994). Role of consciousness and accessibility of death-related thoughts in mortality salience effects. *Journal of Personality and Social Psychology*, *67*, 627–37.
- Han, S., Qin, J., Ma, Y. (2010). Neurocognitive processes of linguistic cues related to death. *Neuropsychologia*, *48*, 3436–42.
- Harmon-Jones, E. (2004). Contributions from research on anger and cognitive dissonance to understanding the motivational functions of asymmetrical frontal brain activity. *Biological Psychology*, *67*(1–2), 51–76.
- Heine, S.J., Proulx, T., Vohs, K.D. (2006). The meaning maintenance model: on the coherence of social motivations. *Personality and Social Psychology Review*, *10*, 88–110.
- Holbrook, C. (2016). Branches of a twisting tree: domain-specific threat psychologies derive from shared mechanisms. *Current Opinion in Psychology*, *7*, 81–6.
- Holbrook, C., Fessler, D.M.T. (2015). The same, only different: threat management systems as homologues in the tree of life. In: Carroll, P.J. Arkin, R.M., Wichman, A.L., editors. *Handbook of Personal Security*, New York: Psychology Press.
- Holbrook, C., Sousa, P. (2013). Supernatural beliefs, unconscious threat, and judgment bias in Tibetan Buddhists. *Journal of Cognition and Culture*, *13*, 33–56.
- Holbrook, C., Sousa, P., Hahn-Holbrook, J. (2011). Unconscious vigilance: worldview defense without adaptations for terror, coalition or uncertainty management. *Journal of Personality and Social Psychology*, *101*, 451–66.
- Huang, Y.Z., Edwards, M.J., Rounis, E., Bhatia, K.P., Rothwell, J.C. (2005). Theta burst stimulation of the human motor cortex. *Neuron*, *45*, 201–6.
- Inzlicht, M., Tullett, A.M. (2010) Reflecting on God: religious primes can reduce neurophysiological response to errors. *Psychological Science*, *21*, 1184–90.
- Inzlicht, M., McGregor, I., Hirsh, J.B., Nash, K. (2009). Neural markers of religious conviction. *Psychological Science*, *20*, 385–92.
- Izuma, K. (2013). The neural basis of social influence and attitude change. *Current Opinion in Neurobiology*, *23*, 456–62.
- Izuma, K., Adolphs, R. (2013). Social manipulation of preference in the human brain. *Neuron*, *78*, 563–73.
- Izuma, K., Akula, S., Murayama, K., Wu, D.A., Iacoboni, M., Adolphs, R. (2015). A causal role for posterior medial frontal cortex in choice-induced preference change. *The Journal of Neuroscience*, *35*, 3598–606.
- Izuma, K., Matsumoto, M., Murayama, K., Samejima, K., Sadato, N., Matsumoto, K. (2010). Neural correlates of cognitive dissonance and choice-induced preference change. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 22014–9.
- Jonas, E., McGregor, I., Klackl, J., et al. (2014). Threat and defense: from anxiety to approach. In: Olson, J.M., Zanna, M.P., editors. *Advances in Experimental Social Psychology*, San Diego, CA: Academic Press, 219–86.
- Jong, J., Halberstadt, J., Bluemke, M. (2013). Foxhole atheism, revisited: the effects of mortality salience on explicit and implicit religious belief. *Journal of Experimental Social Psychology*, *48*, 983–9.
- Jost, J.T., Amodio, D.M. (2012). Political ideology as motivated social cognition: behavioral and neuroscientific evidence. *Motivation and Emotion*, *36*, 55–64.
- Klackl, J., Jonas, E., Kronbichler, M. (2014) Existential neuroscience: self-esteem moderates neuronal responses to mortality-related stimuli. *Social Cognitive and Affective Neuroscience*, *9*, 1754–61.
- Klem, G.H., Luders, H.O., Jasper, H.H., Elger, C. (1999). The twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology Supplement*, *52*, 3–6.
- Klucharev, V., Hytonen, K., Rijpkema, M., Smidts, A., Fernandez, G. (2009). Reinforcement learning signal predicts social conformity. *Neuron*, *61*, 140–51.
- Klucharev, V., Munneke, M.A., Smidts, A., Fernández, G. (2011). Downregulation of the posterior medial frontal cortex prevents social conformity. *Journal of Neuroscience*, *31*, 11934–40.
- Knoch, D., Schneider, F., Schunk, D., Hohmann, M., Fehr, E. (2009). Disrupting the prefrontal cortex diminishes the human ability to build a good reputation. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 20895–9.
- Lieberman, N., Trope, Y. (2008). The psychology of transcending the here and now. *Science*, *322*, 1201–5.
- Luo, S., Shi, Z., Yang, X., Wang, X., Han, S. (2014). Reminders of mortality decrease midcingulate activity in response to others' suffering. *Social Cognitive and Affective Neuroscience*, *9*, 477–86.
- Maier, S., Szalkowski, A., Kamphausen, S., et al. (2012). Clarifying the role of the rostral dmPFC/dACC in fear/anxiety: learning, appraisal or expression? *PLOS One*, *7*, e50120.
- McCrea, S.M., Wieber, F., Myers, A.L. (2012). Construal level mind-sets moderate self- and social stereotyping. *Journal of Personality and Social Psychology*, *102*, 51–68.
- McGregor, H., Lieberman, J.D., Solomon, S., et al. (1998). Terror management and aggression: evidence that mortality salience motivates aggression against worldview threatening others. *Journal of Personality and Social Psychology*, *74*, 590–605.
- McGregor, I., Prentice, M., Nash, K. (2013). Anxious uncertainty and reactive approach motivation (RAM) for religious, idealistic, and lifestyle extremes. *Journal of Social Issues*, *69*, 537–63.
- Nash, K., McGregor, I., Prentice, M. (2011). Threat and defense as goal regulation: from implicit goal conflict to anxious uncertainty, reactive approach motivation, and ideological extremism. *Journal of Personality and Social Psychology*, *101*, 1291–301.
- Navarrete, C.D., Kurzban, R., Fessler, D.M.T., Kirkpatrick, L. (2004). Anxiety and intergroup bias: terror-management or coalitional psychology? *Group Processes & Intergroup Relations*, *7*, 370–97.
- Proulx, T., Inzlicht, M., Harmon-Jones, E. (2012). Understanding all inconsistency compensation as a palliative response to violated expectations. *Trends in Cognitive Sciences*, *16*, 285–91.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, *306*, 443–7.
- Rosenblatt, A., Greenberg, J., Solomon, S., Pyszczynski, T., Lyon, D. (1989). Evidence for terror management theory: I. The effects of mortality salience on reactions to those who violate or uphold cultural values. *Journal of Personality and Social Psychology*, *57*, 681–90.
- Rushworth, M.F., Buckley, M.J., Behrens, T.J., Walton, M.E., Bannerman, D.M. (2007). Functional organization of the medial frontal cortex. *Current Opinion in Neurobiology*, *17*, 220–7.
- Rushworth, M.F., Walton, M.E., Kennerley, S.W., Bannerman, D.M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, *8*, 410–7.
- Shi, Z., Han, S. (2013). Transient and sustained neural responses to death-related linguistic cues. *Social Cognitive and Affective Neuroscience*, *8*, 573–8.

- Shima, K., Tanji, J. (1998). Role for cingulate motor area cells in voluntary movement selection based on reward. *Science*, **282**, 1335–8.
- Tritt, S.M., Inzlicht, M., Harmon-Jones, E. (2012). Toward a biological understanding of mortality salience (and other threat compensation processes). *Social Cognition*, **6**, 715–33.
- Ullsperger, M., Volz, K.G., Cramon, D.Y. (2004). A common neural system signaling the need for behavioral changes. *Trends in Cognitive Sciences*, **8**, 445–6.
- Urry, H.L., Nitschke, J.B., Dolski, I., et al. (2004). Making a life worth living: neural correlates of well-being. *Psychological Science*, **15**, 367–72.
- van Veen, V., Krug, M.K., Schooler, J.W., Carter, C.S. (2009). Neural activity predicts attitude change in cognitive dissonance. *Nature Neuroscience*, **12**, 1469–74.
- Wiech, K., Farias, M., Kahane, G., Shackel, N., Tiede, W., Tracey, I. (2008). An fMRI study measuring analgesia enhanced by religion as a belief system. *Pain*, **139**, 467–76.