

Cognitive and neural foundations of religious belief

Dimitrios Kapogiannis^{a,b}, Aron K. Barbey^{a,c}, Michael Su^a, Giovanna Zamboni^a, Frank Krueger^a, and Jordan Grafman^{a,1}

^aNational Institute of Neurological Disorders and Stroke/National Institutes of Health, MSC 1440, 10 Center Drive, MSC 1440, Bethesda, MD 20892-1440;

^bNational Institute on Aging/National Institutes of Health, 3001 South Hanover Avenue, Baltimore, MD 21225; and ^cDepartment of Psychology, Georgetown University, White-Gravenor Hall 306, 37th and O Street NW, Washington, D.C. 20057

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We propose an integrative cognitive neuroscience framework for understanding the cognitive and neural foundations of religious belief. Our analysis reveals 3 psychological dimensions of religious belief (God's perceived level of involvement, God's perceived emotion, and doctrinal/experiential religious knowledge), which functional MRI localizes within networks processing Theory of Mind regarding intent and emotion, abstract semantics, and imagery. Our results are unique in demonstrating that specific components of religious belief are mediated by well-known brain networks, and support contemporary psychological theories that ground religious belief within evolutionary adaptive cognitive functions.

Religious belief and behavior are a hallmark of human life, with no accepted animal equivalent, and found in all cultures (1). The biological basis of religion, though, is fiercely debated in fields as diverse as evolutionary psychology, anthropology, genetics, and cosmology. Contemporary psychological theories consider religious belief and behavior as complex brain-based phenomena that may have co-emerged in our species with novel cognitive processes for social cognition, such as Theory of Mind (ToM), and successfully engaged fundamental cognitive mechanisms, such as memory (2–4).

Remarkably little is currently known about the neural foundations of religiosity. Cognitive neuroscience studies have so far focused on the neural correlates of unusual and extraordinary religious experiences (5, 6), whereas clinical studies have focused on pathological religious manifestations. Hyperreligiosity in patients with temporal-lobe epilepsy motivated early theories linking religiosity with limbic and temporal areas (7, 8), executive aspects and prosocial roles of religion (9) shifted the focus to the frontal lobes (10), while decreased parietal lobe activity was linked to mystical religious experiences (5). Overall, these findings show a low degree of correspondence and no relationship to any proposed psychological architecture underlying religious belief.

The aim and motivation of our research was to define the psychological structure of religious belief, based on fundamental cognitive processes, and to reveal the corresponding pattern of brain activation to determine the relevance of evolutionary theories of cognitive development to the development of religious beliefs. To this end, it was necessary to model the complexity of religious belief.

Factor analytic studies have demonstrated that an underlying psychological structure can be described for religious belief and have established the perceptions of God's level of involvement and God's level of anger as key organizing components (11). Processing these components presupposes intent-related and emotional ToM being applied to supernatural agents, a fact that links fundamental aspects of social cognition to religious belief. Besides these components, any belief system relies on a body of semantic and event knowledge. One source of semantic knowledge for religious belief is doctrine, a body of concepts regarding supernatural agents and entities, which believers accept as real despite not being verified by personal experience. Aspects of doctrine may be rooted in intuitive world-theory creation inherent in all humans, such as belief in the existence of nonmaterial agents (1), but for the most part doctrine has abstract linguistic content, is specific to the various institutionalized religions, and is culturally transmitted (3). Another source of religious knowledge is event knowledge stemming from personal

experiences explicitly religious (such as prayer or participation in ritual), but also from multiple social and moral events influenced by religion (3). In this view, religious knowledge forms a continuum from doctrinal to experiential, and most beliefs draw from both sources. Moreover, adoption and implementation of religious beliefs is influenced by emotions and goals. For example, a set of doctrinal beliefs about the soul may lead through logical reasoning to a moral rule regarding euthanasia, but an applied moral stance would also draw from experience and take the particular circumstances and their emotional significance into account.

Based on the above psychological structure, we hypothesized that religious belief relates to specific patterns of brain activation. First, we hypothesized that the 2 previously identified components (God's involvement and God's anger) (11) engage ToM-related prefrontal and posterior regions. Second, we hypothesized that the proposed continuum of religious knowledge differentially engages associative processes: doctrinal knowledge engages networks processing abstract semantics (3), whereas experiential knowledge engages networks involved in memory retrieval and imagery (3). Third, we predicted that adoption of religious belief engages networks providing cognitive-emotional interface.

We conducted a multidimensional scaling (MDS) study to determine the psychological components underlying religious belief (Experiment 1) and evaluated their neural foundations by employing a parallel functional neuroimaging study (Experiment 2).

Experiment 1 (Multidimensional Scaling). MDS is a data-reduction technique (conceptually similar to factor analysis) which, for data structures featuring statistical regularities, is able to define a multidimensional space where each data point is represented by a set of coordinates (12, 13). Interpretation of this multidimensional space can be aided by linearly restricting output dimensions to external variables. MDS has been extensively used in cognitive psychology to uncover psychological processes underlying behavioral measures (12). MDS was also successfully used in defining the psychological structure of social-event knowledge, which was then studied with functional neuroimaging (14). In the current study, we applied MDS to ratings of conceptual dissimilarity for pairs of statements regarding religious beliefs, using several variables as linear restrictors of the output dimensions. We recruited 26 subjects with varying degrees of self-reported religiosity to perform the ratings.

MDS Results. The accepted MDS solution was the only 3-dimensional solution with an acceptable stress level (0.0857), in which each output dimension correlated strongly and uniquely with each one of 3 linear restrictors. Moreover, the linear restrictors producing this solution (God's perceived level of involvement, God's perceived emotion, and religious knowledge

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¹To whom correspondence should be addressed. E-mail: grafmanj@ninds.nih.gov.

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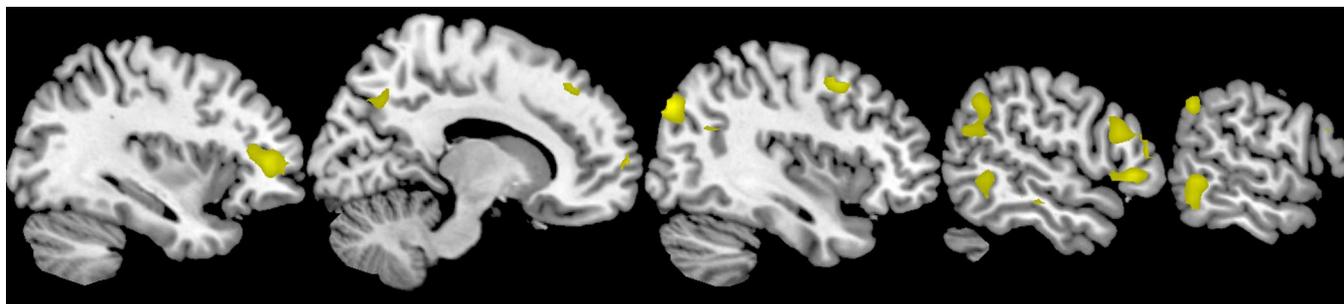


Fig. 1. Effect of God's lack of involvement (D1). Threshold was set to $P < 0.05$, false discovery rate (FDR) corrected. Slices are oriented from L to R. Activations are shown in yellow.

source) had good a priori justification (12, 13) to characterize the psychological processes underlying religious belief.

Dimension 1 (D1) correlated negatively with God's perceived level of involvement (-0.994), Dimension 2 (D2) correlated negatively with God's perceived anger (-0.953) and positively with God's perceived love (0.953), and Dimension 3 (D3) correlated positively with doctrinal (0.993) and negatively with experiential (-0.993) religious content. D1 represents a quantitative gradient of a single concept and we will be referring to it as "God's perceived level of involvement." D2 and D3 represent gradients of contrasting concepts; we will be referring to them as "God's perceived emotion" (D2) and "religious knowledge source" (D3). The MDS solution and analyses regarding the external variables are available as Fig. S1.

God's perceived level of involvement (D1) organizes statements so that "God is removed from the world" or "Life has no higher purpose" have high positive coordinate values, while "God's will guides my acts," "God protects one's life," or "God is punishing" have high negative values. Generally speaking, on the positive end of the gradient lie statements implying the existence of uninvolved supernatural agents, and on the negative end lie statements implying involved supernatural agents.

God's perceived emotion (D2) ranges from love to anger and organizes statements so that "God is forgiving" and "God protects all people" have high positive-coordinate values, while "God is wrathful" and "The afterlife will be punishing" have high negative values. Generally speaking, on the positive end of the gradient lie statements implying the existence of a loving (and potentially rewarding) supernatural agent, and on the negative end lie statements suggestive of a wrathful (and potentially punishing) supernatural agent.

Religious knowledge (D3) ranges from doctrinal to experiential and organizes statements so that "God is ever-present" and "A source of creation exists" have high positive-coordinate values,

while "Religion is directly involved in worldly affairs" and "Religion provides moral guiding" have high negative values. Generally speaking, on the positive end of the gradient lies theological content referring to abstract religious concepts, and on the negative end lies theological content with moral, social, or practical implications.

Experiment 2 (Functional MRI). In Experiment 2, we used event-related functional MRI (fMRI) to reveal brain activity, while 40 new subjects indicated whether they agreed or not to the statements used in Experiment 1. A control (font discrimination) task was also included. In a parametric analysis, we assessed the effect of MDS dimension-coordinate values as parametric modulators of the hemodynamic response function (HRF) and the effect of subjects' religiosity. To better assess individual subjects' belief systems, we also evaluated the combined effects of agreement on individual statements and religiosity in a separate nonparametric analysis. (For behavioral results in Experiment 2, see *SI Text*).

Parametric Analysis

God's Perceived Level of Involvement (D1). Statements reflecting God's lack of involvement ($+D1$) modulated activity within 2 right-sided anterior-posterior networks, one lateral [consisting of: right (R) inferior frontal gyrus (IFG), Brodmann area (BA) 45; R middle occipital gyrus, BA 19; R middle temporal gyrus (MTG), BA 21, R inferior temporal gyrus (ITG), BA 20] and one medial (consisting of: R superior medial frontal gyrus, BA 8 and 10; R precuneus, BA 7), as well as, left (L) IFG, BA 45 (Fig. 1, Table 1). Statements reflecting increasing involvement by God ($-D1$) did not produce a reliable pattern of activity.

God's Perceived Emotion (D2). Statements reflecting God's love ($+D2$) modulated activity within the R middle frontal gyrus (MFG), BA 11

Table 1. fMRI activations with God's level of involvement (D1)

| Regressor | Voxel coordinates | Z value | Cluster size | t-statistics significance | Brodman area | Localization |
|-----------------------------------------------|----------------------|---------|--------------|--------------------------------------------------------------------------|--------------|---------------------------------------------|
| God's perceived lack of involvement ($+D1$) | (39, -78 , 36), | 4.65 | 426 | FDR correction ($P = 0.033$), cluster level correction ($P < 0.001$) | BA 19 | R middle occipital gyrus |
| | (54, 30, 0) | 4.20 | 452 | FDR correction ($P = 0.033$), cluster level correction ($P < 0.001$) | BA 45 | R inferior frontal gyrus, pars triangularis |
| | (9, 66, 6) | 4.09 | 58 | FDR correction ($P = 0.033$) | BA 10 | R superior medial frontal gyrus |
| | (60, -48 , -3) | 4.01 | 158 | FDR correction ($P = 0.033$) | BA 21 | R middle temporal gyrus |
| | (6, 33, 48) | 3.82 | 109 | FDR correction ($P = 0.035$) | BA 8 | R superior medial frontal gyrus |
| | (51, -18 , -18) | 3.59 | 84 | FDR correction ($P = 0.035$) | BA 20 | R inferior temporal gyrus |
| | (12, -63 , 39) | 3.47 | 111 | FDR correction ($P = 0.036$) | BA 7 | R precuneus |
| | (-36 , 42, 6) | 4.17 | 381 | FDR correction ($P = 0.033$), cluster level correction ($P = 0.001$) | BA 45 | L inferior frontal gyrus, pars triangularis |

FDR, false discovery rate.

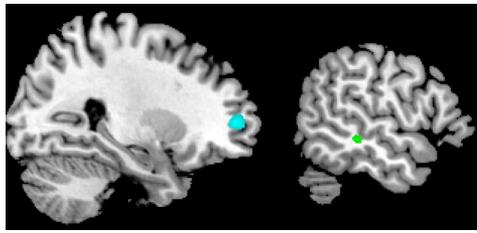


Fig. 2. Effect of God's perceived emotion (D2): Love (Left) vs. Anger (Right). Threshold was set to $P < 0.05$, FDR corrected. Activations are shown in blue for God's perceived love and green for God's perceived anger.

(Fig. 2, Table 2). Statements reflecting God's anger ($-D2$) modulated activity within the L MTG, BA 21 (see Fig. 2, Table 2).

Religious Knowledge Source (D3). Statements reflecting doctrinal religious knowledge ($+D3$) modulated activity within the R ITG and MTG, BA 20 and 21, and the R inferior parietal gyrus, BA 40, the L middle cingulate gyrus, BA 23 and the L superior temporal gyrus, BA 22 (Fig. 3, Table 3). Statements reflecting experiential religious knowledge ($-D3$) modulated activity within a large area in bilateral occipital lobes, with main foci at bilateral calcarine gyri, BA 17 and 18, with activation extending to the L fusiform gyrus, BA 19, and the L precuneus, BA 7. They also modulated activity within L frontal areas, such as the L IFG, pars triangularis, BA 45/47, and the premotor cortex, BA 6 (see Fig. 3, Table 3).

Religiosity. Religiosity covaried across dimensions with activity within the L precuneus, BA 23, the L temporoparietal junction area (BA 39) and the L MFG, BA 47 (Fig. 4, Table 4). A direct comparison of religious and nonreligious subjects did not reveal differences for any of the parametric modulators.

Nonparametric Analysis. Disagreement to the statements (compared with agreement) in religious (compared with nonreligious) participants engaged the anterior insulae, the adjacent R orbitofrontal cortex, BA 47, and the middle cingulate gyri, BA 32 (see Fig. 4, Table 5).

Discussion

The MDS results confirmed the validity of the proposed psychological structure of religious belief. The 2 psychological processes previously implicated in religious belief, assessment of God's level of involvement and God's level of anger (11), as well as the hypothesized doctrinal to experiential continuum for religious knowledge, were identifiable dimensions in our MDS analysis. In addition, the neural correlates of these psychological dimensions were revealed to be well-known brain networks, mediating evolutionary adaptive cognitive functions.

Statements reflecting God's lack of involvement ($+D1$) engaged a lateral network concerned with understanding agents' actions (15), with main foci of activation within bilateral IFG, pars triangularis, BA 45. The pars triangularis relates functionally with the nearby pars opercularis, BA 44, of the human mirror neuron system (16, 17). The R IFG, BA 45, in particular, is involved in action observation (16, 18), action understanding (16, 17), and detection

of intent (15, 19). Understanding agents' actions also involves decoding their emotional impact and the IFG play important roles in emotion processing. The R IFG, BA 45, is involved in detection of emotion from prosody or facial expression (20, 21), whereas the L IFG, BA 45, responds to various negative emotional stimuli (22, 23), monitors semantic-emotional congruency (24), and mediates reappraisal or suppression of negative emotions (25). Furthermore, the coactivated here R BA 20 and 21 may augment emotional understanding by accurately identifying negative emotions (26). Understanding agents' actions also requires them to be related to one's self: the medial network activated by D1 (L medial frontal BA 10 and 8 and precuneus, BA 7), as well as the R MTG, BA 21, may perform this function, given their role in self-processing and self-relevance (27–30). Overall, the D1 pattern of activation implies that ToM processes were engaged to understand God's intent and resolve the negative emotional significance of his lack of involvement.

Statements reflecting God's perceived emotion (D2) engaged areas involved in emotional ToM and higher-order emotional regulation. Statements reflecting God's anger ($-D2$) engaged the L MTG, BA 21, a key area in emotional ToM (21, 31, 32), involved in detection of high-valence emotion in facial expression and linguistic content (21). The same area responds to language-induced fear (33) and mediates conscious reappraisal of perceived negative emotions (25). On the other hand, statements reflecting God's love ($+D2$) activated the R MFG, BA 11, an area involved in positive emotional states and suppression of sadness (34, 35). Activation of the R MFG with $+D2$ may explain the observed negative association of positive God concepts with incidence of depressive symptoms (9).

In regards to the continuum of religious knowledge (D3), the low-imagery content of doctrinal knowledge strongly activated temporal-lobe regions, compared to the high-imagery content of experiential knowledge (36, 37). Statements reflecting doctrine ($+D3$) engaged the R ITG, a key area in decoding metaphorical meaning (38) and abstractness (39). It also engaged the L superior temporal gyrus, BA 22, an area known to process abstract linguistic content less amenable to imagery (36). On the other hand, statements reflecting experiential religion ($-D3$) activated a network including bilateral occipital lobes (including the L precuneus), the L precentral gyrus, and the L IFG. This network classically mediates visual and motor imagery of self in action (36, 40–42), which may be triggered by high-imagery linguistic content (36) and is based on episodic memory retrieval (28, 40, 43).

To assess the overall effect of religiosity on the processing of religious stimuli, we examined how it covaried with brain activation patterns. Religiosity modulated activity within the L precuneus, the L MFG, and the L occipital middle gyrus. This modulation may be related with stronger episodic memory retrieval and imagery (28, 41) and greater effort in representing the meaning of the statements (44) among participants who actively practice their religious beliefs.

To investigate the process of adopting or rejecting religious beliefs and how it relates with religiosity, we performed a nonparametric analysis. Disagreeing (compared to agreeing) with religious statements among religious (compared to nonreligious) participants engaged bilateral anterior insulae and middle cingulate gyri. The anterior insulae are key areas for emotional-cognitive integration (45), and insular recruitment for rejecting religious beliefs

Table 2. fMRI activations with God's perceived emotion (D2)

| Regressor | Voxel coordinates | Z value | Cluster size | t-statistics significance | Brodmann area | Localization |
|---------------------------------|-------------------|---------|--------------|--------------------------------------------|---------------|-------------------------|
| God's perceived love ($+D2$) | (27, 51, 6) | 3.72 | 212 | Cluster level 4 correction ($P = 0.018$) | BA 11 | R middle frontal gyrus |
| God's perceived anger ($-D2$) | (-54, -33, -6) | 4.92 | 141 | FDR correction ($P = 0.038$) | BA 21 | L middle temporal gyrus |

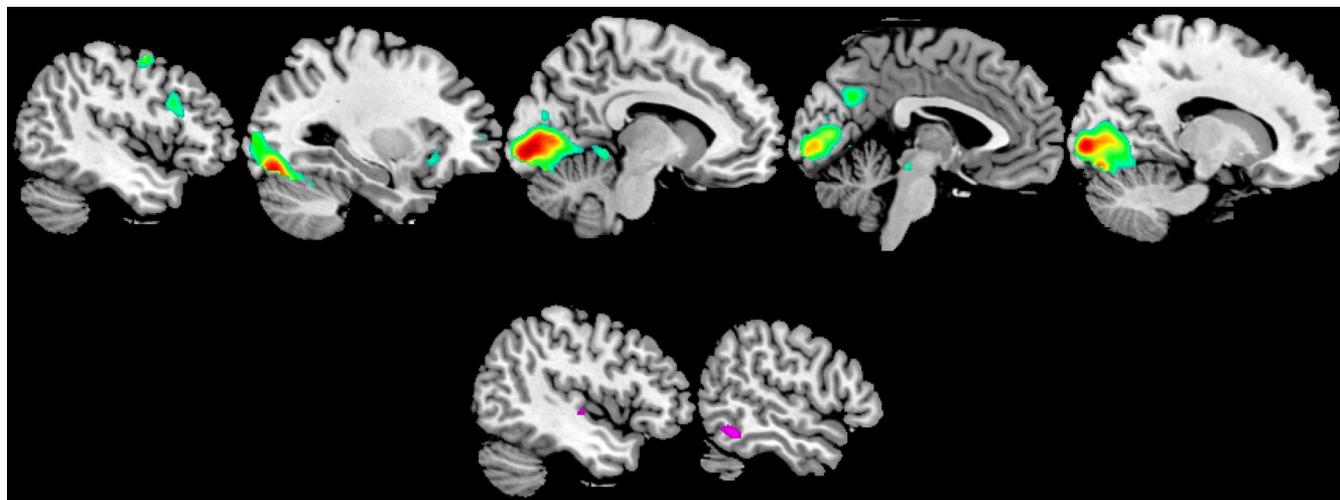


Fig. 3. Effect of religious knowledge (D3): Experiential (*Above*) vs. Doctrinal (*Below*). Threshold was set to $P < 0.05$, FDR corrected. Slices are oriented from L to R. Activations are shown in purple for doctrinal knowledge and as a spectrum for experiential knowledge.

implies a greater role of emotions in the process. Religious subjects may have experienced negative emotions triggered by religious disagreement, such as aversion, guilt, or fear of loss (23, 46, 47), perhaps because the stakes for detecting and rejecting religious statements inconsistent with their religious beliefs were higher in this group. For the same reason, this group may have experienced higher cognitive conflict manifested by middle cingulate gyri recruitment (48, 49).

This study defines a psychological and neuroanatomical framework for the (predominately explicit) processing of religious belief. Within this framework, religious belief engages well-known brain networks performing abstract semantic processing, imagery, and intent-related and emotional ToM, processes known to occur at both implicit and explicit levels (36, 39, 50). Moreover, the process of adopting religious beliefs depends on cognitive-emotional interactions within the anterior insulae, particularly among religious subjects. The findings support the view that religiosity is integrated in cognitive processes and brain networks used in social cognition, rather than being *sui generis* (2–4). The evolution of these networks

was likely driven by their primary roles in social cognition, language, and logical reasoning (1, 3, 4, 51). Religious cognition likely emerged as a unique combination of these several evolutionarily important cognitive processes (52). Measurable individual differences in these core competencies (ToM, imagination, and so forth) may predict specific patterns of brain activation in response to religious stimuli. The framework identified in this study reflects the religiosity (or lack of) of members of a modern Western society. Tribal and non-Western religions may differentially engage the cognitive processes and networks identified here or engage novel ones (3). This conjecture is readily testable in a larger and more religiously diverse group of participants under varying ecological conditions. Regardless of whether God exists or not, religious beliefs do exist and can be experimentally studied, as shown in this study.

Methods

Experiment 1 (MDS). The Neuroscience Institutional Review Board of the National Institutes of Health Intramural Program approved this research. Twenty six right-

Table 3. fMRI activations with religious knowledge source (D3)

| Regressor | Voxel coordinates | Z value | Cluster size | t-statistics significance | Brodmann area | Localization |
|----------------------------------------|-------------------|---------|-----------------|----------------------------------------------------------------------------|---------------|---------------------------------------------|
| Doctrinal religious knowledge (+D3) | (54, -51, -15) | 4.88 | 689 | FDR correction ($P = 0.014$), 4 cluster level correction ($P < 0.001$) | BA 20 | R inferior temporal gyrus |
| | (60, -48, 9) | 4.46 | (Above cluster) | FDR correction ($P = 0.022$) | BA 21 | R middle temporal gyrus |
| | (60, -36, 48) | 3.98 | (Above cluster) | FDR correction ($P = 0.046$) | BA 40 | R inferior parietal/supramarginal gyrus |
| | (-18, -24, 42) | 3.89 | 448 | FDR correction ($P = 0.050$), cluster level correction ($P < 0.001$) | BA 23? | (Below) L cingulate gyrus, middle part |
| | (-45, -15, -3) | 3.96 | 69 | FDR correction ($P = 0.047$) | BA 22? | L Superior temporal gyrus |
| Experiential religious knowledge (-D3) | (-9, -90, -3) | 7.29 | 2,369 | FDR correction ($P < 0.001$), cluster level correction ($P < 0.001$) | BA 17 | L calcarine gyrus |
| | (-30, -78, -15) | 6.50 | (Above cluster) | FDR correction ($P < 0.001$) | BA 19 | L fusiform gyrus |
| | (15, -93, 0) | 6.88 | (Above cluster) | FDR correction ($P < 0.001$) | BA 18 | R calcarine gyrus, |
| | (-3, -63, 33) | 4.67 | 52 | FDR correction ($P = 0.001$) | BA 7 | L precuneus |
| | (-48, -3, 57) | 4.67 | 58 | FDR correction ($P < 0.001$) | BA 6 | L precentral gyrus |
| | (-45, 15, 27) | 3.93 | 191 | FDR correction ($P = 0.002$), Cluster level correction ($P = 0.028$) | BA 44/ BA 47 | L inferior frontal gyrus, pars triangularis |

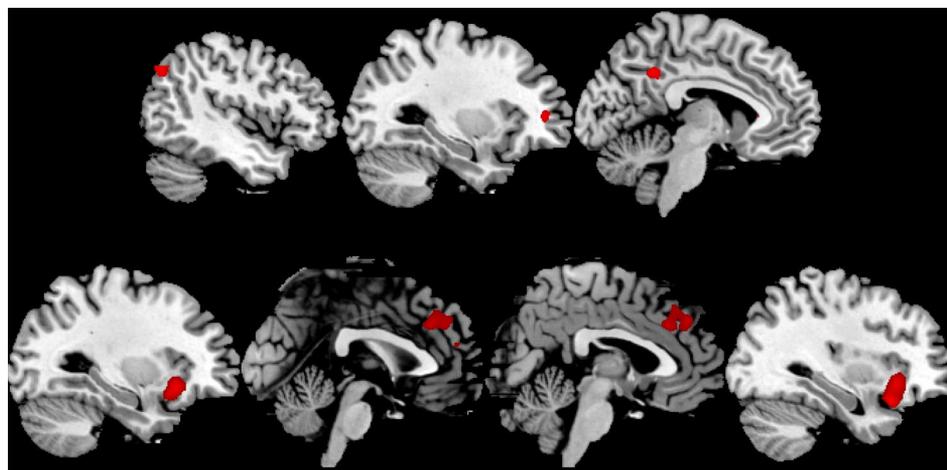


Fig. 4. Effect of religiosity (*Above*) and disagreement (*Below*). The effect of religiosity in the parametric design is shown above. The effect of disagreement (compared to agreement) for religious (compared to nonreligious) participants in the nonparametric design is shown below. Threshold was set to $P < 0.05$, FDR corrected. Slices are oriented from L to R. Activations are shown in red.

handed subjects (11 women and 15 men; mean age, 37.7; mean years of education, 17.9) participated. First, subjects provided conceptual dissimilarity ratings for pairs of statements regarding religious beliefs, using a 7-point Likert scale (from 1 = “extremely similar” to 7 = “not similar at all”). We used 70 statements, derived (and modified to be 3–5 words-long) from previously used questionnaires (11, 53), and formed all possible pairs (Table S1). Subsequently, subjects rated each statement on six 7-point Likert “external” variable scales: God’s level of involvement (from high to low), God’s emotion (from anger to love), religious knowledge source (from doctrinal to experiential), exposure to the concept (from low to high), prospective reward (from punishment to reward), and time horizon (from present to after-life). We applied individual differences MDS for ordinal measures (PROXSCAL, SPSS15) to the dissimilarity ratings, adopting the weighted Euclidean model (to allow for differential weighing of subjects), and using the external variables as linear restrictors of the output dimensions (12, 13). We performed all possible MDS analyses combining 2 to 6 external variables as linear restrictors. The alternative solutions were compared according to established MDS criteria: stress (< 0.10 being the cut-off) and correlation of output dimensions and linear restrictors (the stronger and more unique a correlation, the more confident the interpretation) (12, 13). Generally, higher dimensional solutions have decreased stress up to a plateau, but are harder to interpret (12, 13). Our intent to use the dimension coordinates as parametric modulators in an fMRI study further dictated acceptance of the lowest-dimensional solution possible, to increase the power of the ensuing general linear model. The use of 3 linear restrictors (God’s level of involvement, God’s emotion, and religious knowledge source) provided the best MDS solution.

Experiment 2 (fMRI). Forty right-handed subjects demographically matched to those in Experiment 1 (20 women and 20 men; mean age, 35.7; mean years of education, 17.5) participated in Experiment 2. The 70 statements used in Experiment 1 were also used as stimuli in the scanner.

There were two fMRI tasks: in the judgment task (J), participants were asked whether they mostly agreed or disagreed with a statement, whereas, in the font discrimination task (F), participants were asked which one of 2 fonts (variations of Arial) a statement appeared in. Subjects responded by pressing a key with their right index or middle finger. The key/finger assignment was counterbalanced across subjects. Each experiment contained 2 runs, with 70 trials each. Each trial was preceded by a task cue for 1 sec, followed by a statement for 5 sec. Subjects were instructed to make a decision within this timeframe. A blank screen was presented during intertrial interval (jittered from 2 to 8 seconds). Each statement was presented twice: in one run associated with the J and in the other with the F task, keeping all surface characteristics identical. The order of presentation was

pseudorandomized. Visual stimulus presentation was controlled by E-Prime (v1.2, Psychology Software Tools, Inc.).

A 3-Tesla GE MRI scanner with an 8-channel receiver head coil was used to acquire single-shot, 2-dimensional gradient-echo planar imaging T2*-weighted images with blood oxygenation level-dependent contrast. High-resolution T1-weighted 3-dimensional magnetization-prepared rapid gradient-echo structural images were also acquired. Image preprocessing and statistical analyses were performed using SPM5 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, UCL). Preprocessing included realignment and unwarping, slice-timing correction, normalization (to a $3 \times 3 \times 3$ voxel size), and smoothing (FWHM = 6 mm). Translation and rotation parameters were inspected and all subjects showed < 3 mm of motion.

The fMRI study used an event-related design. Trials were modeled as events assuming a canonical HRF.

For the parametric analysis, we assumed that the MDS dimension coordinates modulated the HRF (14). For single-subject analysis, we constructed the following model (for each run): F, J, JD1, JD2, JD3, 6-motion parameters. Linear contrasts were computed to assess the effect of each parametric regressor compared to the baseline. Then, contrast images were entered in a between-subjects full factorial model with one factor (“Dimension,” with 3 nonindependent levels D1, D2, and D3, and unequal variances) and 4 covariates (age, gender, education, and religiosity). t statistics identified brain regions where the HRF had a positive linear association with each modulator. Because the parametric modulators were dimension coordinates, a negative linear association with a dimension (deactivation) equals to a positive linear association with the opposite of the dimension. Therefore, “activation” and “modulation” in this article refer to positive linear associations. The statistical threshold for individual voxels at the whole-brain level was set to $P < 0.005$, with minimum cluster size of 50, similarly to other studies using parametric modulators (14, 54). We corrected for multiple comparisons for voxels at the whole-brain level by applying FDR correction ($P < 0.05$). Cluster-level correction (when applicable) is also reported.

For the nonparametric analysis, subjects were divided into 20 religious and 20 nonreligious (demographically matched to each other). At the single-subject level, we constructed the following model: F, JA, JDA, 6-motion parameters (where Agreement = A; Disagreement = DA). Linear contrasts were computed to assess the effect of each regressor compared to the baseline. Contrast images were entered in a between-subjects full factorial model with 2 factors (“Agreement,” with 2 levels: A and DA; and “Religiosity,” with 2 levels: “religious” and “nonreligious”) and age,

Table 4. Effect of religiosity (as covariate in parametric analysis)

| Regressor | Voxel coordinates | Z value | Cluster size | t -statistics significance | Brodman area | Localization |
|-------------|-------------------|---------|--------------|--------------------------------------------------------------------------|--------------|--------------------------|
| Religiosity | (−6, −48, 39) | 4.66 | 129 | FDR correction ($P = 0.020$), cluster level correction ($P = 0.004$) | BA 23 | L precuneus |
| | (−45, −72, 39) | 4.50 | 95 | FDR correction ($P = 0.020$), cluster level correction ($P = 0.015$) | BA 39 | L occipital middle gyrus |
| | (−30, 45, 6) | 4.36 | 75 | FDR correction ($P = 0.020$), cluster level correction ($P = 0.035$) | BA 47 | L middle frontal gyrus |

Table 5. Effect of agreement and religiosity (nonparametric analysis)

| Regressor | Voxel coordinates | Z value | Cluster size | t-statistics significance | Brodman area | Localization |
|-----------------------------------------------------------------------------------------|-------------------|---------|-----------------|------------------------------------------------------------------|--------------|--------------------------|
| Disagreement (compared to agreement) in all participants | (-33, -24, 15) | 3.95 | 89 | Cluster level correction (P = 0.010) | ? | L insula |
| Disagreement compared to agreement (in religious compared to nonreligious participants) | (33, 18, -21) | 5.64 | 238 | FDR correction (P < 0.001), cluster level correction (P < 0.001) | BA 47 | R orbitofrontal cortex |
| | (33, 21, -6) | 5.16 | (Above cluster) | FDR correction (P < 0.001) | ? | R insula |
| | (3, 30, 33) | 4.51 | 293 | FDR correction (P = 0.002), cluster level correction (P < 0.001) | BA 24/32 | R middle cingulate gyrus |
| | (-9, 33, 24) | 3.65 | (Above cluster) | FDR correction (P = 0.024) | BA 32 | L middle cingulate gyrus |
| | (-30, 21, -9) | 5.45 | 122 | FDR correction (P < 0.001), cluster level correction (P = 0.002) | ? | L insula |

gender, and education as covariates. Variances were considered unequal and factor levels nonindependent. The statistical threshold for individual voxels was set to $P < 0.001$, with minimum cluster size of 50; correction for multiple comparisons was similarly applied.

Results are reported in the original Montreal Neurological Institute template. Figures display statistical maps overlaid on the T1 anatomical template used by

MRIcron (Chris Rorden's MRIcron, 2005); only voxels passing FDR correction are displayed.

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