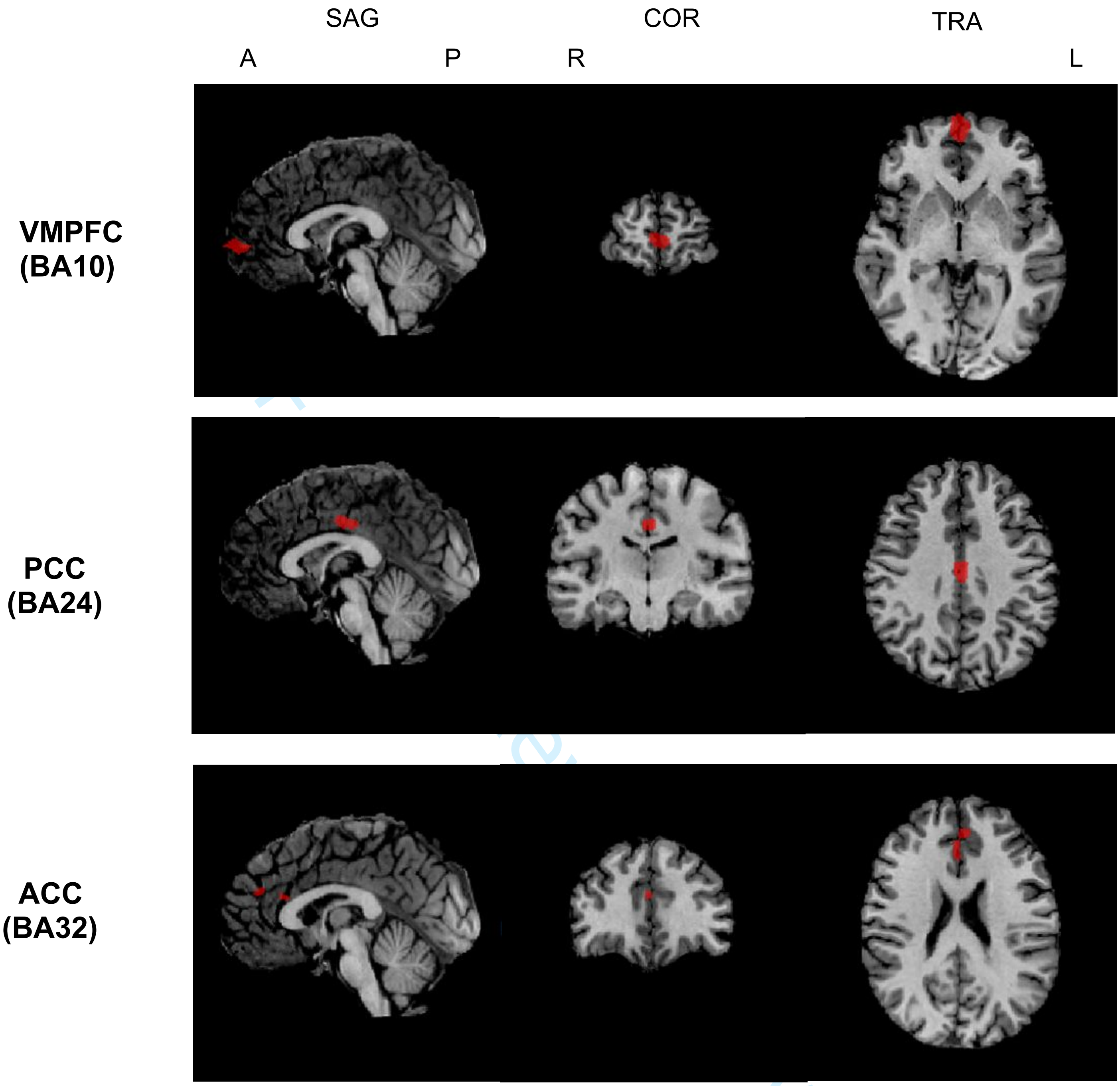
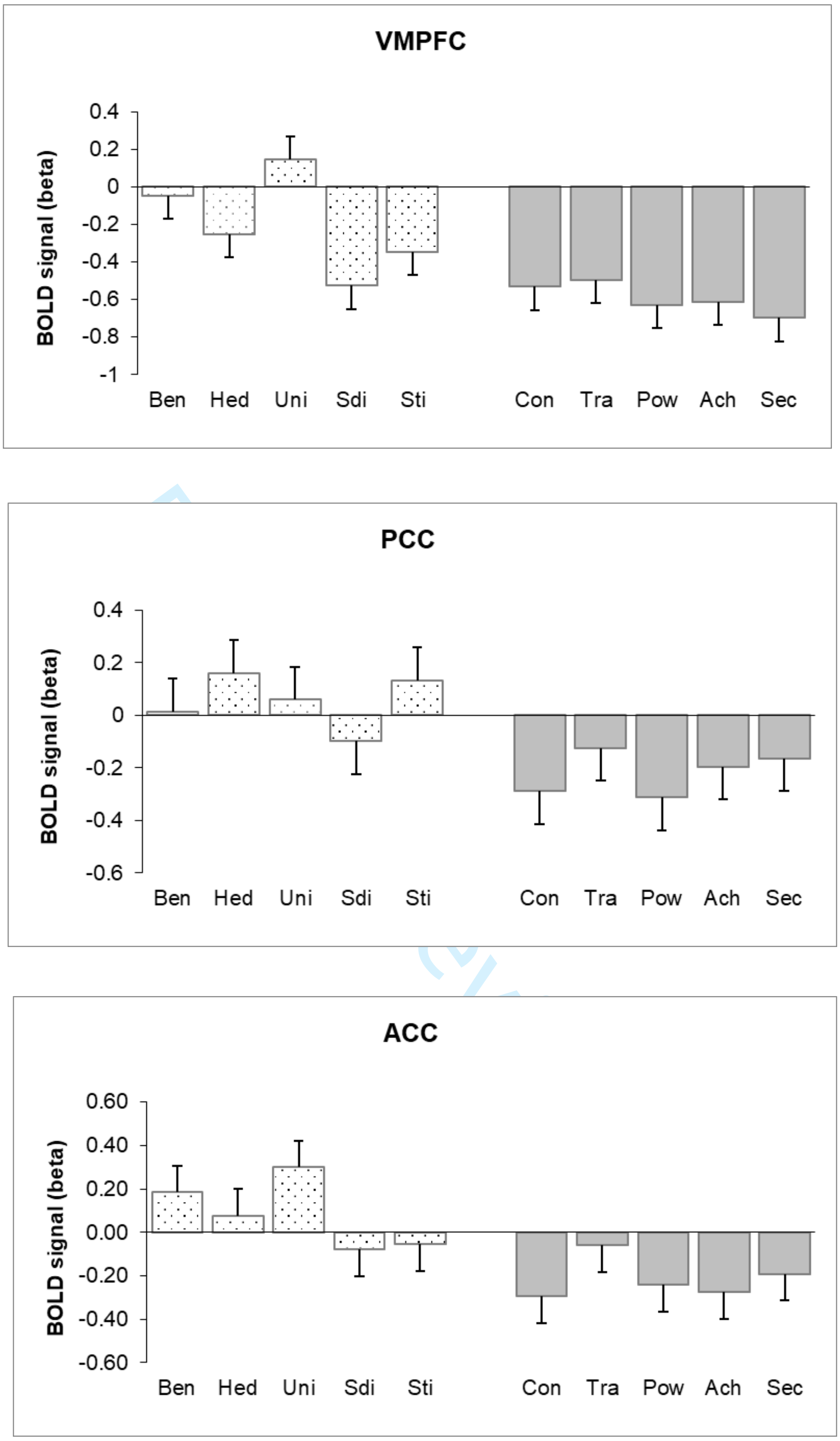
Neural coding of human values is underpinned by brain areas representing the core self in the cortical midline region

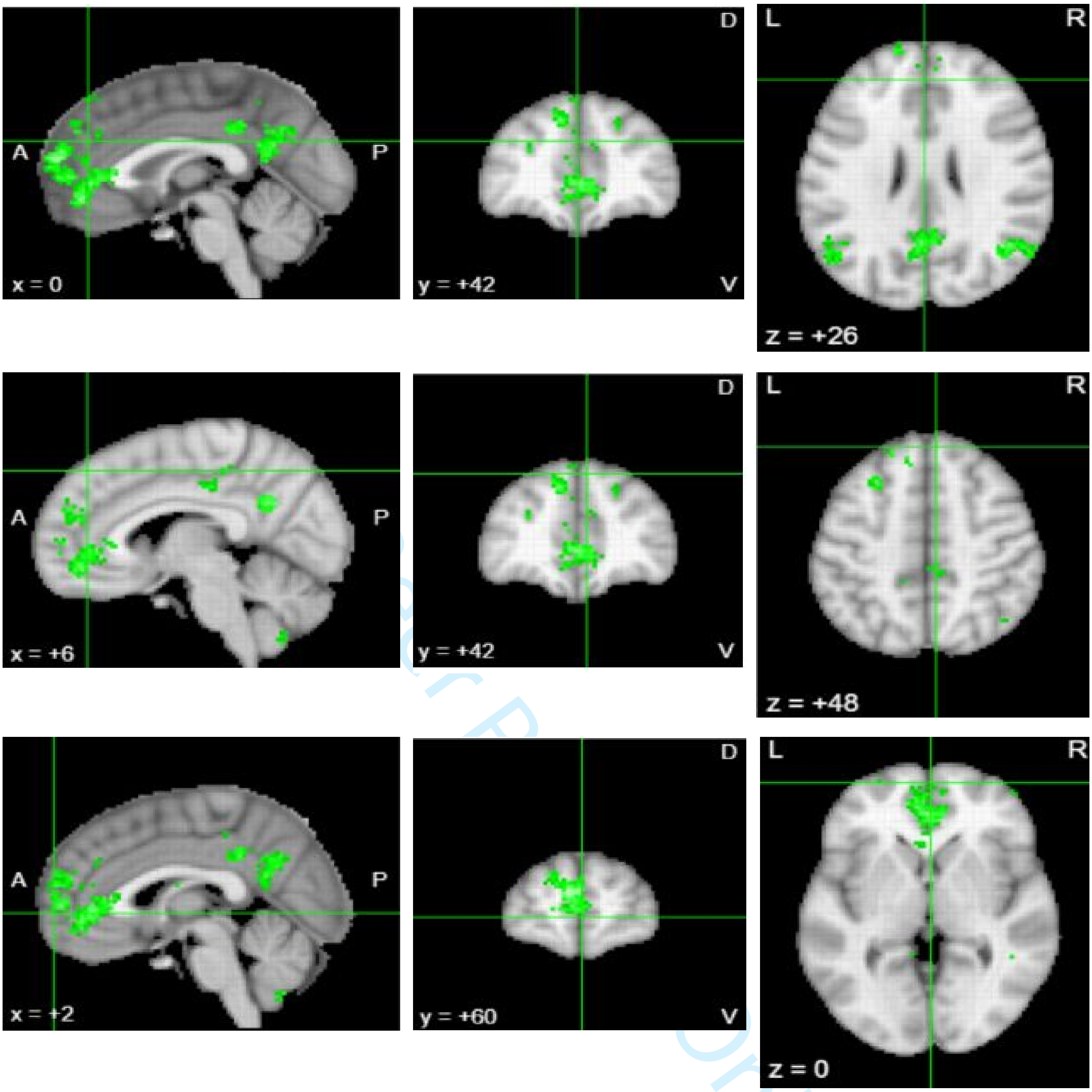
Journal:	*Social Neuroscience*
Manuscript ID	SNS-RP 118.20.R3
Manuscript Type:	Research Paper
Date Submitted by the Author:	20-Jun-2021
Complete List of Authors:	Leszkowicz, Emilia; University of Gdańsk Faculty of Biology, Department of Animal and Human Physiology; Cardiff University Maio, Gregory; University of Bath Linden, David; Maastricht University Faculty of Health Medicine and Life Sciences Ihssen, Niklas; Durham University
Keywords:	Basic human values/Schwartz's value model, self-transcendence, self-enhancement, fMRI



Supplementary Figure 1. Brain regions showing significantly larger activation for Anxiety-Free values compared to Anxiety-Based values. VMPFC = ventromedial prefrontal cortex; PCC = posterior cingulate cortex; ACC = anterior cingulate cortex; BA = Brodmann area; SAG = sagittal view; COR = coronal view; TRA = transversal view; A = anterior; P = posterior; R = right; L = left.



Supplementary Figure 2. Mean beta weights, which correspond to relative activation levels, in brain regions where stronger activation was found for Anxiety-Free values than Anxiety-Based values. Anxiety-Free values (Ben-Sti) are presented at the left and Anxiety-Based (Con-Sec) at the right. VMPFC = ventromedial prefrontal cortex; PCC = posterior cingulate cortex; ACC = anterior cingulate cortex; Ben = Benevolence; Hed – Hedonism; Uni = Universalism; Sdi = Self-Direction; Sti = Stimulation; Con = Conformity; Tra = Tradition; Pow = Power; Ach = Achievement; Sec = Security.



Supplementary Figure 3. Term-based meta-analyses map produced in NeuroSynth for "self-referential" term (an automated meta-analysis of 166 studies). On the map, crosshairs are shown at our peak activity in the DMPFC (BA9; x, y, z = 0, 42, 26) (upper row), DMPFC (BA8; x, y, z = 6, 42, 47) (middle row), and VMPFC (B10; x, y, z = 2, 60, -1) (lower row). The presented map is an *association test* map (z-scores from a two-way ANOVA testing for the presence of a non-zero association between the term „self-referential" and voxel activation). The association test map shows whether activation in a region occurs *more* consistently for studies that mention the term than for studies that do not. Activations and deactivations are not distinguished on NeuroSynth maps. NeuroSynth maps have a resolution of 2 mm, and coordinates are rounded to the nearest point there are data for.

Supplementary Table 1. Brain regions where rating Anxiety-Free values evoked significantly greater activation than rating Anxiety-Based values.

Brain region	BA	Peak coordinates of the activation cluster			Cluster size	*t*-value
		x	y	z		
VMPFC	10	0	59	0	887	5.237
PCC	24	0	-14	35	700	3.649
ACC (L/R)	32	-1	34	22	648	4.078

Note: BA, Brodmann area; L, left hemisphere; R, right hemisphere; VMPFC, ventromedial prefrontal cortex; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex; peak coordinates, Talairach coordinates of a cluster's center of gravity; cluster size, number of 1 x 1 x 1-mm voxels in a cluster; *t*-value, the value of the comparison: Anxiety-Free > Anxiety-Based condition, with $p < .001$.

Neural coding of human values is underpinned by brain areas representing the core self in the cortical midline region

Emilia Leszkowicz, University of Gdansk, Cardiff University; Gregory R. Maio, University of Bath; David E.J. Linden, Maastricht University; Niklas Ihssen, Durham University

Abstract

The impact of human values on our choices depends on their nature. Self-transcendence values motivate us to act for the benefit of others and care for the environment. Self-enhancement values motivate us to act for our benefit. The present study examines differences in the neural processes underlying these two value domains. Extending our previous research, we used fMRI to explore first of all neural correlates of Self-Transcendence vs Self-Enhancement values, with a particular focus on the putative role of the medial prefrontal cortex (MPFC), which has been linked to a self-transcendent mindset. Additionally, we investigated the neural basis of Openness to Change vs Conservation values. We asked participants to reflect on and rate values as guiding principles in their lives while undergoing fMRI. Mental processing of Self-Transcendence values was associated with higher brain activity in the dorsomedial (BA9, BA8) and ventromedial (BA10) prefrontal cortices, as compared to Self-Enhancement values. The former involved activation and the latter deactivation of those regions. We did not detect differences in brain activation between Openness to Change vs Conservation values. Self-Transcendence values thus shared brain regions with social processes that have previously been linked to a self-transcendent mindset, and the "core self" representation.

Keywords: Basic human values/Schwartz's value model; self-transcendence; self-enhancement; fMRI;

Introduction

All individuals hold values that guide their attitudes and motivate their behaviours. Freedom, helpfulness, wealth are just examples of the abstract concepts that people deploy as guiding principles in their lives (Maio, 2017; Schwartz, 1992; Rokeach, 1973). Diverse values form the core of our identity (Hitlin, 2003), and there is abundant precedent for studying values from a neurobiological perspective (e.g. Maio, 2017; Maio et al., 2009). Research has found evidence for a heritable contribution to values (Schermer et al., 2011), especially among values that differ between gender (Knafo & Spinath, 2011), and individual differences in the gene encoding for oxytocin are correlated with prosocial values (Israel et al., 2009). Furthermore, there is an association between the polygenic neuroticism score and ratings of value importance in the Schwartz value survey (Zacharopoulos et al., 2016b), and neural correlates of values have been identified. Previously, using a forced choice task we demonstrated that conflict experienced at the behavioural level when having to choose between similar values engaged those brain structures that were previously associated with conflict in other tasks (Fedota et al., 2014; Carter & van Veen, 2007), that is the supplementary motor area and dorsolateral prefrontal cortex (Leszkowicz et al., 2017). Zacharopoulos et al. (2017) found associations between value types ratings and structural brain parameters, including white matter volume, myelin water fraction, and grey matter parameters in frontal regions. The importance that people attach to hedonistic values ("enjoying life", "pleasure") was associated with left globus pallidus volume (Zacharopoulos et al., 2016a).

Schwartz (1992) proposed that values can be arranged into a circular model that clarifies their motivational interrelations. His widely recognized model of basic human values was studied in over 80 nations (Coelho et al., 2019; Hanel et al., 2018; Schwartz et al., 2012). That model predicts that values are organised around two dimensions (Fig. 1). One dimension taps into motivational conflict between values that transcend self-interest to consider the well-being of others and values that focus on promotion of self-interest: Self-Transcendence vs Self-Enhancement values. The other dimension taps into motivational conflict between values that follow interests in uncertain directions with values that protect the status quo: Openness to Change vs Conservation values. In the present research, we mainly consider the neural correlates of Self-Transcendence vs Self-Enhancement values, with particular attention to the putative role of cortical midline structures. Additionally, we analyse if Openness to Change and Conservation values differ at the neural level. In supplementary exploratory analyses, we look at values related to anxiety, and compare Anxiety-Free (Hedonism, Stimulation, Self-Direction, Universalism, Benevolence) with Anxiety-Based values (Tradition, Conformity, Security, Power, Achievement).

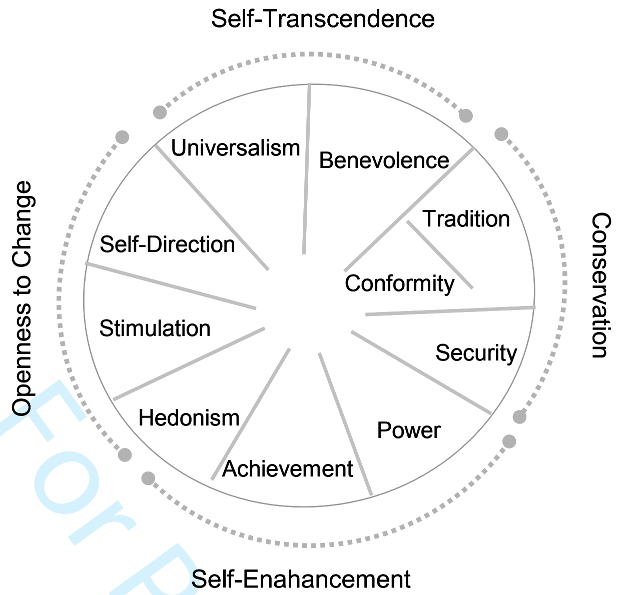


Figure 1. The Schwartz model of basic human values (Schwartz, 1992). Ten basic value types are presented inside the circle. Higher order value domains are shown outside the circle.

Cortical midline structures are engaged in self-referential and other-referential processes, which are relevant to self-enhancement and self-transcendence, respectively, (Araujo et al., 2013; Wagner et al., 2012). For the sake of clarity, we use the term "dorsomedial prefrontal cortex" (DMPFC) in reference to frontal cortical midline areas above the genu of the corpus callosum, broadly comprising BA8 and 9, "ventromedial prefrontal cortex" (VMPFC) in reference to BA10 below the genu (Wagner et al., 2012), which is sometimes referred to as the anteromedial prefrontal cortex (Lieberman et al., 2019), and "orbitofrontal cortex" (OFC) to denote the most ventral part of the cortical midline area comprising BA11, 12, 13 (Rolls et al., 2020). Core regions involved in self- and other-referential processing include the VMPFC, DMPFC, posterior cingulate cortex (PCC), precuneus, and temporo-parietal junction (TPJ) (Denny et al., 2012; Murray et al., 2012; Northoff et al., 2006). The medial prefrontal cortex (MPFC) is differentially activated by the self and others, with most ventral parts more active for the self/self-referential processing, and more dorsal parts more active for the other/other-referential processing (Denny et al., 2012; Murray et al., 2012; Amodio & Firth, 2006). MPFC activity also varies with the closeness, familiarity, or similarity of the other (Krienen et al., 2010; Mitchell et al., 2006). More precisely, the VMPFC is associated with processing of a close other, while the DMPFC is more engaged in processing of socially distant or unknown others (Murray et al., 2012). In some situations, self- and other-referential processes may be represented both in the VMPFC and DMPFC (e.g. Nicolle et al., 2012).

MPFC and cingulate cortex activity is also associated with moral functioning (Han et al., 2016), which is interesting from the perspective of the self that prioritizes moral group-oriented values over selfish self-oriented values. A wide variety of moral tasks devoted to understanding complex aspects of moral cognition engage the VMPFC and DMPFC, which was interpreted in the context of the default mode network (DMN; Han, 2017; Sevinc & Spreng, 2014), and the mentalising network (Eres et al., 2018). The DMN is engaged in various constructs involved in social understanding of others, including morality, emotion perception, empathy, and theory of mind (ToM)

(Li et al., 2014). An overlap between brain regions associated with moral cognition, ToM, which is related to rational/cognitive facets of moral cognition, and with emotional network, which is associated with emotional facets of moral cognition, was demonstrated in the DMPFC, TPJ, and right middle temporal gyrus (Bzdok et al., 2012). Social, as well as moral cognition engages the ventral and dorsal aspects of the MPFC, and a functional ventral-dorsal gradient in the MPFC was suggested for some dimensions of social and moral cognition, such as self-referential/close other – other-referential/distant other, or emotional/automatic/simple – cognitive/mentalising/complex (Lieberman et al., 2019; Sul et al., 2015; Li et al., 2014; Denny et al., 2012; Amodio, & Firth, 2006). Based on the literature reviewed above, we explored whether the other-oriented – self-oriented dimension of human values, as reflected in the processing of Self-Transcendence vs Self-Enhancement values, respectively, may be associated with the MPFC, too.

Moreover, other parts of the DMN, such as the PCC and inferior parietal lobule, or mentalising network, such as the TPJ and lateral temporal cortex, could also be involved in value processing due to their functional connections with the different subregions of the MPFC contributing to various aspects of social understanding of others (Li et al., 2014; Bzdok et al., 2013; Van Overwalle, 2011). We could not exclude the involvement of other possible structures in value processing either, such as limbic regions and reward/pleasure/hedonic system beyond the VMPFC/OFC, including the ACC, and ventral striatum; relevant in particular for Self-Enhancement values (Berridge & Kringelbach, 2015). The present study also explored brain responses to Openness to Change vs Conservation values, and whether similar activation patterns could be identified as in previous studies (Brosch et al., 2011). Given the exploratory nature of our study and the diversity of brain regions associated with the processes described above, we analysed the present data at the whole-brain level rather than responses of selected regions.

Of importance, however, Schwartz's model forms a continuum of related motivations, which gives rise to the circular structure, where value motivations at one end are opposed by value motivations at the other end. It is therefore important in imaging analyses to contrast values at opposing ends in order to tap opposite ends of the same continuum, rather than treat opposing ends as though they are entirely separable processes. For example, a clear separation between Self-Transcendence and Self-Enhancement values in the cortical midline is complicated by the fact that the self-transcendence mindset has been linked with the VMPFC/OFC (BA10/11; Brosch et al., 2018;-Kang et al., 2018; Teed et al., 2019), which is a key area in the reward/pleasure/hedonic system (Berridge & Kringelbach, 2015), more than with the DMPFC, but indirect evidence suggests that Self-Transcendence values may be linked with activity in different medial prefrontal regions (DMPFC, VMPFC, OFC) because these regions are associated with various aspects of self-transcendent mindset such as prosocial attitudes and behaviours, or moral cognition (Han et al., 2016; Moll et al., 2006; Moll et al., 2005). Furthermore, the mental representation of the other and the ability to contemplate others' thoughts, desires, and behavioural dispositions is linked to the mentalising or ToM network, comprising the DMPFC (BA9), STG/TPJ and precuneus (van Veluw & Chance, 2014). There are suggestions that prosocial behaviour may, in part, result from our tendency to consider others' mental states and not from empathic concern per se, which is supported by the fact that altruistic behaviour can engage ToM network with the DMPFC and precuneus/PCC without engagement of the emotional system (Waytz et al., 2012). Thus, a key question is the extent to which the *dimension* from Self-Transcendence vs Self-Enhancement values predicts activity in these regions. Our approach is based on the idea that Self-Transcendence and Self-Enhancement values are not separable at the brain level, and we did not look at them as though they were distinct independent constructs in the brain. Of course, both models could be applied and compared, but at this stage we did not use separate analyses (Self-Transcendence vs control and Self-Enhancement vs control) for brain regions connected with Self-Transcendence and brain regions connected with Self-Enhancement values.

Our own and previous research on values (Teed et al., 2019; Kang et al., 2018; Leszkowicz et al., 2017; Brosch et al., 2011) used tasks in which participants made decisions that were potentially related to the values in an indirect or complex manner (e.g. choices between them). To more directly examine the neural signature of Self-Transcendence vs Self-Enhancement values and Openness to Change vs Conservation values, we set out to investigate brain activity solely while *thinking* about values as personal guiding principles in life. We hypothesised that these two value *dimensions*, Self-Transcendence vs Self-Enhancement and Openness to Change vs Conservation, have distinct neural representations, which can be revealed (among others in the MPFC), when people *reflect on* these value dimensions. We did not aim to identify brain regions associated with those four value domains per se (Self-Transcendence, Self-Enhancement, Openness to Change, Conservation), and our BOLD contrasts did not test for a value domain vs control stimuli.

To test our hypotheses, we asked participants to reflect on and rate values as guiding principles in their lives, while undergoing fMRI. We then compared fMRI BOLD signals for Self-Transcendence vs Self-Enhancement and Openness to Change vs Conservation values during the time period before the onset of the rating response. Potential results obtained with this method may reveal where values could be coded in the brain, before they trigger a particular action which subsequently will involve other relevant brain regions.

Materials and methods

Participants

23 healthy, white-British students or community residents from Cardiff (UK) were paid (15 GBP) for taking part in the study (16 women, 7 men, mean age 26.1 years, age range 19-48 years). All participants were right-handed, had normal or corrected-to-normal vision, and gave written informed consent. The sample size was established following former social neuroscience studies (Han et al., 2016 (n = 16); Cloutier & Gyurovski, 2014 (n = 20); Zelinková et al., 2014 (n = 20); Brosch et al.,

2012 (n = 18)), taking into account a 15% rate of data loss based on insufficient quality or other factors. The study was approved by the School of Psychology Research Ethics Committee at Cardiff University and followed the ethical guidelines of the World Medical Association Declaration of Helsinki.

Stimuli

Participants were presented with 50 original value items (termed “values” henceforth) sampled across all ten basic value types in Schwartz’s (1992) circular model, with 5 values from each type (Table 1). The value types were as follows: Universalism, Benevolence, Tradition, Conformity, Security, Power, Achievement, Hedonism, Stimulation, and Self-Direction. Seven of the original Schwartz's values (Schwartz, 1992; Schwartz et al., 2012) were slightly modified so that the length of words/phrases across conditions was matched. For example, "meeting social expectations" was substituted with "behave properly" and "stability" was replaced by "stability of society". These minor amendments maintained the value meanings and are unlikely to have elicited differences in value activation.

Table 1. Ten basic value types with value items (stimuli) used in the study.

Basic value type	Value (stimulus)	Basic value type	Value (stimulus)
Achievement	achievement ambition aspiration competence success	Security	avoiding danger avoiding sickness cleanliness security stability
Benevolence	dependability faithfulness to friends forgiveness helpfulness honesty	Self-direction	choosing own goals creativity curiosity freedom independence
Conformity	fitting in with my group following rules meeting social expectations obedience politeness	Stimulation	a varied life an exciting life novelty and change seeking adventure taking risks
Hedonism	enjoying life having a good time having fun pleasure self-indulgence	Tradition	acceptance of family beliefs commitment to family religion preservation of customs respect for tradition traditional culture
Power	authority being the leader preserving my public image social power wealth	Universalism	care for environment equal opportunity for all protection of the weak tolerance world peace

Because the main focus of our research were four value domains of a higher order, we also made sure that character counts, including spaces, were comparable for these value domains, which were as follows: Self-Transcendence (15.20 ± 6.58 SD), Self-Enhancement (11.50 ± 5.82 SD), Conservation (17.67 ± 7.39 SD), Openness to Change (13.07 ± 3.79 SD). A Kruskal-Wallis H test showed that there was no statistically significant difference in character counts between the domains, $\chi 2(3) = 5.909$, $p = .1161$.

The values were presented at the center of a black screen in white and green letters. The screen was viewed through a mirror fixed on the MRI head coil.

Procedure

The experimental procedure is illustrated in Fig. 2.

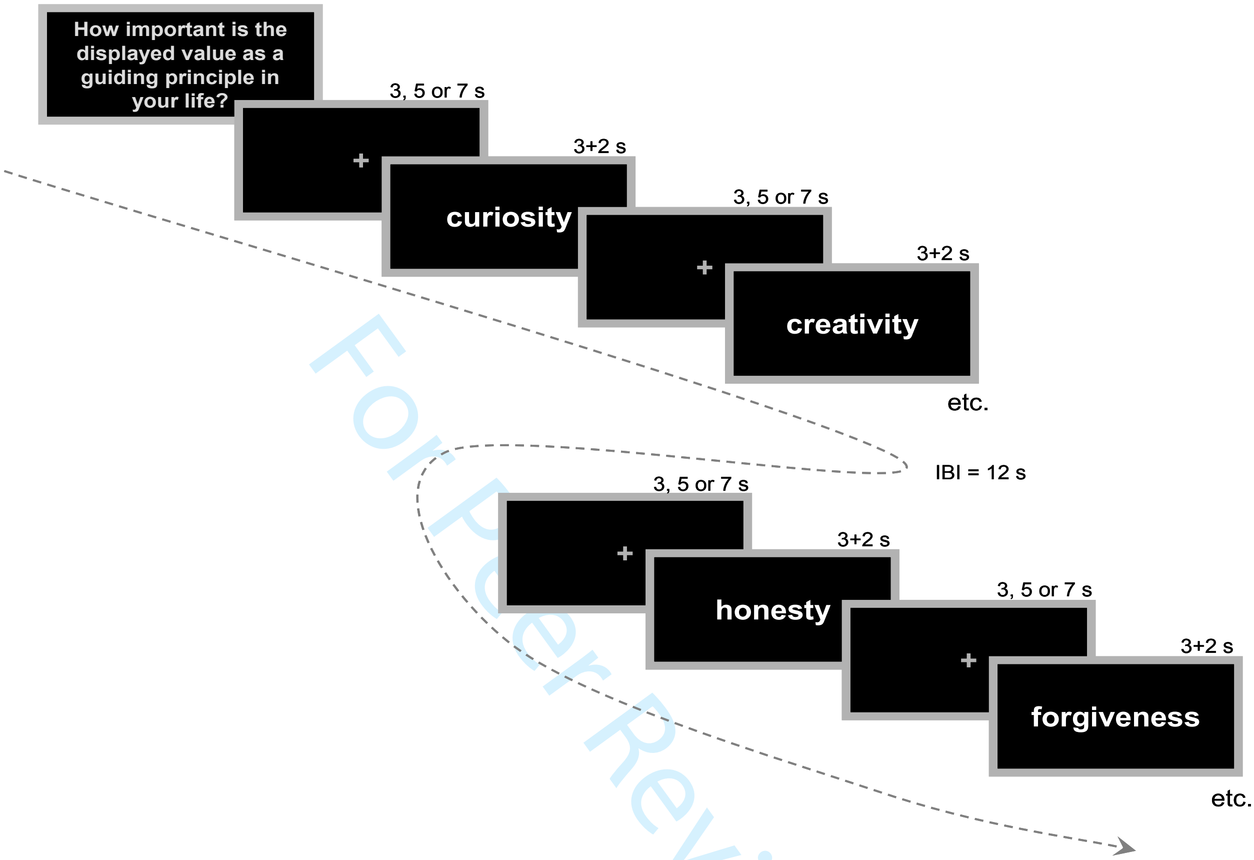


Figure 2. Experimental paradigm. In an fMRI scanner, participants were presented with one value at a time and were asked to decide how important that value was for them as a guiding principle in their life on a scale from 1 to 5. Each trial began with a fixation cross of 3, 5, or 7 s duration, followed by a value displayed for 5 s. Subjects were to decide on the value importance by pressing a response button in the last 2 s of the value presentation. Ten basic value types (with 5 values each) were randomly presented: Universalism, Benevolence, Tradition, Conformity, Security, Power, Achievement, Hedonism, Stimulation, and Self-Direction. They were presented in blocks with inter-block intervals, IBI = 12 s.

At the beginning of the task, participants were presented with the instruction that they should rate the importance of each value as a guiding principle in their life on a scale from 1 to 5 (1 = not important at all, and 5 = extremely important). Participants were also instructed that they should withhold their rating until the value changed its font color from white to green. Participants gave their responses by pressing one of five buttons on a MRI-compatible response box with their right hand, using their thumb for 1 (totally unimportant), and their little finger for 5 (extremely important).

Each trial started with a gray fixation cross of a random duration of either 3, 5, or 7 s, which was later treated as fixation baseline in fMRI data analyses. A value was then displayed in white letters for 3 s, before it changed its color to green, and was displayed for another 2 s. Participants were asked to respond (by pressing a button) after the value had turned to green, in order to separate the motor effect of button pressing from value processing.

Values of one type were presented together in short blocks, with the block order and value order within a block freely randomised. The interval between the blocks was 12 s. No value nor value type was presented repeatedly to a subject. Each participant completed 50 trials, which lasted about 640 s in total, including the instruction display. Structural brain scans were collected at the end of the functional imaging and lasted about 5 min.

At the end of the scanning session, participants answered the HEXACO Personality Inventory-Revised (HEXACO-PI-R) questionnaire, which evaluates major dimensions of personality with 100 questions (Lee & Ashton, 2018). The evaluated personality dimensions included: Honesty-Humility, Emotionality, Extraversion, Agreeableness, Conscientiousness, and Openness to Experience; additionally, the questionnaire evaluated Altruism Participants were not asked to fill in Schwartz's Personal Values Questionnaire because we were interested in the mental processing of values regardless of value preferences.

fMRI data acquisition

FMRI data were acquired on a 3-Tesla General Electric Medical Systems Sigma HDx at the Cardiff University Brain Research Imaging Centre (CUBRIC). BOLD signals were measured with a T2-weighted gradient EPI sequence synchronized to the task onset (the first trial) and covering the whole brain. Volumes comprised 35 slices of 3-mm thickness each, with 1-mm inter-slices spacing (repetition time (TR) = 2000 ms, echo time (TE) = 35 ms, flip angle = 80°, field of view (FOV) = 192 x 192 mm, matrix size = 64 x 64, voxel size = 3 x 3 x 3 mm^3). A total of 314 volumes per participant were acquired, giving a total scanning time of 628 s.

3D high-resolution T1-weighted anatomical images of the whole brain were acquired with a fast spoiled gradient echo sequence (FSPGR), using 190 contiguous axial slices (isotropic voxel resolution = 1 mm, TE = 3 ms, inversion time = 450 ms, flip angle = 15^o, FOV = 256 x 256 mm).

Data analysis

Ten values types were grouped into four higher order domains according to Schwartz's model (Schwartz et al., 2012; Fig. 1). These domains represented the two bipolar dimensions of the value model, and they were as follow: Openness to Change (Stimulation and Self-Direction), Conservation (Tradition, Conformity, and Security), Self-Transcendence (Universalism and Benevolence), Self-Enhancement (Power, Achievement, and Hedonism). Additionally, we contrasted each value type versus all other values types to check if any specific type was related to significantly different brain activity, as well as Anxiety-Free values (Hedonism, Stimulation, Self-Direction, Universalism, Benevolence) vs Anxiety-Based values (Tradition, Conformity, Security, Power, Achievement).

Behavioral data

For each participant, Cronbach's alpha was used to check for internal consistency of their answers in the HEXACO-PI-R questionnaire. We measured mean rating scores for each basic value type and value domain to see if there was any rating bias at the group-level, which could potentially influence fMRI data.

fMRI data

Data was analyzed using the BrainVoyager QX™ software (Brain Innovation, Maastricht, the Netherlands). FMRI data preprocessing involved 3D motion correction for head movements, slice-timing correction and temporal filtering to eliminate signal drifts (high pass filter of 0.006 Hz). Functional images were realigned to participants' structural images, normalized to Talairach space (Talairach & Tournoux, 1988), and spatially smoothed (6 mm FWHM Gaussian kernel).

Standard general linear model (GLM) approaches were used for statistical fMRI analysis. Data from one participant had to be excluded due to technical problems during data acquisition. Ten task predictor time courses were defined based on stimulus (value) onsets and offsets to regress BOLD signal changes induced by the presentation of 10 experimental conditions (10 basic value types). The predictor time courses were convolved with a standard hemodynamic response function. The task predictor modeled the processing of stimulus (value) during the first 3 s of its presentation, when no response was given yet. To denoise BOLD signal, motion confounds were modeled and added to the design matrix, using 6-12 detrended, non-correlated motion parameters and their derivates.

In additional analyses, we added rating scores from the last 2 s of stimulus presentation, when participants responded by button pressing, as parametric predictors to control for non-specific rating effects that are not exclusively related to value processing. Moreover, in separate analyses we modeled the 2-s response period with value as a main predictor and rating score as a parametric predictor. Both parametric analyses were whole-brain conjunction analyses of the main predictor and the de-meaned parametric predictor.

For each value type and participant, regression coefficients (beta estimates) were extracted. Next, multi-subject brain activation maps were generated by entering individual beta estimates into whole-brain random effect analyses. Using t-tests, we intended to find brain regions showing significant differences for the following contrasts: Self-Transcendence (Universalism and Benevolence) vs Self-Enhancement (Hedonism, Power and Achievement), and Openness to Change (Stimulation and Self-Direction) vs Conservation (Security, Tradition and Conformism). In supplementary analyses, we contrasted Anxiety-Free with Anxiety-Based values. The specified RFX GLM contrasts were balanced to compensate for the unequal number of compared conditions.

We controlled for multiple comparisons in voxel-based whole-brain analyses by applying a BrainVoyager cluster-size thresholding tool. This tool uses iterative Monte Carlo simulations to calculate a minimum cluster size for a targeted p-value and given volumetric activation map (Goebel et al., 2006 Forman et al., 1995). Only voxels within clusters that survived the estimated threshold/cluster size were considered to be significantly activated. Here, cluster thresholds were calculated based on activation maps at an uncorrected cluster-defining threshold (CDT) p-level of CDT < 0.001. This procedure resulted in a final cluster-extent threshold determined with a FWE of p = 0.05, and generated minimum cluster sizes of 486 and 324 (1x1x1 mm) voxels for Self-Transcendence vs Self-Enhancement and Openness to Change vs Conservation, respectively (and 405 voxels for Anxiety Free vs Anxiety Based condition in the supplementary analyses). Peak activation coordinates, cluster size (in 1x1x1-mm voxels), mean beta weights (representing contrast of each condition to baseline), and t-values for specific contrasts (z-transformed) were extracted for each brain region showing significant effects in the whole-brain analysis. The reverse contrasts, that is Self-Enhancement > Self-Transcendence and Openness to Change > Conservation, were also performed. They did not present any additional information. Therefore, only the sign of the t-value displayed within the previous contrasts was transformed, so positive became negative and vice versa.

Neurosynth, an automated brain mapping database housing thousands of fMRI studies, gives an opportunity to produce term-based maps (voxel- not cluster-based analysis). Neurosynth maps do not distinguish between activations and deactivations, and individual terms for which these maps are produced are not necessarily a perfect proxy for a cognitive process (as Neurosynth author(s) explains). Nevertheless, those maps can show if there is a striking discrepancy between the vast Neurosynth database and the results of an individual experiment. To compare our results with a Neurosynth map we produced a term-based map for a term "self-referential" (there was no "altruism" or other relevant terms we have used on the Neurosynth term list).

Results

Behavioral data

Personality profiles: HEXACO-PI-R

The HEXACO questionnaire answers were internally consistent: Cronbach's α was between 0.68 for Conscientiousness and 0.90 for Openness to Experience at personality dimension-level, and between 0.55 for Sentimentality and 0.91 for Forgivingness at personality facet-level. We checked average scale scores across all participants (N = 23) to see if a particular personality type predominated among our subjects. On a scale from 1 to 5, the average scores were 3.18 ± 0.69 SD for Agreeableness, 3.18 ± 0.62 SD for Emotionality, 3.38 ± 0.57 for Honesty-Humility, 3.49 ± 0.79 for Openness to Experience, 3.45 ± 0.45 for Conscientiousness, 3.49 ± 0.61 for Extraversion, and 4.04 ± 0.68 SD for Altruism. Friedman test showed no significant effect of personality dimension (χ^2 (5) = 5.95, p = 0.31).

Value ratings

The mean rating scores of value domains were comparable (max difference of 0.86 between Openness to Change and Conservation; Table 2). There was an effect of value domain on rating scores (Friedman test, χ^2 (3) = 24.22, p < .001), and effect size Cohen's d of -0.7 for Openness to Change and Conservation, and -0.4 for Self-Transcendence and Self-Enhancement. Thus, it seems that our participants were more open to change than conservative, which is to be expected in an urban population with university students. We consider these differences irrelevant to the focus of our study (Weinbach, 1989), and they are consistent with relative value priorities in data from diverse samples globally (Schwartz & Bardi, 2001).

Correlations between traits and values

Tests of association between personality profiles and value domains showed moderate positive correlations between Honesty-Humility and Self-Transcendence (r = 0.414, p = .049), Emotionality and Conservation (r = 0.483, p = .020), Openness to Experience and Openness to Change (r = 0.547, p = .007), and a moderate negative correlation between Openness to Experience and Conservation (r = -0.585, p = .003). These correlations are consistent with the theoretical conceptualisations of these traits and values (Roccas et al., 2002).

Table 2. Mean rating scores of four value domains and ten basic value types on the scale 1-5 (n=23).

Value domain	Mean rating (±SD)	Basic value type	Mean rating (±SD)
Self-Transcendence	3.73 ± 0.91	Universalism	3.61 ± 0.87
		Benevolence	3.84 ± 1.03
Self-Enhancement	3.20 ± 0.52	Power	2.48 ± 0.80
		Achievement	3.92 ± 0.67
		Hedonism	3.81 ± 0.93
Openness to Change	3.74 ± 0.78	Self-Direction	3.96 ± 0.89
		Stimulation	3.47 ± 0.95
Conservation	2.88 ± 0.58	Tradition	2.24 ± 0.75
		Conformity	3.04 ± 0.63
		Security	3.40 ± 0.97

Brain imaging data

Self-Transcendence versus Self-Enhancement

Whole-brain analysis identified three brain regions showing higher activity when participants were thinking about and rating Self-Transcendence values vs Self-Enhancement values (Fig. 3, Table 3).

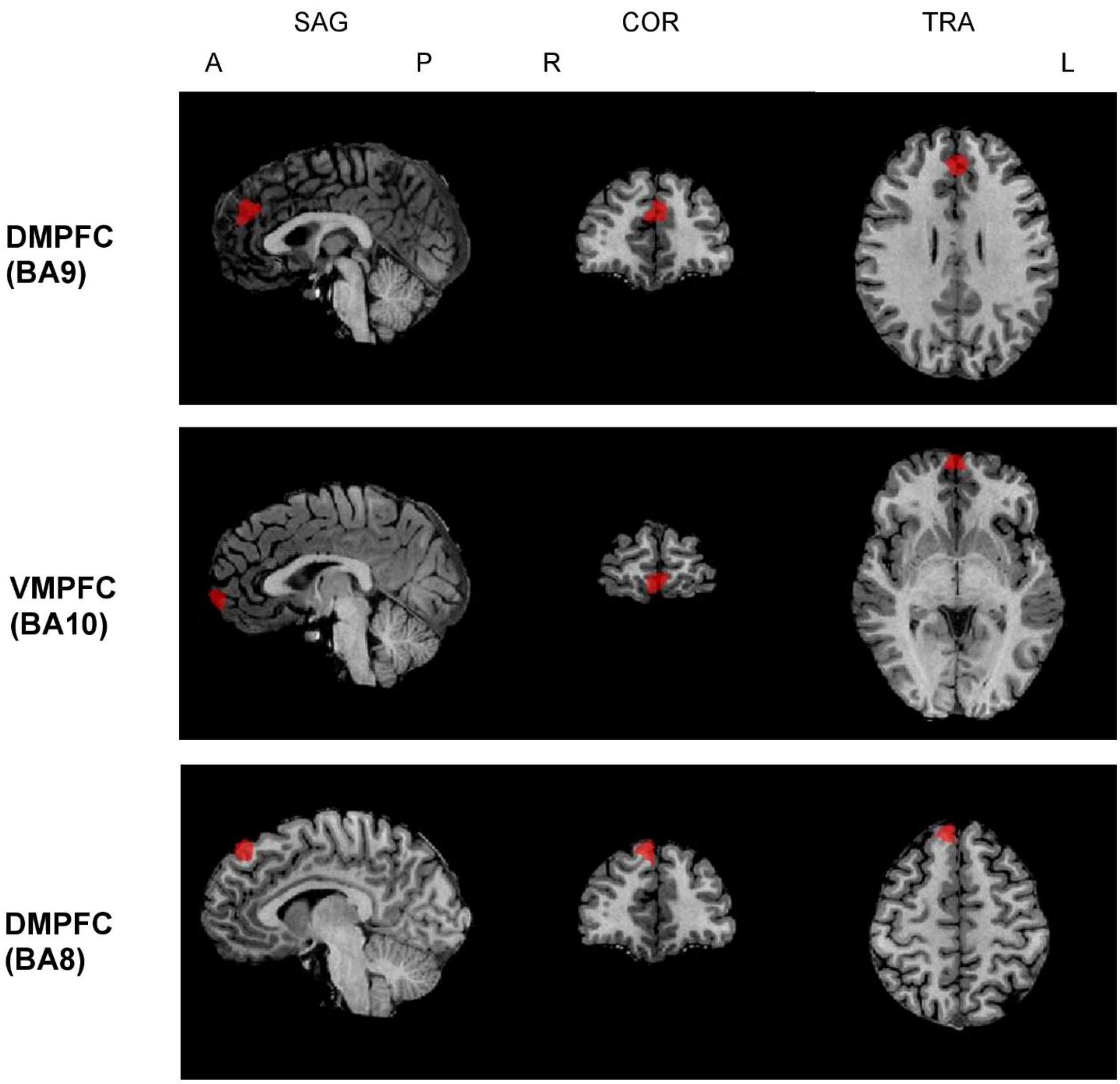


Figure 3. Brain regions showing significantly larger activation for Self-Transcendence values compared to Self-Enhancement values. DMPFC = dorsomedial prefrontal cortex; VMPFC = ventromedial prefrontal cortex; BA = Brodmann area; SAG = sagittal view; COR = coronal view; TRA = transversal view; A = anterior; P = posterior; R = right; L = left.

Table 3. Brain regions where rating Self-Transcendence values evoked significantly greater activation than rating Self-Enhancement values.

Brain region	BA	Peak coordinates of the activation cluster			Cluster size	*t*-value
		x	y	z		
DMPFC (L/R)	9	-0.38	42.46	25.76	1512	4.735
VMPFC (R/L)	10	1.63	60.32	-1.37	891	5.830
DMPFC (R)	8	6.37	41.76	47.02	792	5.289

Note: BA, Brodmann area; L, left hemisphere; R, right hemisphere; DMPFC, dorsomedial prefrontal cortex; VMPFC, ventromedial prefrontal cortex; peak coordinates, Talairach coordinates of a cluster's center of gravity; cluster size, number of 1 x 1 x 1-mm voxels in a cluster; *t*-value, the value of the comparison: Self-Transcendence > Self-Enhancement condition, with an uncorrected p-level of CDT < 0.001, and a final cluster-extent threshold of p = 0.05.

Two clusters were found in the frontal midline areas: in the DMPFC (BA9) and VMPFC (BA10). An additional more lateral cluster was found in the right DMPFC (BA8) close to the midline. A closer look at the obtained clusters showed that, in the Self-Transcendence condition, brain activity was higher compared to baseline, especially in the midline DMPFC (BA9); the opposite tendency was found in the Self-Enhancement condition, where brain activation decreased, especially in the VMPFC, or did not change compared to baseline. Mean beta weights in the identified regions, indicating relative activation levels in the two conditions, are shown in Fig. 4.

Whole-brain analyses using value rating as an additional parametric modulator did not show any significantly activated brain regions during the 3-s value processing period, indicating that the effects described above were not results of differences in value rating. Parametric analysis of the 2-s response periods showed that the effect of value during these periods was modulated by the rating score in relatively small areas in the middle and inferior occipital gyri (BA18), which did not overlap with the regions identified for Self-Transcendence vs Self-Enhancement conditions.

Openness to Change versus Conservation

Whole-brain analysis did not identify any brain regions showing significantly different activity when participants were asked to think about and rate Openness to Change values vs Conservation values.

In additional analyses, we contrasted each of the ten value types vs all other values types. Those comparisons did not reveal any brain region with differential activity for a particular type. Contrasting Anxiety-Free vs Anxiety-Based values revealed greater activity for Anxiety-free values in the VMPFC (BA10), PCC (BA24/23), and ACC (BA32) (Suppl. Fig. 1, Suppl. Table 1). Mean beta weights in these regions, indicating activation levels, are shown in Suppl. Fig. 2. The Neurosynth term-based map for “self-referential” is presented in Suppl. Fig. 3. Although our activation peaks in the DMPFC and VMPFC do not ideally overlap with clusters on the produced map, they are adjacent to those clusters.

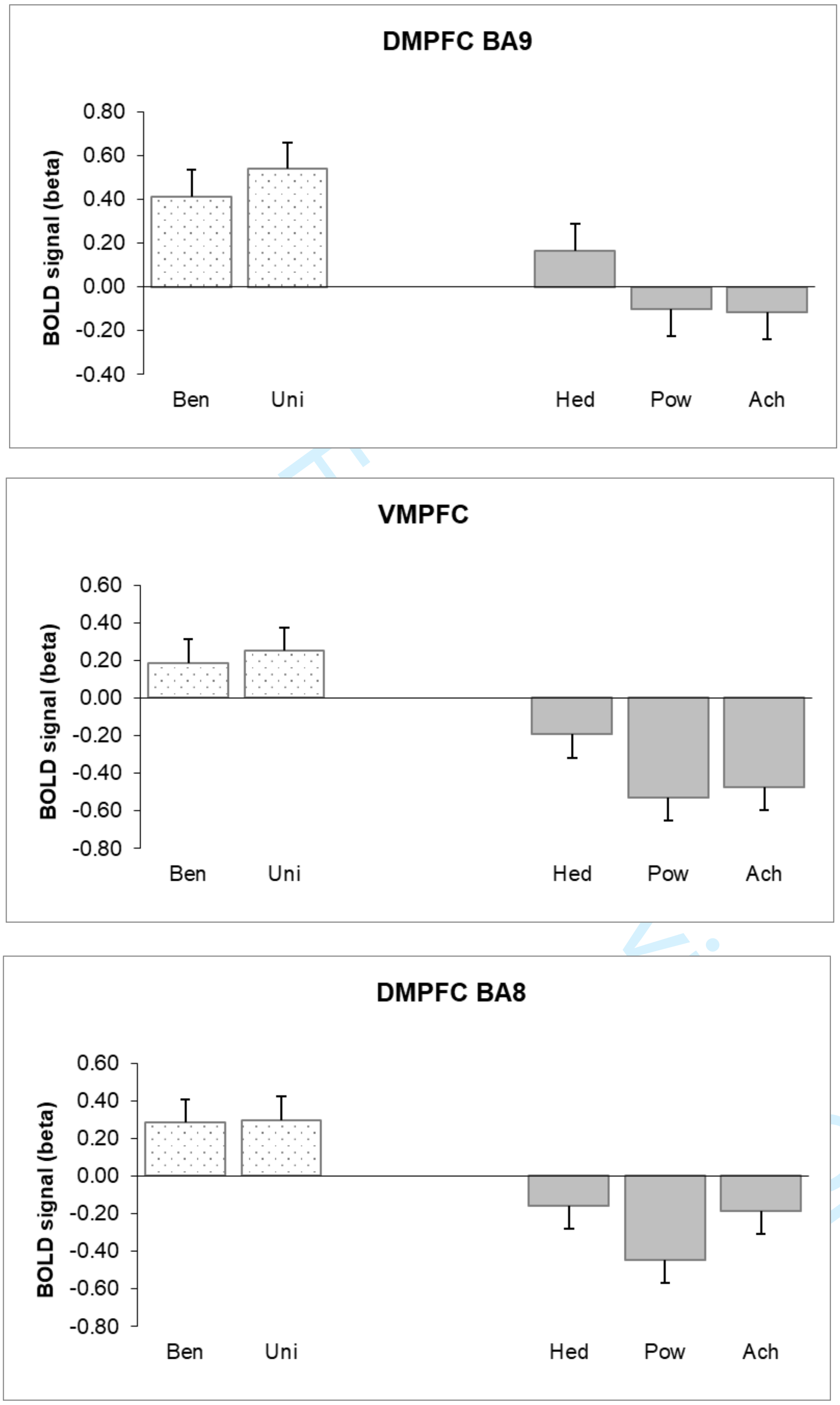


Figure 4. Mean beta weights, which correspond to relative activation levels, in brain regions where stronger activation was found for Self-Transcendence values than Self-Enhancement values. Self-Transcendence (Ben and Uni) is presented at the left and Self-Enhancement at the right (Hed, Pow, Ach). DMPFC = dorsomedial prefrontal cortex; VMPFC = ventromedial prefrontal cortex; BA = Brodmann area; Ben = Benevolence; Uni = Universalism; Hed = Hedonism; Pow = Power; Ach = Achievement.

Discussion

We found that mental processing of social values belonging to the Self-Transcendence domain from Schwartz's value model was associated with significantly higher brain activity in midline cortical regions, that is in the DMPFC (BA9 and BA8) and VMPFC (BA10), as compared to Self-Enhancement values. Moreover, the direction of BOLD signal changes across these two conditions differed. Namely, processing of Self-Transcendence values was related to increases in activity relative to baseline (most pronounced in the DMPFC), while processing of Self-Enhancement values evoked decreases in activity relative to baseline (most pronounced in the VMPFC). We did not detect any significant difference in brain activity between these two conditions in other brain regions. Processing of values from Openness to Change vs Conservation domains did not yield any significant difference in brain activation, even in the striatum, where it had previously been reported (Brosch et al., 2011). Additional analyses in which we contrasted each value type with all the other values together did not reveal any significant difference in brain activity. Yet, values which express anxiety free motivations (Anxiety-Free values) were associated with greater activation in the VMPFC, PCC, and ACC then self protection-oriented values (Anxiety-Based values). Higher cingulate activation for Anxiety-Free values might reflect less de-activation of the DMN during stimulus presentation, as suggested by beta weights corresponding to relative activation levels in both conditions. Overall, the obtained results support our hypotheses that neural representation of Self-Transcendence and Self-Enhancement values differs in the MPFC.

The MPFC activation was associated with representation and evaluation of different types of values, e.g. core and economic values (Brosch et al., 2012), value-related behaviours in the context of moral sentiments (Zahn et al., 2009), and moral functioning (Han et al., 2016). Moreover, Self-Transcendence values were associated with VMPFC activity by Kang et al. (2018), where priming self-transcendent mindset increased receptivity to health messages intervention, and by Teed et al. (2019). In Teed et al.'s (2019) experimental paradigm, MPFC activity (BA10 (x,y,z) = -12, 56, 18) was found when participants were rating their willingness to participate in activities related to Self-Transcendence vs Self-Enhancement values, but not when they were rating how worthwhile those activities were. The authors stated that willingness might represent the individual's subjective preference for an activity, while worthiness might reflect 'personal identification with the intentions and (…) norms'. This interpretation is consistent with MPFC activation found in our study, which was based on ratings of the subjective importance of social values. However, our cluster in the VMPFC (BA10) did not include the right ACC in Self-Transcendence vs Self-Enhancement condition, which contrasts with Teed et al.'s findings (2019). This could have resulted from differences in experimental paradigms because our paradigm consisted in direct examination of the neural processes while thinking about values per se whereas theirs comprised neural processes involved in rating *worthiness* of activities related to values and *willingness* to participate in these activities.

Altruism is a relevant normative behaviour, wherein a person acts with the goal of increasing another person's welfare (Wilson, 1992). Altruism is conceptually a clear behavioural instantiation of Self-Transcendence values (e.g., helpfulness; Maio, 2010), and it is therefore interesting to consider our findings in light of examinations of brain regions related to altruism. Altruistic behaviour is associated with limbic and cortical regions, including the VMPFC and DMPFC (Filkowski et al., 2016). Increased activation of the MPFC (OFC, VMPFC, DMPFC) occurs during charitable donations evoked by different motivations, e.g. empathy or inferring others' thoughts and intentions (Frith & Frith, 2006), and activity in this region discriminates between selfish and generous donation (Tusche et al., 2016). Altruistic decisions can differentially engage ventral and dorsal aspects of the MPFC. The former correlates with the subjective while the latter with the objective value of making an altruistic decision (Waytz et al., 2012; Brosch et al., 2011). Overall, our results concur with these reports: Higher activity in the DMPFC and VMPFC for Self-Transcendence than Self-Enhancement values – with the former anchored in other's welfare, and the latter linked to one's own welfare - is consistent with the neural signature of altruism.

The DMPFC was suggested as one of the key structures involved in mentalising-related altruistic decision-making and behaviour (Filkowski et al., 2016). In an interesting study, the DMPFC was found to mediate the link between mentalising (considering other people) and spending time with others: DMPFC activity during viewing of social scenes was predictive of the time spent with others on a daily basis (Powers et al., 2016). Activity in the DMPFC during a social judgement task also predicted subsequent generosity in donating money and spending time helping others (Waytz et al., 2012). The authors concluded that prosocial behaviour, such as altruism, could result from our broader tendency for social-cognitive thought rather than from affective involvement. That view corresponds with our results: Processing of prosocial Self-Transcendence vs Self-Enhancement values led to differential activity in the MPFC but not in limbic areas typically related to emotions.

Self-Enhancement values include elements of Hedonism (Schwartz et al., 2012). Yet, the reward/hedonic circuit, with its connections between the VMPFC and nucleus accumbens in the ventral striatum was not revealed for Self-Enhancement values in our study. This is not surprising though, because there was no reinforcement or reward in our paradigm, which typically activates the ventral striatum (Haber & Knutson, 2010). Furthermore, Hedonism values are on the border between Self-Enhancement and Openness to Change values, and they vary in position as a Self-Enhancement value vs an Openness to Change value between people (Schwartz, 1992). Thus, these values are only partly captured through analysis of the Self-Enhancement domain.

Our results are in line with previous reports that self-referential processes engage the MPFC. The Neurosynth term-based map shows that our clusters in the VMPFC and DMPFC are adjacent to the clusters produced for the term "self-referential". Though, we did not obtain clusters in the PCC, precuneus, or temporal regions that are visible on that map. Nonetheless, considering how the meta-analysis images are generated in Neurosynth, and Neurosynth's author(s) cautious remarks about concluding based on the maps, in our opinion the produced map does not contradict our interpretation of the results obtained in this study.

It should be noticed that greater activation in the VMPFC and DMPFC (BA8) for Self-Transcendence than Self-Enhancement values resulted not only from increases in BOLD signal in the former condition but also from signal decreases in the latter condition relative to baseline. Deactivation of the VMPFC, together with a set of other DMN structures, for various tasks was reported (Buckner et al., 2008). More specifically, VMPFC deactivation and TPJ activation accompanied difficult moral decisions, and the opposite was true for easy moral decisions, i.e. VMPFC activation and TPJ deactivation (Feldmanhall et al., 2014). VMPFC engagement in self-referential (but not other-referential) judgements involved a decrease in activation relative to baseline (Kelley et al., 2002). Thus, it seems that Self-Transcendence and Self-Enhancement values differently affect MPFC activity, so that the former involve MPFC activation while the latter are associated with its deactivation. There is no clear evidence that reflecting on Self-Enhancement values had self-memory advantage over Self-Transcendence values, or that they differed in the depth of processing, which could potentially account for that difference.

The striatum was reported in a previous study on Openness to Change values (Brosch et al., 2011). Changes in BOLD signal associated with NOGO stimuli in a GO/NOGO task, when subjects had to inhibit a habitual manual movement (pressing a response button) were indicative of the neural correlates of Openness to Change. Correct NOGO responses led to stronger activation in the ventral and dorsal striatum than NOGO error trials. In the dorsal striatum (right caudate nucleus), successful NOGO responses (response inhibition) correlated with the subjective importance of Openness to Change. Data suggest (Baez-Mendoza & Schultz, 2013) that striatal neurons activity is modulated by movements, rewards, and the conjunction of both movement and reward. There are striatal neurons, which code which action is associated to reward and which action is not. These neuronal representations serve many functions like goal directed movements and decision making. Contrary to

GO/NOGO task in Brosch et al.'s (2011) study, in our experiments there was no action nor reward - if a correct response could be subjectively perceived by an individual as a rewarding action (Schultz, 2004) - which could explain the lack of observable striatal involvement.

In conclusion, our results support the social value model developed by Schwartz, providing a neural basis for some of its foundations, including the self-other dimension, which spans Self-Enhancement and Self-Transcendence values. That (but not Openness to Change - Conservation) dimension is reflected in the MPFC. It seems that Self-Transcendence and Self-Enhancement values differently affect MPFC activity, so that the former involve MPFC activation while the latter are associated with its deactivation. Interestingly, Self-Transcendence values are associated with greater activity in both parts of the MPFC that is the VMPFC and DMPFC, which constitute a vital element in the cortical midline area, that is in a brain region where "a core self" is represented (Sui et al. 2015; Northoff & Pankseep, 2008; Northoff & Bermpohl, 2004). No other brain region, beyond the MPFC, showed a significant difference in brain activity between Self-Transcendence and Self-Enhancement values, possibly because our study did not involve execution/implementation of values, which otherwise could have engaged particular neural circuits, such as the reward system or DMN. In future studies, it will be worth examining the value model with multivariate analyses to obtain a more comprehensive picture of its neural basis

Acknowledgements

We thank Armin Heinecke from BrainVoyager for helping with optimization of fMRI data analyses. This study was supported by the National Centre for Mental Health at Cardiff University. NCMH is funded by the National Institute for Social Care and Health Research, Welsh Government, Wales (Grant No. BR09).

References

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*(4), 268–277. https://doi.org/10.1038/nrn1884

Araujo, H. F., Kaplan, J., & Damasio, A. (2013). Cortical midline structures and autobiographical-self processes: an activation-likelihood estimation meta-analysis. *Frontiers in Human Neuroscience, 7*, 548. https://doi.org/10.3389/fnhum.2013.00548

Baez-Mendoza, R., & Schultz, W. (2013). The role of the striatum in social behavior. *Frontiers in Neuroscience, 7,* 233. https://doi.org/10.3389/fnins.2013.00233

Berridge, K. C., & Kringelbach, M. L. (2015). Pleasure systems in the brain. *Neuron, 86*(3), 646–664. https://doi.org/10.1016/j.neuron.2015.02.018

Brosch, T., Coppin, G., Scherer, K., Schwartz S., & Sander, D. (2011). Generating value(s): psychological value hierarchies reflect context-dependent sensitivity of the reward system. *Social Neuroscience, 6*(2), 198-208. https://doi.org/10.1080/17470919.2010.506754

Brosch, T., Coppin, G., Schwartz, S., & Sander, D. (2012). The importance of actions and the worth of an object: dissociable neural systems representing core value and economic value. *Social Cognitive and Affective Neuroscience, 7*(5), 497–505. https://doi.org/10.1093/scan/nsr036

Brosch, T., Stussi, Y., Desrichard, O., & Sander, D. (2018). Not my future? Core values and the neural representation of future events. *Cognitive, Affective, & Behavioral Neuroscience, 18*(3), 476-484. https://doi.org/10.3758/s13415-018-0581-9

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences, 1124*, 1–38. https://doi.org/10.1196/annals.1440.011

Bzdok, D., Langner, R., Schilbach, L., Engemann, D. A., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2013). Segregation of the human medial prefrontal cortex in social cognition. *Frontiers in Human Neuroscience,* 7, e232. https://doi.org/10.3389/fnhum.2013.00232

Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A. R., Langner, R., & Eickhoff, S. B. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure & Function, 217*(4), 783–796. https://doi.org/10.1007/s00429-012-0380-y

Carter, C. S., & van Veen, V. (2007). Anterior cingulate cortex and conflict detection: An update of theory and data. *Cognitive, Affective, & Behavioral Neuroscience, 7*(4), 367–379. doi:10.3758/CABN.7.4.367

Cloutier, J., & Gyurovski, I. (2014). Ventral medial prefrontal cortex and person evaluation: Forming impressions of others varying in financial and moral status. *Neuroimage, 100*, 535–543. https://doi.org/10.1016/j.neuroimage.2014.06.024

Coelho, G. L. D. H., Hanel, P., Johansen, M. K., & Maio, G. R. (2019). Mapping the structure of human values through conceptual representations. *European Journal of Personality, 33*(1), 34-51. https://doi.org/10.1002/per.2170

Denny, B. T., Kober, H., Wager, T. D., & Ochsner, K. N. (2012) A meta-analysis of functional neuroimaging studies of self and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience, 24*(8), 1742–1752. https://doi.org/10.1162/jocn_a_00233

Eres, R., Louis, W. R., & Molenberghs, P. (2018). Common and distinct neural networks involved in fMRI studies investigating morality: an ALE meta-analysis.

Filkowski, M. M., Cochran, R. N., & Haas, B. W. (2016). Altruistic behavior: mapping responses in the brain. *Neuroscience and Neuroeconomics, 5*, 65–75. https://doi.org/10.2147/NAN.S87718

Fedota, J. R., Hardee, J. E., Pérez-Edgar, K., & Thompson, J. C. (2014). Representation of response alternatives in human presupplementary motor area: Multi-voxel pattern analysis in a go/no-go task. *Neuropsychologia, 56*, 110–118. https://doi.org/10.1016/j.neuropsychologia.2013.12.022

Feldmanhall, O., Mobbs, D., & Dalgleish, T. (2014). Deconstructing the brain's moral network: Dissociable functionality between the temporoparietal junction and ventro-medial prefrontal cortex. *Social Cognitive and Affective Neuroscience, 9*(3), 297–306. https://doi.org/10.1093/scan/nss139

Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine, 33*(5), 636–647. https://doi.org/10.1002/(ISSN) 1522-2594

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron, 50*, 531–534. https://doi.org/10.1016/j.neuron.2006.05.001

Goebel, R., Esposito, F., & Formisano, E. (2006). Analysis of functional image analysis contest (FIAC) data with Brainvoyager QX: From single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. *Human Brain Mapping, 27*(5), 392-401. https://doi.org/10.1002/hbm.20249

Haber, S. N., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology, 35*(1), 4–26. https://doi.org/10.1038/npp.2009.129

Han, H., Chen, J. E., Jeong, C., & Glover, G. H. (2016). Influence of the cortical midline structures on moral emotion and motivation in moral decision-making. *Behavioural Brain Research, 302*, (237-251). https://doi.org/10.1016/j.bbr.2016.01.001

Han, H. (2017). Neural correlates of moral sensitivity and moral judgment associated with brain circuitries of selfhood: A meta-analysis. *Journal of Moral Education, 46*(2), 97-113. ttps://doi.org/10.1080/03057240.2016.1262834

Hanel, P., Litzellachner, L., & Maio, G. (2018). An empirical comparison of human value models. *Frontiers in Psychology: Personality and Social Psychology, 9*, e1643. https://doi.org/10.3389/fpsyg.2018.01643

Hitlin, S. (2003). Values as the core of personal identity: Drawing links between two theories of self. *Social Psychology Quarterly*, *66*(2), 118-137. https://doi.org/10.2307/1519843

Israel, S., Lerer, E., Shalev, I., Uzefovsky, F., Riebold, M., Laiba, E., Bachner-Melman, R., Maril, A., Bornstein, G., Knafo, A., & Ebstein, R.P. (2009). The oxytocin receptor (OXTR) contributes to prosocial fund allocations in the dictator game and the social value orientations task. PLoS ONE, 4(5), e5535. https://doi.org/10.1371/journal.pone.0005535

Kang, Y., Cooper, N., Pandey, P., Scholz, C., O'Donnell, M. B., Lieberman, M. D., Taylor, S. E., Strecher, V.J., Dal Cin, S., Konrath, S., Polk, T. A., Resnicow, K., An, L., & Falk, E. B. (2018). Effects of self-transcendence on neural responses to persuasive messages and health behavior change. *PNAS, 115*(40), 9974-9979. https://doi.org/10.1073/pnas.1805573115

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience, 14*(5), 785–794. https://doi.org/10.1162/08989290260138672

Krienen, F. M., Tu P. C., Buckner R. L. (2010). Clan mentality: Evidence that the medial prefrontal cortex responds to close others. *Journal of Neuroscience, 30*(41), 13906-13915. https://doi.org/10.1523/JNEUROSCI.2180-10.2010

Knafo, A., & Spinath, F.M. (2011). Genetic and environmental influences on girls' and boys' gender-typed and gender-neutral values. *Developmental Psychology, 47*(3), 726-731. https://doi.org/10.1037/a0021910

Lee, K., Ashton, C. (2018). Psychometric properties of the HEXACO-100. *Assessment, 25*, 543-556. https://hexaco.org/hexaco-online, https://hexaco.org/scaledescriptions

Leszkowicz, E., Linden, D. E. J., Maio, G. R., & Ihssen, N. (2017). Neural evidence of motivational conflict between social values. *Social Neuroscience, 12*(5), 494–505. https://doi.org/10.1080/17470919.2016.1183517

Lieberman, M. D., Straccia, M. A., Meyer, M. L., Du, M., Tan, K. M. (2019). Social, self, (situational), and affective processes in medial prefrontal cortex (MPFC): Causal, multivariate, and reverse inference evidence. *Neuroscience and Biobehavioral Reviews, 99*, 311-328. https://doi.org/10.1016/j.neubiorev.2018.12.021

Li, W., Mai, X., Liu, C. (2014). The default mode network and social understanding of others: What do brain connectivity studies tell us. *Frontiers in Human Neuroscience, 8*(1), 74. https://doi.org/10.3389/fnhum.2014.00074

Lombardo, M. V., Chakrabarti, B., Bullmore, E. T., Wheelwright, S. J., Sadek, S. A., & Suckling, J., MRC AIMS Consortium, Baron-Cohen S. (2010). Shared neural circuits for mentalizing about the self and others. *Journal of Cognitive Neuroscience, 22*(7), 1623-1635. https://doi.org/10.1162/jocn.2009.21287

Maio, G. R. (2010). Mental representations of social values. In M. P. Zanna (Ed.), *Advances in Experimental Social Psychology, 42,* 1-43. Academic Press. https://doi.org/10.1016/S0065-2601(10)42001-8

Maio, G. R. (2017). *The psychology of human values. (European Monographs in Social Psychology)* (1st ed.). Routledge.

Maio, G. R., Pakizeh A., Cheung W-Y., & Rees, K. J. (2009). Changing, priming, and acting on values: Effects via motivational relations in a circular model. *Journal of Personality and Social Psychology, 97*(4), 699-715. https://doi.org/10.1037/a0016420

Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron, 50*(4), 655–663. https://doi.org/0.1016/j.neuron.2006.03.040

Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the*

National Academy of Sciences U S A, 103(42), 15623-15628. https://doi.org/10.1073/pnas.0604475103

Moll, J., Zahn, R., De Oliveira-Souza, R., Krueger, F., & Grafman, J. (2005). Opinion: The neural basis of human moral cognition. *Nature Reviews Neuroscience, 6*(10), 799–809. https://doi.org/10.1038/nrn1768

Murray, R. J., Schaer, M., & Debbane, M. (2012). Degrees of separation: a quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. *Neuroscience & Biobehavioral Reviews, 36*(3), 1043–1059. https://doi.org/10.1016/j.neubiorev.2011.12.013

Nicolle, A., Klein-Flügge, M. C., Hunt, L. T., Vlaev, I., Dolan, R. J., & Behrens, T. E. (2012). An agent independent axis for executed and modelled choice in medial prefrontal cortex. *Neuron, 75*(6), 1114–1121. https://doi.org/10.1016/j.neuron.2012.07.023

Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences, 8*(3), 102-107. https://doi.org/1016/j.tics.2004.01.004

Northoff, G., Heinze, A., Greck, M. De, Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain – a meta-analysis of imaging studies on the self. *Neuroimage, 31*(1), 440–457. https://doi.org/10.1016/j.neuroimage.2005.12.002

Northoff, G., & Panksepp, J. (2008). The trans-species concept of self and the subcortical-cortical midline system. *Trends in Cognitive Sciences, 12*(7), 259-264. https://doi.org/10.1016/j.tics.2008.04.007

Powers, K. E., Chavez, R. S., & Heatherton, T. F. (2016). Individual differences in response of dorsomedial prefrontal cortex predict daily social behavior. *Social Cognitive and Affective Neuroscience, 11*(1), 121-126. https://doi.org/10.1093/scan/nsv096

Roccas, S., Sagiv, L., Schwartz, S. H., & Knafo, A. (2002). The big five personality factors and personal values. *Personality and Social Psychology Bulletin, 28*(6), 789–801. https://doi.org/10.1177/0146167202289008

Rokeach, M. (1973). *The nature of human values*. Free Press.

Rolls, E. T., Cheng, W., & Feng, J. (2020). The orbitofrontal cortex: reward, emotion and depression. *Brain Communications*, *2*(2), fcaa196. https://doi.org/10.1093/braincomms/fcaa196

Schermer, J. A., Vernon, P. A., Maio, G. R., & Jang, K. L. (2011). A behavior genetic study of the connection between social values and personality. *Twin Research and Human Genetics, 14*(3), 233-239. https://doi.org/10.1375/twin.14.3.233

Schwartz, S. H. (1992). Universals in the content and structure of values: Theoretical advances and empirical tests in 20 countries. In M. Zanna (Ed.), *Advances in experimental social psychology* (pp. 1–65). Orlando, FL: Academic Press. https://doi.org/10.1016/S0065-2601(08)60281-6

Schwartz, S. H., & Bardi, A. (2001). Value hierarchies across cultures: Taking a similarities perspective. *Journal of Cross-Cultural Psychology, 32*(3), 268–290. https://doi.org/10.1177/0022022101032003002

Schwartz, S. H., Cieciuch, J., Vecchione, M., Davidov, E., Fischer, R. Beierlein, C., Ramos, A., Verkasalo, M., Lönnqvis, J-E., Demirutku, K., Dirilen-Gumus, O., & Konty, M. (2012). Refining the theory of basic individual values. *Journal of Personality and Social Psychology, 103*(4), 663-688. https://doi.org/10.1037/a0029393

Schultz, W. (2004). Neural coding of basic reward terms of animal learning theory, game theory, microeconomics and behavioural ecology. *Current Opinion in Neurobiology, 14*(2), 139–147. https://doi.org/10.1016/j.conb.2004.03.017

Sevinc, G., & Spreng, R. N. (2014). Contextual and perceptual brain processes underlying moral cognition: a quantitative meta-analysis of moral reasoning and moral emotions. *PLoS One, 9*(2), e87427. https://doi.org/10.1371/journal.pone.0087427

Sui, J., Enock, F., Ralph, J., & Humphreys, G. W. (2015). Dissociating hyper and hypoself biases to a core self-representation. *Cortex, 70*, 202-212. https://doi.org/10.1016/j.cortex.2015.04.024

Sul, S., Tobler, P. N., Hein, G., Leiberg, S., Jung, D., Fehr, E., & Kim, H. (2015). Spatial gradient in value representation along the medial prefrontal cortex reflects individual differences in prosociality. *Proceedings of the National Academy of Sciences, 112* (25), 7851-7856. https://doi.org/10.1073/pnas.1423895112

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotactic atlas of the human brain*. Stuttgart: Thieme.

Teed, A., Rakic J., Mark, D. B., & Krawczyk, D. C. (2019). Relative activation patterns associated with self-transcendent and self-enhancement core values: an fMRI study of basic human values theory concepts in males. *Social Neuroscience, 25*(1), 1-14. https://doi.org/10.1080/17470919.2019.1598893

Tusche, A., Böckler, A., Kanske, P., Trautwein, F. M., & Singer, T. (2016). Decoding the charitable brain: Empathy, perspective taking, and attention shifts differentially predict altruistic giving. *Journal of Neuroscience, 36*(17), 4719–4732. https://doi.org/10.1523/JNEUROSCI.3392-15.2016

Van Overwalle, F. (2011). A dissociation between social mentalizing and general reasoning. *Neuroimage, 54*(2), 1589–1599. https://doi.org/10.1016/j.neuroimage.2010.09.043

van Veluw S. J., Chance S. A. (2014). Differentiating between self and others: an ALE meta-analysis of fMRI studies of self-recognition and theory of mind. *Brain Imaging and Behavior 8*(1), 24-38. https://doi.org/10.1007/s11682-013-9266-8. PMID: 24535033

Wagner D. D., Haxby, J. V., Heatherton, T. F. (2012). The representation of self and person knowledge in the medial prefrontal cortex. *Wiley Interdisciplinary Reviews: Cognitive, 3*(4), 451–470. https://doi:10.1002/wcs.1183

Waytz, A., Zaki, J., & Mitchell, J. P. (2012). Response of dorsomedial prefrontal cortex predicts altruistic behavior. *Journal of Neuroscience, 32*(22), 7646–7650. https://doi.org/10.1523/JNEUROSCI.6193-11.2012

Weinbach, R. W. (1989). When is statistical significance meaningful? A practice perspective. *The Journal of Sociology & Social Welfare, 16*(1), 31-37. https://scholarworks.wmich.edu/jssw/vol16/iss1/4

Wilson, D. S. (1992). On the relationship between evolutionary and psychological definitions of altruism and selfishness. *Biology & Philosophy, 7*(1), 61–68. https://doi.org/10.1007/BF00130164

Zacharopoulos, G., Lancaster, T. M., Bracht, T., Ihssen, N., Maio, G. R., & Linden, D. E. J. (2016a). A hedonism hub in the human brain. *Cerebral Cortex, 26*(10), 3921-3927. https://doi.org/10.1093/cercor/bhw197

Zacharopoulos, G., Lancaster, T. M., Maio, G. R., & Linden, D. E. (2016b). The genetics of neuroticism and human values. *Genes, Brain and Behavior, 15*(4), 361-366. https://doi.org/10.1111/gbb.12286

Zacharopoulos, G., Hanel, P. H. P., Lancaster, T. M., Ihssen, N., Drakesmith, M., Foley, S., Maio, G. R., & Linden, D. E. J. (2017). Nonlinear associations between human values and neuroanatomy. *Social Neuroscience, 12*(6), 673-684. https://doi.org/10.1080/17470919.2016.1229215

Zahn, R., Moll, J., Paiva, M., Garrido, G., Krueger, F., Huey, E. D., & Grafman, J. (2009). The neural basis of human social values: evidence from functional MRI. *Cerebral Cortex, 19*(2), 276–283. https://doi.org/10.1093/cercor/bhn080

Zelinková, J., Shaw, D. J., Mareček, R., Mikl, M., Urbánek, T., Havlíčková, D., Zámečník, P., Haitová, P., & Brázdil, M. (2014). An evaluation of traffic awareness campaign videos:

Empathy induction is associated with brain function within superior temporal sulcus.

Behavioral and Brain Functions, 10, e27. https://doi.org/10.1186/1744-9081-10-27