Non-linear Associations between Human Values and Neuroanatomy

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Abstract

Human values guide behaviour and the smooth functioning of societies. Schwartz's circumplex model of values predicts a sinusoidal waveform in relations between ratings of the importance of diverse human value types (e.g., achievement, benevolence) and any variables psychologically relevant to them. In this neuroimaging study, we examined these non-linear associations between values types and brain structure. In 85 participants, we found the predicted sinusoidal relationship between ratings of values types and two measures of white matter, volume and myelin volume fraction, as well as for grey matter parameters in several frontal regions. These effects reveal new functional associations for structural brain parameters and provide a novel cross-validation of Schwartz's model. Moreover, the sinusoidal waveform test can be applied to other circumplex models in social, affective and cognitive neuroscience.

Keywords: human values, MRI, non-linear associations

INTRODUCTION

The world "value" has at least two sub-definitions. According to the Oxford Dictionary of English, it can denote "the material or monetary worth of something" and "the principles or standards of behaviour, one's judgment of what is important in life" (Soanes & Stevenson, 2003). The former meaning relates to the study of values in the context of neuroeconomics, while the latter meaning relates to the study of values in the social cognitive context of culture, political ideology, morality, and attitudes. The present work is primarily focused on the latter definition.

In this latter context, human values are regarded as part of the psychological foundations for ethical behaviour and a crucial element in social functioning (Turiel, 1983). Allport's seminal "Study of values" (1960) proposed six value types, representing the kind of future activity that one wishes to perform (e.g., "social" values entail helping people and occupations such as social work, whereas "theoretical" values involve the search for truth and occupations such as scientific study). Subsequent theories emphasize that values should be assessed as idealized standards that have an ''ought'' character, rather than a mere assessment of subtle likes and dislikes toward activities and occupations. For example, Rokeach (1973) developed a list of thirty-six values and asked people to rank them in terms of their importance, finding that the relative differences in value importance are more psychologically meaningful than the importance of any single value on its own.

The relations between values are the central feature of the most widely used models of values at this time: Schwartz's (1992) circumplex model and its closely linked successor (Schwartz et al., 2012). The circumplex model of human values (Schwartz 1992) posits the existence of 10 value types (e.g., achievement, power), each of which comprises several individual values. The 10 value types are organized along two value dimensions. One dimension contrasts motives to promote the self (self-enhancement) against motives that

transcend personal interests (self-transcendence), while the other dimension contrasts motives to follow the status quo (conservation) against motives to pursue personal intellectual and emotional interests in uncertain directions (openness). The motivational relations between the human value types form the basis for organizing them into value dimensions, which have been revealed through two-dimension smallest space analysis and multidimensional scaling of ratings of value importance (Schwartz and Bliksly, 1987; Schwartz, 1992), while being confirmed with confirmatory factor analysis (Schwartz & Boehnke 2004).

Figure 1. The circumplex structure of personal values (modified from Schwartz, 1992)

Compared to other models, Schwartz's theory has received extensive validation (Schwartz, 1992). The consistent support for the model recently led to a revised version containing 19 value types, but subsumes the same higher-order dimensions as the earlier model and the same predictions about patterns of relations between values and external values (Schwartz et al., 2012). In fact, these dimensions are apparent in patterns of interrelations between the value types across samples from over 70 nations (Schwartz et al., 2012).

The extensive cross-cultural support may imply that values express motives that have been evolutionarily conserved. Relevant to this possibility, one characteristic feature of this circumplex model of values is that it makes specific predictions about *sinusoidal* associations between social values and external variables. In other words, if the values are ordered according to their positions along the value circle, then an external variable that is positively related to a particular value type should manifest lower positive correlations with adjacent values and an opposing relation with the opposing value type. This pattern should follow a sine wave, similar to those shown in Figure 2.

Figure 2. Plot of hypothesized relationships between three external variables (A, B, C) and the 10 Values (SD= Self-direction, ST=Stimulation, HE=Hedonism, AC=Achievement, PO=Power, SE=Secirity, CO=Conformity, TR=Tradition, BE=Benevoelnce, UN=Universalism). Each point in a curve represents a hypothetical correlation (adapted from Schwartz 1992).

This prediction has indirectly received support in many studies that have sought evidence that values at opposite ends of the circumplex model exhibit opposing relations to other judgments and behavior (see Maio, 2010; Schwartz et al., 2012). This approach is less precise than methods specifically looking at sinusoidal tests of patterns of associations between values and other variables, but one study has recently found evidence of a sinusoidal pattern in relations between values and personality traits (Parks-Leduc, L., Feldman, G., & Bardi, A., 2014). This pattern supports the model's assumptions about latent motivational conflicts, and, together with evidence of genetic contributions (Knafo & Spinath, 2011; Schermer, Vernon, Maio, & Jang, 2011), suggests that some aspects of human value orientation are entrenched in biological traits. Indeed, the polygenic score of neuroticism has been recently shown to be associated (Zacharopoulos et al., 2016) to all ten human value types in a sinusoidal manner as predicted by the Schwartz's circumplex model of values.

The present work focuses on the neurostructural properties of the motivational underpinning of human value orientations. To be clear, our chief interest was whether the motivational conflicts described in Schwartz's model have neurological components. That is, we did not focus on specific values, but devised a test of the roles of value types organized along the two motivational dimensions described by Schwartz. This focus enabled us to rely

upon the motivational aspects of values predicted by the model – aspects which are distinct from the abstract meaning of specific values per se (Schwartz & Bilsky 1987).

Values and Brain Anatomy

Whether this putative evolutionarily conserved set of values and their latent conflicts might be reflected in brain anatomy has hitherto not been explored. We can test this by assessing whether human values also exhibit a sinusoidal relationship with brain anatomical parameters (i.e. volume, myelin volume fraction).

Our knowledge regarding the brain correlates of human values is diverse, including evidence derived from functional and structural brain imaging studies of associations with values and value-related traits (Kanai & Rees, 2011) and from specific moral deficits in patients with brain lesions (Koenigs et al., 2007). These studies illustrated the role of cortical, mainly frontal regions, as well as subcortical cortices as the neural machinery in processing human values and morally-relevant behaviours. With regard to values, Zahn et al. (2009) demonstrated that values' abstract (i.e. context-independent) meaning is represented in the right superior anterior temporal lobe, whilst the motivational properties of values are represented in frontal and subcortical areas. A recent subcortical neurostuctural study from our group demonstrated that the value of hedonism is positively related to the volume of the left globus pallidus (Zacharopoulos et al, 2016). In addition, Brosch et al. (2011) found that subjective human value ratings correlated with activation in the anterior prefrontal cortex and insula, whereas reading examples of actions reflecting human values (e.g., correcting injustice) and reflecting on the importance of these values activated the medial prefrontal cortex.

In the context of motivational properties of value-related behaviour, Moll et al (2012) demonstrated that affiliative emotion (induced by kinship-related social scenarios) is

associated with activation of basal forebrain structures, especially the septo-hypothalamic area. Moreover, in an examination of one type of value-related behaviour, prosociality, Moll et al. (2006) showed that the subgenual cingulate cortex and septal region were selectively activated for donations vs selfish rewards, and the same regions tracked individual differences in beliefs about family entitativity (i.e., the perception of a group as a pure entity), which are similar to family-related values, such as family security (Rusch et al., 2014). In other studies, pictures or narratives of moral violations activated the orbitofrontal gyrus and the medial prefrontal cortex (Moll et al., 2002; Berthoz et al., 2002; Takahashi et al., 2004), and the medial PFC and OFC were involved when participants engaged in costly and non-costly monetary decisions to oppose societal causes (Moll et al., 2006). Ventromedial PFC and OFC were also involved in a condition facilitating mutual cooperation in the Prisoner's Dilemma (Rilling et al., 2002), and patients with medial frontal and orbitofrontal deficits demonstrate abnormalities in morally relevant behaviours (Ward, 2012).

Studies of brain anatomy have also explored psychological variables related to human values, but distinct from them. These variables include political attitudes, personality traits, and moral beliefs. With regard to political attitudes, Kanai, Feilden, Firth and Rees (2011) found that greater liberalism was associated with increased grey matter volume in the anterior cingulate cortex and that greater conservatism was associated with increased volume of the right amygdala. However, the links between these political ideologies and values is unclear, because ideologies are related to multiple values (e.g., liberalism to the value dimensions of self-transcendence, self-enhancement) in ways that vary across nations and not to any particular values distinctly (e.g., Ashton et al., 2005; Greenberg & Jonas, 2003).

With regard to personality traits, Gardine et al. (2009) investigated the association between grey matter volume and personality scores using the Three-dimensional Personality Questionnaire. Higher novelty seeking, an inclination similar to Schwartz's stimulation

values, was associated with more grey matter volume in the right frontal and posterior cingulate regions. Higher reward dependence, similar to Schwartz's hedonism value, was correlated with less grey matter volume in the caudate nucleus and in the rectal gyrus, a part of the frontal lobe. Persistence, a tendency conceptually related to Schwartz's achievement value, showed a positive correlation with grey matter volume in the precuneus, paracentral lobule and parahippocampal gyrus. Thus, traits that are associated with some of the values in Schwartz's model, including the portion covering self-enhancement and openness values in particular, were empirically linked to brain morphology in this study.

Links between moral beliefs and brain structure have been also been investigated. In a voxel-based morphometry (VBM) study of the relationship between grey matter volume and scores on the Moral Foundation Questionnaire, Lewis et al. (2012) found that moral individualizing (conceptually similar to Schwartz's self-enhancement) was positively associated with grey matter volume in the dorsomedial prefrontal cortex and negatively with grey matter volume in the bilateral precuneus. Conversely, moral binding (conceptually similar to Schwartz's conservation value dimensions, Boer and Fischer (2013)) was positively associated with grey matter volume in the bilateral subcallosal gyrus of the frontal lobe.

Overall, previous studies have found some structural brain correlates of psychological variables that are relevant to values, but the past research was not designed to examine structural correlates of values directly. Schwartz's model offers an opportunity to close this gap through its description of motivational dimensions in values. Together, the prior findings suggest that value-relevant judgements are supported by a number of brain regions, but with particular relevance to the frontal regions where the motivational functioning of values is concerned.

The Present Research

The present study directly examined brain structural correlates of the Schwartz value system for the first time. To test the model's applicability in this context robustly, we specifically applied a sinusoidal waveform test appropriate to the model's predictions regarding motivational conflicts and compatibility between values, based on the full set of value types. The sinusoidal pattern of relations is more specific to this motivational pattern than the mere detection of linear associations without any theoretical foundation, which is beset by multiple testing problems. To enhance the power of the study, we initially focused our sinusoidal analysis on gross brain parameters, white and grey matter volume across the whole brain, and regions in the frontal lobe, all of which were selected on the basis of the neuropsychological literature (Lewis et al., 2012, Rilling et al., 2002).

METHODS

Participants

Eighty-five right-handed Caucasian university students between 19 and 42 (55 females; mean age=24.03 ± 4.025 SD) participated in the study as part of an imaging cohort that underwent detailed phenotyping and genotyping. Data from the same participants were used in our study of subcortical volume correlates of human values (Zacharopoulos et al., 2016). Participants were informed that the study examined value-morality judgments with anatomical neuroimaging. Participants gave written informed consent, and the study was approved by the local ethics committee of Cardiff University. Human value scores beyond three standard deviations away from the mean were excluded from the analysis (to induce normality): specifically, if a participant had a score falling beyond three standard deviations in a particular value, we merely excluded the outlier score and not all the value scores of that participant. We therefore made one exclusion for each of six participants, excluding (1) conformity (conservation), (2) myelin volume faction, (3) hedonism (openness and self-enhancement), (4) security, or (5) achievement (6) myelin volume fraction.

Human Values

Participants completed the Schwartz value survey (SVS; Schwartz, 1992), which was administered in the laboratory prior to the scanning session. This is a 56-item scale that can be used to measure the value types shown in Figure 1. Participants are asked to rate the importance of each of the 56 values as a guiding principle in their lives, using a quasi-bipolar 9-point scale ranging from -1 (opposed to my values), 0 (not important), 4 (important), to 7 (of supreme importance). Examples of SVS items are as follows: "Equality: Equal opportunity for all" (Universalism); "Pleasure: Gratification of desires" (Hedonism); "Obedient: Dutiful meeting obligations" (Conformity). The average score across the 56 items was calculated and subtracted from each of the 56 initial raw scores, prior to calculating the average of the value scores within each of the 10 value types. Schwartz recommends this procedure to help control for superfluous individual variations in rating styles (e.g. Schwartz, 1992). The reliability for the values was moderate to good (see, Supplementary Material 2).

MATRICS Consensus Cognitive Battery

Participants completed all seven cognitive domains of the MATRICS Consensus Cognitive Battery (Nuechterlein & Green, 2006): Speed of processing (Brief Assessment of Cognition in Schizophrenia (BACS): Symbol-Coding, Category Fluency: Animal Naming, Trail Making Test: Part A), Attention/Vigilance (Continuous Performance Test—Identical Pairs (CPT-IP), Working memory (Wechsler Memory Scale®—3rd Ed. (WMS®-III): Spatial Span, Verbal learning Hopkins Verbal Learning Test—Revised™ (HVLT-R™), Visual learning Brief Visuospatial Memory Test—Revised (BVMT-R™), Reasoning and problem solving (Neuropsychological Assessment Battery® (NAB®): Mazes, Social cognition (Mayer-Salovey-Caruso Emotional Intelligence Test (MSCEIT™): Managing Emotions).

MRI Data Acquisition

MRI images were acquired with a General Electric 3T scanner equipped with an 8HR Brain parallel head coil for radio frequency transmission/reception. Anatomical high-resolution T1-weighted volume scans (1 mm^3) were acquired using FSPGR 256*192 3-D sequence (TR=7.849ms; TE=2.984ms; field of view=256x256 mm; voxel size=1x1x1 mm).

Structural Imaging Processing

VBM pre-processing and statistical analysis was performed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). All structural images were visually checked for artefacts. Customized T1 templates and prior images of grey Matter (GM), white matter (WM) and cerebrospinal fluid (CSF) were created from all participants. For the segmentation, we followed the steps provided by the SPM8 guidelines (light bias regularisation (0.001), 60mm bias FWHM cut-off, warping regularisation of 4, affine regularisation to the ICBM European brain template (linear registration), sampling distance of 3). The normalization was performed using the DARTEL method and the images were modulated only by the non-linear component (i.e., the affine scaling factor was ignored). Finally, the images were smoothed (Ashburner & Friston, 2000) with a Gaussian kernel of 8mm (FWHM), whereby the intensity of each voxel was replaced by the weighted average of the surrounding voxels.

Relaxometry MRI acquisition

Myelin measures were derived using Multi-Component Driven Equilibrium Single Pulse Observation of T1 and T2 (mcDESPOT) (Deoni et al., 2008). The acquisition consists of Spoiled Gradient Recall (SPGR) images across eight flip angles, one inversion recovery SPGR (IR-SPGR) and steady-state free precession (SSFP) images across eight flip angles and two phase-cycling angles. All images were acquired in a 3T GE HDx MRI system (General Electric Healthcare). A total of 25 images were acquired for each subject. All images were acquired in sagittal orientation with a slice matrix of 128x128 (1.72x1.72mm resolution) with

a minimum of 88 slices (slice thickness = 1.7mm). Additional slices were added for some subjects to ensure full head coverage.

Sequence-specific parameters were: SPGR: TE=2.112ms, TR=4.7ms, flip angles = 3°, 4°, 5°, 6°, 7°, 9°, 13° and 18°. IR-SPGR: TE=2.112ms, TR=4.7ms, IR=450ms, flip angle = 5°. SSFP: TE = 1.6ms TR=3.2ms, flip angles of 10.59°, 14.12°, 18.53°, 23.82° 29.12° 35.29°, 45°, 60° and phase-cycling angles of 0° and 180°.

mcDESPOT processing

All images were linearly coregistered to the 13° SPGR image to correct for subject motion. Non-brain tissue was removed using a mask computed with the BET algorithm [Smith, 2002]. Registration and brain masking were performed with FSL (http://www.fmrib.ox- .ac.uk/fsl/) The images were then corrected for B1 inhomogeneities and off-resonance artefacts, using maps generated from the IR-SPGR and 2 phase-cycling SSFP acquisitions, respectively. The 3-pool mcDESPOT algorithm was then used to identify a fast (water constrained by myelin) and slow (free-moving water in intra- and extra-cellular space) components of the T1 and T2 times, and a non-exchanging free-water component (Deoni et al., 2013). The fast volume fraction was taken as a map of the myelin-water fraction.

Voxel-based Morphometry (VBM)

Voxel-based morphometry, implemented in SPM8 (http://www.fil.ion.ucl.ac.uk/spm) and MATLAB 7.9 (Math-Works, Natick, MA, USA), was utilised to probe the association between human value scores and the white (and grey matter) volume. First, MR images were segmented into GM, WM and CSF by utilising a method used previously (Ashburner & Friston, 2005). The covariates entered in the design matrix were the gender and age of the participants. We initially identified the clusters of voxels that exceeded an uncorrected threshold of voxel-wise $p<0.001$. To control for multiple comparisons, we applied a family-

wise error (p(corr)<0.05) correction across the whole-brain volume at a cluster level using non-stationary correction. Regular normalisation (healthy controls) was used in the study. The data were pre-processed and analyses using SPM8 using the VBM8 toolbox.

Grey and White Matter Structures-Based Correlation Analysis

Cortical reconstruction and volumetric segmentation of 32 cortical (64 in total, Left and Right regions in Supplementary Material 7) and 7 subcortical (14 in total, Left and Right: Amygdala, Accumbens, Caudate, Hippocampus, Pallidum, Putamen, Thalamus) areas (Deskian atlas) was performed with the FreeSurfer image analysis suite, which is documented and freely available for download on-line (surfer.nmr.mgh.harvard.edu). These variables we corrected for age gender and Intracranial Volume (ICV). The ICV was extracted using the toolbox VBM8 on SPM8 instead of Free Surfer, because it was previously suggested (http://freesurfer.net/fswiki/eTIV) that researches may use calculate the ICV from an image modality other than Free Surfer when possible. All correlation analyses were performed on the Software Package for Social Sciences (SPSS for Windows version 19.0).

Sinusoidal Relationship Analysis

To test the sinusoidal pattern, we employed a new methodology (Zacharopoulos et al., 2016; Hanel et al., 2016) and an established one (Boer & Fischer, 2013, Supplementary Material 6). We focus here on the new, more conservative approach, but parallel findings for the other test are described in Supplementary Material 6.

To test the sinusoidal pattern for every brain anatomy measure, the correlation coefficients with the 10 value types were calculated. The fit of the sinusoidal function presented below (1) was calculated using the programming language R

$$(1) \qquad \hat{y} = f(x) = a + b*\sin(c*x + d)$$

where ŷ are the estimated numerical values (e.g., estimated correlation coefficients), x is a vector containing the numbers 1 to 10, the parameter a is the y-offset that moves the function up and down along the ordinate (y-axis), the parameter b determines amplitude of the sinus wave on the y-axis, the parameter c is the period of the sine wave and finally the parameter d (x-offset) moves the sinusoidal function along the x-axis.

The script that was written to calculate the sinusoidal fit index is composed of build-in mathematical functions available in R. Here we provide a description of the main functions used in the Sinusoidal Fit Index. To optimize the four parameters (a, b, c, d) of the sine function (equation 1) we used the 'brute force method', an exploration approach utilised to determine the starting points for the actual optimization function, using the R command optim (general-purpose optimization function, https://stat.ethz.ch/R-manual/R-devel/library/stats/html/optim.html). This is because the R command optim that is often used for optimizations, only searches for local minima (i.e., stabilizes to the closest local minima) – as do all optimization algorithms. The optim function takes 4 arguments-inputs (the a, b, c, and d of the eq1 and produces 4 outputs through Nelder–Mead, quasi-Newton and conjugate-gradient algorithms (Nelder & Mead, 1965; Nash, 1990). For all the parameters a, b, c, and d 50 numerical values were selected, resulting in 50x50x50x50 = 6,250,000 combinations. Specifically, we tested which of 6,250,000 combinations of the parameters a, b, c, and d of the sinusoidal function results in a sine function that has the smallest deviation to the empirical data. The selection of numerical values (i.e., the 6,250,000 combinations) was done to achieve both a range that is as large as necessary – more combinations can increase the fit slightly – but still manageable in computational terms.

For each parameter, the numerical values were selected from a specific range according to the theoretical predictions of Schwartz (1992) and Schwartz et al. (2012). The

50 numerical values selected for the parameter a were -1, -.96, -.92, …, .96, 1. In other words the values of parameter a were restricted from -1 to 1 because this is the range within which a correlation coefficient can range. For the same reason, the same restrictions were applied to parameter b, which determines amplitude of the sinus wave on the y-axis (i.e., the distance between the turning points of the sinusoidal function). The parameter c, the period of the sine wave, was restricted to range from 85-95% of a full sine wave. This restriction was based on the circular model's assumption that "the distances between the values around the circle may not be equal" (Schwartz et al., 2012, p. 669). Given that the first value type was plotted at x = 1, the parameter d (x-offset), which moves the sinusoidal function along the x-axis, was set to the interval [1 + 10/2, 1 – 10/2]. The parameter d was restricted by 10 which is the number of correlation coefficients between the external variable and the 10 value types. This is because there was no hypothesis regarding the exact starting point of the sine wave for each brain parameter. To be able to define a lower and upper bound given these constraints, a method developed by Byrd, Lu, Nocedal, and Zhu (1995) was used.

We calculated the sum of the squared residuals divided by the variance to estimate the model fit indices for the sinusoidal function. This fit is called, for the sinusoidal function, "Sinusoidal Fit Index" (SFI) (Hanel, Zacharopoulos, Megardon & Maio, 2016) and is presented below (2).

$$(2)\ SFI = \frac{\frac{1}{K-1}\sum_{k=1}^{K}(y_k - \hat{y}_k)^2}{\frac{1}{K-1}\sum_{k=1}^{K}(y_k - \bar{y}_k)^2}$$

In this equation (2), K represents the number of correlation coefficients, yk represents the correlation coefficients, ŷk represents the estimated correlation coefficient through the optimization function, and yk represents the mean of the correlation coefficients. The denominator is the formula for the variance.

To obtain the number of false-positive results for the SFI, three simulations of m = 100,000 samples each were conducted with the programming language R. To simulate a random pattern of correlation coefficients, we tested different assumptions of the distribution of the correlation coefficients. (1) We sampled 10 numbers (i.e., number of human values) between -.5 and .5, with k being the number of correlation coefficients, assuming a uniform distribution. The numbers -.5 to .5 represent the interval in which most correlation coefficients of values with external variables usually fall. (2) We sampled k numbers from a normal distribution with ~N(0, .1), and (3) ~N(0, .3). Numbers >|1| were restricted to -1 or 1, respectively.

The proportion of false positives was well below 1% for all three different simulations for SFI < .20. The percentage of false positives was slightly larger if a uniform distribution was assumed. The percentage of false positives for an SFI < .20 was 0.49 (i.e., less than 5 false positive results per one thousand comparisons) assuming normal distribution. This means that 200 SFI tests will yield merely one false positive result. Therefore, our statistical threshold is considerably more conservative than typical statistical thresholds (i.e., p<.05). The percentage of false positives were 0.20%, 0.05% and 0.005% for SFI <.15, SFI <.10 and SFI < .05, respectively. Please note that the main reason for our cut-off values (SFI < .20 etc.) were not the results of the simulations, but the careful examination of many plots. An SFI of < .20 can still be considered as following a sine wave, but it is harder to recognize an SFI of .30 as following a sine wave.

RESULTS

Initial Checks

To validate Schwartz's hypothesised circular structure in our sample, we conducted two MDS analyses (Bilsky et al., 2011). The first analysis plotted the 56 value items, and the second analysis plotted the 10 value types; both analyses use the respective correlation matrix

to plot the values in a two dimensional space. The first analysis yielded S-stress =.167 and Stress I= .274, while the second analysis yielded S-Stress=.032 and a Stress-I=.115. The stress value is an index of how well the data fit the hypothesized configuration; higher stress values signify a poorer configuration. The stress values and the patterns in the MDS (see Supplementary Material 3) supported to a large extent to the structure hypothesized by Schwartz (1992). Given this convergence, we proceeded to examine the association between the values scores and neuroanatomical indices.

To rule out a potential confounding effect of intelligence, we performed correlations between the human values and all subscores of the MATRICS. All correlations (Pearson's *r*) were between .29 and -.24, and no correlation survived the multiple comparison correction for significance. Thus, intelligence did not have a significant influence on value orientation in our sample.

Fitting the Sinusoidal Model to Whole Brain Indices

We tested whether the relationship between brain parameters and value scores follows the sinusoidal pattern. We plotted the correlation coefficients between a particular brain parameter on the y-axis and each of the 10 lower-order values on the x-axis (in an order that follows their circular structure). Our analyses revealed a strong sinusoidal association (SFI=.07) between human values and overall white matter volume (Figure 3, Panel A), but no significant association with overall grey matter volume (SFI=.61). To check the robustness of the white matter finding, we also performed the sinusoidal test on various unmodulated (1-3) and modulated (4) white matter indices: (1) raw white matter while controlling for age, gender and intracranial volume (SFI=.13), (2) raw white matter to intracranial volume ratio (SFI=.19), (3) raw white matter to intracranial volume ratio while controlling for age and gender (SFI=.13) and (4) modulated non-linear only (SFI=.20). In all instances, the sine wave was of a similar form (i.e., negatively associated with self-transcendence and positively with

self-enhancement) and the SFI indicated good fit (SFI<.20). Of note, intracranial volume was significantly associated with five out of ten values: stimulation (r(83)=.27, p=.011), self-direction (r(83)=.26, p=.018), benevolence (r(83)=-.27, p=.012) as well as the value dimension of Openness (r(83)=.25, p=.022). To control for the potential confound of intelligence, we regressed out of each individual value the effect of all the MATRICS domains including the total score (i.e., speed of processing, attention/vigilance, working memory, verbal learning, visual learning, reasoning and problem solving, Social cognition and the total score). The SFI was virtually the same (SFI=.10, see Supplementary Material 4A).

Figure 3. Correlation coefficients between the 10 value types (x-axis) and the White (Panel A) and Grey (Panel B) matter volume (cubic decimetres dm^3).

The white matter parameter estimate from VBM, however, is not a direct measure of myelination and it can arise from various contributing sources that cannot be discriminated with VBM analysis of standard contrast-based MR data. To further test the relationship between white matter and human values, we obtained the myelin volume fraction of the overall brain using Multicomponent Relaxometry (mcDESPOT) (see Methods, Deoni et al., 2013). We then tested the sinusoidal association between human values and myelin volume fraction, a direct measure of myelination. As expected, the wave form was sinusoidal and exhibited the same form as the white matter volume (SFI=.12, Figure 4). As was the case for white matte volume, the myelin volume fraction was associated with the human values even after regressing out the intelligence variables (SFI=.10, see Supplementary Material 4B).

Figure 4. Correlation coefficients between the 10 value types (x-axis) and overall myelin volume fraction (ratio of myelin-bound water to total water).

Investigation of Regional Differences using Voxel Based Morphometry

Having identified a sinusoidal association between white matter and the 10 value types, we investigated the specific anatomical contributions. Based on inspection of the sinusoidal waveforms, we expected a negative linear association of regional white matter volume with the value dimensions of conservation (composed of conformity, security and tradition) and self-transcendence (composed of universalism and benevolence). Conversely, we expected a positive linear association of regional white matter volume with openness (composed of hedonism, self-direction and stimulation) and self-enhancement (composed of power, achievement and hedonism).

When we examined the associations at the level of higher-order value dimensions, conservation values were negatively associated with the volume of the white matter underlying the parahippocampal and lingual gyri (pFWE=.047; t=4.78, -22-54 4, Montreal Neurological Institute: MNI space, k=1, Figure 5, Left panel, see also Supplementary Material 9). In addition, self-transcendence was negatively associated with the white matter underlying the middle temporal gyrus (pFWE=.009; t=5.27, 60-37 -11, k=30, Figure 5, Right Panel).

Figure 5. VBM results for the relations between white matter volume and values: Negative association with conservation (pFWE=.047; t=4.80, -22-54 4, k=1, uncorrected cluster shown, Top Left Panel), and negative association with self-transcendence (pFWE=.009; t=5.27, 60-37 -11, k=30, Top Right Panel). The Bottom Panels are the scatter-plots with the

human value score on the y-axis and the beta-weights of the corresponding regions in the x-axis.

Because of the strong inverse relation between conservation and openness, we tested whether these values' associations with the white matter parameter are underpinned by the shared variance between the values. Removing the variance of openness from conservation, and vice versa, revealed no significant associations with brain structure. Similarly, when the self-enhancement variance is regressed out from self-transcendence, self-transcendence is no longer associated with brain structure. These analyses show that our findings were driven by the shared variance of the two opposing ends of the same motivational dimension (see Figure 1), underlining the importance of the motivational conflicts predicted by Schwartz's (1992) model.

Fitting the Sinusoidal Model to Cortical and Subcortical Regions of Interest

Based on the brain imaging and lesion work that indicated the involvement of regions across the whole brain as putative structures encoding human values, we probed sinusoidal associations between human values and the volume of the structures across the whole brain. With respect to the cortical regions,The volume of one frontal brain region (Figure 6), the right medial orbitofrontal cortex (SFI=.15), as well as the thickness of the left lateral orbitofrontal and caudal middle frontal exhibited the strongest sinusoidal association with human values (Supplementary Material 5). As can been seen in Supplementary Material 5, these frontal-related sinusoidal associations were driven by higher grey matter volume/thickness for self-transcendence (i.e., highest positive peak of the sine wave) and lower grey matter volume/thickness for openness (i.e., highest negative peak of the sine

wave). In respect of the volume of the 14 subcortical regions, none of them was statistcially related to the values in a sinusodal manner.

Figure 6. Correlation coefficients between the 10 value types (x-axis) and the volume (mm^3) of the right medial orbitofrontal cortex. For completeness, the grey matter regions (Supplementary Material 7) that show a sinusoidal association with human values (i.e., SFI<.20) are depicted in Supplementary Material 5.

DISCUSSION

The present research investigated the neuroanatomical correlates of human values using structural imaging. Three main results emerge from this study. First, we demonstrated sinusoidal associations between overall white matter volume and the values described in Schwartz's (1992, 2012) cross-cultural model of values. Second, we identified specific white matter regions that were associated with human values, mainly in the temporal lobe. Thirdly, the results supported our hypothesis that volumetric differences in the frontal lobes are related to values; this relation was found in prefrontal grey matter, portions of which exhibited a sinusoidal waveform of association with human values.

The main finding here concerns the novel sinusoidal relationship between overall white matter volume and myelination and human values. People who attach more importance to self-enhancement and openness values possess higher white matter volume, whereas people who attach more importance to self-transcendence values possess lower white matter volume. Furthermore, this pattern of association was not influenced by any putative confounds with intelligence as assessed by the MATRICS battery. Nonetheless, we acknowledge that a nonclinical intelligence assessment tool would be a more robust device to

employ in future research. Overall, then, we can be confident that this sinusoidal waveform is an accurate description of the associations with values.

The associations are consistent with previous findings regarding the relationship between white matter and risk taking. A recent study (Jacobus et al., 2013) demonstrated that *reduced* white matter integrity in a number of brain regions (including fornix, superior corona radiata, superior longitudinal fasciculus, and superior fronto-occipital fasciculus) predicted substance use and risk-taking behaviours. Here, we complement these findings by showing that *increased* white matter volume is associated with self-enhancement and openness values, which are underlined by the need for control and mastery in one's behaviour (Schwartz, 2009). We further show, beyond simply looking at white-matter volume, that the myelin content of white matter, as measured from the myelin volume fraction (Deoni et al., 2008) reveals a congruent pattern of association with values. This result provides more information about the tissue composition of white matter, independent of volume (to which other parameters such as axon diameter and inter-axonal space can contribute). Myelin enables faster and more efficient propagation of action potentials along axonal pathways, via regulating the speed and synchronicity of neuronal firing between cortical regions (Fields, 2008), which in turn can contribute to faster information processing capabilities (Turken et al., 2008). This might enable individuals to be more adapted to changing human environments, which may explain why increased myelination is associated with openness to change values. Of course, we cannot make any statements about causation. Value orientations might be associated with specific behavioural factors, such as physical activity, which is associated with increased myelination (Bracht et al, 2016), and future independent studies would be useful because a multiple comparison correction for the number of values and regions tested could not be carried out here.

In general, we need to exercise caution when interpreting relatively global brain parameters like overall white matter. It is important to consider such associations in light of the findings in more specific brain regions. In this regard, our study showed that individual variability in both conservation and openness orientations is associated with structural variability in brain structure. Removing the variance of openness from conservation, and vice versa, revealed no significant associations with brain structure. The same effect was observed for the second value dimension, self-enhancement vs. self-transcendence. After variance related to self-enhancement was removed from self-transcendence, self-transcendence was no longer associated with brain structure. This suggests that our findings have been driven by the shared variance between the two opposing motivational ends of the same value dimension, congruent with Schwartz's (1992) model. Schwartz's model indicates that the two opposing ends of a value dimension express opposing motivational needs. If this motivational opposition is crucial to an association (e.g., the volume of a brain region), then the variance shared between the two opposing value types should be a crucial component of the association. This neurostructural evidence therefore provides a novel cross-validation of Schwartz's circumplex model of the motivational relations between values using neuroanatomical data. Previously, the motivational oppositions in the circular model of values received support at the behavioural level, but here we see new neural markers of the motivational oppositions.

Our findings also reveal novel aspects of the psychological functioning of prefrontal regions. As noted earlier, prior lesion and fMRI studies demonstrate a link between prefrontal regions, mPFC and OFC, and value-related constructs (Anderson et al., 1999, Grafman et al., 1996, Rilling et al., 2002). Here, we extend these findings by showing that the right medial OFC is directly related to the whole spectrum of human values in a sinusoidal manner, driven especially by higher right medial OFC activation among those who attach higher importance

to self-transcendence values. This evidence ties in with previous structural and functional findings investigating self-transcendent-related behaviours and deficits. For example, in a voxel-based morphometry study (de Oliveira-Souza et al., 2008), psychopathic patients (i.e. individuals with moral deficits) showed reduced grey matter in a number of regions including OFC. In addition, Hare et al. (2010) found that higher mOFC (vmPFC) activity was associated with the higher subjective liking of donations at the time of the decision making.

Of importance, a strong and significant, association between an external variable and a particular value does not guarantee that the external variable is associated with the whole human value space in a sinusoidal manner (i.e., a good SFI). That is, sinusoidal relations do not depend solely on the correlations between values in the circumplex model (Hanel et al., 2016). For example, as can be seen in the results, the 10 correlation coefficients between ICV and human values are stronger and more significant (3 of which are at a $P<.05$) than the correlations between white matter volume and human values (none of which is at $P<.05$). If the sinusoidal pattern were carried by a single strong association, the SFI for ICV should be better than the SFI for white matter volume. However, this is not the case; the SFI for ICV is worse ($SFI>.2$) than that for white matter volume. The sinusoidal relationship depends on more than the co-variation between the 10 values. There is a great number of inter-human value covariance sources with which a given external variable may co-vary.

Moreover, if we had employed a research methodology using merely classical linear models, we would not have been able to capture all the available information from the values and imaging data. Our development of a specific test for a sinusoidal pattern is a novel data-reduction approach, which increases the power to detect otherwise unobserved relationships, and can be utilised for other circumplex models in psychology, such as influential circumplex models of affect (Russell, 1980) and personality (Wiggins, 1996). In the present project, this methodology helped to combine a well-informed psychological model, which features

specific predictions, with neuroimaging techniques. This approach enabled more robust modelling of the connections between human values and the brain, but this approach can be extended usefully to other domains of psychology.

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