

Running title: VALUE CONFLICT IN THE BRAIN

Neural evidence of motivational conflict between social values

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Abstract

Motivational interdependence is an organizing principle in Schwartz's (1992) circumplex model of social values, which has received abundant cross-cultural support (Schwartz et al., 2012). We used fMRI to test whether motivational relations between social values predict different brain responses in a situation of choice between values. We hypothesized that differences in brain responses would become evident when the more important value had to be selected in pairs of congruent (e.g., *wealth* and *success*) as opposed to incongruent (e.g., *curiosity* and *stability*) values as they are described in Schwartz's model, because the former serve mutually facilitating motives, whereas the latter serve mutually inhibiting motives. Consistent with the model, choosing between congruent values led to longer response times and more activation in conflict-related brain regions (e.g., the supplementary motor area, dorsolateral prefrontal cortex) than selecting between incongruent values. These results provide novel neural evidence supporting the circumplex model's predictions about motivational interdependence between social values. In particular, our results show that the neural networks underlying social values are organized in a way that allows activation patterns related to motivational similarity between congruent values to be dissociated from those related to incongruent values.

Keywords: Human values; Schwartz's value model; Supplementary motor area; Dorsolateral prefrontal cortex; fMRI.

Many aspects of human behavior are guided by *social values*, which determine what we consider important and which goals we choose to pursue (Rokeach, 1973). *Social values* (e.g., *freedom, authority*) are conceptually distinct from *economic values* (i.e., reward associated with a specific choice option), which have been the subject of extensive research in the fields of human decision-making, behavioral economics, and neuroeconomics. Economic values reflect the computation of choice propensities that are attached to specific stimuli (or responses, rewards) in a given situation. In contrast, social values can be seen as transsituational goals that vary in importance between individuals and serve as general guiding principles across contexts (Schwartz, 1992) and are intrinsically linked to the self-schema (Brosch & Sander, 2013).

In particular situations, usually involving reward or altruistic decisions, social and economic values can engage the same or overlapping brain areas, such as the mesolimbic reward system (VTA-striatum) (Moll, Krueger, Zahn, Pardini, de Oliveira-Souza, & Grafman, 2006), the ventromedial prefrontal cortex/orbitofrontal cortex (Hare, Camerer, Knoepfle, & Rangel, 2010) or the dorsomedial prefrontal cortex (Brosch, Coppin, Scherer, Schwartz, & Sander, 2011). It has been suggested that social values may exert their effects on decisions and behaviors via modulations of the neural regions involved in the computation of economic values (Brosch & Sander, 2013).

A critical advance in research on social values was Schwartz's (1992) proposition that it is important to model the motivational interdependence among values. The starting point for this model was the assumption that values are representations of three universal requirements of human beings: biological needs of individuals, coordinated social interactions and societal demands for group welfare and survival (Schwartz, 1992; Schwartz & Bilsky, 1987). The motivational types of values were derived from these three universal human requirements and

thus reflect a joint function of social normative influence and personal priorities. Indeed, Schwartz, Verkasalo, Antonovsky, and Sagiv (1997) showed that the whole motivational continuum described by the value circle was coherently related to socially desirable responding (measured with The Marlowe-Crowne scale). The correlations between social desirability and value priorities contributed to the validation of the value measurement.

Schwartz's (1992) model postulates a continuum of 10 motivational value types, which underline decision-making, attitudes and behavior, constituting an important organizing principle of both the individual's life and the functioning of society as a whole. According to Schwartz, the pursuit of a particular value has consequences compatible with some values but incompatible with others. As shown in Fig. 1, adjacent types share compatible motivations, those on opposite sides of the circle serve incongruent motivations, while orthogonal ones are in between. For example, the pursuit of *novelty* and *change* (stimulation values) is likely to undermine preservation of *time-honored customs* (tradition values), while it can amplify *creativity* and *freedom* (self-direction values).

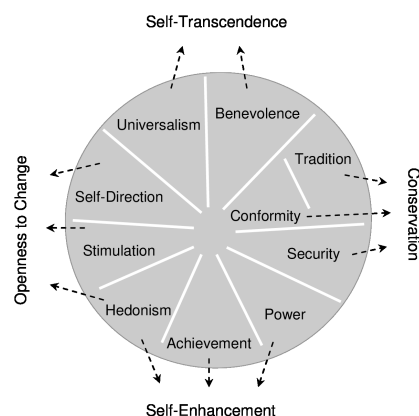


Figure 1. Schwartz's (1992) model of values. Value types are presented inside the circle. Higher dimensions of motivational aims are shown outside the circle.

The circumplex model has been highly influential in social and cultural psychology. It has been cited in over 50,000 publications used to help integrate diverse findings in studies of emotions, attitudes and behavior relevant to cultural psychology, intergroup behavior, personality, and political psychology (Boer & Fischer, 2013). Furthermore, supportive evidence for motivational interdependence between values as postulated by the circumplex model exists at the behavioral level (e.g., Bardi, Lee, Hofmann-Towfigh, & Soutar, 2009; Boer & Fischer, 2013; Maio, Pakizeh, Cheung, & Rees, 2009; Pakizeh, Gebauer, & Maio, 2007; Pulfrey & Butera, 2013), including evidence of genetic contributions (Knafo & Spinath, 2011; Schermer, Vernon, Maio, & Jang, 2011).

However, these behavioral findings rely on the correct identification of value-relevant behaviors, which is problematic if more than one value is promoted by a behavior (which is often the case). For this reason among others (e.g., behavioral measurement reliability, paucity of studies with multiple behavioral variables at once), it is important to further test the motivational relationships between values as delineated in the circumplex model, and triangulation with other types of data. The inclusion of neuroimaging data would be particularly useful because it can identify cognitive and emotional processes without relying on participants' self-reports or inferences from overt behavioral data.

Of importance, the aim here is different from simply identifying neural networks involved in the representation of social values. Research has already made strides in mapping these networks. For instance, increased activation in the medial prefrontal cortex and dorsal striatum were found during "core value" computations, while value ratings correlated with activity in the precuneus and anterior prefrontal cortex (Brosch, Coppin, Schwartz, & Sander, 2012). Others have investigated the neural basis of moral sentiments like pride and guilt, gratitude and indignation/anger in the context of social values expressed by social concepts

such as generosity and stinginess (Zahn et al., 2009). The authors demonstrated that regions in the superior anterior temporal lobe, which represent abstract social concepts, were recruited during emotional judgment of social values and were stable across different contexts of moral sentiments. The authors showed that context-dependent moral sentiments were encoded in fronto-mesolimbic regions. That is, pride correlated with activity in the septum, the ventral tegmental area (VTA), the parahippocampal gyrus, and the anterior ventromedial prefrontal cortex. Guilt was associated with activity in the anterior ventromedial prefrontal cortex as well, and also in subgenual cingulate cortex; indignation/anger activated the orbitofrontal cortex, the dorsolateral prefrontal cortex, and the insula; gratitude correlated with hypothalamus activation. Other commonly studied social concepts whose neural underlying systems have been mapped include moral cognition and altruism (e.g., Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005; Moll et al., 2006); the former was related to activation in cortical-limbic networks including the prefrontal cortex, anterior and posterior temporal cortex, and limbic/paralimbic structures, and the latter to the mesolimbic reward system (VTA-striatum), the orbitofrontal cortex/subgenual cingulate, and the anterior prefrontal cortex.

Although these studies help to outline the neural networks involved in values, they do not address the neuronal signature of the motivational conflicts in Schwartz's social value types. This question was the focus in the present research. Specifically, we used functional magnetic resonance imaging (fMRI) to test whether the circumplex model's predictions about value congruence versus incongruence are supported at the neural level. If the circumplex model's predictions about motivational conflicts between values are correct, then there should be higher conflict (in the sense of mentally struggling to choose between two alternatives, either desirable or undesirable) evoked by choices between congruent values versus

incongruent values. Selecting between congruent as compared to incongruent values should entail more psychological conflict, because the former serve mutually facilitating motives, whereas the latter serve mutually inhibiting motives (Bardi et al., 2009; Schwartz et al., 2012). Incongruent values are inherently contrasted and those who emphasize a specific value tend to de-emphasize the opposing value (e.g., Borg, Bardi, & Schwartz., 2015; Sverdlik, 2012). Therefore, in cases that contrast incongruent values, individuals tend to show a clear preference of one value over the contrasting one, so they experience less psychological conflict. Furthermore, even in cases where the preference is equivalent, there can still be more *subjective* conflict with motivationally opposing values than congruent values (Maio, 2010; Pakizeh et al., 2007). Consistent with these observations and rationale, we expected to see activation in brain regions associated with conflict processing in a situation of choice – when one value had to be selected as more important from two motivationally congruent values versus two motivationally opposing (incongruent) values.

Prior theory and evidence points to specific regions as being important in the processing of psychological conflict. An important role in detection of conflict and in conflict monitoring has been assigned to the anterior cingulate cortex (ACC), in a model proposed by Botvinick, Braver, Barch, Carter, and Cohen (2001). According to this model, the ACC is not only involved in the detection of conflict but its activation also signals a demand for increased control to meet tasks demands. One could thus predict that the crosstalk among pathways processing different values may thus constitute a conflict that is detected by the ACC mechanism.

Neuroscientific evidence examining psychological conflict has supported a role for the ACC, as well as for the dorsolateral prefrontal cortex (DLPFC) and the supplementary motor area (SMA). This research has relied on classic conflict paradigms, such as moral dilemma

situations, moral judgements, Stroop tasks, go/no-go or stop-signal tasks. For instance, high conflict between self-interest and collective interest in the Prisoner's dilemma game was associated with increased activity in the ACC and DLPFC (Emonds, Declerck, Boone, Vandervliet, & Parizel, 2012). In another interesting example of a psychological conflict in a moral dilemma situation, the ACC and DLPFC exhibited increased activity during difficult as compared to easy personal moral judgments (Greene, Nystrom, Engell, Darley, & Cohen, 2004). More specifically, utilitarian judgments that violated personal norms but were perceived as "appropriate" led to increased activity in brain regions associated with cognitive control, particularly in the DLPFC, relative to non-utilitarian judgments perceived as "inappropriate".

The importance of the DLPFC in psychological conflict is consistent with additional evidence looking at value-based decisions. For instance, a distinctive pattern of prefrontal activation was found in a study in which value-based decisions in conflict situations were investigated in individuals with either a predominant collectivistic (altruistic) or individualistic (egocentric) value system (Caspers et al., 2011). Both collectivists and individualists recruited the DLPFC equally strongly, yet individualists additionally activated the medial superior frontal cortex, while collectivists showed increased engagement of the middle cingulate cortex. The DLPFC was also important in a study by Christensen, Flexas, de Miguel, Cela-Conde, and Munar (2014), who found that the DLPFC, temporal poles and posterior cingulate cortex were activated during utilitarian but not during deontological moral judgments in Catholics. Deontological moral judgments likely involved less cognitive/psychological conflict compared to utilitarian judgments because they are based on rules and norms rather than on anticipated consequences (as utilitarian norms).

The SMA is important because successful goal-directed behavior requires the selection of an appropriate response for the task at hand, while stopping an inappropriate response. Stopping a selected (by a participant) action and specified (by an experimenter) action recruits the SMA, indicating that this area supports both action selection and stopping and thus helps to resolve conflict between competing available responses (Rae, Hughes, Weaver, Anderson, & Rowe, 2014). Recent findings support the view that the SMA plays a central role in conflict resolution and encodes response alternatives as opposed to simply the presence of conflict (Fedota, Hardee, Pérez-Edgar, & Thompson, 2014). In a go/no-go task, the SMA was activated in response to both go and no-go stimuli, but with a different activation pattern associated with these the two stimuli, which supported a direct role for the SMA in response selection. Thus, the SMA may be involved in the representation and maintenance of task sets and response alternatives as a final step before motor program execution (Banich, 2009).

In our experimental paradigm, we expected that forced choice between motivationally congruent (and thus either similarly compelling or similarly undesirable) values would produce conflict and therefore engage some of the above mentioned brain areas. To test this hypothesis and thus a central assumption in Schwartz's model, we presented participants with pairs of motivationally congruent or incongruent values. Participants were asked to choose as quickly as possible the more important value in each pair, while we recorded response times and brain activation using fMRI.

METHODS

Participants

Twenty-three healthy participants (16 women, 7 men, mean age 26.1 years, age range 19-48 years) were paid (15 GBP) for taking part. They were all right-handed, white-British

university students or community residents from Cardiff (Wales) and had normal or corrected vision. The sample size was established before the start of data collection. Following previous social neuroscience studies (Cloutier & Gyurovski, 2014; Zelinková et al. 2014), we aimed for a sample size of 20 to remain after allowing for a 15% rate of data loss, insufficient data quality, or exclusions. Therefore, we tested 23 participants.

The research project was approved by the School of Psychology Research Ethics Committee at Cardiff University and carried out in accordance with the provisions of the World Medical Association Declaration of Helsinki.

Stimuli

Participants were presented with 60 pairs of values randomly sampled across nine value types in Schwartz's (1992) circular model (Fig. 1): universalism, benevolence, tradition, conformity, security, power, achievement, stimulation, and self-direction. (One value type [hedonism] was not included because it shares elements of two motivational dimensions and therefore could not be used to test our hypothesis.) Each type contained five mainly original Schwartz's value items (Schwartz, 1992; Schwartz et al., 2012).

Following Schwartz's value model, we systematically created pairs of values, such that each pair was categorized as either congruent (compatible) or incongruent (conflicting). We presented 20 pairs per condition. The congruent value types were conformity and security, power and achievement, stimulation and self-direction, universalism and benevolence; the incongruent value types were benevolence and achievement, conformity and self-direction, security and stimulation, power and universalism (Table 1, Fig. 1). In addition, we included 20 pairs of orthogonal values for follow-up tests of the extent to which the differences between congruent and incongruent values might be more strongly attributable to either or

both motivational pairings: these orthogonal value types were benevolence and security, power and stimulation, stimulation and universalism, tradition and power (Table 1, Fig. 1). Results of those additional tests are presented and discussed in the supplementary material. Specific items (e.g., *cleanliness*) from within each value type were sampled randomly. No value pair was presented repeatedly to a subject.

To match phrase length across conditions, seven of the original Schwartz's items (Schwartz, 1992; Schwartz et al., 2012) had to be modified. For example, we presented *meeting social expectations* instead of *behave properly/avoid doing anything people say is wrong* and *stability* instead of *stability of society*. These minor adjustments preserved the value meanings and are unlikely to have evoked differences in basic value activation. Stimuli were matched for word length across conditions: mean character counts including spaces were identical for congruent and incongruent values (13.6, 95% CI [11.8, 15.4]) and comparable for orthogonal values (15.6, 95% CI [13.6, 17.5]), $F(2,78) = 2.25, p = .113$. The values in a pair were presented simultaneously one above the other at the centre of a black screen in white letters. The screen at the rear of the MRI bore was viewed through a mirror mounted on the MRI head coil.

Procedure

Participants were screened for fMRI safety hazards and familiarized with the task. The scanning session started with an instruction displayed on the monitor: "You will see a sequence of value pairs. For each pair, decide as quickly and accurately as possible which value is more important as a guiding principle in your life". Participants were asked to give their responses by pressing the left or right button on a response box with their left or right index finger, respectively. Each trial began with a gray fixation cross having a random

duration of either 4, 6, or 8 s (Fig. 2), which was used as fixation baseline in fMRI data analyses (see below). A value pair was then displayed for 4 s before the next trial started. The order of value pairs was freely randomized. Each participant completed 60 trials, which lasted about 610 s in total, including the instruction display. Additionally, to monitor the potential motor effect of button pressing force, which could differ in the three conditions, pressure sensors (water-filled detector pads) were mounted on the response buttons to measure response force (RF), as an indicator of motor activation. It is possible that the congruence conditions could evoke motor activation of varying intensity, which might lead to differences in RF, thus affecting brain activity. To exclude this potential motor confound, we examined if our experimental conditions were related to RF differences. Due to technical reasons, pressure data could be recorded from a subgroup of 17 of the 23 participants only. Response force was recorded with the Spike2™ software (CED, Cambridge, UK).

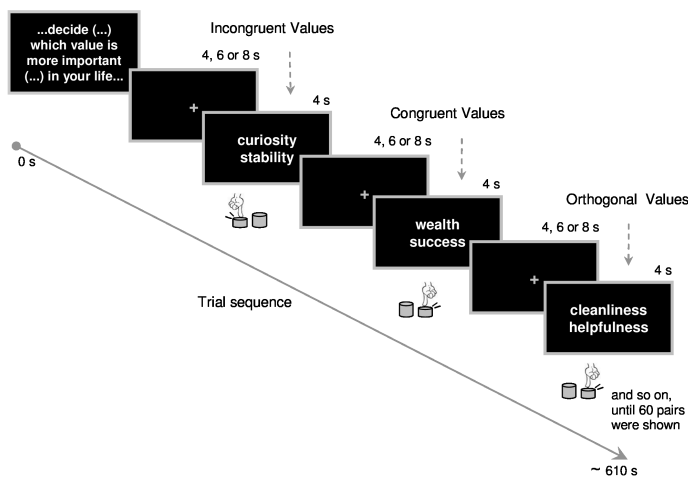


Figure 2. Experimental paradigm. While undergoing fMRI scanning, participants were asked to choose as quickly and accurately as possible which of two simultaneously presented values was more important for them as a guiding principle in their life. Each trial began with a fixation cross of 4, 6, or 8 s duration, followed by a value pair displayed for 4 s. Three types of pairs were randomly presented: motivationally incongruent, congruent and orthogonal value pairs (see figure for examples).

fMRI data acquisition

fMRI images were acquired using the 3.0 Tesla General Electric Medical Systems Signa HDx at Cardiff University Brain Research Imaging Centre (CUBRIC). Blood-oxygenation level dependent (BOLD) signals were measured during the experimental task using a T2-weighted gradient echo planar imaging (EPI) sequence that was synchronized to the onset of the task (the first trial) and covered the whole brain. Each volume (whole brain coverage) contained 35 slices of 3-mm thickness, with 1-mm inter-slices spacing (parameters: voxel size = 3 x 3 x 3 mm³, matrix size = 64 x 64; field of view = 192 x 192 mm, time repetition = 2000 ms, time echo = 35 ms, flip angle = 80°). A total of 304 volumes per participant were acquired, yielding a total scanning time of 608 s.

Also, we obtained 3D high-resolution T1-weighted anatomical images of the whole brain immediately after functional scanning using a fast spoiled gradient echo sequence (FSPGR) with 190 contiguous axial slices and an isotropic voxel resolution of 1 mm (time echo = 3 ms, inversion time = 450 ms, flip angle = 15°, field of view = 256 x 256 mm).

Data analysis***Behavioral data***

For each condition and participant, we computed mean response time (RT, N = 23) and mean response force (RF, N = 17). RFs were calculated based on the peak force amplitude after stimulus presentation. All responses before onset of the next value pair were included to compute RTs and RFs. Mean RTs and RFs were submitted to paired samples *t*-tests. Effect sizes for significant differences between conditions were calculated using Cohen's *d* for paired samples ($d = D / SD_D$, where *D* is the mean difference score and *SD_D* is standard deviation of the difference scores). Data are presented with 95% confidence intervals.

fMRI data

Data analysis was conducted using the BrainVoyager QX™ software (Brain Innovation, Maastricht, the Netherlands). fMRI data preprocessing included 3D motion correction for head movements, slice scan time correction and temporal filtering to remove signal drifts (high pass filter of 0.006 Hz). Functional images were realigned (coregistered) to participants' anatomical images and normalized to Talairach space (Talairach & Tournoux, 1988). 3D functional images were spatially smoothed using a Gaussian kernel with a full width at half maximum (FWHM) of 4 mm.

Statistical fMRI analysis was performed using standard general linear model (GLM) approaches (N = 22, one participant was excluded due to technical problems during data acquisition). Based on stimulus onsets and offsets of each value pair, we defined three predictor functions to regress BOLD signal changes elicited by the presentation of each of the three experimental conditions. The predictor time courses were convolved with a hemodynamic response function to account for the hemodynamic delay of the BOLD signal. Our task predictor modeled both stimulus (value) processing and motor processes, which are not separable in time with the resolution of the fMRI signal. Moreover, we refrained from including RTs as a separate predictor, because effects of conflict and prolonged stimulus processing (RT delays) were inherently linked in our paradigm (see also discussion). However, to control for non-specific motor effects that are not related to conflict processing we added RF as a parametric predictor in additional parametric analyses (N = 17). In these analyses, we tested if and where in the brain RF modulated the effects of condition (main predictor) using whole-brain conjunction analyses of the main predictors and the de-meaned RF predictor.

For each participant and predictor, regression coefficients (beta estimates) were extracted. To generate multi-subject brain activation maps, we then entered individual beta estimates into whole-brain random effect analysis. Specifically, we aimed to identify brain regions showing significant differences for the comparisons between congruent versus incongruent pairs using *t*-tests. We followed-up with additional comparisons (presented in supplement) between both sets of values and the orthogonal values.

To control for multiple comparisons in voxel-based whole-brain analyses, we used a cluster-level statistical thresholding approach, which calculates - for a targeted *p*-value and given volumetric activation map - a minimum cluster size using iterative Monte Carlo simulations (Forman, Cohen, Fitzgerald, Eddy, Mintun, & Noll, 1995). We considered voxels within clusters to be significantly activated only when they survived the estimated threshold/cluster size. Here, cluster thresholds were calculated based on activation maps at an uncorrected (voxel-based) *p*-level of $p < .005$ and resulted in a cluster-corrected *p*-level of $p < .05$, and a cluster threshold level of 351 voxels (1x1x1 mm) for the congruent versus incongruent contrast. Thresholded activation maps with significant clusters were converted into brain regions of interests (ROI) and subjected to detailed ROI analysis. For each ROI, we extracted cluster size (in 1x1x1-mm voxels), mean beta weights, and *t*-values for specific contrasts, which were *z*-transformed to allow for comparisons between ROIs.

RESULTS

Behavioral data

Response time

On average, there were fewer than two missed responses per participant. Replicating past evidence (Pakizeh et al., 2007), paired-samples *t*-test showed that participants took

longer to select the more important value in pairs of congruent ($M = 2149$ ms; $SD = 462$ ms) as compared to incongruent values ($M = 1964$ ms; $SD = 389$ ms), $t(22) = 3.68$, $p = .001$, Cohen's $d = .77$ (Fig. 3).

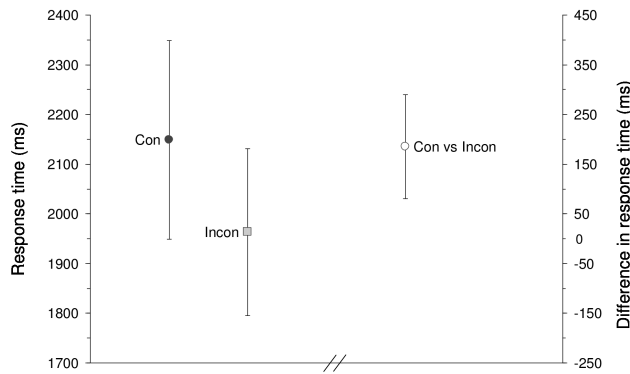


Figure 3. Mean response times (RTs; left) and the mean of RT difference (right) when participants were selecting the more important value in pairs of congruent (Con) or incongruent (Incon) values. Error bars show 95% confidence intervals (paired data).

Response force

Paired-samples t -test showed no difference in RF between congruent and incongruent conditions, $t(16) = -0.04$, $p = .970$.

Brain imaging data

One participant was excluded from fMRI analyses because of technical problems during data acquisition. Whole-brain analyses using RF as an additional parametric modulator did not show any significantly activated brain regions, suggesting that the effects described below were not attributable to between-condition differences in RFs.

Whole-brain analysis identified several brain regions in the left frontal lobe showing larger activation when participants were asked to choose between two congruent versus two incongruent values (Table 2, Fig. 4). As expected, the active regions were those that have been previously identified as being important in the processing of psychological conflict. The

largest activation cluster was found in the SMA, other clusters were located in the DLPFC, the ventrolateral prefrontal cortex (VLPFC), and in the inferior frontal junction (IFJ). Stronger activation in the congruent versus incongruent condition was also found in the right inferior semi-lunar lobule (ISLL) of the cerebellum. The exploration of activation levels in these areas across conditions revealed that, in both conditions and in all regions, brain activity increased relative to the fixation baseline; yet, this increase was significantly more pronounced when subjects were choosing between congruent values. Mean beta weights in the identified clusters, indicating relative activation levels in the two conditions (congruent or incongruent pairs), are shown in Fig. 5.

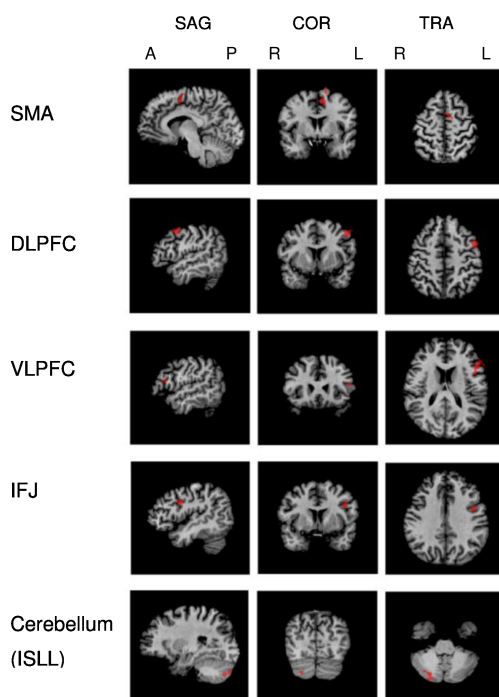


Figure 4. Brain regions showing larger activation in the congruent versus incongruent condition. SMA = supplementary motor area; DLPFC = dorsolateral prefrontal cortex; VLPFC = ventrolateral prefrontal cortex; IFJ = inferior frontal junction; ISLL = inferior semi-lunar lobule; SAG = sagittal view; COR = coronal view; TRA = transversal view; A = anterior; P = posterior; R = right; L = left.

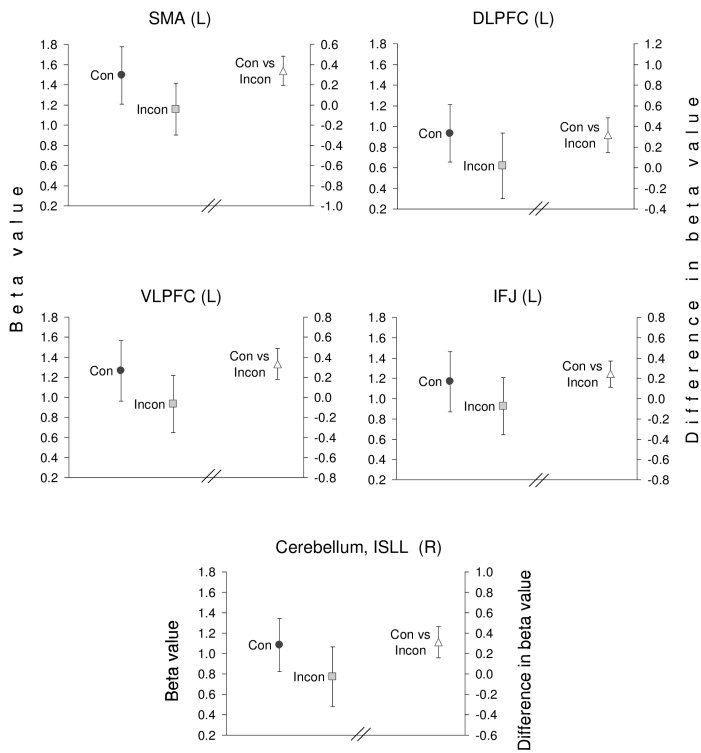


Figure 5. Mean beta weights in brain regions where stronger activation was found for congruent versus incongruent value pairs. Betas (corresponding to relative activation levels) of single conditions are shown at the left and beta differences between the conditions at the right. Error bars show 95% confidence intervals (paired data). SMA (L) = left supplementary motor area; DLPFC (L) = left dorsolateral prefrontal cortex; VLPFC (L) = left ventrolateral prefrontal cortex; IFJ (L) = left inferior frontal junction; ISLL (R) = right inferior semi-lunar lobule; Con = pairs of congruent values; Incon = pairs of incongruent values; Con vs Incon = difference between the two conditions.

DISCUSSION

Despite evidence of attitudinal and behavioral implications of motivational conflicts between human values, research has not previously examined whether signatures of value conflict are also detectable at the neural level. Choices between values should reveal heightened activity in brain regions implicated in conflict resolution, but more so when the choices involve two motivationally compatible rather than opposing values. The present study tested whether Schwartz's (1992) circular model of values is capable of identifying the value choices that lead to more activation in regions that have been linked to processing conflict (e.g., Caspers et al., 2011; Christensen et al., 2014; Fedota et al., 2014; Rae et al., 2014). Supporting the model, choosing between values that it identifies as serving congruent motives led to more

activation than choosing between values that it identifies as serving incongruent motives. This difference arose within several regions previously linked to processing conflict, the left SMA, DLPFC, and VLPFC, as well as in the left IFJ and the right cerebellar ISLL.

The SMA is involved in situations of response conflict, like motor response inhibition in the go/no-go and stop-signal tasks (Fedota et al., 2014; Rae et al., 2014). It is activated when cognitive requirements are complex, and SMA activity is mainly driven by increased attentional and working memory load, not by response inhibition per se (Criaud & Boulinguez, 2013). This corroborates the results of our study, where cognitive demands including attention and self-reflection are likely to have been high and a 4-s response window allowed the completion of meaningful decisional processing (see Pakizeh et al., 2007).

The DLPFC has been associated with BOLD activity related to “cognitive” conflict, such as response inhibition, conflict monitoring or task switching (Gläscher et al., 2012), but also with “social” conflict as studied in moral dilemma tasks. Referring to the latter, the DLPFC was engaged in responding to difficult as compared to easy personal moral dilemmas, in which utilitarian values require “personal” moral violations (Greene et al., 2004), and in utilitarian moral judgments to impersonal moral dilemmas (Christensen et al., 2014).

Moreover, and consistent with our results, Caspers et al. (2011) found increased DLPFC activation during value-related conflicts when participants had to reject a value that was congruent with their own value orientation. Similarly, neural correlates of norm compliance, which involved the requirement to curb immediate self-interest in order to obey a fairness norm under the threat of punishment, included activation of the DLPFC, and VLPFC (Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007).

Conflict-related effects were also reported in the VLPFC, where Sommer et al. (2010) found higher activity during moral relative to “neutral” conflicts. Moreover, both the DLPFC

and VLPFC have contralateral projections to the cerebellar ISLL (Krienen & Buckner, 2009). We therefore speculate that the present activation in the right cerebellum may be related to the left prefrontal effects.

We observed activation in the IFJ, a region adjacent to the middle DLPFC (BA 46 and 9) (Brass, Derrfuss, Forstmann, & von Cramon, 2005). Some researchers have argued for a structural and functional distinction between the IFJ and the DLPFC in cognitive control (Brass et al., 2005). The authors suggest that the IFJ plays an important role in cognitive control tasks, such as task switching and Stroop tasks. In a meta-analysis comparing Stroop tasks, two areas in the fronto-lateral cortex showed a consistent activation: the IFJ and middle DLPFC (Neumann, Lohmann, Derrfuss, & von Cramon, 2005).

A central role in the detection and monitoring of conflict is often assigned to the ACC (Botvinick et al., 2001). ACC activation has been associated with tasks requiring the participant to override relatively automatic but task-inappropriate responses (Swick & Jovanovic, 2002) or to select among equally dominant (allowed) responses (Barch et al., 2001), tasks leading to the commission of errors (Carter et al., 1998; van Veen & Carter, 2006), or difficult, as compared to easy, personal moral dilemmas (Greene et al., 2004). The question arises why we did not observe ACC activation in our congruent condition in which participants had to choose between almost equally dominant response options (i.e., none of the values was more compelling than the other). One tentative account for this divergence is that tasks for which ACC activation has been reported typically require choices where “dominant” responses in prior tasks have a different meaning than here. The congruent values are associated with high importance but are not automatic elicitors of some pre-potent response (as in cognitive conflict tasks), and have to be compared in order to make a decision.

This deliberative comparison process is inherently different from the control-focused tasks usually linked to ACC activation.

The DLPFC and VLPFC have been shown to be interconnected in humans (Goulas, Uylings, & Stiers, 2012; Morawetz, Bode, Baudewig, Kirilina, & Heekeren, 2015). Direct connections between the SMA areas and both the DLPFC and cingulate areas have also been established (Lu, Preston, & Strick, 1994; Luppino, Matelli, Camarda, & Rizzolatti, 1993; Nachev, Kennard, & Husain, 2008), with much stronger intrinsic connections from the DLPFC to SMA than from the SMA to DLPFC (Morawetz et al., 2015). The SMA makes also a direct and substantial contribution to the corticospinal tract, and termination patterns of SMA corticospinal cells resemble those of primary motor cortex projections, suggesting that these SMA cells make direct connections to motor neurons (for review see Nachev et al., 2008). Thus, considering the anatomical connections of the DLPFC and SMA and the existing conflict and cognitive control hypotheses, it seems conceivable that a conflict signal reached the DLPFC (and VLPFC) which exerted cognitive control to overcome the conflict (Barch, Braver, Sabb, & Noll, 2000; Carter et al., 1998; Carter & van Veen, 2007), possibly via the SMA. The SMA plays a central role in conflict resolution and encodes response alternatives as opposed to simply the presence of conflict (Fedota et al., 2014). The SMA is theorized to implement the appropriate tasks sets as performance demands evolve (Dosenbach et al., 2006). As the response set is accessed, the differentiated response representations encoded in the SMA are activated as part of a direct conflict resolution mechanism (Petersen & Posner, 2012). Thus, the SMA may be involved in the representation and maintenance of active task sets and response alternatives as a final step before motor program execution (Banich, 2009).

As in all studies that link brain activity with particular psychological constructs, it is important to consider potential alternative interpretations of the psychological processes

putatively revealed by the brain activity. One alternative interpretation is relevant to our finding that, as expected, RTs were longer when participants were selecting a value which was more important to them as a guiding principle in their lives from pairs of congruent values as opposed to pairs of incongruent values, which was previously observed by Pakizeh et al. (2007). The question arises whether these RT effects reflect a mere “distance effect”, which is usually found in cognitive comparison tasks wherein participants are faster to compare items that *differ* more on a given dimension (Ogata, Horaguchi, Watanabe, & Yamamoto, 2011). In Schwartz’s circular model, greater distance does not signify greater difference as much as it signifies motivational opposition. The circular arrangement of values in the model represents a motivational continuum from congruence to antagonism: the closer any two values, the more congruent their underlying motivations, and the more distant any two values, the more antagonistic their underlying motivations. In fact, the opposing values are similar insofar as they reside on opposite ends of the *same* motivational dimension. This motivational opposition, which also entails self-reflection and moral judgment, is therefore distinct from the manipulations of distance in much simpler cognitive comparison tasks (e.g., when selecting the larger of two letters). Moreover, distance effect tasks engage parietal and temporal regions, with a central role typically assigned to the intraparietal sulcus (IPS; Mussolin, Noël, Pesenti, Grandin, & De Volder, 2013). We did not find activation differences in the IPS, suggesting that conflicting processing related to values can be neurally dissociable from conflict processing related to cognitive/perceptual comparisons.

Another potential interpretation of our findings is that the present BOLD effects (especially the increase of frontal activation) simply reflected increased attention and prolonged stimulus/motor processing in high-conflict trials. Thus, the frontal activity patterns may have been caused by differences in task difficulty (and associated changes in executive

control), rather than a psychological conflict per se (Shenhav, Straccia, Cohen, Botvinick, & 2014). Such concerns have recently been raised in relation to work showing that comparing economic values in reward-based decision making, namely the choice between engaging in a given option and searching for alternatives, leads to distinct activation in the ACC (Kolling, Behrens, Mars, & Rushworth, 2012). Further, Yarkoni, Barch, Gray, Conturo, and Braver (2009) demonstrated that the longer it takes an individual to respond, the more activation is seen in a given brain region, especially when participants are experiencing increased task difficulty or conflict. Critically, in contrast to choices based on economic values, our task entails no “optimal” or objectively correct choice; instead value comparisons and associated conflicts are idiosyncratically defined by each individual’s value hierarchy, which in turn mitigates confounds from general task difficulty. However, we acknowledge that in our task “subjective difficulty” and psychological conflict were inherently linked. That is, the difficulty of choice increased when the conflict entailed in choosing between two “similarly” important values increased.

Finally, the absence of response force differences between conditions adds further support to the notion that RT and brain activation effects were caused by differences in psychological conflict and not by differences in motor processes, and we should note that semantic relatedness was not a major factor in influencing RTs. Previous research has found that judgments of semantic relatedness were independent of RT effects (on speed of rating of the second value in a pair) in a similar experimental paradigm presenting pairs of congruent, incongruent, and orthogonal values (Pakizeh et al., 2007).

It is worth noting that Schwartz recently added other principles into the structure of relations among values proposed in his original model (Schwartz, 2012). He recognized interests that are served by value attainment, such as personal or social interests, and relations

of values to anxiety and self-protection, such as anxiety-based/self-protection or anxiety-free/self-expansion values. In our study, we decided to examine motivational conflicts based on the two original dimensions in Schwartz's model. Yet, it would be interesting in future research to explore the neuronal basis of these additional dimensions, which also place values on opposite ends in the value circle. Some neuroimaging evidence for the relevance for these dimensions indicates that the activation pattern in the left posterior insula differentiates between the processing of self-protection and self-expansion values (Brosch et al., 2012). Nonetheless, as described in our introduction, prior analyses have not looked at the neural associates of value conflict, which is the novel contribution from our research. By looking at value conflict across two dimensions of the circle, while yielding evidence converging with prior studies of psychological conflict, our findings make it seem likely that similar results will arise if we look at other dimensions within the circle (i.e., rotated 45 degrees). This is an interesting question for future research.

In summary, our results provide novel evidence for differences in neural responses to human values as a function of their motivational compatibilities/conflicts, particularly as described within Schwartz's model (1992, 2012). This model has received abundant cross-cultural support, but it had been unclear whether the motivational relations between values predicted by the model might have a theoretically consistent neural signature. Our fMRI results thus extend behavioral evidence in support of Schwartz's model by identifying neural signatures of value conflict and may provide a useful neuroscientific paradigm for future research manipulating and measuring motivational connections between values.

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TABLE 1

Values types used in the study

<i>Motivational type</i>	<i>Value (stimulus)</i>	<i>Motivational type</i>	<i>Value (stimulus)</i>
Power	authority being the leader preserving my public image social power wealth	Benevolence	dependability faithfulness to friends forgiveness helpfulness honesty
Achievement	achievement ambition aspiration competence success	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	Tradition	acceptance of family beliefs commitment to family religion preservation of customs respect for tradition traditional culture

Self- direction	choosing own goals	Security	avoiding danger
	creativity		avoiding sickness
	curiosity		cleanliness
	freedom		security
	independence		stability

Universalism	care for environment
	equal opportunity for all
	protection of the weak
	tolerance
	world peace

TABLE 2

Brain regions showing larger activation for congruent versus incongruent value pairs

Notes: BA = Brodmann area; mean 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 = *t*-value of the contrast congruent versus opposing pairs; L = left hemisphere; R = right hemisphere; SMA = supplementary motor area; DLPFC = dorsolateral prefrontal cortex; VLPFC = ventrolateral

Brain region	BA	Mean coordinates of the			Cluster size	<i>t</i> -value
		x	y	z		
SMA (L)	6	-8.3	0.3	55.2	1420	4.817
DLPFC (L)	6	-48.5	5.6	47.3	812	3.852
VLPFC (L)	45	-51.4	21.1	17.9	523	4.464
IFJ (L)	9	-43.4	3.73	32.2	380	3.933
Cerebellum: ISLL (R)		23.6	-72.5	-38.4	635	4.262

prefrontal cortex; IFJ = inferior frontal junction; ISLL = inferior semi-lunar lobule.