The Neurostructural and Genetic basis of Human Values

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A thesis submitted to the School of Psychology, Cardiff University, in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY

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To an angel…

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Abstract

This thesis is aimed at investigating the neurobiology underlying individual variation in human value orientation. In over 80 nations, human values have been investigated under the framework of the circumplex model of human values (Schwarz, 1992). The present research probes specific biological markers of the human values described in this model, including macrostructural and microstructural properties of the human brain, brain activation and genetic components.

The first section of the thesis investigates human values in the context of behavioural genetics. The motivation of this research is to identify the genetic representation of human values. To this end, I utilized knowledge in personality genetics to investigate an association between values and a specific genetic component: the polygenic neuroticism score. The results indicated that the polygenic neuroticism score was associated with individual differences in human values in a sinusoidal manner that is consistent with Schwartz's (1992) model of values. These results suggest that it is useful to consider human values in analyses of genetic contributions to personality traits.

The second section of the thesis describes two studies aimed at identifying the neurostructural basis of values. Specifically, this first study aimed at identifying the neural substrates that account for individual variation in the values assessed within Schwartz's model. This individual variation was reflected in both macrostructrual (volume) and microstructural (myelin volume fraction) properties of brain white matter. The second study focused on a specific type of human values: hedonism values. It aimed at identifying the neurostructural link between hedonism and reward-related processing. The results provided evidence of a "hedonic hub" in the human brain by delineating how an intricate network of structures is associated with hedonism. These findings establish the first neurostructural link between hedonism values and the classical neurobiological pathways of the reward circuitry.

Building on the previous section, the last chapter investigates the effect of human values on reward-related processing in the context of economic decision making and self-interest. Participants made foraging decisions for themselves and for a charity of their choice in two different foraging paradigms. Across both foraging tasks, self-focused individuals, compared to social-focused individuals, obtained more rewards when foraging for themselves than when foraging for others. This evidence reveals a dynamic interplay between an evolutionarily entrenched decision making system and the higher order belief system of individuals.

Taken together, these findings provide new information helping to delineate the biology of values. They also pave the way for a more detailed explanation of psychopathological syndromes such as neuroticism and anhedonia in major depression.

Table of Contents

Chapter 1. General Introduction: Schwartz's circumplex model of values

Chapter 2. Human Values and Genetics: The Genetics of Neuroticism and Human Values

Chapter 3: Human Values and Neuroanatomy

Chapter 4: The effect of Human Values on Personal and Social Foraging Behaviour

Chapter 5. General Discussion

Supplementary Material

Supplement for Chapter 2

Supplement for Chapter 3

Supplement for Chapter 3

List of Figures

Figure title

Abbreviations

PNS	Polygenic Neuroticism Score
NS	Neuroticism Score
fMRI	Functional Magnetic Resonance Imaging
MRI	Magnetic Resonance Imaging
DTI	Diffusion Tensor Imaging
FA	Fractional Anisotropy
L1/AD	Axial Diffusivity
MD	Medial Diffusivity
RD	Radial Diffusivity
MFB	Medial Forebrain Bundle
GP	Globus Pallidus
GM	Grey Matter
WM	White Matter
ICV	Intracranial Volume
SVM	Schwartz circumplex model of human values

Impact of this thesis

Please note that the following chapters have been amended from published/submitted papers:

Chapter 2 is based on:

Zacharopoulos G, Lancaster T.M., Maio G.R., Linden D.E. (2016). The genetics of neuroticism and human values. *Genes Brain and Behaviour*, 15(4), 361-366.

Chapter 3 is based on:

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Zacharopoulos, G., Lancaster, T., Bracht, T., Ihssen, N., Maio, G. and Linden, D. E. J. (2016). A hedonism hub in the human brain. *Cerebral Cortex*, doi: 10.1093/cercor/bhw197

Chapter 1

General 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 thesis is primarily focused on the latter definition. However, the last experimental chapter on economic decision making attempts to investigate the interplay between the two kinds of values.

1.1. Human Values.

1.1.1. The progression of value models

Human values are regarded as part of the psychological foundations for ethical behaviour and a crucial element in social functioning (Turiel, 1983). Allport’s and colleagues (Allport, Vernon & Lindzey, 1960) seminal “Study of values” 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 emphasized 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 36 values, such as freedom, equality, and broadmindedness. He 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. However, an important missing element in these accounts of value orientations was the omission of predictions about relations between values.

1.1.2. Schwartz's Circumplex Model

The relations between values are the central feature of the most widely used model of values at this time: Schwartz's (1992) circumplex model and its closely linked successor (Schwartz et al., 2012). Schwartz's (1992) model posits the existence of 10 value types (Figure 1, Panel A), with each expressing motives that can be discerned from Multi-Dimensional Scaling (MDS) analyses of responses to 56 separate values. These motives are organized along two main 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).

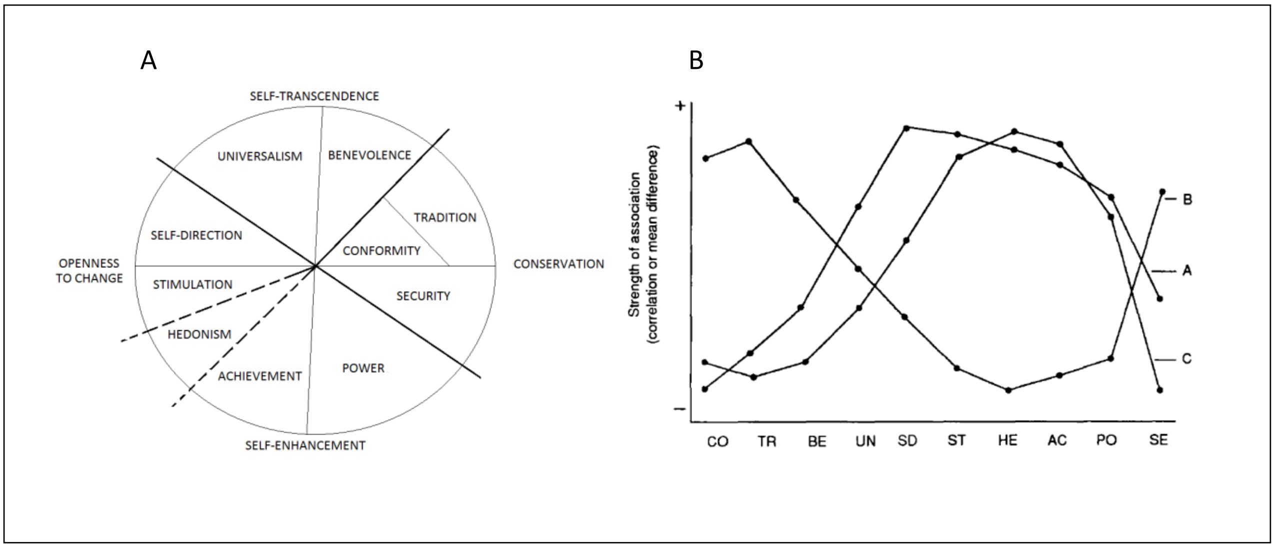

Figure 1.1. A. The circumplex structure of personal values (modified from Schwartz, 1992). B. Plot of hypothesized relationships between three external variables (A, B, C) and the 10 values (SD= Self-direction, ST=Stimulation, HE=Hedonism, AC=Achievement, PO=Power, SE=Security, CO=Conformity, TR=Tradition, BE=Benevolence, UN=Universalism). Each dot point could represent a correlation coefficient (adapted from Schwartz 1992).

Compared to other models, Schwartz's theory has received extensive validation (Schwartz, 1992). By building on the idea of the motivational continuum, a revised version of the theory "partitions the continuum into a finer set of meaningful, conceptually distinct values with greater universal heuristic and predictive power" (Schwartz et al., 2012). This 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 the circumplex model of values is that it makes specific predictions about sinusoidal associations between 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 1B.

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. This approach is less precise than methods specifically looking at sinusoidal tests of patterns of associations between values and other variables, because it focuses only on the opposing ends of each dimension and not on the correlations in between. Nonetheless, one study has recently found evidence of a sinusoidal pattern in relations between values and personality traits in an analysis that considered correlations across all the values (Parks-Leduc, Feldman, & Bardi, 2015). In particular, the personality trait openness to experience was positively associated with the value types stimulation and self-direction and negatively associated to the value types conformity, tradition and security.

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. Therefore, this circumplex model of values offers a suitable avenue for probing the neurobiology of human values.

1.2. Social Psychology and Social Cognitive Neuroscience

As introduced above, human values were initially conceptualized in the field of social psychology, which is "an attempt to understand and explain how the thoughts, feelings, and behaviors are influenced by the actual, imagined, or implied presence of others" (Allport, 1985). However there has been an increasing realization from the researchers studying social psychological behavior of the importance of biological studies. The importance of biological studies in social psychology is underscored by several general principles (Cacioppo et al., 2000). The first principle, the multiple determinism, posits that most if not all social phenomena are multiply determined, including biological apart from social determinants. For example a number of important social phenomena including morality, anger, fear, social propriety and sexuality have been shown to have direct biological determents including lesions in ventromedial prefrontal cortex and amygdala (Damasio, 1994; Macmillan, 1986; Klein & Kihlstorm, 1998). Therefore, focusing exclusively on social determinants in isolation when investigating a social phenomenon, could hinder the discovery of associations and interactions among the social and biological determinants (Cacioppo et al., 2000). Another general principle is the reciprocal determinism, which suggest that there are mutual influences between microscopic (e.g., biological) and macroscopic (e.g., social) factors in determining social phenomena and behaviour. For instance, Zillmann (1984) demonstrated that the sympathetic arousal in males is influenced when they are exposed to violent and erotic material and most importantly this level of arousal has a reciprocal effect on how they perceive sex and aggression. These results, again, suggest that is it difficult to provide a comprehensive account of social behaviours if either the biological or social levels of organization are considered unnecessary or irrelevant. The present thesis embraces these principles and aims, though social psychological and biological methodologies, to provide a more comprehensive account of human values by utilizing the most recent technical and methodological developments including functional brain imaging, and genetic techniques.

As a result, despite initially being studied mainly in the context of social psychology, many human value-related social psychological phenomena including altruism, trust and cooperation, are now being explored in a multi-disciplinary approach, within social cognitive neuroscience.

The emergence of this relatively recent field has been “an attempt to understand and explain, using the methods and theories of neuroscience (Magnetic Resonance Imaging (MRI), functional Magnetic Resonance Imaging (MRI) , Electroencephalography (EEG), Magnetoencephalography (MEG) and genetics (twin studies and Genome Wide Association

Studies in particular), how the thoughts, feelings, and behaviors of individuals are influenced by the actual, imagined, or implied presence of others" (Ward, 2012). It was initially introduced by Cacioppo and Berntson in 1992 as the "Social psychological contributions to the decade of the brain: Doctrine of multi-level analysis." This approach recognizes that psychological phenomena/processes can be explained at multiple levels: at the cultural/societal, personal, brain, cellular and molecular. The field of social psychology focuses particularly on the cultural/societal and personal level by explaining psychological phenonomena in terms of inter-group processes, group processes, social interactions and encounters, personality traits of the individual etc. Neuroscience on the other hand focuses on the brain, cellular and molecular levels, by explaining psychological phenomena in terms of neural circuits, neurons, chemicals and genes.

The pivotal aim of social cognitive neuroscience has been to create bridges between these different levels of explanation (Ward, 2012). Creating bridges across these different levels of explanation can be beneficial to both social psychology and neuroscience for a number of important reasons, including the explication of psychological mechanisms and theoretical development. This thesis aims to take advantage of both of these benefits in the context of human values.

Firstly, most psychological processes (such as altruistic giving) are usually comprised of several sub-processes often occurring in close temporal proximity or even simultaneously (Lieberman, 2010). To be able to explain and predict a given psychological process, the psychological researcher needs to be able to clarify the nature of the underlying sub-processes and the relationships between them. However, it is often a difficult task to outline all the specific psychological computations of psychological process if one merely employs the knowledge and tools of a single discipline (e.g., social psychology). On the other hand, years of neuroscience research have resulted in the insight that a great number of processes that are directly related to human values, such as calculations of reward and punishment, pain and pleasure, mentalizing, delaying gratification and emotion regulation, are implemented by specific brain systems (Lieberman, 2010). Social psychology can utilize this neuroscientific knowledge to produce inferences about the specific sub-processes of a multi-dimensional psychological phenomenon. For example, if a group of individuals exhibits more benevolent behavior than another group, there may be a number of psychological sub-processes (e.g., individual differences in the ability to understand others or in the subjective liking of donating money to others) that are connected to these behavioral differences. Teasing apart putative psychological mediators is often difficult when looking at a gross behavioral measure, such as total amount of money given to charity or reaction times, metrics that are usually recorded by a social psychologist. However, these putative psychological computations can be interrogated by examining whether such behaviors are related to brain regions or pathways that are particularly associated with the ability to understand the emotions of other people or the subjective liking of donating money to others or even both. All in all, the tool of neuroimaging can aid the psychological scientist to interrogate simultaneous psychological processes which are often hard to interrogate otherwise. However, it is important to note that despite the potential insights for employing such methodologies, this “reverse inference” approach (i.e., where the engagement of a particular cognitive process is inferred from the activation of a particular brain region) has been shown to be problematic especially when the selectivity of the region in question cannot be established or is known to be weak (Poldrack, 2006).

Second, applying neuroscience methods to the study of human values can help to update social psychological models, like Schwartz’s circumplex model of values. For example, psychological processes that were traditionally thought of being distinct, such as social vs physical pain, or social vs physical reward or even social vs physical disgust, are now understood to be underpinned by overlapping structures. For example, anterior cingulate cortex is active both during physical or social pain (Eisenberger, Lieberman, Williams, 2003) and the physical pain reliever acetaminophen (Tylenol) was shown to additionally reduce social pain (DeWall et al., 2010). These findings of similarities in the neural processing of social and physical pain challenge Maslow’s theory (1943) of a hierarchy of needs. This theory predicts that individuals will prioritize the prevention of physical pain over social pain. However, in the light of these recent social cognitive neuroscience findings, we may revise how we think about these hierarchical priorities (Lieberman, 2010). For example, the priority to prevent physical pain and certain types of social pain may be clustered in the same hierarchical level, and this revised version would now predict that, when prevention of certain types of physical and social pain compete, individuals would not have a particular preference to prevent one type over the other.

Similarly, in light of neurobiological evidence in the context of human values, we might revise our current notion about the structure of human values. For example, if particular pathways in the brain (e.g., the volume of reward-related neural regions, the integrity of reward-related tracts connecting these regions) are found to be strongly associated to a particular value (e.g., hedonism) but not associated (or associated in the opposite direction) to the adjacent value (e.g., stimulation) then this finding may challenge the hypothesized motivational congruence of these adjacent values (which formed the basis to place them next to each other in the circular model in the first place), or suggest a unique way in which this congruence is encoded in the brain (e.g., through diffuse indirect brain pathways).

The ability of social cognitive neuroscience to help elucidate mechanisms and develop theory may have diverse benefits. One important benefit is to help addressing social psychological questions that have gone unanswered for years (Lieberman, 2010). For example, it is commonly known that there is individual variation in the relative importance of human values (e.g. hedonism) as a guiding principle in one's life. Why do some people have a strong tendency to value hedonism and live hedonic lives while others appear to choose more restraint? Questions such as this have diverse answers, including roles for a range of cultural, social, personal, and biological factors. The field of social-cognitive neuroscience helps to utilize the knowledge of reward-related biological pathways of the brain derived from years of human and animal neuroscientific research, thereby gaining insight into neurological mediators in such questions. Also, a number of psychiatric conditions have been previously linked to human-value related behaviours (Hanel & Wolradt, 2016). For example, people suffering from depression tend to avoid interacting with others; psychopaths tend to undermine and even violate social norms and manipulate others. Employing the methods of neuroscience to study brain abnormalities in response to human-related deficits can help illuminate the neural systems underlying such social deficits and the values to which they relate. Moreover, developing certain biomarkers can help in the assessment and/or intervention of such deficits.

Taken together, the pivotal aim of the present thesis is to take advantage of the social cognitive neuroscience approach to bridge different levels of explanation in the context of human values. This is important because values act through processes that can be found in the brain. Therefore, elucidating these processes and their connections to values has the potential to help us learn more about what values do (their functions) and how they are interrelated to each other and to other constructs (their structure).

1.3. The evolution of human values and the "social brain" hypothesis

Human values are thought to help us to achieve a smooth social functioning in the complex societies in which we live (Schwartz, 1992). This functioning is interesting in light of evidence examining brain properties (e.g., size) and social characteristics in animals. Compared to other animals, humans live and interact with other conspecifics in considerably more complex social environments. There is now converging evidence of a positive association between relative brain size and the social complexity in which organisms live. In fact, the best predictor of brain to body ratio across primate species is the individuals' social group size. Moreover, relative brain size correlates with many indices of social complexity, including social group size, number of females in the group, grooming clique size, frequency of coalitions, male mating strategies, frequency of social learning, frequency of tactical deception, and prevalence of social play (reviewed in Dunbar & Shultz, 2007). As can be seen in Figure 1.2., humans have the highest brain-to-body ratio and they live in the largest groups. Taken together, this evidence implies that the larger the brain, the greater the number of social relationships that can be sustained (Ward, 2012).

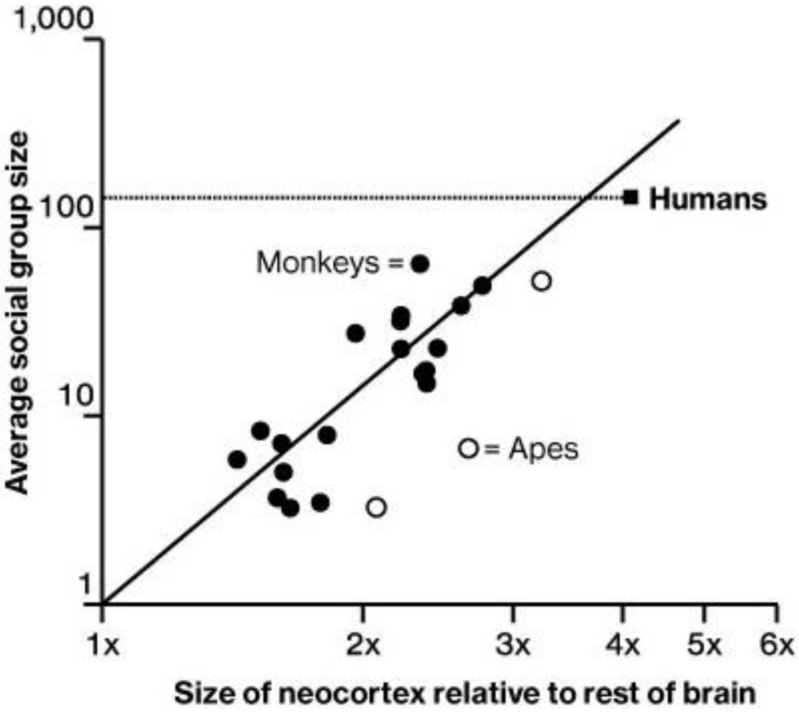

Figure 1.2. Scatter-plot exhibiting a strong positive association between neocortex size and social network size in primates. (Adapted from Kudo & Dunbar, 2001).

Despite the general agreement on humans' unique social complexity, and the relationship between this social complexity and relative brain size, there has been debate on the exact nature of the neural underpinning of our ability for this social complexity. Indeed, a perennial neuroscientific question in the context of human evolution is whether the brain has a specialized social module that exclusively computes social-related information (also known as the "social brain"), or whether our remarkable social abilities are mere applications of our general ability to think and reason analytically (Ward, 2012).

The "social brain" view suggests that there are particular regions or networks in the brain (notably amygdala, orbital frontal cortex and temporal cortex (Brothers, 1990)) involved in social-related processing (or specific types of social-related processing), but not involved in other types of cognitive processing. A number of previous studies (cited in Ward,

2012) support this modular view. For example, it has been demonstrated that there are certain regions in the brain that exclusively process the sight of faces (e.g. Kanwisher, 2000), the detection of cheating (Cosmides, 1989) or the mental state of others (Saxe, 2006). This latter mentalizing network (which is composed of dorsomedial prefrontal cortex, precuneus, posterior cingulate cortext, temporoparietal junction and anterior temporal cortex) has been studied extensively and is thought to support thinking about the thoughts, feelings, and goals of others (Liebermann, 2012). By contrasting it with the structure of other networks for analytic thought and memorization, and using a see-saw analogy, Liebermann and others provided evidence that there is a competition between the mentalizing and working memory networks in many settings. In other words, when one network is active, the activity of the other decreases and vice versa (Lieberman, 2012). For example, at rest, there is a negative correlation between the activities of these two networks (Fox et al., 2005). Moreover, certain cognitive tasks that recruit the lateral frontoparietal working memory regions significantly decrease the concurrent neural activity of the medial frontoparietal mentalizing regions (McKiernan, Kaufman, Kucera-Thompson & Binder, 2003). Furthermore, higher activity in the mentalizing network during analytic processing leads to poorer task performance (Li, Yan, Bergquist & Sinha, 2007; Weissman, Robert, Visscher & Woldorff, 2006). Of note however these two networks are thought to operate in concert in other settings (Lieberman, 2012). Lastly, patients with social functioning deficits (but not general intelligence deficits) such as autism typically show abnormal activation of the social brain network during social-processing tasks (Hadjikhani, Joseph, Snyder & Tager-Flusber, 2007). Taken together, these findings suggest that there may be some modules in the brain that are specialized for the processing of social information. However, contrary to the social brain view, others disagree with the notion that brain contains specialized modules exclusively devoted for social-related processing and argue that the so called social regions compute both social and non-social aspects of cognition such as reasoning (e.g., Gould, 1991).

A related debate considers the origins of humans' remarkable social abilities and their associated biological underpinnings. According to the first view, the social-intelligence hypothesis (Humphrey, 1976), also termed social-brain hypothesis (Dunbar, 1998) or the Machiavellian intelligence hypothesis (Whiten & Byrne, 1988), the environmental pressures of living in highly complex social lives in large groups triggered the unusual enlargement of the brain in primates causing an increase in their general intellect. Such pressures include meeting one's requirements, while coordinating one's behaviour with other group members. According to the opposite view (cited in Holekamp, 2007), the greater intellect and larger brains did not evolve because of social complexity but because of selective forces in the non-social physical environment, including the need to learn and recall when and where food might become available.

In alignment with the social-intelligence hypothesis, it is possible that the manifestation of human values over the course of evolution has arisen in response to social complexity, as a tool enabling smooth functioning within large social groups. It is also conceivable that different human values existed over the course of evolution. Indeed, as discussed above, Schwartz circumplex model features a set of human values that are present across cultures supporting the evolutionary conserved idea. Nonetheless, a set of values, the ones that provided the best social functioning, may have been most strongly conserved. This may explain why most cultures attach the highest levels of importance to values that are relatively important in social functioning (e.g., Bard et al., 2009), including Schwartz's self-transcendence values in particular. One of the aims of the present thesis is to test the hypothesis that the human values recognised by all cultures may be reflected in biological indices, including measures of genetic factors, brain structure, and brain function.

1.4. Human Values and Genetics

Knowledge of the genetic underpinnings of human values is scarce. To investigate whether human values has a strong genetic component previous studies (see below) utilized the twin study methodology. Twin studies are important because they allow researchers to disentangle the genetic (nature) vs the environmental (nurture) determinants of a trait or a behavior. A twin study is usually consisted of two types of twins. The first type is monozygotic or identical twins who are genetically identical to each other (i.e., they share 100% of their genes) and they share 100% of their prenatal and family environment. The second type of twins is the dizygotic or fraternal twins who like identical twins share 100% of their environment but crucially they share 50% of their genes. The twin study methodology allows the researcher to isolate these genetic and environmental factors, for it allows the examination of the effect of genes while the environment is help constant. This is usually achieved by comparing, for example, the correlation coefficient of a human value score between monozygotic twins and the corresponding correlation coefficient of dizygotic twins. If the monozygotic coefficient is significantly higher than the dizygotic then it would support that human values have a strong genetic component.

Despite the ability to isolate the genetic from environmental factors, twin studies are unable to provide information on the specific genetic locations that account for differences at the phenotypic level. To this end, a number of techniques, such as linkage analysis and candidate gene association studies have been used for several decades. These techniques are particularly powerful in the identification a specific genetic variant of traits or diseases that are genetically determined by a very small number of genetic factors. However, when the trait or the disease does not fulfill this criterion (i.e., are influenced by a large number of common low penetrant variants) such approaches are insensitive to identify a genetic association explaining the phenotype. Indeed, complex traits such as human values, are known to have many environmental and genetic contributions many of which have subtle individual effects. Therefore variations at the phenotypic level of such traits are unlikely to be explained by a small number of genes.

However, recent technological advances made it possible to investigate the subtle genetic contributions (i.e., many genetic variants) that are collectively associated to a complex trait. This can be achieved with a Genome Wide Association Study (GWAS) which is an unbiased examination (in that it does not require the selection of a specific candidate gene in advance) of a genome-wide of genetic variants in different individuals to examine whether any genetic variant is associated with the trait or disease under investigation. Since human values are particularly complex traits and thus influenced by a large number of interacting genetic and environmental factors, the most suitable genetic methodology for investigating the genetic components of human values is GWAS. However, no GWAS study was ever conducted on human values.

1.5. Human Values and Brain Anatomy

Our knowledge regarding the brain correlates of human values derives from a variety of sources, including functional and structural brain imaging studies of associations with values and value-related traits (Kanai & Rees, 2011) and neuropsychological studies of patients displaying specific moral deficits (Koenigs & Tranel, 2007). These studies illustrated the roles 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. In addition, reading examples of actions reflecting human values (e.g., correcting injustice) and reflecting on the importance of these values has been shown to recruit the medial prefrontal cortex (Brosch, Coppin, Schwartz & Sander, 2012).

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 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, Armony, Blair & Dolan, 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, Gardini, Clininger and Venneri (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, Kanai, Bates & Rees, 2012), the authors 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, see Boer & Fischer (2013)) was positively associated with grey matter volume in the bilateral subcallosal gyrus of the frontal lobe. Overall, then, previous studies have found some structural brain correlates of psychological variables that are relevant to values, but no previous study tested the sinusoidal hypothesis (Figure 1B) using neuroanatomical data.

1.6. Human values and brain functions

An important attribute of the animal brain is its ability to derive indices of reward and punishment from different objects and behaviour. These indices help us to make choices in complex environments. For humans, these complex environments are very social in nature, bringing social values into play. Thus, an interesting question is how social values relate to reward processing in the brain.

1.6.1. The motivational nature of human values and the reward circuitry in the brain

One of the most central properties of human values is their motivational nature. The motivational nature of human values as well as the impact on the reward-circuitry of the brain raises the possibility that they might be underpinned by certain subcortical brain regions that are particularly involved in motivated behavior and reward processing, a hypothesis that has never been directly tested at the level of brain anatomy. The putative reward system of the human brain is centered on hubs in the basal ganglia (striatum and Globus Pallidus) and includes the ventral tegmental area (VTA), prefrontal brain regions, and parts of the limbic system (Haber and Knutson 2010). Studying the association between hedonism-related values and the structural properties of the reward system, which is a classical circuitry of the brain, would substantiate the evolutionary account of human values, and is an objective of some of the research reported in this thesis.

1.6.2. Human values and reward-related processing in a foraging context

Apart from merely looking at the neuroanatomy, the relationship between human values and reward-related processing can also be investigated at the level of behavior and brain function. Two types of economic decision-making paradigms are particularly relevant to this possibility, both of which are reward-related tasks: classical economic decision making and foraging. Classical economic decision making mainly involves a binary choice between two currently available options. Previous neuroimaging classical economic decision making work in the context of charitable donations (Brosch, Coppin, Scherer, Schwartz & Sander, 2011) showed that human values motivate behaviour through their impact on the reward-circuitry of the brain.

Foraging, on the other hand which has been recently investigated with neuroimaging methods (see below), involves a binary choice between staying with the currently available option or leaving it to search for alternative ones. Many life decisions can be conceptualized as foraging problems (Charnov 1976; Constantino & Daw, 2015). Employment decisions, mate selection, and internet searches are just a few examples of scenarios wherein people must choose whether to engage with the currently available options or to search for alternative ones. To solve this type of problem, an ideal forager compares the value of two strategies -- engaging with the currently available option or foregoing it to search for alternatives -- and chooses the one of highest value. This is the optimal solution described in the Marginal Value Theorem (Charnov 1976) which requires comparing the value of the current option to the overall value of the alternative, foraging environment. Previous neuroimaging foraging studies found that the anterior cingulate cortex (ACC) is positively associated with the overall value of foraging (Kolling, Behrens, Mars & Rushworth, 2012). However, this psychological function of the ACC was subsequently challenged by research showing that, when choice difficulty is properly controlled, ACC activity is no longer associated with the overall value of foraging. However, there is still an active debate on the issue (Kolling, Behrens, Wittmann & Rushworth, 2016; Shenhav, Straccia, Botvinick & Cohen, 2016).

Classical economic decision making (Brosch et al., 2011), as opposed to foraging, has been previously studied in the context of human values. Brosch and colleagues showed that human values were involved in classical economic decision making via the reward-system of the brain. However, it is currently unknown whether human values are also involved in foraging behaviour, which is considerably more complex than classical decision making (Shenhav, Straccia, Cohen & Botvinick, 2014), and whether they recruit brain systems other than the reward-circuitry of the brain. The aim of the last experimental section of the thesis is to investigate these questions.

1.7. Structure of the thesis

Taken together, it is currently feasible to provide evidence testing a neurological contribution to human values if one carefully utilizes the reliable neuroscience markers, such as polygenic scores, brain anatomy and reward-related decisions. This thesis investigates the neurobiology of human values in three areas/sections: genetics, neuroanatomy, and reward-related decisions. The neuroanatomy section consists of two studies. In the first neuroimaging study, I examined non-linear associations between values and brain structure. In 85 participants, I found the predicted sinusoidal relationship between ratings of values 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.

The general research question in the second study was whether the motivational nature of human values is underpinned by brain structures that are particularly involved in motivated behaviour and reward processing. I hypothesized that variation in subcortical hubs of the reward system and their main connecting pathway, the medial forebrain bundle (MFB) is associated with individual value orientation. This was the first study to illuminate the associations between the importance people attach to the human value of hedonism and structural variation in reward-related subcortical brain regions.

The second main section of this thesis deals with the genetic underpinnings of human values. Indeed, human values and personality have been shown to share genetic variance in twin studies. However, there is a lack of evidence about the genetic components of this association. This study examined the interplay between genes, values, and personality in the case of neuroticism, because polygenic scores were available for this personality trait (but not for others). As described later in the thesis, the results pave the way for an investigation of the biological mechanisms contributing to human value orientations.

The third, and last, experimental section aims at investigating how human values affect economic decision making (foraging and classical) and its neural underpinnings in the context of charitable donations. I found that self-focused individuals, compared to the social-focused ones, kept more money for themselves than for a charity. There was a negative relationship between the self-focus score and dorsal anterior cingulate cortex (ACC) during the personal compared to social foraging but not during the classical economic decision making. This finding complements those of the previous sections.

Together, all of the findings support the main hypothesis of the thesis. The results consistently support the assumption that human values are associated with a number of markers across multiple levels of neurobiology. The General Discussion elaborates on the ramifications of these findings, limitations of the current evidence, and future research directions.

Chapter 2: Human Values and Genetics:

The Genetics of Neuroticism and Human Values

2.1. Introduction

The prior work investigating the genetic component of human values is currently very limited. A recent extended twin family (also known as nuclear twin family study) study (Kandler et al., 2016), which included data from twins and their parents, allowed researchers to disentangle genetic from environmental transmission between parents and their offspring. In particular, they investigated whether the parent-child similarity in human values is primarily determined by the environmental or the genetic transmission of human values. The results indicated that human value parent-child similarity was primarily due to their shared genetic makeup instead of environmental parent-child transmission. Another twin study (Knafo & Plomin, 2006) investigated the genetic and environmental influences explaining the stability and change of prosocial behavior in children from early to middle childhood. Using longitudinal genetic analyses, the authors found that genetic influences explain both change and continuity in prosocial behavior while nonshared environment contributes mainly to change.

Another set of previous studies on this topic have focused on the genetic components of relations between human values and personality traits (Schermer, Feather, Zhu & Martin, 2008; Shermer et al., 2011). The reason for this is twofold: (1) there is a growing body of knowledge of the genetic basis of personality (but not of human values) and (2) human values are reliably associated with certain personality traits at the behavioral level (Parks-Leduc et al., 2015; Rim 1984). Extending this connection, studies of twins have found that the shared variance between human values utilized Schwartz's (1992) circular model of values and personality has a significant heritable component (Schermer et al., 2008, 2011).

However, the exact genetic loci driving this association between values from Schwartz's model and personality have remained obscure. This association can be investigated by utilizing a growing body of knowledge on personality genetics. As complex psychological dispositions, human values and personality traits are both likely to be affected by numerous genes simultaneously (in addition to strong environmental influences). To capture the genetic influence of complex traits and values, it is therefore useful to focus on genetic indices that reflect the contribution of a great number of single nucleotide polymorphisms (SNPs), such as polygenic scores derived from Genome-Wide Association Studies (GWAS).

A polygenic neuroticism score (PNS) has been available through a recent meta-analysis of GWAS of personality traits (N = 63 661) (Genetics of Personality Consortium et al., 2015). Neuroticism is a personality factor ranging from emotional stability to high nervousness, tension and moodiness. In the meta-analysis, a neuroticism score (NS) was derived from a number of measures including the NEO Personality Inventory, the Eysenck Personality Questionnaire, the International Personality Item Pool inventory, harm avoidance scores in Cloninger's Tridimensional Personality Questionnaire and negative emotionality scores in the Multidimensional Personality Questionnaire. The meta-analysis showed that 0.6% of the variance in this NS was explained by the PNS. Although this low percentage suggests only a small genetic component, it was reliable and potentially important, making it a relevant candidate for studying genetic contributions to neuroticism and other individual differences related to neuroticism. The shared genetic associations between personality traits and human values and the recent identification of the polygenic neuroticism score provide a foundation for expecting that the polygenic association with neuroticism may also relate to value orientations. Human values are particularly interesting in connection to neuroticism. A recent meta-analysis of the relations between human values and the Big Five traits found reliable trait-value associations, *except* when looking at neuroticism (Parks-Leduc et al, 2015). The authors explained this non-association using Cloninger's (1994) proposition that neuroticism is more appropriately described as a temperament (i.e., an automatic associative response to emotional stimuli) than as a character trait (i.e., a self-aware volitional concept related to behavioural intentions). This indicates a stronger biological component to neuroticism than to other traits, which, like human values, may be amenable to higher levels of cognitive processing and control. Thus, from this perspective, neuroticism may manifest a genetic component, but little association with human values.

However, a different possibility emerges if we consider relevant research examining links between neuroticism and relevant affective states and attitudes. Neuroticism is associated with a higher likelihood of anxiety and depression, which are two hallmarks of emotional instability that lead people to withdraw from the world around them (Angst, Gamma, & Endrass, 2003; Thompson, Berenbaum, & Bredemeier, 2011). This pattern suggests that emotionally instability may cause people to be less open to new experiences, ideas, and feelings, because of potential threats to their fragile emotional state. Convergent with these observations, lower levels of neuroticism are associated with more liberal, curious, and open-minded attitudes (e.g., Carney, Jost, Gosling & Potter, 2008; van Hiel & Mervielde, 2004). Strong links between such attitudes and Schwartz's openness value type (Ashton et al., 2005) suggests that an inverse relation between openness values (see Figure 1A) and neuroticism is viable.

The present research was therefore motivated by the shared genetic variance between human values and personality, the existence of a polygenic score for neuroticism, and the ambiguity about neuroticism-value relations. I sought to test whether the potential genetic contribution to neuroticism has similar patterns of the association with human values and the trait on a phenotypic level. To be clear, the prediction was *not* that values mediate the link between genes and traits or that traits mediate the link between genes and values. In theory, values and traits should reciprocally influence each other, as stable individual differences over time, leading to an association that is bidirectional. Our principal aim was to test whether associations with genes emerged for *both* the trait and values. Moreover, we wished to detect whether any observed associations arose in a sinusoidal pattern congruent with Schwartz's circumplex model of values. This is because one of the core aims of the present thesis is to test whether the motivational relations within the value system itself (i.e., the relationship between the 10 human values) is reflected in these neurobiological markers including genetic data. The chief interest was whether the motivational conflicts described in Schwartz's model have neurological components. That is, I did not focus on specific values, but utilized a test of the roles of value types organized along the two motivational dimensions described by Schwartz. This focus enabled me 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).

2.2. Material and Methods

Participants and Procedure

The studies described in this and the next chapter (neurostructural) were performed on the same cohort of participants. Eighty one right-handed Caucasian university students between 19 and 42 (50 females; mean age=23.85 ± 3.71 SD) participated in the study, which was approved by the Ethics Committee in the School of Psychology, Cardiff University. Participants were informed that the study examined the connection between value-morality judgments and biological indices. They took part individually in the laboratory, wherein they completed the measures of human values and personality, provided a saliva sample, and were then debriefed. The sample used consisted of an existing sample collected for behavioural analysis. The present study included all the participants from the existing sample for which the human value score, personality score and the genetic score was available.

Human Values

Participants completed the 56-item Schwartz Value Survey (SVS; Schwartz, 1992). Participants rated the importance of each of the 56 values is 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 then calculated and subtracted from each of the 56 initial raw scores. Schwartz recommends this procedure to help control for superfluous individual variations in rating styles (e.g. Schwartz, 1992). The individual centred item scores were then averaged to form scores for each type of value examined in Schwartz’s model (see Figure 1A). The internal consistency of these indices was moderate to good (Supplementary Material 2.1).

Personality Measure

We quantified NS using the 100-item self-report version of the HEXACO Personality Inventory-Revised (HEXACO-PI-R) (Lee & Ashton, 2004). In the HEXACO-PI-R, NS is termed emotionality, and it features subscales for fearfulness, anxiety, dependence, and sentimentality. These subscales are combined together as the total emotionality score (α = .64). Furthermore, many influential research programs have interpreted and labelled Neuroticism from the Big Five as Emotional Stability (e.g., De Raad et al., 2010; Goldberg, 1990; Saucier, 1994). It was previously shown that HEXACO Emotionality represents an alternative rotation of Big Five Neuroticism (Ashton, Lee & de Vries, 2014) and that they are similar constructs (Ashton et al., 2014; Romero, Villar & López-Romero, 2015). Furthermore, the emotionality score provides a particularly interesting and important rendition of neuroticism in this context because of its relative emphasis on emotional instability, which leads people to withdraw from the world around them (Angst et al., 2003; Thompson et al., 2011), and HEXACO's emotionality dimension is well-suited to detecting the links with values (Pozzebon & Ashton, 2009).

DNA Extraction and Genotyping

Genomic DNA was obtained from saliva using Oragene OG-500 saliva kits. Genotyping was performed using custom genotyping arrays (Illumina HumanCoreExome-24 BeadChip), which contain 570,038 genetic variants (Illumina, Inc., San Diego, CA). Quality control was implemented in PLINK (Purcell et al., 2007) to ensure that the genotypes did not display ambiguous sex, cryptic relatedness (up to third degree relatives by identity of descent), genotyping completeness < 97%, and non-European ethnicity admixture (detected as outliers in iterative EIGENSTRAT analyses of an LD-pruned dataset; Price et al., 2006). SNPs were excluded where the minor allele frequency was < 1%, if the call rate <98%, or if the $\chi 2$-test for Hardy-Weinberg Equilibrium had a *p*-value < 1 e-04. Individuals' genotypes were imputed using the pre-phasing/imputation stepwise approach implemented in IMPUTE2/SHAPEIT (Delaneau et al., 2012, Howie et al., 2009) and 1000Genomes (December 2013, release 1000 Genomes haplotypes Phase I integrated variant set) as the reference dataset.

Generation of Risk Profile Scores

PNS was calculated using the method described by the International Schizophrenia Consortium (International Schizophrenia et al., 2009). PNS was estimated using publicly available data from the international GWAS (Genetics of Personality et al., 2015). SNPs were subsequently pruned for linkage disequilibrium (r^2<0.2). This method ensured that all SNPs included in the PNS model were fairly independent. PNS scores were calculated using the 'score' command in PLINK, which averages the number of risk alleles for each index SNP, weighted by the natural logarithm of the SNP's odds ratio extracted from the GWAS results (Genetics of Personality et al., 2015). From the 6949612 SNPs, a total of 206516 quasi-independent SNPs were considered in the PNS ($p < .5$). PNS was calculated at the liberal p-threshold (p<. 5), because it best predicted NS in the GWAS reference data (Genetics of Personality et al., 2015). There were no outliers in the PNS scores, and the scores were normally distributed (Shapiro-Wilk: p >.3).

Sinusoidal Relationship Analysis

To test the sinusoidal pattern, I employed a new methodology (Hanel, Zacharopoulos, Megardon & Maio, 2016) and an established one (Boer & Fischer, 2013, Supplementary Material 2.3.). The text in this chapter focuses on the new, more conservative approach, but parallel findings for the other test are described in Supplementary Material 2.3. Similar to previous approaches the aim of our methodology is simply to test the sinusoidal prediction of Schwartz circumplex model. Before describing the model in great detail, it would be appropriate to introduce the two-fold value of this new methodology to the non-specialist. First, compared to previous approaches, this new methodology is an unbiased, agnostic approach in that it does not require the researcher to specify in advance *how* the 10 human value types should be associated to the external variable. Rather, it empirically calculate whether an external variable has a sinusoidal relationship to the human value types. Second, substantiated by various simulations (see below), this approach is considerably conservative in that it minimizes the chance of committing a type 1 error.

To test the sinusoidal pattern for an external variable, 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 I 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), the ‘brute force method’ was used. This method is 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, I 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 et al., 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 ȳk 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, different assumptions of the distribution of the correlation coefficients were tested. (1) I 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) I 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.

2.3. Results

Replicating the Link Between PNS and NS

Our first aim was to provide further evidence on the association between emotionality (NS from HEXACO-PI-R) and PNS. As expected, there was a positive association between these variables, *r*(79)=.22, *p*=.048 (Figure 2.1.), replicating the findings of the personality GWAS (2015).

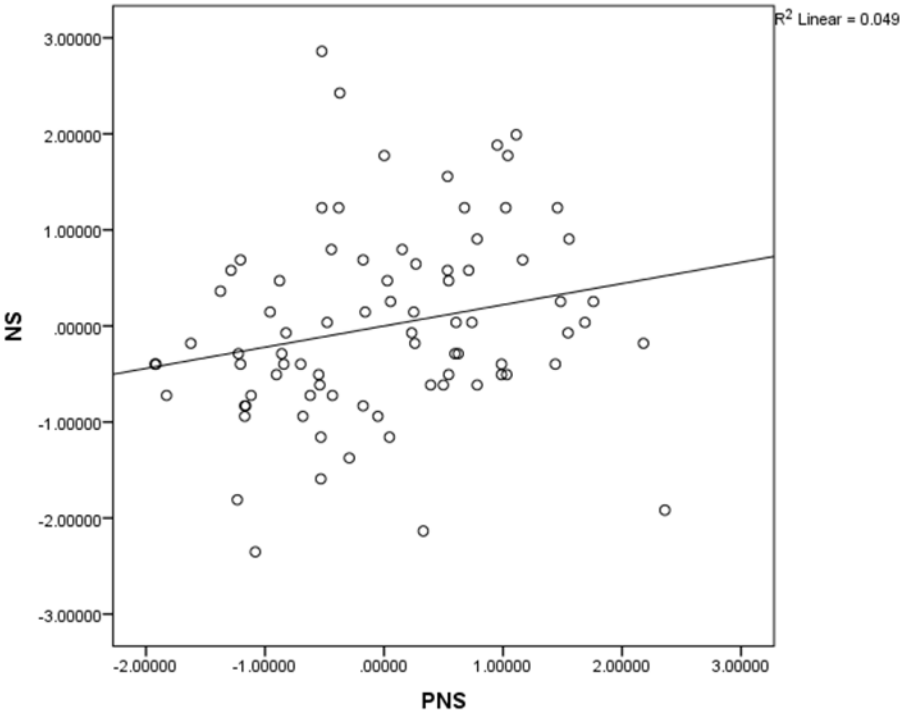

Figure 2.1. Scatter-plot depicting the positive association between NS and PNS, *r*(79)=.22, *p*=.048. Each dot represents a participant.

Structure of Values

Before testing for a sinusoidal waveform in the pattern of associations between values and NS, and PNS, I validated Schwartz's hypothesised circular structure in our sample. This test used two Multi-Dimensional Scaling (MDS) as recommended by Schwartz (e.g., Bilsky, Janik & Schwartz, 2011). The first analysis plotted the 56 value items, and the second analysis plotted the 10 higher-order values. 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.

Fitting the Sinusoidal Model to the NS and PNS

Given the replication of Schwartz's circular structure in the MDS analyses, the analysis turned to testing whether there are sinusoidal patterns of association between values and NS and PNS. To address this question, I plotted the correlation coefficients between NS and PNS on the y-axis and each of the 10 lower-order values on the x-axis in an order that follows their circular structure. The patterns are shown in 2.2. A pattern of sinusoidal association was found between human values and PNS, particularly near the inflection points (Figure 2.2.A), which was significant, *SFI*=.19; false positives=0.6%. Similarly, our analysis of NS reveal a sinusoidal association of a similar form (Figure 2.2.B) but the fit to the sine wave was not reliable, *SFI* = .29; *p*>.05. Visual inspection of Figure 2.2.A shows that the correlation between NS and the human value Benevolence (BE) deviated from the sine-wave; running the sinusoidal test while excluding BE yields a significant *SFI*=.08 (Supplementary Material 2.2.). Overall, NS and PNS map onto the human value space in similar, sinusoidal waveforms. Furthermore, in addition to testing the patterns of correlations using the *SFI* method, this study replicated the PNS and NS findings using two previously established methods, with even more robust results (Roccas, Sagiv, Schartz & Knafo, 2002; Boer & Fischer, 2013) (Supplementary Material 2.3.).

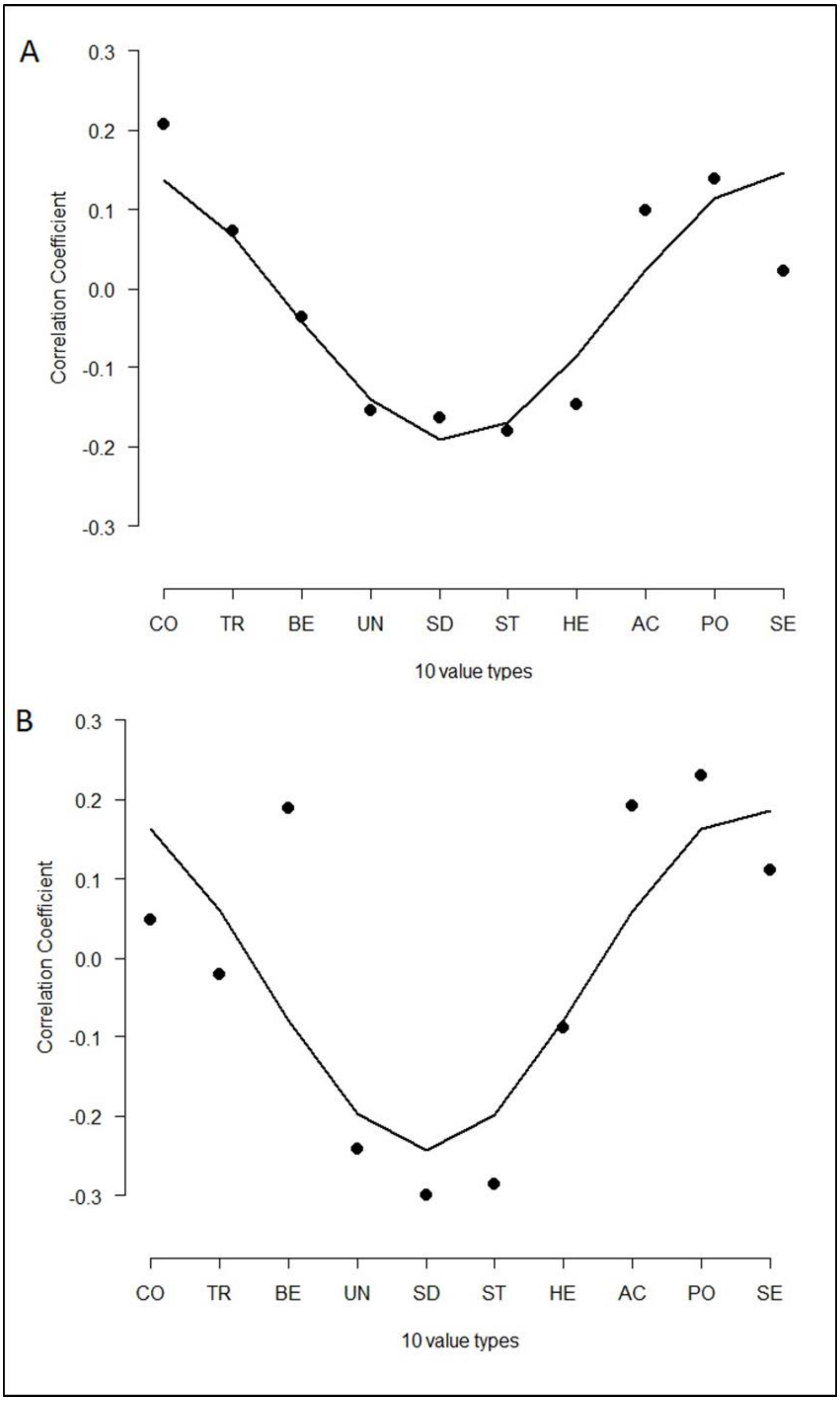

Figure 2.2. Correlation coefficients between the 10 value types (x-axis, Conformity, Tradition, Benevolence, Universalism, Self-Direction, Stimulation, Hedonism, Achievement, Power, Security) and PNS (Panel A) and NS (Panel B).

Discussion

The present research investigated the genetic components connected to the relations between human values and an important dimension of personality, neuroticism. The present study used empirically robust measures of human values, neuroticism, and genetic neuroticism. The results replicated the association between NS and PNS despite using a different measure of neuroticism than in prior research (i.e., emotionality from HEXACO-PI-R). This result adds to the evidence that the polygenic neuroticism score derived by GWAS helps to explain individual variation in neuroticism (Genetics of Personality et al., 2015). Moreover, it laid the foundation for testing whether human values are linked to both NS and PNS. Results indicated that human values were indeed associated with NS and PNS, following the sinusoidal pattern predicted by Schwartz and colleagues (2012) cross-cultural model.

These findings fundamentally extend understanding of human values. Previous twin studies (Schermet et al., 2011; Schermer et al., 2008; Waller, Kojetin, Bouchard, Lykken, & Tellegen, 1990; Keller, Arvey, Dawis, Bouchard & Segal, 1992) have documented that human values may have a genetic component, but this has occurred without simultaneously pinpointing relevant patterns of genes, the pattern of associations with the values, and the nature of the common association to the behavioural phenotype for personality. Here, we document a novel sinusoidal relationship between human values and a specific genetic marker, the PNS – a relationship that was very similar to that found between NS and values.

Furthermore, as expected, Figure 2.2 shows that the sinusoidal waveforms were anchored at one end by negative relations between values promoting stimulation or self-direction and NS or PNS at the other end. This pattern fits links between neuroticism and anxiety and depression. As noted earlier, anxiety and depression lead people to withdraw from the world around them (Angst et al., 2003; Thompson et al., 2011). In addition, higher levels of neuroticism are associated with less liberal, curious, and open-minded attitudes (e.g., Carney et al., 2008; van Hiel & Mervielde, 2004). Neuroticism may contribute to lower openness to new experiences, ideas, and feelings because of the threats posed by novelty. At the same time, the pattern of withdrawal elicited by lower stimulation and self-direction values may contribute to emotional instability by increasing rumination, perseveration in an isolated environment, and self-absorption. Further evidence is needed to explore these possibilities.

The authors acknowledge that the strong sinusoidal association between human values and neuroticism found here is not inconsistent with the meta-analytic finding showing the absence of a sinusoidal association (Parks-Leduc et al, 2015). A number of factors may explain this discrepancy. The measures of neuroticism used in the meta-analytic study (Neuroticism from Five-Factor Model, FFM) and here (Emotionality from HEXACO) are similar but not identical with correlation coefficients around *r*=.55 (Ashton et al., 2014; Romero, Villar & López-Romero, 2015). This raises the possibility that the unique variance of HEXACO's emotionality (rather than the shared variance with FFM's Neuroticism) may be related to human values and thus explain the discrepancy. Future studies administering both personality measures and human values can interrogate this possibility.

Two other aspects of our results merit further discussion. First, it is informative to contrast the sinusoidal pattern, which is a test of association across *all* values, with the strength of the correlations with *specific* values. This is interesting in part because most of the correlations between specific values and PNS or NS were weak and unreliable, aside from the significant theoretically congruent correlations discussed above (see Supplementary

Material 2.4). Nonetheless, the sinusoidal fit reveals a crucial pattern that is missing from univariate tests that focus on one value at a time. It is possible for individual relations to be weak at the same time as their combined pattern is meaningful and reliable. In analyses of values, this difference between individual correlations and the net pattern is crucial, because the relative roles of different values are more psychologically important and meaningful than the roles of any single value type in isolation, due to competing implications between values (Rokeach, 1973; Schwartz, 1992).

Second, the NS variance explained from the PNS was much higher in the present study (4%) than in the initial discovery sample (0.6%). A number of factors may account for the larger relation in this study. First, the present study measured neuroticism using a single scale in a single homogeneous cohort, whereas the meta-analytic study assessed neuroticism from multiple instruments (even in the same cohort). Second, the present study used a single measure of neuroticism with subscales (Fearfulness, Anxiety, Dependence, and Sentimentality) that are different and more emotional in focus than in the replication cohort in the meta-analytic study (NEO-FFI's Neuroticism: anxiety, hostility, depression, self-consciousness, impulsiveness, vulnerability to stress and Amsterdam Biographical Questionnaire). Third, the power of the current study merely allows the detection of a moderate effect, and future replication studies may yield a smaller effect; therefore, future research should interpret the current effect size with caution. Despite these possibilities, the current replication of the NS-PNS relation is promising for future research attempting to learn more about this relation and its implications.

Chapter 3: Human Values and Neuroanatomy

3.1. Non-linear association between human values and Neuroanatomy

3.1.1. Introduction

In the preceding chapter, I tested and accepted the sinusoidal hypothesis by using genetic data. The current sub-section of this experimental chapter directly tested the sinusoidal hypothesis using brain structural correlates. Whether Schwartz's putative evolutionarily (see General Introduction) conserved set of values and their latent conflicts might be reflected in brain anatomy has hitherto not been explored.

As discussed in the general introduction, previous studies have found some structural brain correlates of psychological variables that are relevant to values. In the context of political attitudes, Kanai et al. (2011) showed a positive association between liberalism and grey matter volume in the anterior cingulate cortex and a positive association between conservatism and the volume of the right amygdala. Gardini et al. (2009) explored the link between grey matter volume and personality scores using the Three-dimensional Personality Questionnaire. They found grey matter volume in the right frontal and posterior cingulate regions to be associated with higher novelty seeking, an inclination similar to Schwartz's stimulation values. Moreover, they demonstrated less grey matter volume in the caudate nucleus and in the rectal gyrus, a part of the frontal lobe, to be correlated to higher reward dependence, similar to Schwartz's hedonism value. 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. Lewis et al. (2012) conducted a voxel-based morphometry (VBM) study of the relationship between grey matter volume and scores on the Moral Foundation Questionnaire, and 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, see Boer and Fischer (2013)) was positively associated with grey matter volume in the bilateral subcallosal gyrus of the frontal lobe. Finally, a number of clinical studies also demonstrate an association between brain anatomy, primarily in frontal lobes, and value-related behaviours. For example, patients with ventromedial prefrontal damage (Koenigs & Tranel, 2007) exhibited irrational economic decision-making behaviour when playing the ultimatum game, in that they exhibited a greater rejection rate compared to controls in response to each of the most unfair offers. In addition, patients with medial frontal and orbitofrontal deficits demonstrate abnormalities in morally relevant behaviours (Ward, 2012). Despite the fact that prior findings suggest that value-relevant judgements are supported by a number of brain regions, with particular relevance to the frontal regions where the motivational functioning of values is concerned, 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.

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, this research 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, the analyses initially focused on testing for the sinusoidal waveform 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).

3.1.2. Material and 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, Lancaster, Bracht, Ihssen, Maio & Linden, 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.A. 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 2.1.).

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, Rutt, Arun, Pierpaoli & Jones, 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, Matthews & Kolind, 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 (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 3.1.6) and 7 subcortical (14 in total, Left and Right: Amygdala, Accumbens, Caudate, Hippocampus, Pallidum, Putamen, Thalamus) areas (Desikan 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 researchers may 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).

3.1.3. Results

Initial Checks

To validate Schwartz's hypothesised circular structure in our sample, two MDS analyses (Bilsky et al., 2011) were conducted. 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 3.1.2) 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 sub-scores 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

I tested whether the relationship between brain parameters and value scores followed the sinusoidal pattern. This analysis 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). The results revealed a strong sinusoidal association (*SFI*=.07) between human values and overall white matter volume (Figure 3.1.1, Panel A), but no significant association with overall grey matter volume (*SFI*=.61). To check the robustness of the white matter finding, the sinusoidal test was also performed 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, 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) was regressed out of each individual value. The *SFI* was virtually the same (*SFI*=.10, see Supplementary Material 3.1.3).

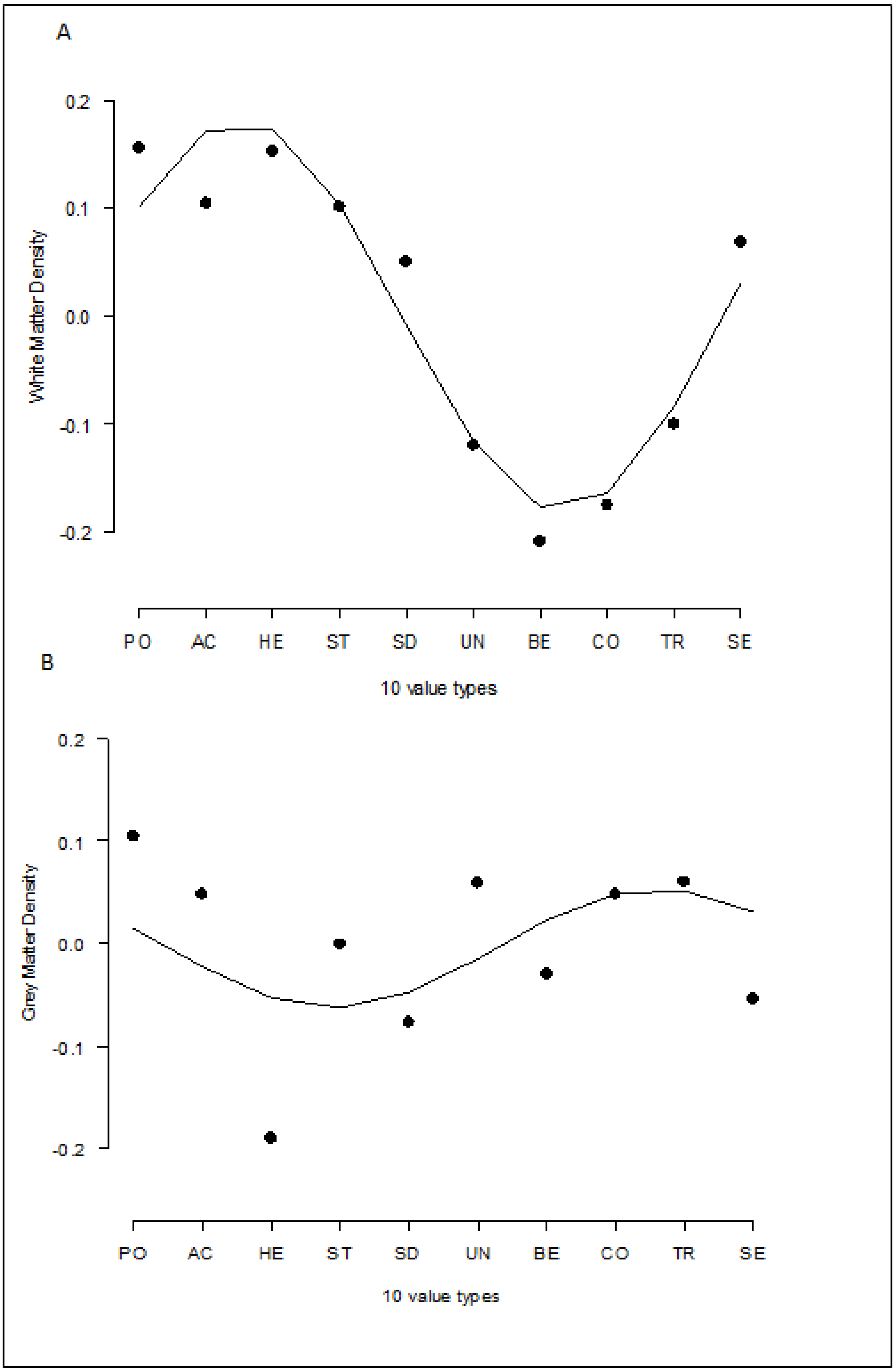

Figure 3.1.1. Correlation coefficients between the 10 value types (x-axis) and the White (Panel A) and Grey (Panel B) matter volume (cubic decimetres dm^3).

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, the myelin volume fraction of the overall brain was obtained using Multicomponent Relaxometry (mcDESPOT) (see Methods, Deoni et al., 2013). This enabled a test of 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 3.1.2). As was the case for white matter volume, the myelin volume fraction was associated with the human values even after regressing out the intelligence variables (*SFI*=.10, see Supplementary Material 3.1.3).

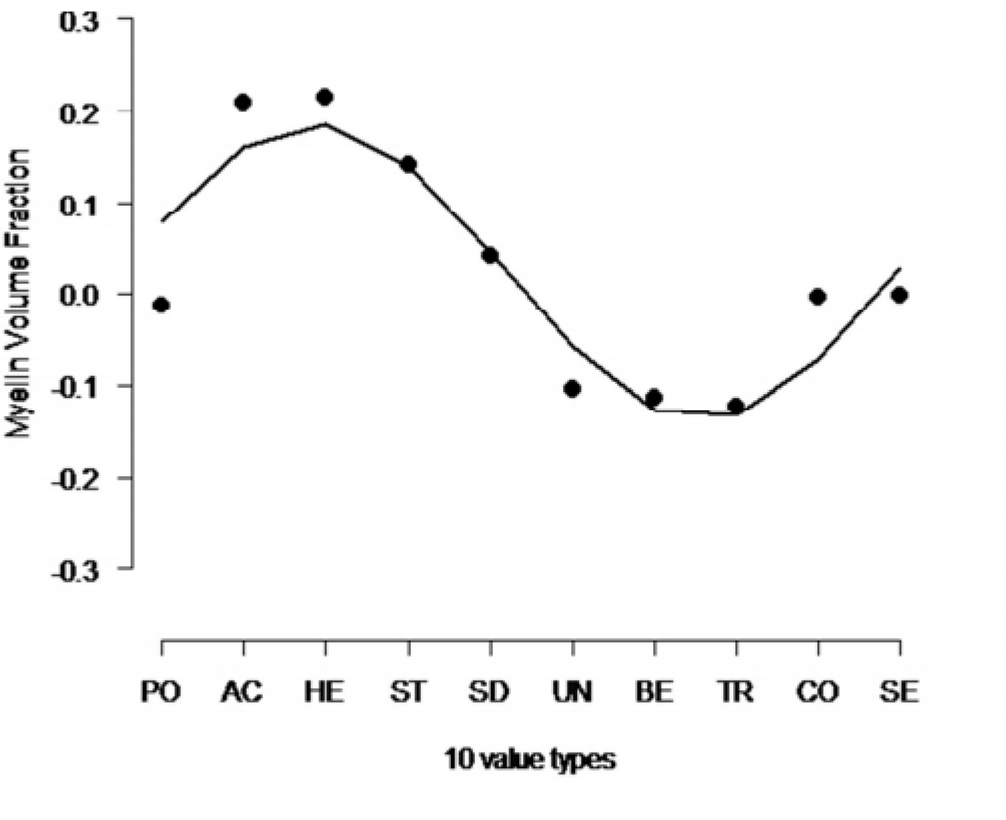

Figure 3.1.2. Correlation coefficients between the 10 value types (x-axis) and overall myelin volume fraction (ratio of myelin-bound water to total water).

Investigation of Regional Differences using Voxel Based Morphometry

Having identified a sinusoidal association between white matter and the 10 value types, it was useful to turn to the specific anatomical contributions. Based on inspection of the sinusoidal waveforms, I 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 the associations at the level of higher-order value dimensions were examined, conservation values were negatively associated with the volume of the white matter underlying the parahippocampal and lingual gyri (*p*FWE=.047; *t*=4.78, -22-54 4, Montreal Neurological Institute: MNI space, k=1, Figure 3.1.3, Left panel, see also Supplementary Material 3.1.8). In addition, self-transcendence was negatively associated with the white matter underlying the middle temporal gyrus (*p*FWE=.009; *t*=5.27, 60-37 -11, k=30, Figure 3.1.3, Right Panel).

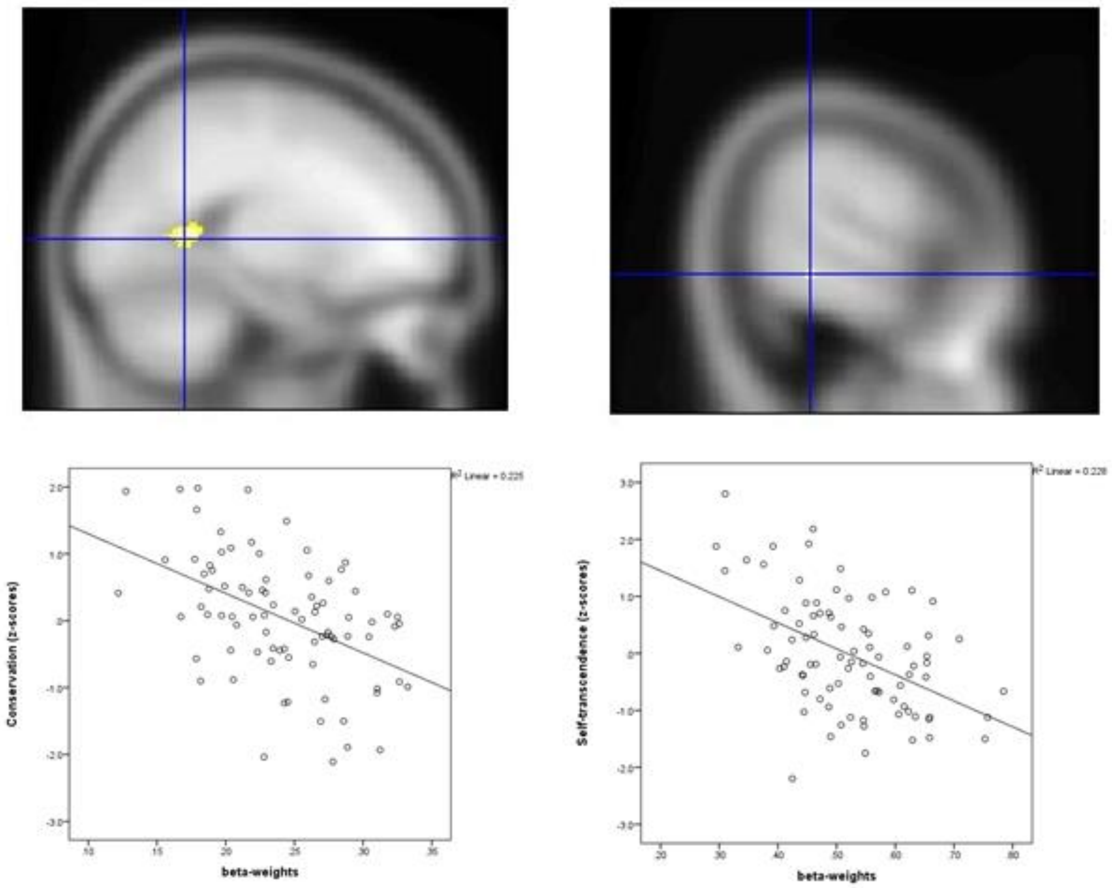

Figure 3.1.3. VBM results for the relations between white matter volume and values: Negative association with conservation (*p*FWE=.047; *t*=4.80, -22-54 4, k=1, uncorrected cluster shown, Top Left Panel), and negative association with self-transcendence (*p*FWE=.009; *t*=5.27, 60-37 -11, k=30, Top Right 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, I 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 was regressed out from self-transcendence, self-transcendence was no longer associated with brain structure. These analyses show that the findings were driven by the shared variance of the two opposing ends of the same motivational dimension (see Figure 1.A), 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, further analyses 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 3.1.4), the right medial orbitofrontal cortex (*SFI*=.15), as well as the thickness of the left lateral orbitofrontal and caudal middle frontal regions, exhibited the strongest sinusoidal associations with human values (Supplementary Material 3.1.4). As can been seen in Supplementary Material 3.1.4, 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). With regard to the volume of the 14 subcortical regions, none of them was statistcially related to the values in a sinusodal manner.

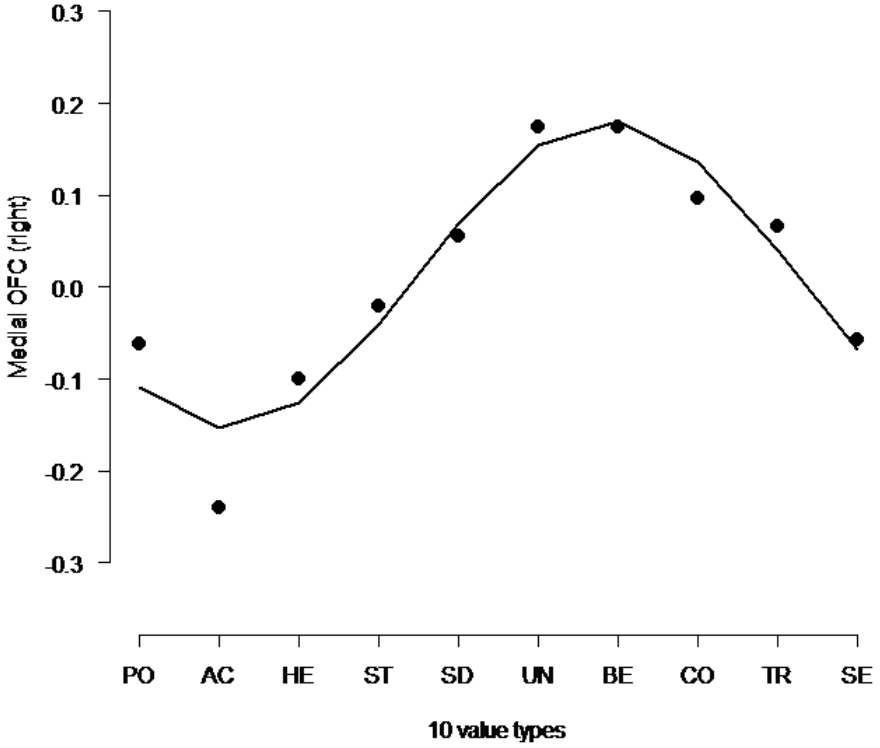

Figure 3.1.4. Correlation coefficients between the 10 value types (x-axis) and the volume (mm^3) of the right medial orbitofrontal cortex. For completeness, the grey matter regions (Supplementary Material 3.1.7) that show a sinusoidal association with human values (i.e., *SFI*<.20) are depicted in Supplementary Material 3.1.4.

Discussion

The present research investigated the neuroanatomical correlates of human values using structural imaging. Three main results emerge from this study. First, the findings demonstrated sinusoidal associations between overall white matter volume and the values described in Schwartz's (1992, 2012) cross-cultural model of values. Second, the results identified specific white matter regions that were associated with human values, mainly in the temporal lobe. Thirdly, the results supported my 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. Of course, a nonclinical intelligence assessment tool would be a more robust device to employ in future research, but the current findings nonetheless indicate that this sinusoidal waveform is an accurate description of the associations with values.

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, this 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 the 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.

The 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, Bechara, Damasio, Tranel & Damasio, 1999; Grafman et al., 1996; Rilling et al., 2002). Here, these findings are extended 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, higher mOFC (vmPFC) activity was associated with the higher subjective liking of donations at the time of the decision making (Hare, Camerer, Knoepfle & Rangel, 2010).

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 this study had employed a research methodology using merely classical linear models, I would not have been able to capture all the available information from the values and imaging data. The 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.

3.2. A hedonism hub in the human brain

3.2.1. Introduction

In the previous sub-section, I illustrated that certain cortical white matter parameters (e.g., volume, myelin volume fraction) are consistently associated with human values in a sinusoidal way as predicted by the Schwartz's circumplex model. However, previous work on the neurostructural correlates of human values has been exclusively focused on the cortex but excluded the subcortical regions. Indeed, the motivational nature of human values raises the possibility that they might be underpinned by certain subcortical brain regions that are particularly involved in motivated behavior and reward processing, a hypothesis that has never been directly tested.

As discussed in the general introduction, the putative reward system of the human brain is centred on hubs in basal ganglia (striatum and GP) and includes the VTA, prefrontal brain regions and parts of the limbic system (Haber & Knutson, 2010). These grey matter regions are structurally connected by white matter pathways. At the core of these connection pathways is the MFB, which connects the ventral tegmental area (VTA) with the nucleus accumbens (NAcc), the medial and lateral orbitofrontal cortex (mOFC, lOFC) and the dorsolateral prefrontal cortex (dlPFC) (Bracht et al., 2014). Two different branches of the MFB have been described previously: the infero-medial medial forebrain bundle (imMFB) and the supero-lateral medial forebrain bundle (slMFB) (Coenen et al., 2012). The latter may be of particular importance for reward processing. However, no study thus far has investigated associations between the slMFB and the values most related to reward processing: hedonism values. It is the aim of this study to investigate if structural properties of basal ganglia and slMFB reflect human values. This aim required examination of correlations between human value scores, as assessed by the Schwartz Value Scale (Schwartz, 1992), and the volume of 14 subcortical areas (left and right: GP, thalamus, caudate nucleus, putamen, hippocampus, amygdala, nucleus accumbens) as well as the slMFB that connects many of these regions. I hypothesized a positive association between the hedonism score and the microstructural parameters within slMFB as well as the volume of the subcortical regions connected to slMFB.

3.2.2. Materials and Methods

Participants

Eighty-seven right-handed Caucasian university students between 19 and 42 (56 females; mean age=23.97 ± 3.92 SD) participated in the study, all of whom were university students or graduates. 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. I identified one such instance in three (hedonism, achievement, conformity) out of ten values.

MRI Data Acquisition

All MRI Data were acquired in the Cardiff University Brain Research Imaging Centre (CUBRIC) on a 3 T GE SignaHDx system (General Electric, Milwaukee, USA) equipped with an 8HR Brain parallel head coil for radio frequency transmission/reception.

Structural MRI

Anatomical high-resolution T1-weighted volume scans (1 mm^3) were acquired using a fast spoiled gradient echo (FSPGR) 3-D sequence (TR=7.849ms; TE=2.984ms; field of view=256x256 mm; voxel size=1x1x1 mm).

Multi-component relaxometry

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. 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). 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, flipangle = 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°.

Diffusion weighted imaging

Diffusion MRI comprising a cardiac-gated diffusion-weighted spin-echo echo-planar imaging sequence was used to acquire high angular resolution diffusion weighted images (HARDI). 30 gradient orientations (b=1200 s/mm^2) and 3 unweighted (b=0 s/mm^2) images were acquired with the following parameters: TE=87 ms, 60 slices, slice thickness=2.4mm, FoV=230×230 mm, acquisition matrix=96×96, resulting in data acquired with a 2.4×2.4×2.4mm isotropic resolution following zero-filling to a 128x128 in-plane matrix for the fast Fourier transform. The final image resolution was therefore 1.8×1.8×2.4mm.

Pre-processing

Structural MRI

Cortical reconstruction and volumetric segmentation of 14 subcortical areas (Supplementary Material 3.2.1. left and right: GP, thalamus, caudate nucleus, putamen, hippocampus, amygdala, nucleus accumbens) was performed with FreeSurfer image analysis software v4.4.0, which is documented and freely available for download on-line (surfer.nmr.mgh.harvard.edu). All correlation analyses were performed on the Software

Package for Statistical Analysis (SPSS for Windows version 19.0). As subcortical volume may be confounded by age, gender and overall intra-cranial volume (ICV) we controlled for these effects in the regression analysis ICV derived from VBM8 (Gaser, 2009), SPM8, (http://www.fil.ion.ucl.ac.uk/spm/software/spm8).

Multi-component relaxometry

All images were linearly co-registered 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 water fraction was taken as a map of the myelin-water fraction.

Diffusion MRI

Data were analysed using *ExploreDTI* 4.8.3 (Leemans, Jeurissen, Sijbers & Jones, 2009). Eddy-current induced distortion and motion correction was performed using an affine registration to the non-diffusion-weighted B_0-images, with appropriate re-orienting of the encoding vectors (Leemans & Jones, 2009). Field non-homogeneities were corrected for using the approach of (Wu et al., 2008). The diffusion weighted images (DWIs) were non-linearly warped to the T_1-weighted image using the fractional anisotropy map, calculated from the DWIs, as a reference. Warps were computed using Elastix (Klein, Staring, Murphy, Viergever & Pluim, 2010) using normalized mutual information as the cost function and constraining deformations to the phase-encoding direction. The corrected DWIs were therefore transformed to the same (undistorted) space as the T_1-weighted structural images. A single diffusion tensor model was fitted to the diffusion data in order to compute quantitative parameters such as FA (Basser, Mattiello & LeBihan, 1994). A correction for free water contamination of the diffusion tensor based estimates was applied, before sampling diffusion properties (e.g., FA) along the fornix and the PHC (Pasternak, Sochen, Gur, Intrator & Assaf. 2009; Metzler-Baddeley, O'Sullivan, Bells, Pasternak & Jones, 2012). The fractional anisotropy (FA), radial, axial, and mean diffusivities (RD, AD, MD) was then computed from the DT.

Tractography of the supero-lateral medial forebrain bundle

Whole brain tractography was performed using the damped Richardson-Lucy algorithm (Dell'acqua et al., 2010), and an algorithm similar to that described by (Basser et al., 1994). Termination criteria were an angle threshold > 45 degrees and FA < 0.2. The slMFB was reconstructed as described in (Bracht, Doidge, Keedwell & Jones, 2015). One horizontal ROI was placed surrounding the ventral tegmental area (VTA). Anatomical borders were laterally the substantia nigra, anteriorly the mammillary bodies and posteriorly the red nucleus (Nieuwenhuys, Voogd & Huijzen, 2008). A second ROI was drawn surrounding caudate and putamen on a coronal section at the height of the nucleus accumbens (NAcc). Due to the particular interest in the role of the MFB in reward processing, the focus was placed on segments of the slMFB dorsal to the VTA including projections from the VTA to NAcc, GP, hypothalamus and the OFC, core regions of reward processing.

Human Values

Participants completed the Schwartz value survey (SVS; Schwartz 1992), which was administered in the laboratory prior to the scanning session. Participants were asked to rate how important each of 56 values is 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 then calculated and subtracted from each of the 56 initial raw scores. Schwartz recommends this procedure to help control for superfluous individual variations in rating styles (e.g. Schwartz 1992). The raw value distribution of the Schwartz Value Survey can be seen in Supplementary Material 3.2.3. The internal consistency, as measured by the Cronbach’s alpha, of these indices was moderate to good (Supplementary Material 2.1.). Moreover, to validate Schwartz’s hypothesised circular structure in our sample, I conducted two Multi-Dimensional Scaling (MDS) analyses (Bilsky et al., 2011). The first analysis plotted the 56 value items, and the second analysis plotted the 10 higher-order values; both analyses used 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 one 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 (Supplementary Material 3.1.2) supported to a large extent to the structure hypothesized by Schwartz (1992).

Of greater interest were the correlations between the human value scores (i.e. 10 values) and the residual scores of all 14 subcortical measures as well as 5 medial forebrain bundle microstructural measures (after regressing out the age, gender and intracranial volume or overall microstructural properties). A Bonferroni correction was calculated using the R^{TM} 3.0.2. software package using the code, p.adjust(p, method = "bonferroni"). Bootstrapped confidence intervals (95%) were computed using AMOS software. To conduct an internal replication analysis of the primary findings, the correlations were calculated in two randomly selected subsets of the participant sample. The volume of left GP significantly predicted hedonism scores in both sub-samples, $r(42)=425$, $p=.005$; $r(43)=.353$, $p=.02$.

3.2.3. Results

The first analyses compared the volume of the left to the right GP. Left GP (M=1667 mm^3) was significantly larger ($t(86)=p<.00001$) than the right (M=1490 mm^3), as reported previously (Kooistra & Heilman, 1988). I then investigated the association between the subcortical volume of 14 structures, as well as 5 microstructual properties of the slMFB, and the 10 human values. After a robust (Bonferroni) multiple comparison correction (i.e., 10 values x (14 subcortical structures+5 slMFB measures)), the results indicated that people who rated hedonism as important in their life had a larger GP in the left hemisphere, $r(84)=.393$, $p_{(BONF)}=.035$ (Figure 3.2.) (($p_{(UNCORR)}=.000182$). The robustness of the association between left GP volume and hedonism score was confirmed by internal replication (Material, Human Values section) and bootstrapping (95% confidence intervals: $r=.393$ lower=.232 upper=.537 $p=.002$ (N=1000), $r=.398$ lower=.241 upper=.540 $p<.0005$ (N=5000)). The next highest correlation between any value and any of the examined brain areas was observed for stimulation and the volume of the left GP, $r(85)=.231$, $p_{(UNCORR)}=.032$, although this correlation did not reach the corrected significance level. The relationship between hedonism score and left GP when including the outlier scores was $r_s(85)=.398$, $p_{(UNCORR)}=.000134$; $p_{(BONF)}=.025$. In addition, similar to left GP, the right GP was also positively related to hedonism ($r(84)=.218$, $p_{(UNCORR)=.}044$), but this association did not survive the Bonferroni correction. Because of this relative difference between left and right, I also examined whether the left minus right GP volume may be associated to hedonism. Indeed, there is a positive association between the left minus right GP volume and hedonism *r*(84)=.266, $p_{(UNCORR)}$=.013 (the correlation coefficient can be seen in Supplementary Material 3.2.4. For completeness, the association between the rest of subcortical measures and hedonism can be seen in Supplementary Material 3.2.3. This pattern of associations suggests that hedonism is specifically related to GP and not to any other subcortical structure.

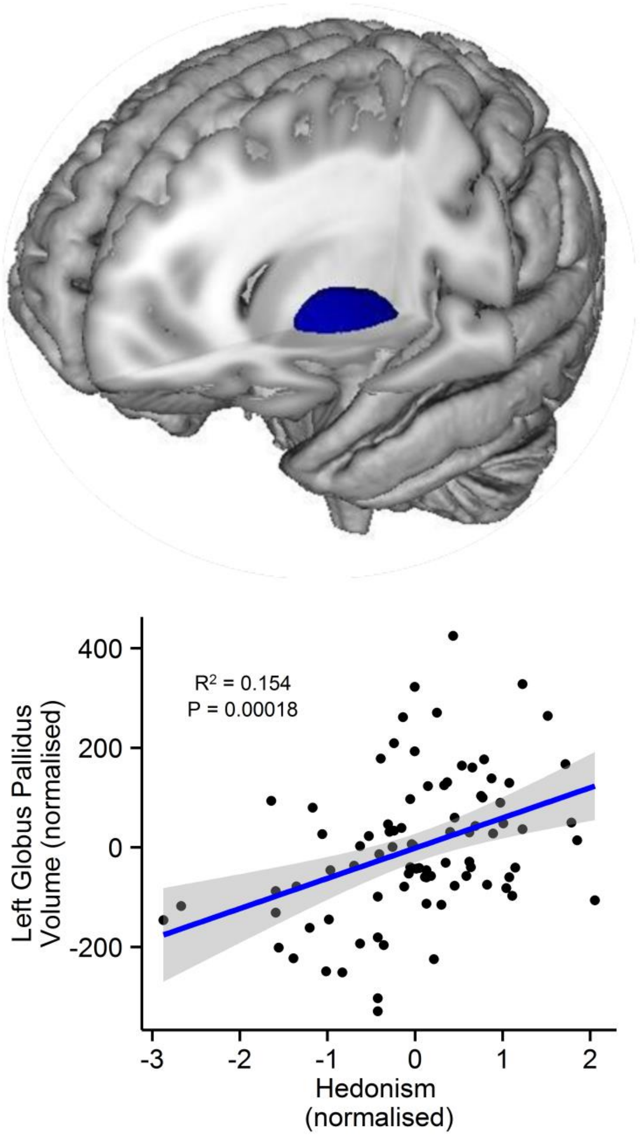

Figure 3.2. A 3d-mesh of the left GP (above) and a scatter-plot of the correlation ($r(84)=.393$, $p_{(BONF)}=.035$) between the volume of the left GP (i.e., the residual scores with age, gender and intracranial volume regressed out) (x-axis) and the standardized hedonism scores (y-axis). Each dot represents one participant. The volume of the left GP significantly predicts hedonism scores. Grey shading around the regression line represents the 95% confidence interval.

Although none of the slMFB and hedonism survived the aforementioned Bonferroni correction, we present here the strongest slMFB associations to hedonism. There was a positive association between the myelin volume fraction of the left slMFB, $r(79)=.312$, $p_{(\text{UNCORR})}=.005$) (Supplementary Material 3.2.3) and right slMFB, $r(79)=.266$, $p_{(\text{UNCORR})}=$. =.017, (corrected for overall whole brain myelin volume fraction, age and gender) and hedonism. These associations still hold, at an uncorrected level, when correcting for overall white matter restricted myelin volume fraction, age and gender (Left, $r(79)=.245$, $p_{(\text{UNCORR})}=.028$; Right, $r(79)=.220$, $p_{(\text{UNCORR})}=.049$). For completeness, we present the association between hedonism and Fractional Anisotropy, Medial Diffusivity, Radial Diffusivity and L1 of left and right MFB (Supplementary Material 3.2.3).

Discussion

The present study investigated the neural representation of the motivational nature of human values by testing for associations between the scores of 10 values and the volume of 14 subcortical regions as well as the myelin volume fraction of slMFB. The results demonstrate, for the first time, a direct association between the value that people attach to hedonism and the volume of a specific brain structure, the left GP as well as the myelin volume fraction of slMFB.

The slMFB has been previously associated to hedonic-related mechanisms (Bracht, Linden & Keedwell, 2015). Specifically Bracht et al. (2014) found that mean-FA within the MFB was correlated negatively with depression scale rating scores. In contrast to the direction of this finding, Bracht et al. (2015) found that hedonic capacity was correlated negatively with mean FA of the left slMFB. The present research calculated both FA and MWF of the slMFB, but only the MWF showed a clear trend with hedonism. Compared to FA, MWF is considered a more biologically interpretable proxy of white matter myelination. Myelin enables faster and more efficient propagation of action potentials along axonal pathways, which in turn can contribute to faster information processing capabilities (Turken et al., 2008). Specifically, it provides more information about the tissue composition of white matter connections, independent of volume (to which other parameters such as axon diameter and inter-axonal space can contribute).

GP is a relatively large subcortical structure which is in a dorsal and a ventral segment. The dorsal segment is particularly implicated in motor control, while the ventral segment, which receives input from the nucleus accumbens, has been involved in hedonic-related processing (see below). The GP region in the present study includes both dorsal and ventral GP segments (Supplementary Material 3.2.1). The GP is a central node not only in the direct and indirect pathways that govern motor control (underpinned mainly by the dorsal segment), but also in the “executive” and “limbic” circuits of the basal ganglia (Rodriguez et al., 2009). The limbic circuit, in particular, has been implicated in motivated behavior. This circuit originates from the projections of the ventral striatum to the GP and continues to the thalamus. Inferences from the size of a region onto its function are limited, but one might speculate that a larger volume of the GP, presumably reflecting a higher number of neurons and/or more neuropil, would result in hypermotivated states, such as those associated with hedonism. Previous lesion studies have indeed implicated the GP in reward activation. For example, Rochat et al. (2013) conducted a voxel-based lesion-symptom mapping, which showed that damage to the GP was associated with poorer reward sensitivity. In addition, a case study described a patient who developed severe anhedonia after he sustained bilateral GP lesions (Miller et al., 2006).

With respect to laterality, it has been previously demonstrated (Kooistra & Heilman, 1988) that the left GP is often larger than the right GP and this finding was replicated here. A previous study (Glick, Ross & Hough, 1982) on neurochemical asymmetries showed a leftward asymmetry in dopamine levels in GP. A later study (Lauterbach, Jackson, Wilson, Dever & Kirsh, 1997) on focal subcortical lesion patients, suggested that depression onset may be caused specifically after left posterior GP lesions potentially by disturbing basal ganglia thalamocortical mood circuits. Taken together, these structural, neurochemical and lesion laterality studies suggest that the left GP is a subcortical structure particularly associated with the maintenance of healthy reward-related mechanisms.

Functional imaging studies have also supported the role of GP in reward sensitivity. A recent meta-analysis (Arsalidou, Duerden & Taylor, 2013) revealed the involvement of the left lateral GP in reward processing and of the left medial GP in tasks that required eliciting or judging emotions. Lastly, prior animal work supports a hedonic function for networks involving the GP. For example, Ho and Berridge (2013) investigated the neuronal connections of the orexin terminals in the posterior half of ventral pallidum, a region in close proximity to opioidergic hedonism “hotspots”. By injecting orexin-A into this region, they enhanced the hedonic impact of sucrose, as assessed via affective taste reactivity (Ho & Berridge 2013).

The present study, which is the first to demonstrate a robust role for the GP in hedonism in healthy humans, thus fits with neuropsychological and animal models of “wanting” and “liking” (Smith, Berridge & Aldridge, 2011). The results have potential implications for both clinical and social neuroscience. Individual variation in GP volume might partly determine susceptibility to hedonic deficits associated with addiction or mood disorders. More broadly, it is also possible that this variation might contribute to our understanding of the role of impulsive, hedonistic inclinations in a number of difficult societal behavior change issues, such as attempts to attenuate increasing levels of obesity, damage to the environment, and antisocial behavior (see Maio et al., 2008 for a review).

Another important question is whether larger GP volume leads to high importance of hedonism or vice-versa. Previous behavioural genetics studies (Shermer et al., 2008, 2011; Zacharopoulos, Lancaster, Maio & Linden, 2016) demonstrated that human values may have genetic aetiology. However, the behavioural genetics of human values is a relatively new field and thus knowledge on the specific genetic markers for particular human values, such as hedonism, are still poorly understood. The findings of the present study provide the first endophenotype (i.e., volumetric variation in the GP) that may mediate the association between specific genetic markers and hedonism. The direction of the GP-hedonism link can be determined in future mediational studies. In particular, if the relationship between specific genetic components and the relative importance of hedonism is mediated by the volumetric variation of left GP, while the relationship between the same genetic components and volumetric variation of left GP is not mediated by hedonism, then one could make the case for left GP volume causes changes in the subjective value of hedonism.

In sum, the present research (a) demonstrated a strong positive association between the volume of left GP and the human value of hedonism, and (b) extended prior findings on the association between hedonic processes and the microstructural properties of slMFB. Together, these results provide the first direct association between the importance people attach to the human value of hedonism and structural variation in reward-related subcortical brain regions. This provides a novel source of evidence pertinent to affective neuroscience research on reward-related deficits, such as the anhedonia in major depression.

Chapter 4: The Effect of Human Values on Personal and Social Foraging Behaviour

4.1. Introduction

In the previous chapter, I investigated the neuroanatomical link between values and reward-related processing. Here I conducted a functional magnetic resonance imaging experiment with the aim to investigate how human values affect reward-related processing at the level of actual behaviour, in particular prosocial behaviour, and the associated neural underpinnings. Specifically, I study the neural correlates of foraging behaviour (see below) because the effect of human values on prosocial behaviour in foraging tasks has never been addressed before.

Many life decisions can be conceptualised as foraging problems (Charnov, 1976; Constantino & Daw, 2015). Employment decisions, mate selection, and internet searches are just a few examples of scenarios wherein people must choose whether to engage with the currently available options or to search for alternative ones. To solve this type of problem, an ideal forager compares the value of two strategies -- engaging with the currently available option or foregoing it to search for alternatives -- and chooses the one of highest value. This is the optimal solution described in the Marginal Value Theorem (Charnov, 1976), which requires comparing the value of the current option to the overall value of the alternative, foraging environment.

Due to their ubiquity in everyday decisions, there has been a recent interest in the behavioural and neural aspects of foraging problems. Previous neuroimaging studies have primarily focused on foraging for oneself (Kolling et al., 2012; Shenhav et al., 2014; Constantino & Daw, 2015). This focus ignores the fact that both humans and animals often forage on behalf of other conspecifics. To my knowledge, there are no existing experiments contrasting personal and social foraging in order to examine their potential behavioural and neural differences. Valuing another person's welfare, or indeed failing to do so, has diverse potential implications in our myriad foraging decisions within the human social environment. An open question is whether the foraging for others involves substantively different psychological and neural processes from foraging for the self, and whether this depends on individual differences. Understanding how selfish and prosocial brains function differently with regard to valuing the welfare of others in a forage context may have a beneficial societal impact.

Particularly relevant individual differences are human value orientations. Here, as in the earlier chapters, it is useful to utilise Schwartz's (1992, Figure 4.1; 2012) Circumplex Model of Values, which has been validated in over 80 nations, and been subjected to experimental, longitudinal, and cross-sectional tests (Maio, 2010). Of particular relevance here is the contrast between self-focused values and social-focused values (Schwartz et al., 2012, for an overview of the value model, see Supplementary Material 3.1.1)

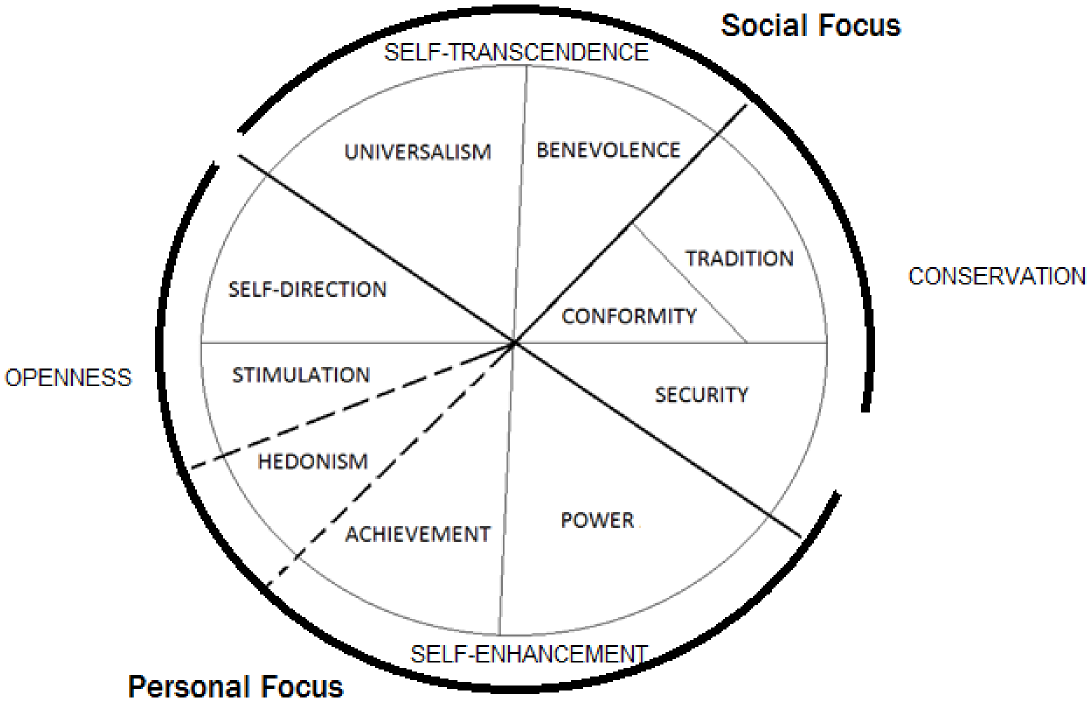

Figure 4.1. The circumplex structure of human values (modified from Schwartz, 1992). Self-focused individuals score high on the value types self-direction, stimulation, hedonism, achievement, power and security, while the social-focused individuals score high on universalism, benevolence, tradition, conformity and security.

This personal vs social distinction in values should be pivotal in how people construe personal vs social foraging tasks. While personal foraging behaviour should be influenced by how people assign reward value to choices that have varying degrees of personal costs and benefits, the social foraging behaviour should be influenced by how people assign reward value to choices that have varying degrees of costs and benefits for others. These reward assignments are conceptually linked to individual differences in the extent to which people prioritize these personal or social concerns. In line with previous findings in classical economic decision making involving charitable donations (Brosch et al., 2011), the key prediction of this study is that personal/self-focused individuals will gather more money for themselves (personal foraging) than for charity (social foraging). The aforementioned work (Kolling et al., 2012; Shenhav et al., 2014; Constantino & Daw, 2015) demonstrated individual variation in foraging behaviour for the self, but provided little information on putative determinants of this variation. Thus, it is important to test whether, for example, a self-focused individual may obtain more reward during personal foraging than a social-focused person.

It is also important to understand how individual variation in human values affects the *process* of foraging, and not just the amount of foraging for the self vs others. It is conceivable that this individual variation affects the parameters that are considered within foraging decisions. For example, self-focused individuals may rely more strongly (compute differently) the overall foraging value than social-focused individuals for personal foraging, but not for social foraging. If the process is different, then this suggests that research needs to model such differences in order to better understand personal and social foraging. Alternatively, if the parameters of foraging decisions are comparable, then the task may be mechanistically equivalent to people, regardless of whether it emphasises personal or social rewards.

This chapter presents two experiments that were designed to examine the behavioural and neural correlates of these issues. In both experiments, participants alternated between foraging for themselves and foraging for a charity of their choice. In Experiment 1, participants decided whether to engage with a given choice of options or to keep looking for better options (foraging). When they chose to engage with a given option, they were asked to make a classical economic decision between two outcomes with known reward magnitudes and probabilities. In Experiment 2, participants were presented with a video simulation of apple harvesting. They were presented with an apple tree and asked to decide whether to harvest it for apples and incur a short harvest delay, or move to a new tree and incur a longer travel delay. The design of Experiment 1 was useful because it involves two distinct modes of decision making, and thus allowed the investigation of how human values may affect behaviour and associated neural systems during foraging and during classical economic decision making separately. Therefore another key hypothesis in this study is whether there is a differential involvement of the previously identified neural regions during the foraging decision and the classical economic decision between the self and charity trials (see below) and most crucially the modulation of these differences based on the self-focus score.

The design of Experiment 2, which only included the foraging stage (equivalent to stage 1 of Exp. 1 below), was useful for testing whether similar patterns of behaviour are obtained in a foraging design directly related to the classical animal foraging literature (e.g. Stephens & Krebs, 1987; Charnov, 1976). Because several analyses could be replicated across these experiments, they are presented together below. For simplicity in this combined presentation, Experiment 1 is abbreviated as EXP 1 and Experiment 2 as EXP2.

4.2. Material and Methods

Participants

Thirty undergraduate and postgraduate university students between 18 and 37 years of age (9 males) took part in the study. Participants were informed that the study investigates the neural (EXP 1) and behavioural (EXP 1 & EXP 2) mechanisms of foraging behaviour. All participants completed EXP 1 before EXP 2. For the behavioural analysis In EXP 1, three participants were excluded because of incomplete scanning sessions, and one participant was excluded because she foraged fewer than seven times (i.e., only once) during social foraging (Kolling et al., 2012 exclusion criterion). For the neuroimaging analysis in EXP1 apart from these four participants, seven additional participants were excluded because of excessive motion in that at least a single image exceeded a voxel's worth of motion >2mm during realignment within a single run. In EXP 2, one participant was excluded because of excessive time outs (i.e., more than 3 standard deviations above the mean). The study was approved by the Cardiff University School of Psychology ethics committee, and all participants gave written informed consent.

Experimental design and task

Charity Selection

Participants were explicitly informed during the instruction phase of the experiment that the number of points (EXP1) or apples (EXP2) would be converted into real money at the end of the experiment, and that the reward obtained during personal foraging would be paid to them (on top of the fixed participation payment, £15, EXP1 and £6, EXP2), while the reward obtained during social foraging would be given to the charity. Participants then were asked to select one from the following charities: British Red Cross, Save the Children Fund, Oxfam, The Salvation Army, Cancer Research UK, Macmillan Cancer Support. Participants were free to choose different charities in the two experiments.

EXP 1

In EXP 1, participants performed a decision-making task (Kolling et al., 2012; Shenhav et al., 2014, Figure 4.2., Panel A), which involved two stages. In Stage 1, participants decided whether to engage with a given choice of options or to keep looking for better options (foraging). In Stage 2, participants made a classical economic decision between two outcomes with known reward magnitudes and probabilities. On each trial in Stage 1 (upper panels, Figure 4.2.A), participants were offered a pair of potential rewards (large numbers). They could choose to forage for a better pair of rewards from the set shown at the top of the screen (smaller numbers in the red box), in which case a random pair from that set was swapped with the current offer. Participants who made this choice would incur a forage cost (shown on the left, below the red box) and a delay until the new choice was shown. Participants could forage any number of times (or not at all) before opting to proceed to Stage 2 (lower panel). Once they entered Stage 2, a probability was randomly assigned to each of the reward options (height of violet bar beside each number), and participants were prompted to choose one of the magnitude-probability pairs. Participants received the outcome of the gamble on each Stage 2 trial, and these were displayed as accumulating points at the bottom of the screen (not shown).

Participants completed a total of eight fMRI runs (4: personal foraging, 4: social foraging). Before each of the 8 blocks, participants were informed with a short message on the screen whether the forthcoming block was personal or social. Participants experienced the foraging conditions in one of two orders: (1) personal, social, personal, social, social, personal, personal, social or (2) social, personal, social, personal, personal, social, social, personal. A block typically lasted for 11 minutes.

The analysis of the behavioural data of EXP 1 focused on the reward during (1) personal foraging (i.e., the total number of points obtained for self during the four personal foraging runs), (2) social foraging (i.e., the total number of points given to the charity during the four social foraging runs) and (3) the difference of the two (i.e., the reward obtained for self minus the reward given to the charity).

EXP 2

In EXP 2, participants completed an adapted version of a virtual patch-foraging task (Figure 4.2.B; Constantino & Daw, 2015). Each run consisted of approximately 50 trials. Participants foraged (Figure 4.2.B) for apples in four 14-min (i.e., 7m Personal Foraging, 7m Social Foraging) virtual patch-foraging orchards (i.e., Long-Shallow, Long-Steep, Short-Shallow, Short-Steep). The recipient of reward (i.e., self, charity) was signalled with a letter ("S", self, or "O", other) that was presented throughout each block (not shown in the figure).

On each trial, participants were presented with a tree and had to decide whether to harvest it for apples and incur a short harvest delay, or move to a new tree and incur a longer travel delay. Harvests at a tree earned apples, albeit at an exponentially decelerating rate. Similar to Constantino and Daw's (2015) study, this experiment varied the quality of the foraging context by manipulating two environmental parameters: depletion rate and travel time. The depletion rate determines the rate at which earned apples decrease with subsequent harvest decisions at a given tree. It is a fixed multiplicative decay κ, such that if a participant harvests 8 apples in the current trial, the number of apples to be harvested in the next trial will be the depletion rate multiplied by 8. By manipulating the depletion rate, the experiment included one environment with fast depletion (steep) and one with slower depletion (shallow). Additionally, it included two more types of orchards -- long (9s) and short (6s) – by manipulating the travel time, the time it takes to travel to a new tree. Combining these two manipulations resulted in the four orchard-types that participants visited during the task: Long-Shallow, Long-Steep, Short-Shallow, Short-Steep.

New trees were drawn from a Gaussian distribution and the environmental richness or opportunity cost of time was varied across blocks by changing the travel time and/or the apple depletion rate (see below). The quality of the tree, depletion rate, and richness of the environment were *a priori* unknown to the subject. The aim of the participants was to maximize their reward (i.e., number of apples) for themselves or for a charity of their choice, depending on their assigned experimental condition. Similar to EXP 1, this was a within-subject design.

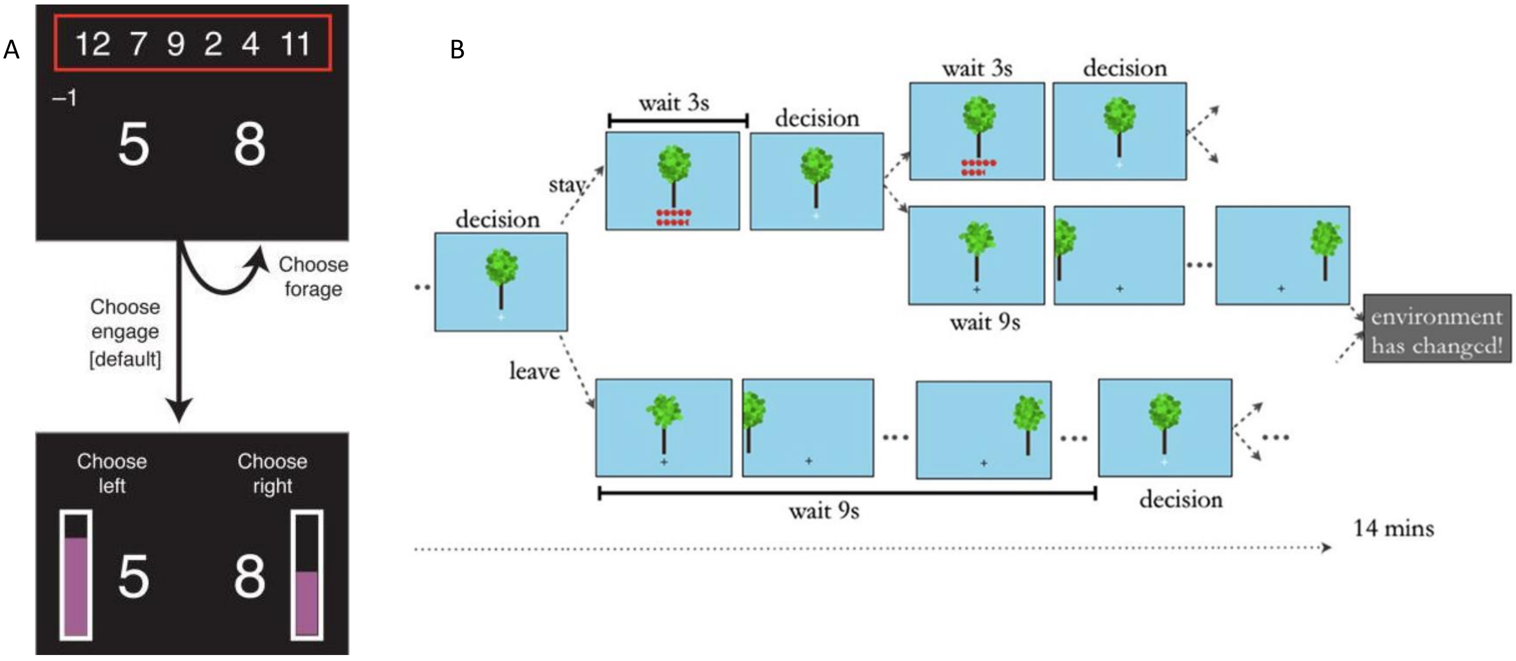

Figure 4.2. Graphical depictions of a trial in Experiment 1 (Panel A, adapted from Shenhav et al., 2014) and Experiment 2 (Panel B, adapted from Constantino & Daw, 2015).

Participants foraged in each orchard for a fixed amount of time: 14m (7m personal and 7m for social foraging). Similar to EXP 1, EXP 2 focused on the reward during (1) personal foraging (i.e., the total number of apples obtained for self during the personal foraging), (2) social foraging (i.e., the total number of apples given to the charity during the social foraging), and (3) the difference of the two (i.e., the reward obtained for self minus the reward given to the charity). In addition to the reward, EXP 2 looked at individual exit thresholds, defined as the mean number of apples at which the participants choose to switch to a new tree in each of the environment types. This was calculated by averaging the number of apples at exit across trees in a given orchard. For example, an exit threshold of 9 means that participants tended to leave a tree when the last harvest yielded 9 apples. Each orchard has an optimal, average reward-maximizing exit threshold given by the Marginal Value Theorem (Charnov, 1976). A higher than optimal empirical exit threshold signals underharvesting bias (i.e., leaving trees too early), while one that falls below the optimal threshold signals an overharvesting bias (i.e., staying with trees too long). For the purposes of this study, the exit threshold was calculated separately for personal and social foraging.

MRI Data Acquisition

All MRI Data were acquired at the Cardiff University Brain Research Imaging Centre (CUBRIC) on a 3 T GE SignaHDx system (General Electric, Milwaukee, USA) equipped with an 8HR Brain parallel head coil for radio frequency transmission/reception.

Structural MRI

Anatomical high-resolution T1-weighted volume scans (1 mm^3) were acquired using a fast spoiled gradient echo (FSPGR) 3-D sequence (TR=7.849ms; TE=2.984ms; field of view=256x256 mm; voxel size=1x1x1 mm).

Functional MRI

Functional images were acquired with a gradient-echo EPI sequence [repetition time (TR) 3000ms, echo time (TE) = 30ms, flip angle 87°, gap=1mm, number of slices=43, voxel dimension=3.5x3.5x4.4, tilted 15° relative to the AC/PC plane).

MRI Data Pre-processing

The general procedure for fMRI analysis was similar to a previous study of non-social foraging (Shenhav et al., 2014). Imaging data were analyzed in SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK). Functional volumes were motion corrected, normalized to a standardized (MNI) template (including resampling to 2mm isotropic voxels), spatially smoothed with a Gaussian kernel (8mm FWHM), and high-pass filtered (0.01 Hz cut-off). Separate regressors were included for the Stage 1 and Stage 2 decision phases. These regressors were all modelled as stick functions (which sets the duration of events to 0 and the event is modelled using HRF, GLM#1). GLM#2 featured the two main predictors of GLM#1 but additionally included separate parametric regressors. Stage 1 featured 3 parametric regressors: (i) task difficulty, (ii), search evidence (iii) search cost (i.e., the amount of points the participant will deterministically lose if they choose to forage) while Stage 2 featured one parametric regressor, relative value (i.e., the difference between reward magnitude of the left option * reward probability of the left option and the reward magnitude of right option * reward probability of the right option). All analysis presented below refer to GLM#1 unless the replication analysis. In all SPM analysis, the extent threshold was set at 50 voxels, and the text below reports the clusters that survived an FWE-cluster level correction at an uncorrected *p*-value of 0.01 (apart from the replication analysis which was performed at a FWE-voxelwise level). Of note, all clusters presented below also survived an FWE-cluster level correction at an uncorrected p-value of 0.001.

Human Values

Participants completed the Schwartz Value Survey (SVS; Schwartz, 1992). As described earlier in this thesis, this 56-item scale can be used to measure the value types shown in Figure 4.1. 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 self-focus score was calculated from the average score of self-direction, stimulation, hedonism, achievement, power and security values. The social-focus score was calculated from the average score of universalism, benevolence, tradition, conformity and security values. The behavioural human-value related statistical analyses were conducted using a one-tail test because there was a directional hypothesis derived from research by Brosch et al. (2011) -- self-focus should be positively associated with points obtained during personal foraging -- and because this threshold is relatively efficient on a relatively small (when considering individual variation studies) sample size.

4.3. Results

Behavioural data (EXP 1 & 2)

The analyses first compared the decision weights between personal and social foraging (i.e., personal beta-weight minus social beta-weight) for EXP 1 (Figure 4.3, Panel top left). Results indicated no significant difference in any of the estimates (beta-weights from binary logistic regression for Stage 1 and Stage 2, Figure 4.3, Panel top left) or in the number of points, number of forages or amount of incurred cost (Figure 4.3, Panel top right). The outcome of EXP 2 (Figure 4.3, bottom Panels) was similar: As shown in Figure 4.3, there was no difference in the number of apples (*t*=.088, *p*=.931, two-tailed) or exit thresholds (*t*=1.449, *p*=.158, two-tailed) between the personal and social foraging scenarios. Taken together, this data reveals no difference between participants' approaches to the personal and social foraging tasks in both foraging experiments.

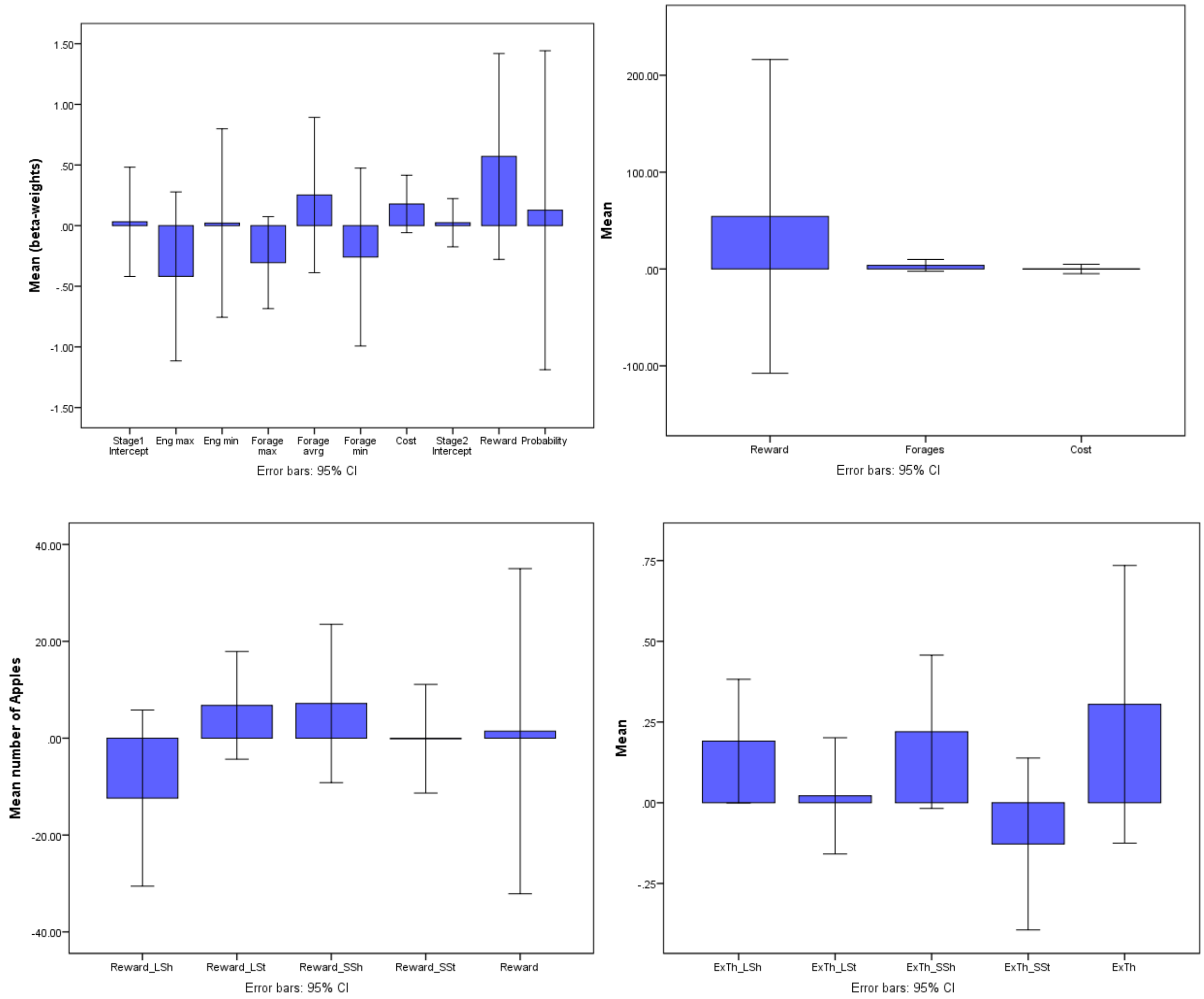

Figure 4.3. All variables in the figure represent the personal minus social foraging (top panels are from EXP1 and bottom panels are from EXP 2). In the top left panel, the Stage 1 intercept is the constant from the foraging binary logistic regression predicting foraging vs engaging based on 6 continuous predictors the beta-weights of which are plotted here (the higher engaging value, the lower engaging value, highest foraging value, average foraging value, lowest foraging value, search cost). In the top right panel, the Stage 2 intercept is the constant from the classical economic decision making. The binary logistic regression predicted the left or right option, with beta-weights for reward and probability. In the top right panel, the number of overall points, number of overall forages and number of overall

cost incurred is represented. The bottom left panel shows the number of apples in each of the four orchards (Long Shallow, Long Steep, Short Shallow, Short Steep) and across all four. The bottom right panel shows the exit threshold in each of the four orchards (Long Shallow, Long Steep, Short Shallow, Short Steep) and across all four.

I then tested the association between self-focused values and reward during personal and social foraging. Participants who exhibited higher self-focus score earned higher overall reward during personal foraging in EXP 1 ($r(24)=.413$, $p=.016$, one-tailed Figure 4.4, Panel top left) and in EXP 2 ($r_s(27)=.411$, p=.013, one-tailed, Figure 4.4, Panel bottom left). During social foraging, no relationship was found between self-focus and the overall reward given to the charity in EXP 1 ($r(24)=-.141$, $p=.246$, one-tailed) and in EXP 2 ($r_s(27)=.164$, $p=.199$, one-tailed), respectively. In addition self-focus was not associated with the overall amount of points across personal and social foraging (i.e., number of points obtain for themselves + number of points given to the charity) in EXP1 ($r(24)=.178$, $p=.384$) and EXP2 ($r_s(27)=.256$, $p=.181$). Most importantly, the self-focus dimension was positively associated with the overall reward during personal minus social foraging in EXP 1 ($r(24)=.413$, $p=.018$, one-tailed Figure 4.4., Panel top middle) and showed a trend in EXP 2 ($r(27)=.294$, $p=.061$, one-tailed 4.4, Panel bottom middle). When adding the z-scores of personal minus social reward across both EXP 1 and EXP 2, self-focus was positively associated with amount of reward during personal foraging ($r(23)=.529$, $p=.004$, one-tailed Figure 4.4., Panel top right) as well as with the amount of reward during personal minus social foraging ($r(23)=.463$, $p=.010$, one-tailed, Figure 4.4., Panel bottom right)).

To complement this approach, I also investigated whether the correlation coefficient of self-focus score and overall reward during personal foraging was significantly different from the correlation between the self-focus score and the overall reward during social foraging (Steiger, 1980). In EXP 1 ($z=2.124$, $p=.016$, one-tailed) and in EXP 2 ($z=1.667$, *p*=.047, one-tailed), the two correlation coefficients were significantly different from each other. Finally, I checked whether the number of points obtained during personal foraging in EXP 1 was related to those obtained in EXP 2. The number of points in EXP 1 were not related to the number of apples in EXP 2 (r_s(23)=.113, *p*=.225, one-tailed).

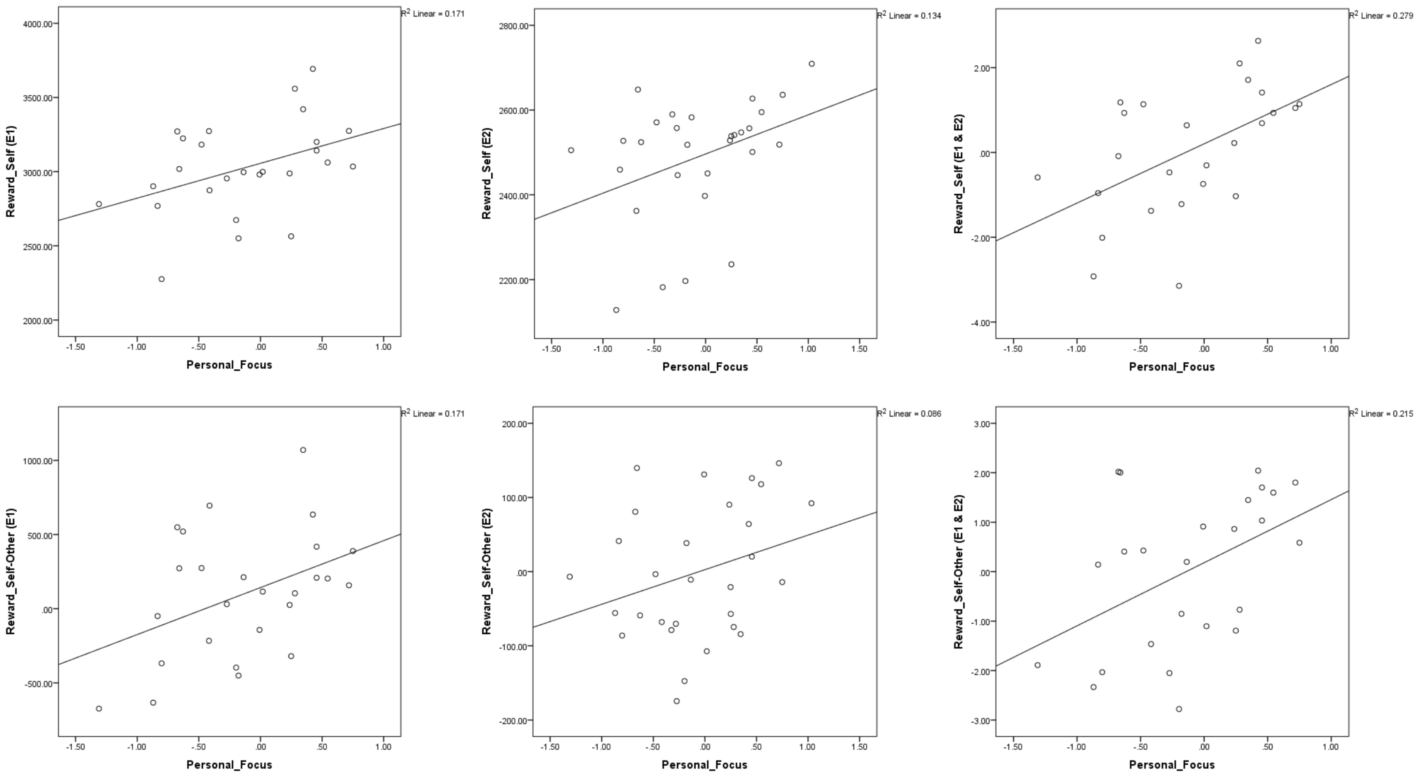

Figure 4.4. Scatterplots depicting the associations between human-value orientation and overall reward obtained during personal and personal-social foraging. These depict a positive association between self-focused values and overall reward during personal foraging for EXP 1 (top left), EXP 2 (top middle) and EXP1 & EXP2 combined (top right), as well as a positive association between self-focused values and overall reward during personal versus social foraging for EXP 1 (bottom left), EXP 2 (bottom middle) and EXP1 & EXP2 combined (bottom right). I also tested and found that these self-focus-overall reward associations were significantly influenced by the variables signalling the overall foraging value (average foraging value in EXP 1, and exit threshold in EXP 2; see Supplementary Material 4.2).

Functional Magnetic Resonance Imaging Results

I initially tested whether there was a positive association between task difficulty and dACC, as reported previously. This finding was replicated reliably (*p*FWE-CORR-CLUSTER-level<.0005; *t*=8.79, MNI coordinates, x=6 y=22 z=44, k=59, Figure 4.5A, uncorrected cluster shown). After this initial check, the analyses probed the difference between personal and social (i.e., contrast self minus charity conditions) foraging (stage 1) and classical economic decision making (stage 2). Reflecting the absence of a statistically significant difference in the behavioural data, no brain region was differentially engaged in either stage 1 or stage 2 when contrasting the personal and the social conditions.

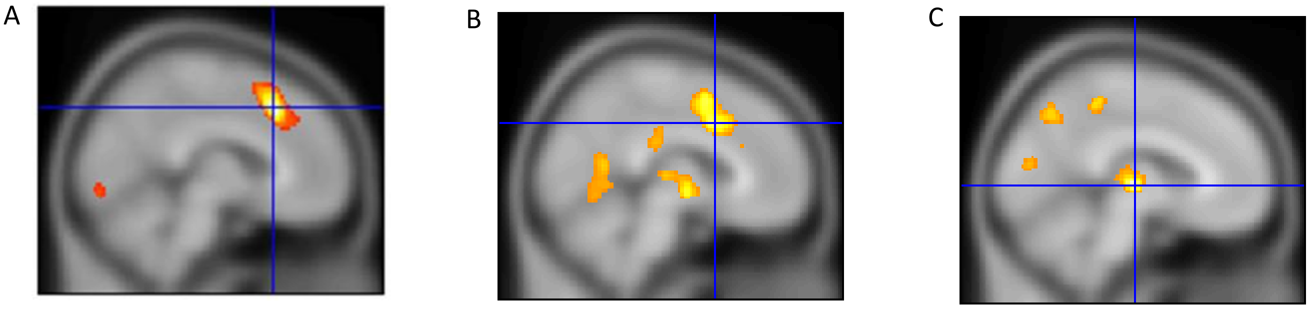

Figure 4.5. Replication analysis (A) and the investigation of the impact of the self-focus score on neural regions reflecting personal vs social foraging (B) and classical economic decision making (C) behaviour. Panel A shows dACC activation during foraging in response to task difficulty averaged across the personal and the social conditions. In Panel B, there is a negative lineal relationship between the self-focus score during foraging (Stage 1) for oneself compared to social foraging which included activation in a cluster compassing the dACC. In Panel C, there is a negative lineal relationship between the self-focus score during classical

economic decision making (Stage 2) for oneself compared to charity which included activation in a big cluster encompassing the thalamus.

Relating the Human Value Orientation to Personal > Social contrasts

I then investigated the neural mechanisms of the value-related behavioural effects. I probed how the self-focus score is associated with the neural activation of the difference between personal and social (i.e., contrast self minus other) foraging (stage 1) and economic decision making (stage 2). During Stage 1, self-focus was negatively related to activation in a large cluster encompassing dACC (PFWE-CORR-CLUSTER-level =.011, *t*=5.27, x=-2 y=6 z=52 (x=-2 y=18 z=40, x=6 y=10 z=38), k=2655, Figure 4.5B, the 6,10,38 coordinates are shown). During Stage 2, self-focus was negatively related to activation in a big cluster thalamus (PFWE-CORR-CLUSTER-level <.0005, *t*=7.87, x=-6 y=-16 z=2 (x=10 y=-12 z=0, x=-48 y=-56 z=10), k=26534, Figure 4.5C).

Discussion

The present study investigated the effect of self-focus on foraging behaviour by examining the role of human value orientations in personal and social foraging behaviour across two experiments. The results demonstrate, for the first time, a direct association between individual variation in values and the amount of reward earned when foraging for oneself, rather than on behalf of a charitable organization.

Human values have been previously associated with personal and social point allocations in classical economic decision making in the context of charitable donations (Brosch et al., 2011). Specifically, Brosch et. al. (2011) found that self-centred participants kept more money for themselves instead of donating it to charity. The present experiments extend these findings by showing that self-focused value preferences have an effect on behaviour that extends beyond classical economic decision-making to the context of foraging decisions.

From a social psychological perspective, the effect of self-focused values on foraging fits the nature of self-focused values (Schwartz et al., 2012). They include values that focus on openness to new experiences and challenging the status quo (e.g., “creativity,” “curiosity,” “freedom”), along with values that promote personal achievement (e.g., “wealth”, “success”, “power”). Foraging is inherently about embracing the unknown, with risk but potentially high gains, which serve personal achievement even more when the foraging is for the self. It therefore makes sense that individual differences in values can help to explain the substantial individual differences in foraging behaviour – the bases for which have not been examined in past research. Apart from overall number of forages, the intercept of Stage 1 binary logistic regression, which reflects the overall tendency of the participant towards foraging or engaging (and this is related to the overall earnings, r(23)=.571, *p*=.003, two-tailed), can also be conceptualized as a status-quo marker. Again, there was no significant association between the overall tendency to forage and openness values. In EXP 2, the variable reflecting status-quo is the harvest options (i.e., the number of apples to be obtained if participant choose to harvest the tree), while the option to travel to a new tree can be conceptualized as challenging the status-quo. The behavioural measures reflecting the extent to which participants are willing to challenge the status-quo are the overall number of times they travel to a new tree, but this variable was not significantly associated with Openness, and it was not even related to the overall earnings in the task in the first place. Thus, the behavioural effects do not appear to be accounted for by variation in openness.

The second putative mechanism is more related to the value dimension self-enhancement. In this account, people with high self-enhancement scores are more likely to earn more money during personal foraging because they spend more time (i.e., higher reaction time) trying to figuring out the optimal choice during the personal vs social foraging. In both EXP 1 and EXP 2, the reaction time was not related to self-enhancement scores, thereby casting doubt on this putative mechanism.

Of importance, the design also allowed me to probe the neural underpinnings of these behavioural effects. Previous foraging studies found that the ACC is positively associated with the overall value of foraging (Kolling et al., 2012). However, this psychological function of the ACC was subsequently challenged (Shenhav et al., 2014) by showing that, when choice difficulty is properly controlled, ACC activity is no longer associated with the overall value of foraging (although there is an active debate on this account: Kolling et al., 2016; Shenhav et al., 2016); a result that replicated here. Moreover, the self-focus human value orientation score was negatively associated with the activation within the ACC during the foraging stage (personal vs social foraging), but not associated with classical economic decision making. The self-focus individuals who exhibited a higher bold-response within ACC when playing for charity relative to the self may have done so because playing for charity may have been a more challenging task compared to playing for self. The reason for this may be the product of two opposing motivations 1) the lack of motivation to help others and 2) the social pressure to behave altruistically. I attempted to minimize this latter factor by informing participants that this was an anonymous study, but this may not have been adequate to significantly diminish the social pressure.

A potential limitation of this study involves the threshold choice (i.e., a liberal primary threshold p=.01 and an extent threshold of k=50). Since this analysis was conducted, there has been increased focus on the appropriate balance in threshold setting between false negative and false positive errors (Eklund, Nichols & Knutson, 2016; Woo, Krishnan & Wager, 2014). The present thesis might incur criticism, but I still think that the threshold approach used is appropriate for a study of a novel paradigm due to its high sensitivity (Friston, Worsley, Frackowiak, Mazziotta & Evans, 1994; Smith & Nichols, 2009).

Taken together, these results extend the psychological properties of ACC in foraging behaviour by providing a prosocial account for the activity of this region, while showing its connection to individual differences in human value orientations. The findings expand the scope for understanding foraging behaviour to include the varied motivations expressed by values.

Chapter 5: General Discussion.

5.1. Results Summary

The main aim of this thesis was to investigate the extent to which human values are reflected in human neurobiology. By employing methodologies in social-cognitive neuroscience, I associated individual variation in human values with a range of neurobiological indices, including genetic, brain structural and brain functional parameters. A second, related aim was to test whether the motivational relations within the value system itself (i.e., the relationship between the 10 human values) are also reflected in these neurobiological markers. Schwartz circumplex model of values predicts that an external variable should be associated with the human values in a sinusoidal waveform, underpinned by the motivational compatibilities and oppositions of human values. To meet this particular aim, I employed a recently developed as well as previously established sinusoidal tests. Taken together, the results of this thesis suggest that human values are indeed represented in all three aspects of biology tested. Moreover, the brain structural and genetic studies suggest that the motivational relations among human values are also represented in neurobiology.

Taken together these various neurobiological findings suggest that human values, at least those that are included in the circumplex model of Schwartz, may have in part an evolutionary basis. There is the possibility that during the course of evolution humans may attempted to use various human values but some of those may have been extinct and some may have been conserved. The latter values, or at least some of them, may have been captured by the circumplex model of Schwartz. Moreover, throughout the course of evolution the values that have been evolutionary conserved may have started forming relationships between each other (e.g., incompatibilities) and the evolutionary marker of these relationships may have been captured by the sinusoidal association between human values scores and different neurobiological markers presented in this thesis. Another potential contribution of the present thesis with respect to the evolutionary account of values and how can that may affect the updating of our social psychological models in light of the neural findings is the emerging possibility that some values may be more weighted at the neurobiological level than others. For example I have found that the human value type hedonism is very strongly associated with classical reward pathways (volume of left Globus Pallidus and microstructural properties of the Medial Forebrain Bundle) compared to other values types. This suggest that even though a set of values may be evolutionary conserved still some values may be more strongly associated to neurobiology than others. This piece of finding may help updating the psychological models of values in a number of ways. For example, new items in the human value scale can be added to interrogate the potential different components of hedonism and most importantly the content of these items should be based on the neuroscientific knowledge on classical reward pathways in the brain that has been accumulated over the years. However, I acknowledge that these above conclusions and suggestions are rather speculative considering the findings of the present thesis alone.

With regard to the tests involving genetic markers, the current state of affairs at the time of present thesis was the converging evidence that individual variation in both human values and personality traits are underpinned by shared genetic variation. Despite this link, no specific genetic markers had been connected to human values. The first experimental chapter of the thesis tested the sinusoidal prediction of Schwartz’s Circumplex model of values utilising the polygenic score of neuroticism. After I replicated prior evidence (Genetics of Personality, 2015) of a polygenic contribution to neuroticism using a novel measure of the trait (using the HEXACO), I demonstrated that the whole human value spectrum is significantly associated with the polygenic score of neuroticism in a sinusoidal manner, as predicted by Schwartz’s value model, providing the first association between human values and a specific genetic marker. This finding provides support for the evolutionary account (see General Introduction) of the 10 universal human value types, featured in Schwartz Circumplex model, and their relations, something that is particularly difficult to achieve when merely employing behavioural methodologies. Together, these results show that it is useful to include value orientations as relevant individual differences in polygenic contributions to neuroticism-related traits and that future research should consider values in investigations of polygenic contributions to other traits. Finally, this genetic finding also paved the way for an investigation of the biological mechanisms contributing to human value orientations which was the focus of the following experimental chapters.

Similar to the polygenic neuroticism score, the overall white matter volume and myelin volume fraction (as well as some grey matter regions particularly within the frontal lobes), which have a strong genetic component (Kanai & Rees, 2011), were also significantly associated with the whole human value space in a sinusoidal manner as predicted by the Schwarz Circumplex model. Indeed the white matter 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. 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 in clarifying whether such behavioural factors mediate the relationship between white matter and human values. Taken together, the genetic and brain structural data provide support for the circular structure of Schwartz value model, a support that spans different levels of neurobiology.

Apart from testing the overall structure of human values (i.e., analysing all 10 human value types at a time), the other main aim of the thesis was to investigate the extent to which neurobiological markers are related to human values at the level of individual values types and value dimensions. In particular, building on previous work, I looked at the neurostructural underpinning of the value type hedonism and the behavioural and neurofucntional link between the value dimension personal-focus vs social-focus in two prosocial reward-relate experiments. With respect to the value type of hedonism, I found that the volume of the subcortical structure left globus pallidus as well as the microstructural properties of left medial forebrain bundle, a white matter tract connecting a number of reward-related structures including the left globus pallidus, are positively associated with the value type hedonism. The observed association between structural variability in the slMFB- and hedonism complements previously established links between fronto-striatal and limbic-striatal microstructural connectivity, striatal reward-related processing and personality traits

(Cohen, Schoene-Bake, Elger & Weber, 2009). For example, individual differences in novelty seeking were associated with the microstructural strength of connections between hippocampus, ventral striatum and midbrain, while the microstructural strength of the tracts between prefrontal cortex and striatum explained individual differences in reward dependence (Cohen et al., 2009). Furthermore, novelty seeking and the reward dependence temperaments were associated with fronto-striatal fiber connectivity (Lei et al., 2014). Moreover, in a DTI-fMRI study, fractional anisotropy of cortico-striatal fiber tracts was related to NAcc reward-related activation (Koch et al., 2014).

At the level of value dimensions, this research studied the effect of selfishness/prosociality (i.e., value dimension personal focus vs social focus) on economic design making behaviour and neural activation in the context of charitable donations. Recent studies (Brosch et al., 2011) showed that human values are significant predictors of behaviour (i.e., point allocation) in a classical decision making task in the context of charitable donations. These studies showed that selfish participants kept more money for themselves than for a charity. Here, I extended the effect using a task that involved both a foraging stage and a classical economic decision making stage, as well as including a foraging task similar to those in the animal literature. Across both foraging tasks, self-focused individuals, compared to social-focused individuals, obtained more rewards when the foraging was for themselves or for themselves compared to the charity, but did not obtain more rewards when the foraging was simply for the charity. Most importantly, the higher level self-focus human value orientation score was negatively associated with the activation within the ACC during the foraging stage (personal vs social foraging). This evidence reveals a dynamic interplay between an evolutionarily entrenched decision making system and the higher order belief system of individuals.

All in all, these results showed that human values have an intricate link with classical neuroscience computations such as reward-related processing and economic decision making. Together, the findings further establish the diverse (i.e., spanning multiple levels) representation of human values in human neurobiology.

5.2. Limitations

A great number of the findings in the present thesis rely on novel statistical tests and methodologies. Chief among these are the sinusoidal test of associations with the human value types and the inclusion of neurobiological markers, such as the polygenic neuroticism score and brain structural parameters. Despite the significantly more conservative nature of our novel sinusoidal approach (i.e., *SFI*, Hanel et al., 2016) compared to the previously established approaches (e.g., Boer & Fischer, 2013), there are still some issues to consider in its application. In particular, to be certain that an external variable (e.g., a genetic score or the volume of brain region) is associated with human value types in a sinusoidal manner, I recommend the following suggestion. In the sinusoidal test, the inputs to the statistical test are the 10 correlation coefficients between the external variable and the 10 human value types, but this does not take into account the variance of a particular coefficient (i.e., distance between the empirical correlation coefficient of the sample and the real correlation coefficient in the population). However, as far as I am aware, none of the currently available sinusoidal tests take the correlation coefficient variance (i.e., confidence intervals) into account. This point requires special attention because the empirical sinewave (black sinewave, Figure 5) may differ from the population sine wave (red sinewave, Figure 5, hypothetical), which may not be a sinewave at all. This point is illustrated in the following figure (Figure 5). This unresolved issue can be addressed in at least two ways. First, future sinusoidal tests should take as an input not only the correlation coefficients (i.e., 10 numbers) but also the confidence intervals of each correlation coefficient and then utilise or control for this variance during the calculation of the fit. An alternative approach would be to independently replicate the effect of interest in a number of samples, and each correlation coefficient could be the mean correlation coefficient across samples, with error bars representing the spread across the samples. After this is done, the researcher can then run the *SFI* approach to test for significance. These methods would strengthen the test, although the strong *a priori* ordering of the values in the predicted sinusoidal waveform inspires confidence that the patterns of association are not merely occurring by chance (i.e., the wave would be perturbed by different real orderings which are not allowed for in the test), and the test remains an important advance beyond past methods.

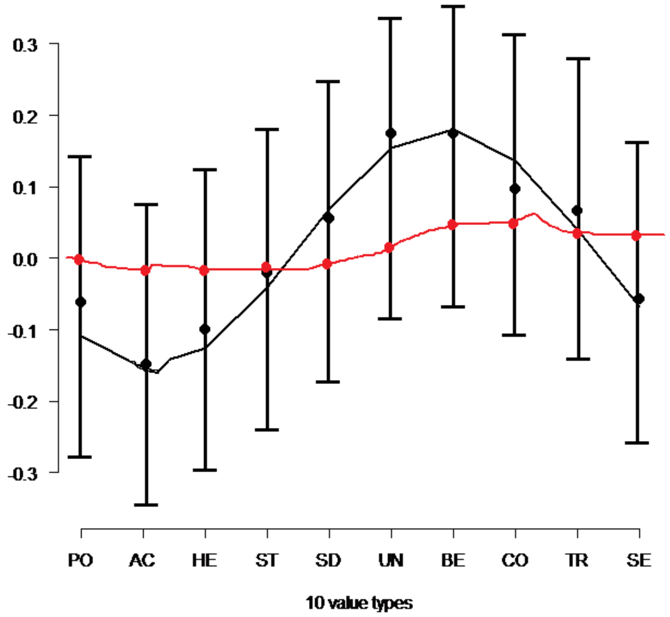

Figure 5. A methodological consideration for the Sinusoidal Fit Index. The empirical-sample (black line) and the population *SFI* may differ significantly. Error Bars are for demonstration purposes (fictitious). Black dots= empirical correlation coefficients, Black line= empirical *SFI*, Red dots= population correlation coefficients, Red line= population *SFI*.

Lastly, in relation to the foraging research, a significant limitation is that participants' choices may have been drastically different had they not felt the need to behave according to the social standards (i.e., act prosocially). Indeed, it was previously shown that participants' prosocial behaviour and corresponding neural activation when playing a similar economic decision-making game was significantly different depending on whether they were told that information about their choices are public or private. To minimize the social desirability effect, we specifically informed participants that the data are stored anonymously. However, this does not ensure that social desirability effects were eliminated. Congruent with abundant social psychological research utilising this method, social biases should have been attenuated, but it is not possible to be certain they were eliminated completely or sufficiently. Nevertheless, there is a question about mundane validity here: To extrapolate to the real world, total elimination of social desirability influences may not be untenable and raise its own limitations in interpretation.

Lastly, another limitation of this thesis is the fact human values were merely assessed via self-report items. This method poses some challenges because individuals might not accurately report their value orientation. Accuracy may be diminished for a variety of reasons, such as social desirability and not paying enough attention when completing the assessment tool. This can be somewhat corrected if the researcher replicates or extends the findings by using implicit measures of human values (for a review of implicit social cognition measures, see Nosek, Hawkins & Frazier, 2011) or other explicit measures similar to the Schwartz Value Scale, such as the Portrait Value Questionnaire (Schwartz et al., 2001), which measures the same 10 value types.

5.3. Future Directions

It is becoming increasingly apparent that individual variation in human values is associated with a range of neurobiology markers, including genetic, brain structural and brain functional parameters. However, a number of questions unanswered in this thesis can be investigated in the future work. For example, previous work (Brosch et al., 2011) showed that human values are associated with activation of reward-related regions of the brain in classical economic decision making tasks. Here, I found the value of hedonism is associated with the volume of left globus pallidus as well as with the microstructural properties of the left medial forebrain bundle, a white matter tract connecting a number of reward-related structures including the left globus pallidus. Given that the left medial forebrain bundle connects the reward-related areas found by Brosch et al (2011), future studies can investigate whether the effects of human values (and in particular hedonism) on reward-related neural activation is mediated/influenced by the integrity of the left medial forebrain bundle.

Another unresolved issue of this thesis is the elucidation of the process whereby the polygenic score of neuroticism is associated with human values. A polygenic score is derived from the genome wide association study, and it reflects variation of the whole genome, which is significantly associated with the variable of interest (neuroticism in this case). As such, it is a non-specific specific biological marker, and it is thus very hard to characterize the exact nature of the biological connection between this score and human values. Future studies can investigate the human values in relation to more specific neuroticism-related markers, as they become available, which would ideally control well-characterized endophenotypes. Of course, another future direction would be to associate human values with the polygenic scores of other personality traits, especially extraversion, because this personality trait has been shown to be associated with the whole human values space in a sinusoidal way at the behavioural level (Parks-Leduc et al., 2015). Indeed, a polygenic score for extraversion (van den Berg et al., 2016) has very recently been made available. Polygenic scores for well-being (Okbay et al., 2016) and depressive symptoms (Okbay et al., 2016) have also just become available. Similar to extraversion, previous studies showed a consistent link between well-being and human values (Bilsky & Schwartz, 1994; Oishi, Diener, Suh & Lucas, 1999; Sagiv & Schwartz, 2000), and this behavioural association can now be replicated and be extended at the genetic level. Lastly, future studies can interrogate the possibility whether the unique of HEXACO's emotionality or the shared variance with Big Five's extraversion is associated with human values in a sinusoidal way.

5.4. Final Conclusion

In sum, the present thesis tested the hypothesis that human values and the relationships between human values are represented at different levels of biology. I showed that individual variation in human values is associated with genetic, neurostructural and neurofunctional measures. Moreover, I demonstrated that the intrinsic patterns of associations within the value system itself, as predicted by Schwartz's circumplex model, are also linked to different levels of neurobiology. These data provide support for the circumplex structure of Schwartz's model and lay the foundation for future investigations into the neurobiology of values.

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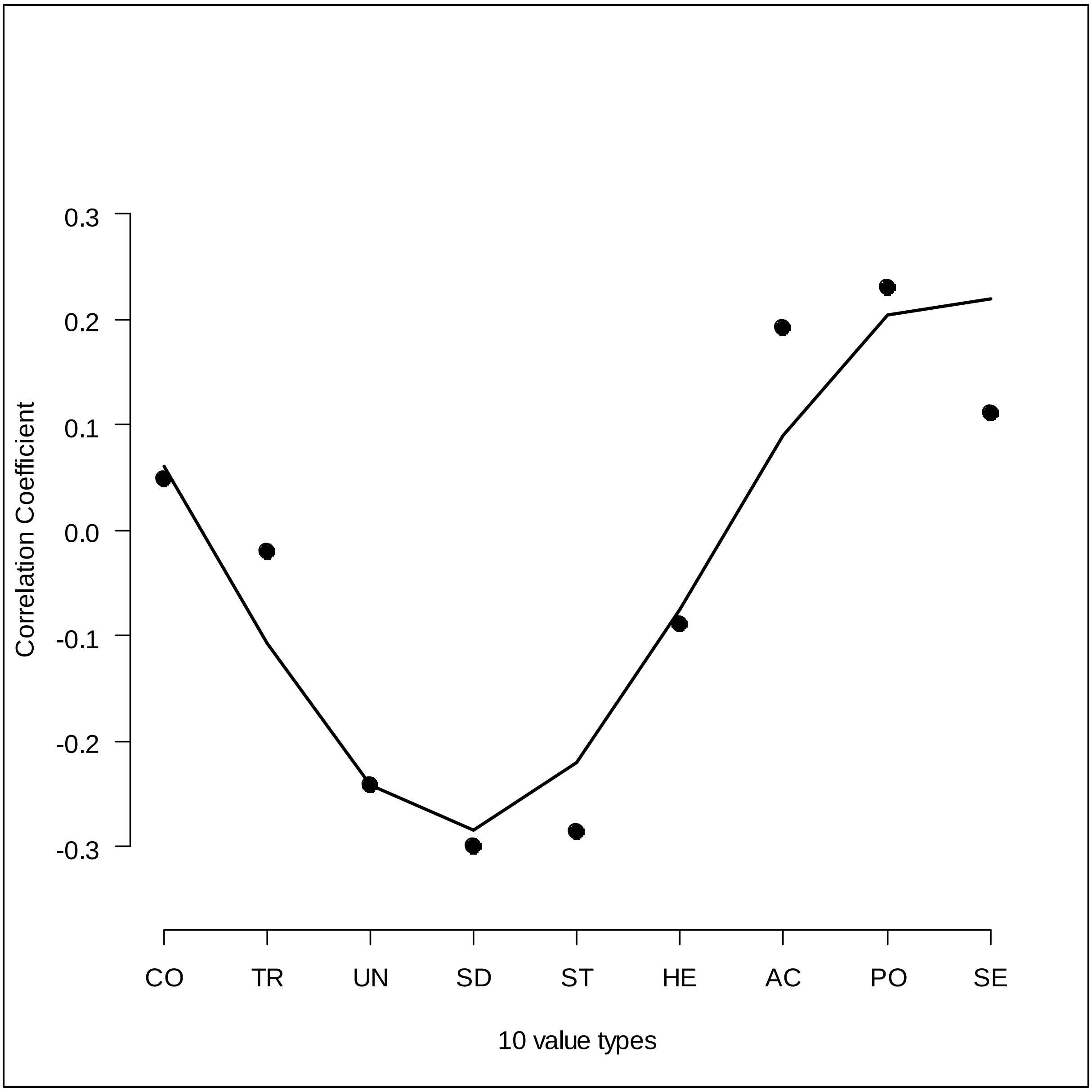
Supplementary Material

Supplementary Material 2.1. Cronbach's alpha for each of the 10 values (experimental chapters 2 & 3).

Value	Number of items	Cronbach's α
Universalism	7	.76
Benevolence	9	.76
Tradition	6	.63
Conformity	4	.63
Security	6	.68
Power	5	.79
Achievement	6	.67
Hedonism	2	.74
Stimulation	3	.79
Self-direction	6	.65

Supplementary Material 2.2. Correlation coefficients between the 9 value types (x-axis, Conformity, Tradition, Universalism, Self-Direction, Stimulation, Hedonism, Achievement, Power, Security) and NS.



Supplementary Material 2.3. Replication of sinusoidal results using previously established methods.

Apart from the sinusoidal approach discussed here, two alternative methods (Roccas et al. 2002; Boer & Fischer, 2013) for testing whether an external variable (e.g., PNS) is associated with the whole value space were utilised in the prior work. The method used in Roccas et al (2002) is composed of three steps. First, researchers derive hypotheses regarding the strongest positive and strongest negative correction between the external variable and the 10 value types. For example, in the case of extraversion discussed in their paper, it was hypothesized that the strongest positive correlation was with Stimulation and the strongest negative with Tradition. Next, researchers specify the expected order of correlations by assigning numbers 1 to 10 to the ten human values, with 1 assigned to the value with the strongest positive correlation and 10 to the value with the most negative correlation following the circular model (e.g., Stimulation=1, Hedonisms and Achievement=2, Self-direction and Power=4.5, Security and Universalism=6.5, Benevolence, Conformity=8.5, Tradition=10). After this is done, the researcher performs a spearman correlation correlating the expected orders of correlations (step 2) with the observed order of correlation (i.e., empirical correlations). A significant correlation suggests that the external variable is associated with the whole value space as predicted by Schwartz's circular model of values. By assigning the following values in step 2 (Stimulation=1, Hedonisms and Self-direction=3.5, Universalism and Achievement=6, Benevolence and Power=8, Security=9 and Conformity and Tradition=10), I replicated the PNS (r_s=.8, p=.008) and NS (r_s=.5, p=.112) findings using this approach. The exact same results also occur when assigning slightly different values in step 2 (Stimulation=1, Hedonisms and Self-direction=3, Universalism and Achievement=5, Benevolence and Power=7.5, Security=9 and Conformity and Tradition=10). The second approach discussed in Boer and Fischer (2013) tests four correlation patterns (i.e., two prototypical correlation patterns including the reversed patterns). The first pattern is termed SET-shape consistency, and it indicates that correlations with the external variable are highest for self-transcendence values, lowest for self-enhancement values, while the correlations with other values are in between. Similar to the first pattern, the second pattern is termed OC-shape consistency, and it indicates that correlations with the external variable are highest for openness values, lowest for conservation values, while the correlations with other values are in between. Each of the correlation patterns are assigned the output statistic, which is a number that ranges from -1 to 1. An absolute value greater of .4 indicates a small value consistent, .6 a medium value consistency and .8 a large value consistency. Again, I replicated the findings using this approach for PNS (SET-Shape=-.40, OC-Shape=.88). However, this latter approach deemed the correlation pattern of NS also significant (SET-Shape=-.47, OC-Shape=.74).

Supplementary Material 2.4. Pearson correlation coefficients between PNS and NS with the 10 human values (Conformity, Tradition, Universalism, Self-Direction, Stimulation, Hedonism, Achievement, Power, Security).

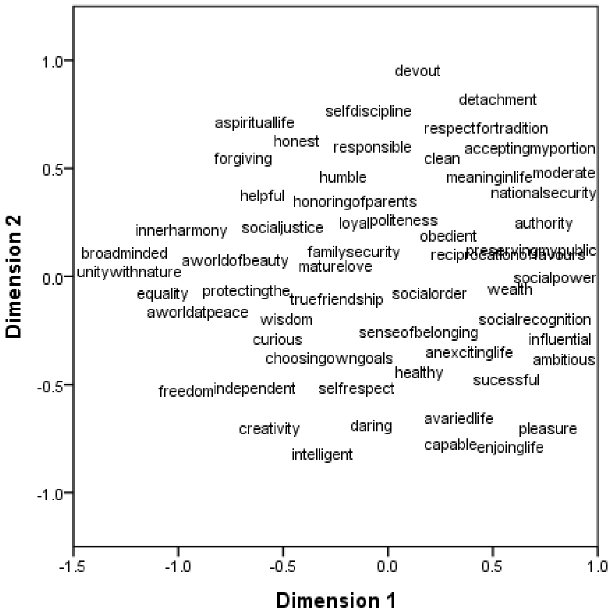
	CO	**TR**	**BE**	**UN**	**SD**	**ST**	**HE**	**AC**	**PO**	**SE**
PNS	.208	.073	-.035	-.155	-.163	-.180	-.146	.099	.139	.023
Sig. (2-tailed)	.067	.518	.758	.166	.145	.108	.196	.383	.216	.840
NS	.048	-.020	.189	-.242*	-.299**	-.285**	-.088	.192	.230*	.111
Sig. (2-tailed)	.673	.860	.091	.029	.007	.010	.437	.090	.039	.327

Supplementary Material 3.1.1. Schwartz's (1992) 10 value types and their principal values (adapted from Maio, Pakizeh, Cheung & Rees, 2009).

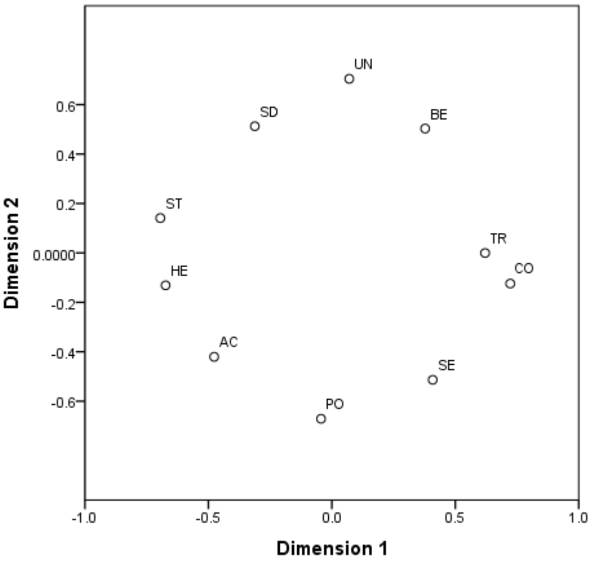
Value Type	Definition	Values
Power	Social status and prestige, control or dominance over people and resources	Social power, wealth, authority, preserving my public image
Achievement	Personal success through demonstrating competence according to social standards	Successful, ambitious, capable, influential
Hedonism	Pleasure and sensuous gratification for oneself	Pleasure, enjoying life
Stimulation	Excitement, novelty, and challenge in life	A varied life, daring, an exciting life
Self-direction	Independent thought and action-choosing, creating, exploring	Creativity, freedom, independent, curious, choosing own goals
Universalism	Understanding, appreciation, tolerance, and protection for the welfare of all	Broadminded, wisdom, a world of beauty, equality, unity with nature, a world at peace, social justice, protecting the environment
Benevolence	Preservation and enhancement of the welfare of people with whom one is in frequent personal contact	Honest, loyal, helpful, forgiving, responsible
Tradition	Respect, commitment, and acceptance of the customs and ideas that traditional culture or religion provide the self	Respect for tradition, humble, accepting my portion in life, devout, moderate
Conformity	Restraint of actions, inclinations, and impulses likely to upset or harm others and violate social expectations or norms	Self-discipline, obedient, politeness, honoring of parents and elders
Security	Safety, harmony, and stability of society, relationships, and self	Family security, national security, reciprocation of favors, social order, clean

Supplementary Material 3.1.2. Multidimensional Scaling Analyses

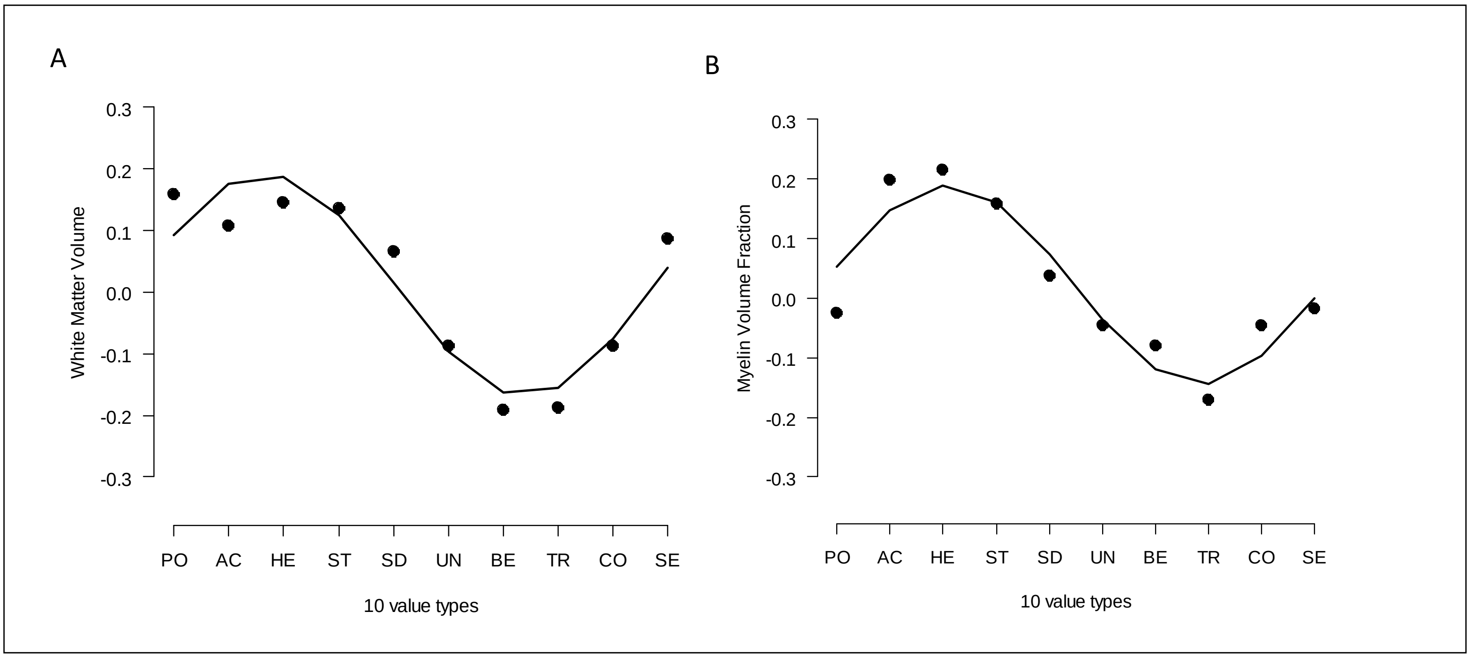
3.1.2.1. Multi-Dimensional Scaling: Multi-dimensional scaling analysis of 56 items.



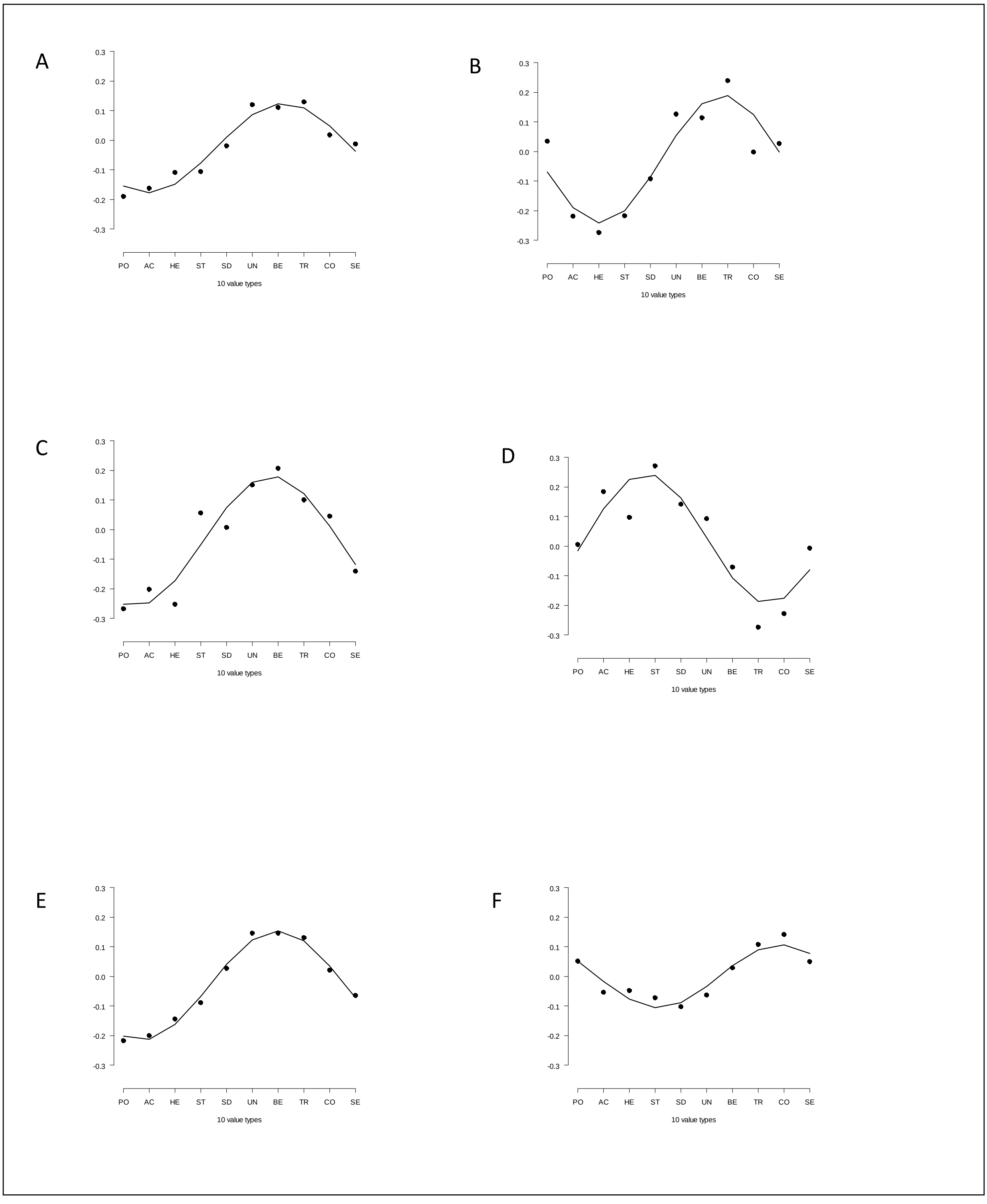
3.1.2.2. Multi-Dimensional Scaling: Multi-dimensional scaling analysis of 10 values.



Supplementary Material 3.1.3. Correlation coefficients between the 10 value types and the white matter volume (Panel A) and myelin volume fraction (Panel B). Unlike Figure 3 and 4, here I control for the potential confound of intelligence by regressing 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).



Supplementary Material 3.1.4. Parameters of brain regions that correlate with the social values scores in a sinusoidal fashion (*SFI*=goodness of fit). A. Left thickness of caudal middle frontal (*SFI*=.07), B. Left thickness of lateral orbitofrontal (*SFI*=.17), C. Left volume isthmus cingulate (*SFI*=.10), D. Left volume lateral occipital (*SFI*=.16), E. Left volume superior parietal (*SFI*=.02) and F. Right volume superior parietal (*SFI*=.10).



Supplementary Material 3.1.5. Replication of the sinusoidal finding using the Boer and Fischer (2013) method.

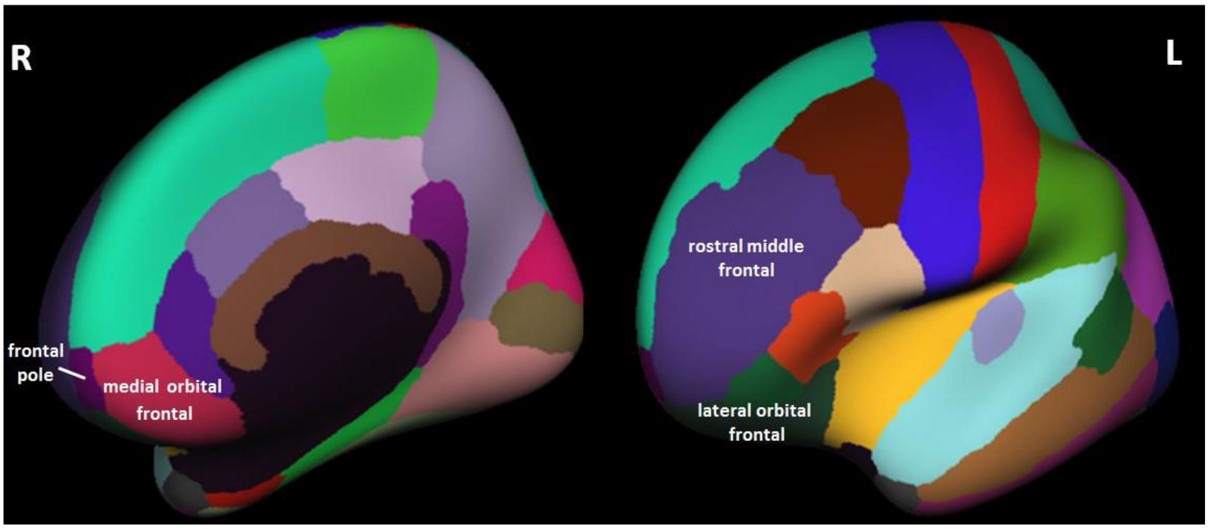
Despite the fact that the *SFI* approach is a more rigorous and conservative approach than Boer and Fischer's method (2013), it nevertheless revealed the same conclusions. That is, their method also brought out the association between values and white matter volume as well as with myelin volume fraction. The approach discussed in Boer and Fischer (2013) tests four correlation patterns (i.e., two prototypical correlation patterns including the reversed patterns). The first pattern is termed SET-shape consistency, and it indicates that correlations with the external variable are highest for self-transcendence values, lowest for self-enhancement values, while the correlations with other values are in between. Similarly to the first pattern, the second pattern is termed OC-shape consistency, and it indicates that correlations with the external variable are highest for openness values, lowest for conservation values, while the correlations with other values are in between. Each of the correlation patterns are assigned an output statistic, which is a number that ranges from -1 to 1. An absolute value greater than .4 indicates a small value consistency, .6 a medium value consistency and .8 a large value consistency.

	shapeSET	**shapeOC**
White matter volume	-.80	-.23
Myelin volume fraction	-.66	-.38
White matter volume (MATRICS regressed out)	-.77	-.26
Myelin volume fraction (MATRICS regressed out)	-.55	-.53

Supplementary Material 3.1.6. The 32 cortical labels (per hemisphere) of the DKT (Desikan-Killiany-Tourville (DKT) protocol to define the regions of interest (ROI) in the analysis.

1) caudal anterior cingulate
2) caudal middle frontal
3) cuneus
4) entorhinal
5) fusiform
6) inferior parietal
7) inferior temporal
8) isthmus cingulate
9) lateral occipital
10) lateral orbitofrontal
11) lingual
12) medial orbitofrontal
13) middle temporal
14) parahippocampal
15) paracentral
16) pars opecularis
17) pars orbitalis
18) pars triangularis
19) pericalcarine
20) postcentral
21) posterior cingulate
22) precentral
23) precuneus
24) rosterior anterior cingulate
25) rostral middle frontal
26) superior frontal
27) superior parietal
28) superior temporal
29) supramarginal
30) transverse temporal
31) insula
32) frontal pole

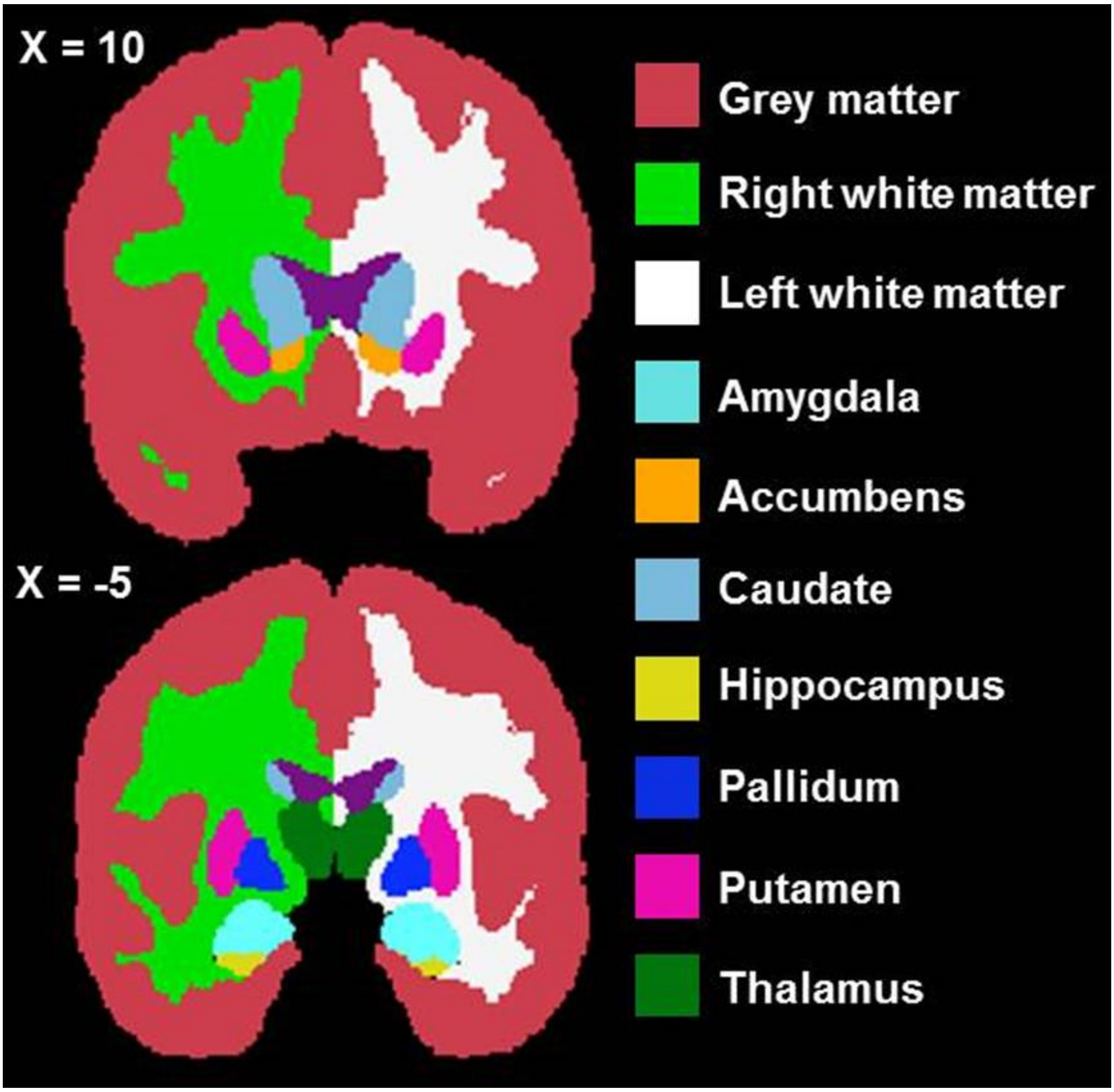
Supplementary Material 3.1.7. Frontal regions of interest: frontal pole, medial orbital frontal, rostral middle frontal, lateral orbital frontal



Supplementary Material 3.1.8. Voxel-based morphometry results representing negative associations between value dimensions and white matter across the whole brain.

Value Dimension	Coordinates	Cluster size	Cluster level	Peak Level	*T* value
Conservation	-22 -54 4	1	.044	.047	4.80
Self-Transcendence	60 -37 -11	30	.015	.009	4.87

Supplementary Material 3.2.1. Coronal sections showing the segmented subcortical regions and white and grey matter (x=coronal slice, Montreal Neurological Institute space)



Supplementary Material 3.2.2. Correlation coefficients between the ten human values (CO=Conformity, TR=Tradition, BE=Benevolence, UN=Universalism, SD= Self-direction, ST=Stimulation, HE=Hedonism, AC=Achievement, PO=Power, SE=Security) and the 14 subcortical structures (left and right: globus pallidus, thalamus, caudate nucleus, putamen, hippocampus, amygdala, nucleus accumbens), as well as with several fractional anisotropy and myelin volume fraction indices (wm: restricted to white matter mask, wb=whole brain, #: controlling for age, gender and overall fractional anisotropy within the white matter mask, +: controlling for age, gender, and overall fractional anisotropy).

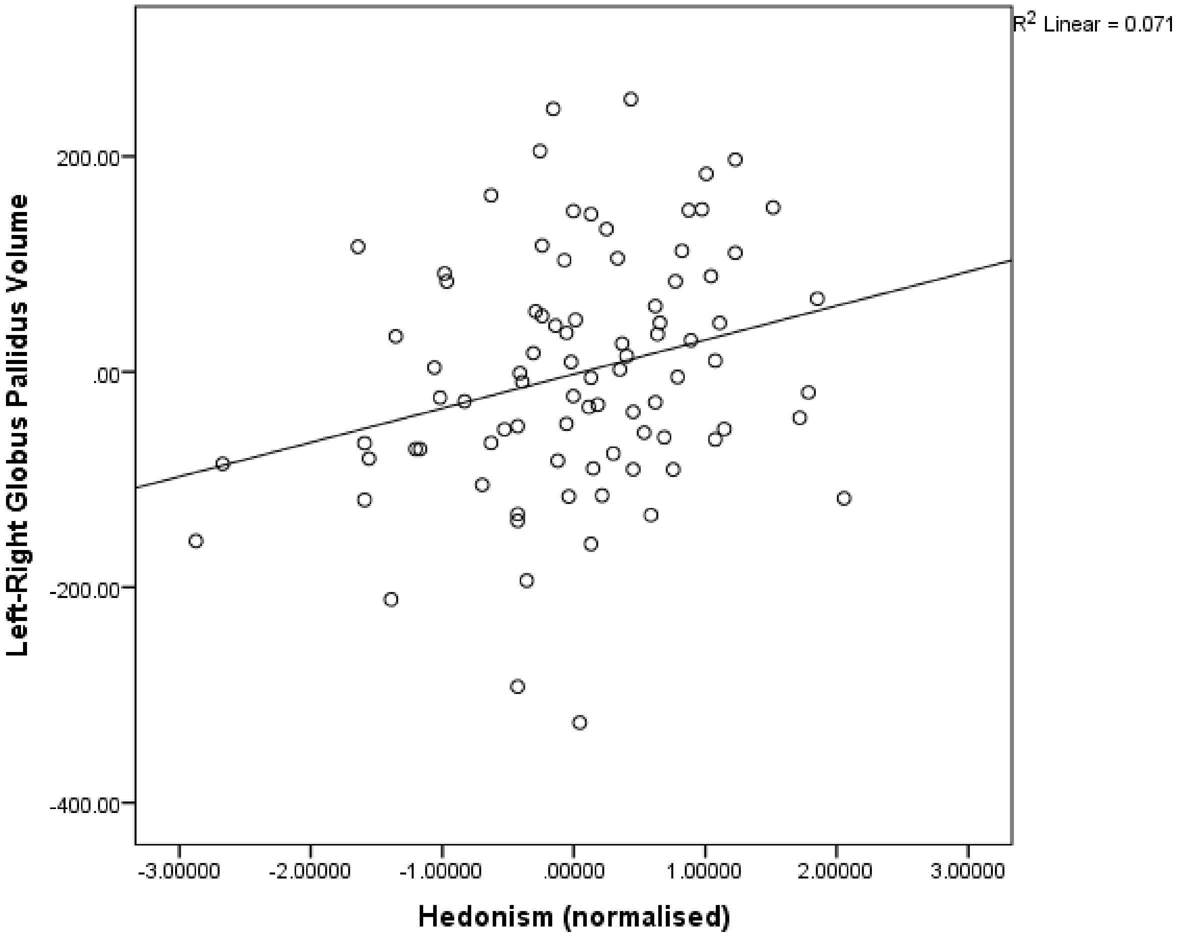
	CO	TR	BE	UN	HE	SD	ST	AC	PO	SE
L_Thalamus	0.033	-0.011	0.064	-0.127	0.105	-0.054	0.021	-0.026	-0.091	0.15
R_Thalamus	0.032	-0.055	-0.084	-0.119	0.192	-0.088	0.114	0.027	0.041	0.109
L_Caudate	-0.088	-0.08	-0.052	0.078	0.149	0.055	0.041	0.145	-0.113	-0.036
R_Caudate	-0.035	-0.038	0.002	0.129	0.144	0.021	0.03	0.018	-0.099	-0.08
L_Putamen	-0.076	-0.002	-0.106	-0.059	0.053	-0.101	0.142	-0.005	0.188	-0.02
R_Putamen	-0.037	0.033	-0.129	-0.025	-0.005	-0.144	0.13	-0.079	.217*	0.044
L_Pallidum	0	-0.182	-0.021	-0.152	.393**	0.036	.231*	0.083	-0.058	0.002
R_Pallidum	-0.1	-0.152	0.085	-0.125	.218*	0.001	0.052	0.014	0.039	-0.035
L_Hippocampus	0.042	0.042	-0.062	-0.003	-0.021	-0.105	0.096	-0.007	-0.004	0.014
R_Hippocampus	-0.035	0.073	-0.023	0.024	0.072	-0.134	0.183	-0.048	-0.004	0.082
L_Amygdala	-0.142	-0.029	-0.068	0.073	-0.124	-0.069	0.033	0.036	0.205	-0.115
R_Amygdala	0.084	-0.002	-0.081	-0.013	-0.15	0.014	-0.038	0.077	0.045	-0.046
L_Accumbens	0.075	0.166	0.061	-0.13	-0.09	-0.038	-0.056	-0.053	0.012	-0.016
R_Accumbens	-0.092	-0.079	-0.115	0.018	0.114	0.072	0.055	0.179	0.091	-0.182
L_MVF_wm	0.061	0.09	0.035	-0.198	.245*	-0.163	0.06	0.134	0.038	0.032
R_MVF_wm	-0.058	0.012	0.153	-0.027	.220*	-0.089	0.041	0.011	-0.004	0.049
L_MVF_wb	0.013	0.021	0.066	-0.2	.312**	-0.142	0.051	0.108	0.03	0.145
R_MVF_wb	-0.066	-0.049	0.122	-0.064	.266*	-0.067	0.041	0.023	-0.013	0.155
L_FA_wm#	0.007	0.106	-0.001	-0.176	0.107	-0.042	0.144	0.145	0.001	-0.062
R_FA_wm#	-0.042	0.091	0.105	-0.027	0.056	-0.031	0.112	-0.014	-0.096	0.006
L_FA_wb+	-0.037	0.087	0.007	-0.211	0.136	-0.051	0.091	0.157	0.034	0.003
R_FA_wb+	-0.062	0.072	0.098	-0.058	0.071	-0.032	0.068	0	-0.075	0.058

* p< 0.05, ** p< 0.01 (2-tailed).

Supplementary Material 3.2.3. Raw value distribution of all 10 human values

	N	Minimum	Maximum	Mean	Std. Deviation
Conformity	86	.75	7.00	4.4913	1.20321
Tradition	86	.17	5.67	2.5891	1.26664
Benevolence	87	2.50	6.63	5.0848	.85643
Universalism	87	2.44	6.89	4.9757	1.01120
Self- Direction	87	3.17	7.00	5.3257	.86150
Stimulation	87	1.33	7.00	4.8199	1.36948
Hedonism	87	2.00	7.00	5.5517	1.08648
Achievement	86	2.40	7.00	5.1186	1.02228
Power	87	-.80	6.60	2.5011	1.41318
Security	87	1.29	6.71	4.7274	1.03237
Valid N (listwise)	85				

Supplementary Material 3.2.4. A scatterplot depicting the association between hedonism and the left minus right GP volume.



Supplementary Material 4.1. Instructions to participants for the foraging Exp1 (4.1.1.) and Exp2 (4.1.2.).

Before reading the instructions and performing the practise sessions participants were told that they will be playing a game with the goal to maximize the number of points (Exp1) or apples (Exp2), which would be converted into real money at the end. In addition, participants were apprised that they will be playing these games for themselves for half of the trials and for a charity of their choice for the other half. Participant could select a different charity in Exp2. The list of charities was the following: British Red Cross, Save the Children Fund, The Salvation Army, Oxfam, Cancer Research, and Macmillan Cancer Support.

4.1.1. The instructions for EXP 1 were as follows.

"Thank you for participating. Today you will be earning money above pay/credits from coming in. It will be in the form of points shown in a reward bar. These points will turn into cash at the end of the experiment. Please press any key to continue.

You are now going to begin the main task

You will see a blue bar fill up to a golden line as you collect rewards. Each time you fill that bar we will add £0.20 to your final compensation.

Each trial of this task will involve two stages:

In stage 2 you will be choosing between two randomly chosen numbers at a time that are each GAMBLES. These numbers represent the amount of reward you get if the gamble wins. These numbers will each have a probability of winning between 20% and 90%. We will show you a purple bar next to each number that represents the probability of getting the reward for that number. The purple bars will perfectly represent the probability of winning for each symbol, and these probabilities will be assigned at RANDOM before each trial (i.e., they will have nothing to do with the amount of reward you can get from each number).

This all means that if you choose a certain number there is a chance that you will not receive the reward associated it, and that it will not necessarily benefit you to just choose the number associated with higher reward on each trial. On any given trial, it is possible that NEITHER, ONE, or BOTH gambles will be successful, but you will only the reward for the number you chose if it is successful.

Stage 1 takes place before you get to see the probabilities.

During Stage 1 you will simply see the two numbers you could choose between in the middle of the screen. You will ALSO see six other numbers in a box at the top of the screen.

At this stage you can press the A key to choose to swap out the two numbers you were given for two others from that box. When you do this, two numbers will be randomly chosen for that box and the two numbers previously in the middle will go into the box.

You can swap from this box as many times as you'd like. However, there is a cost for each of these swaps. The number of points you would lose is determined by the number to the left of the box.

Whenever you decide you want to stick with the number in the middle of the screen you can press the S key. You will then be shown the probabilities for each number and choose between them.

You will choose between numbers in the middle by pressing the K for the LEFT number and the L key for the RIGHT number. After you make a choice you will see the outcome of BOTH gambles. A plus (+) will appear next to each gamble that was successful (i.e., the purple bar beat the probability that was chosen), and an X will appear next to each one that was unsuccessful.

If the gamble you chose won, those points will be added to the reward bar. If you were unsuccessful, the bar will stay the same.

Note that each time you choose to swap for a new set of numbers or to make a choice between the numbers in front of you, there will be a few seconds delay before moving on to the next part of the trial. This is normal. You will get a better sense for all of this when you do the practice, but one thing to keep in mind is that the only time you will be able to make a response is when you see question mark (?) in the middle of the screen.

Finally, remember that the only time you can get rewards on this task is during the SECOND stage choice. There are a FIXED number of times total (200) that you will get to make this choice, meaning that you will not get the opportunity for more of these choices if you decide to swap more or fewer times during the first stage. These swaps will only affect which numbers you ultimately choose between, not how many times you will have an opportunity for reward."

4.1.2.

The instructions for EXP2 were as follows.

"Thank you for participating! For the next 30 minutes you will be asked to make choices that can earn you money.

In this game, you are in an orchard where you visit trees to harvest apples. You have a limited amount of time in the orchard and you need to decide whether to spend this time harvesting apples at a tree or moving to a brand new tree. Some trees produce more apples than others and each apple is worth money. Your goal is to earn as many apples (money) as possible.

On each trial you will see a tree. You can decide to harvest apples by pressing the Down arrow or move to a new tree by pressing the Right arrow.

Harvesting apples takes up some time but earns you money. However, you will tend to find that the more times you harvest apples at a tree the fewer apples it produces. Each time you harvest, the tree will produce only a fraction of the apples you earned on the previous turn

Going to a new tree also takes up time but the new tree has never been visited and so has a full supply of apples. There is an endless supply of new trees in each orchard, and you will never return to an already visited/harvested tree.

You have a limited amount of time to harvest apples in each orchard and this time starts counting down when you start the game. Harvesting apples takes time and each harvest decision results in fewer apples produced by that tree. Going to a new tree takes time but the tree has not been depleted by apple picking. Your goal is to tradeoff time spent harvesting and time spent moving to a new tree.

When the circle at the bottom of the tree turns white you should enter your decision to harvest apples (Down arrow) or move to a new tree (Right arrow). You won't have long to make a choice!

If you don't respond in time, you miss a turn. The more turns you miss, the less time you have left in the game to harvest apples and you will collect less apples (money).

A time out looks like this: “Time Out!” ;

You will harvest apples in different orchards. Some orchards have spread out trees and it takes longer to reach a new tree. Other orchards are more packed together and it takes less time to reach a tree. You will spend a limited and equal amount of time in each type of orchard.

The time it takes to go to a new tree can only change when you switch to a new orchard. Once in an orchard, the time it takes to go to a new tree does not change.   You will know when you switch orchards by a change of color, a message and a short break.

You will notice that at some trees you will harvest a larger initial number of apples than at others. The quality of any given tree is random but the likelihood of a good, bad, or average tree never changes. It is unrelated to which orchard you are in or the physical appearance of the tree.

When you harvest apples you may also get portions of whole apples. These are still worth money but at a fraction of a whole apple. You earn the apples on the screen after each harvest. Your goal is to earn as many apples (money) as possible. Your earnings are totaled throughout and paid to you at the end. Every decision counts!

SUMMARY: * Limited and equal time per orchard * Tradeoff time harvesting vs. switching trees * Number of apples produced by each tree varies the same way in every orchard * Harvesting apples depletes the supply in the same way in every orchard * Time to go to a new tree changes only when you switch orchards * Nothing changes until you switch orchards * The apples you earn on every choice count!

Remember, you can earn more by noticing how: * the apples you earn decrease as you harvest from the same tree * the quality of the trees varies * long it takes to go to a new tree or harvest apples.

You are now ready to try a short practice session

Supplementary Material 4.2: Personal foraging analyses

Given the effect of individual variability in self-focus on rewards during personal and social foraging, we investigated whether the average foraging value (i.e., the reward participants would earn if they choose to forage in a given trial) has an impact on the relationship between self-focus and reward. These analyses tested whether the effect of self-focus was significantly weakened when the overall foraging value variables were added into the regression model.

In EXP 1, the estimate signalling the average value of foraging was the average of the 6 numbers in the box (Figure 2), and the impact of that estimate on participants' decisions was the corresponding beta-weights from the logistic regression (Figure 3). Indeed, the standardized self-focus coefficient changed from significant (β=413, p=.036) to nonsignificant (β=.308, p=.103), while the standardized coefficient of the average forage value during personal foraging was still significant in the multiple regression model (β=.381, p=.046) predicting number of points during personal foraging. More interestingly, the standardized self-focus coefficient changed from significant (β=413, p=.036) to nonsignificant (β=.225, p=.157) ,while the standardized coefficient of the average forage value during personal minus social foraging was still significant in the multiple regression model (β=.609, p=.001) predicting number of points during personal minus social foraging.

In EXP 2, the variable that reflects how participants' decisions are influenced in response to the average foraging value is the exit threshold. We focused our analysis on the second visit of each environment, to eliminate the learning confound. (Of note, the reason we include all visits in EXP1 was because EXP1 is not a learning task). Similar to EXP 1, the self-focus coefficient changed from significant (β=.372, p=.047) to insignificant (β=.191, p=.305), while the coefficient of the average forage value was still significant in the multiple regression model (β=-.429, p=.026), during the personal foraging but not during the personal minus social foraging.