scientific reports

OPEN

Whole-brain white matter correlates of personality profiles predictive of subjective well-being

Raviteja Kotikalapudi, Mihai Dricu ✉, Dominik Andreas Moser & Tatjana Aue

We investigated the white matter correlates of personality profiles predictive of subjective well-being. Using principal component analysis to first determine the possible personality profiles onto which core personality measures would load, we subsequently searched for whole-brain white matter correlations with these profiles. We found three personality profiles that correlated with the integrity of white matter tracts. The correlates of an "optimistic" personality profile suggest (a) an intricate network for self-referential processing that helps regulate negative affect and maintain a positive outlook on life, (b) a sustained capacity for visually tracking rewards in the environment and (c) a motor readiness to act upon the conviction that desired rewards are imminent. The correlates of a "short-term approach behavior" profile was indicative of minimal loss of integrity in white matter tracts supportive of lifting certain behavioral barriers, possibly allowing individuals to act more outgoing and carefree in approaching people and rewards. Lastly, a "long-term approach behavior" profile's association with white matter tracts suggests lowered sensitivity to transient updates of stimulus-based associations of rewards and setbacks, thus facilitating the successful long-term pursuit of goals. Together, our findings yield convincing evidence that subjective well-being has its manifestations in the brain.

What makes one experience more frequent positive feelings, become better adjusted socially and stay in good mental and physical health? A large body of research has shown that subjective well-being, which includes perceived mental and physical health as well as rewarding social interactions[1], has less to do with objective circumstances such as age, gender, race, income, education or marital status and more to do with stable personality traits[2–5]. Although the effects of outside circumstances on well-being are often statistically weak[6–8], people persist in their impression that factors such as a relocation, a higher income, getting married or having children would lead to a substantial increase in subjective well-being[9–11]. This perceived importance of outside circumstances is likely the result of a focusing illusion[12–14], i.e., the tendency to focus on the changes that singular events bring while overlooking various other factors that will eventually also influence the actual feeling states. This is of course not to say that situational factors are not influential in subjective well-being.

The current understanding of well-being[15–18] is that genes (temperament) and personality together dictate a baseline of happiness. There is a range of values by which this baseline can fluctuate (i.e. a dynamic equilibrium;[16]), and this is where external events[19,20], an individual's goals and values[21,22] as well as social comparisons with peers[23–25] can exert most of their influence. Consequently, it is the interaction between genes and personality, on one hand, and situational factors and their interpretations, on the other hand, that give a complete picture to understanding well-being. The current study investigates the existence of well-being correlates in brain anatomy. Because we cannot study variations in brain anatomy for the person × situation interaction in total (i.e., across a multitude of different situations), and because the situation factor alone cannot be expected to manifest in brain anatomy, we concentrate on the person factor here.

Among personality factors that influence subjective well-being, the most researched ones have been a dispositional optimistic outlook on life[26–28], a particular pattern of Big Five personality dimensions (i.e. high extraversion and low neuroticism;[29–32]), higher dispositional sensitivity to rewards than to setbacks (i.e., a high aroused behavioral activation (BAS) and/or a lowly aroused behavioral inhibition system (BIS);[33–36]) as well as the habitual use of particular emotion regulation strategies (i.e. a frequent use of cognitive reappraisal and/or a rare use of suppression of negative affect;[37–39]). These personality factors not only independently predict subjective well-being but they also share significant variance with each other (e.g. Big Five with cognitive reappraisal[40–43] and with BIS/BAS[44]; optimism with Big Five[45–48] and with cognitive reappraisal[49]; BAS with use of cognitive reappraisal and/or low suppression of negative emotions[35,50,51]). The question then arises of how exactly these personality factors position themselves in relation to each other and in their predictive power over subjective well-being. Our

Institute of Psychology, University of Bern, Fabrikstrasse 8, 3012 Bern, Switzerland. ✉email: mihai.dricu@unibe.ch

study aimed to investigate this by running a principal component analysis (PCA) that revealed the underlying commonalities between these psychological constructs.

One of the objectives of neuroscience is to map brain-behavioral connections which may yield important insights about the processes that possibly underlie psychological constructs. Several studies exist already on the gray and white matter correlates of personality measures[52–56] and of subjective well-being[57]. However, a limitation of these studies is that they have focused on one personality measure at a time (see[58]). A likely possibility is that some personality measures cluster more often together than others, giving rise to personality "profiles" or "types"[59–61]. For example, high extraversion and high conscientiousness tend to cluster together but are both separate from high neuroticism[60,62]. Therefore, it might be wiser to investigate the neural correlates of personality profiles instead of individual factors. This has only very recently been attempted. For example, Li et al.[63] have looked into the grey matter correlates of personality profiles. However, no study to our knowledge has investigated the white matter correlates of personality profiles, particularly profiles that predict subjective well-being.

White matter tracts connect various grey matter regions and their integrity is a marker of how well the corresponding grey matter regions communicate with each other (e.g.,[55]). Therefore, individual variability in white matter tracts may underlie variability in personality profiles. Accordingly, in our study, we correlated the "positive personality profiles" from the PCA with the markers of white matter integrity. Because no other study has investigated the white matter correlates of personality profiles that are predictive of subjective well-being, we based our hypotheses on the few studies that independently probed relevant concepts (i.e., Big Five, BIS/BAS, emotion regulation strategies) in relation to white matter integrity.

For example, several studies have linked neuroticism to decreased integrity of white matter tracts in the cingulum (CNG[56,64]), the uncinate fasciculus (UNC;[56,65]), the body of the corpus callosum (CC[66,67]) as well as increased integrity of the posterior CC, the corticospinal tract (CST), the inferior fronto-occipital fasciculus (IFOF;[68]) and the inferior longitudinal fasciculus (ILF;[67,68]). Extraversion correlates negatively with white matter integrity in the posterior CC[67,69] and the CNG and the IFOF[69]. Furthermore, the BIS scale correlates positively with the integrity of the CNG, UNC, IFOF and superior longitudinal fasciculus (SLF;[68]). We note that some other studies have failed to find a meaningful relationship between white matter integrity and the Big Five dimensions[54,58,70] or the BIS/BAS[71]. By contrast, the association between the habitual use of cognitive reappraisal and white matter integrity has been rather consistent, implicating the UNC[72–75] and the CNG[72,73]. Given the above-reported correlates for isolated personality characteristics, we expected the implication of these areas in our profile study, too.

To measure white matter tracts, we used diffusion tensor imaging (DTI) tract-based spatial statistics, which is a commonly used voxel-based statistical framework for understanding white matter integrity[76]. To operationalize white matter integrity, we looked at widely used measures in DTI: (a) fractional anisotropy (FA), a measure that describes the directionality strength of local white matter tracts, (b) axial diffusivity (AD), a measure of the degree of diffusion of water molecules parallel to the axonal tracts, and (c) radial diffusivity (RD), a mean diffusion coefficient of water molecules diffusing orthogonally to the axonal tracts. These diffusivity measures provide complementary information about white matter integrity: as FA and AD values increase (integrity increases), RD values decrease.

Results

Principal component analysis results. The PCA analysis revealed that the 16 behavioral measures loaded on five principal components (eigenvalue > 1, serving as a cutoff) (Table 1). Together, these five principal components or personality profiles explained 60.8% of the total variance (Fig. 1).

The first component, which we call "*Optimism*" loaded the LOT Optimism, COS Optimism and Satisfaction with Life positively and LOT Pessimism negatively. The second component, dubbed "*Avoidant behavior*", loaded the BIS, BFI Conscientiousness and BFI Neuroticism positively and BAS Fun Seeking negatively. The third component, "*Short-term approach behavior*" loaded BFI Extraversion, BFI Agreeableness and BAS Fun Seeking positively but ERQ Suppression negatively. The fourth component, "*Long-term approach behavior*", loaded all three BAS components and BFI Openness positively. Finally, the fifth component "*Pessimistic reappraisal*" loaded COS Pessimism and ERQ Reappraisal positively (Table 1).

White matter voxel-based results. The tract-based spatial statistics correlations between personality profiles and diffusion maps are presented with Table 2. Of these five PCA components, "*Optimism*" (PCA 1), "*Short-term approach behavior*" (PCA 3) and "*Long-term approach behavior*" (PCA 4) revealed tract-based findings for the probabilistic diffusion maps. Specifically, the "*Optimism*" component correlated positively with AD values in the right hemisphere exclusively (Fig. 2): the corticospinal tract (CST), the superior longitudinal fasciculus (SLF), anterior cingulum bundle (CNG), anterior corpus callosum (CC), anterior thalamic radiation (ATR) and uncinate fasciculus (UNC). The component for "*Short-term approach behavior*" correlated negatively with the FA values in the left hemisphere exclusively, namely the splenium of the CC, inferior longitudinal fasciculus (ILF), and UNC (Fig. 3). This component further correlated positively with the RD values in the right UNC/inferior fronto-occipital fasciculus (IFOF) and right SLF and left CNG (Fig. 4). Lastly, the component for "*Long-term approach behavior*" correlated positively with the RD values in the right UNC (Fig. 5).

Discussion

Our study is the first to investigate the white matter correlates of personality profiles that are predictive of subjective well-being. We used PCA to determine the possible profiles onto which dispositional optimism, Big Five dimensions, BIS/BAS, ERQ and SWL would load. We then searched for whole-brain white matter correlations with these profiles, and we based our hypotheses on past structural findings for each separate psychological construct. The PCA revealed five distinct profiles, three of which correlated to white matter measures: (a) "*Optimism*"

Behavior data			Personality profiles derived from PCA				
Psychological constructs	Mean	Standard deviation	PCA 1 Optimism	PCA 2 Avoidant behavior	PCA 3 Short-term approach behavior	PCA 4 Long-term approach behavior	PCA 5 Pessimistic reappraisal
LOT optimism	8.71	2.08	**0.77**	−0.24	0.05	0.04	0.02
LOT pessimism	4.04	2.02	**−0.69**	0.08	−0.23	−0.07	−0.17
Satisfaction with life	26.51	5.33	**0.70**	−0.02	0.25	0.11	−0.05
COS optimism	69.94	11.01	**0.48**	−0.12	−0.31	0.30	−0.01
COS pessimism	76.99	14.50	0.00	0.00	−0.03	−0.12	**0.78**
BIS	20.01	3.64	−0.10	**0.80**	0.04	0.04	0.08
BAS drive	12.34	2.10	0.17	0.00	−0.01	**0.73**	−0.08
BAS fun seeking	12.26	1.63	−0.11	**−0.39**	0.41	**0.41**	0.33
BAS reward response	16.59	2.04	0.08	0.00	0.18	**0.78**	−0.08
BFI openness	7.49	1.88	−0.27	−0.31	0.25	**0.55**	0.14
BFI Conscientiousness	7.16	1.77	0.17	**0.44**	−0.01	0.26	−0.11
BFI extraversion	6.89	1.98	0.12	0.03	**0.75**	0.21	−0.13
BFI agreeableness	7.05	1.33	0.15	0.11	**0.64**	−0.13	0.11
BFI neuroticism	5.79	1.88	−0.16	**0.82**	0.03	0.00	0.00
ERQ reappraisal	29.34	5.65	0.18	0.13	0.09	0.29	**0.51**
ERQ suppression	13.45	4.75	−0.13	−0.03	**−0.69**	−0.03	−0.01

Table 1. PCA results derived from the questionnaire data. Descriptive statistics of mean and standard deviation of the behavioral questionnaires are presented. Bend correlations 'rho' between derived components and individual questionnaires are also provided. Bold indicates significant correlations (alpha = 0.05, corrected for multiple comparisons).
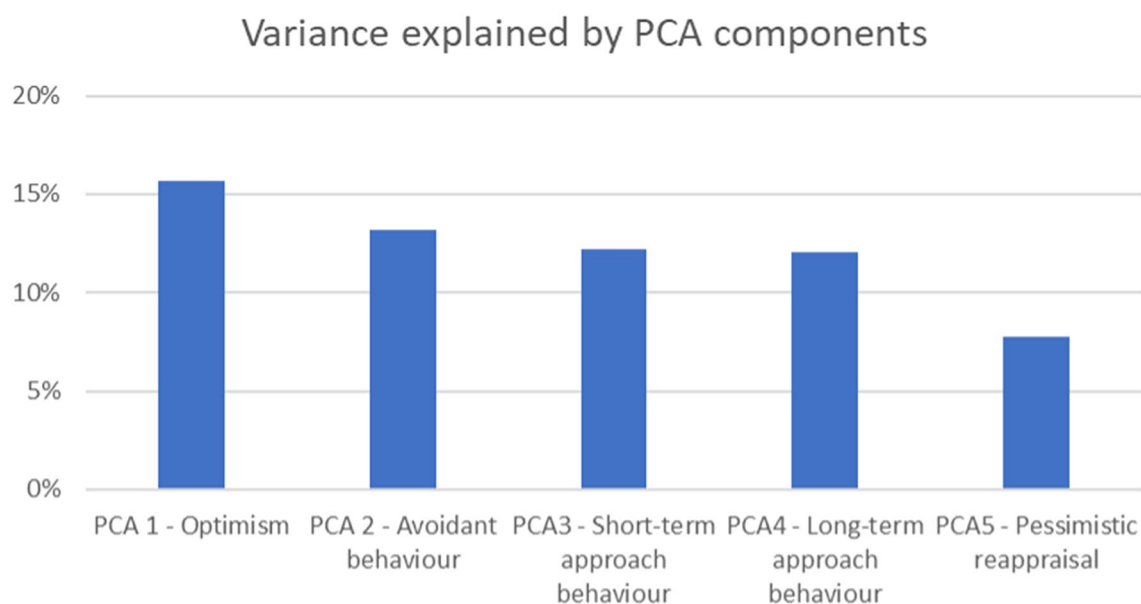
Figure 1. Total variance explained (60.8%) by the five PCA components with an eigenvalue > 1.

profile, onto which LOT Optimism, COS optimism and SWLS loaded positively and LOT Pessimism loaded negatively; (b) "*Short-term approach behavior*" profile, onto which Extraversion, Agreeableness and BAS Fun Seeking loaded positively and EQ Suppression loaded negatively; (c) "*Long-term approach behavior*" profile, onto which BAS Drive, BAS Reward Responsiveness and, to a lesser degree, BAS Fun Seeking and Openness loaded.

We found that the "*Optimism*" profile correlated positively with AD values in white matter tracts exclusively in the right hemisphere: the CST, the SLF, and the anterior CNG, CC and ATR. Similar to FA values, the AD reflects the magnitude of diffusion parallel to fiber tracts and thus the integrity of axons[77,78]. The exclusivity of our findings in the right hemisphere is in line with the proposed functional asymmetry between the left and right hemispheres concerning complementary modes of processing incoming information (e.g.[79,80]). While the left hemisphere processes the information in a strictly sequential and unambiguously understood monosemantic context[81], the function of the right hemisphere is to simultaneously capture a vast number of possible connections and to integrate them in an ambiguous but polysemantic context[81–83]. Because of this functionality, the right

Behavioral component	DTI marker	Cluster size	Peak voxel	Anatomy	Projections to gray matter regions
Positive correlation with diffusion maps: PC 1—Optimism 1. LOT (+) 2. SWLS (+) 3. COS optimism (+) 4. LOT pessimism (−)	AD	1781	[21, − 18, 43]	R corticospinal tract 72.5% R dorsal superior longitudinal fasciculus 33.7%	From primary motor and primary somatosensory cortex to afferent nerves in the body[106,184]
		102	[17, 20, 39]	R anterior corpus callosum 100% R anterior thalamic radiation 100% R anterior cingulum bundle 92.2%	Connecting the ventromedial prefrontal cortex, anterior cingulate cortex and frontal poles[135,136,185,186]
		81	[40, − 12, 28]	R dorsal superior longitudinal fasciculus 100% R corticospinal tract 50.6%	From angular gyrus to premotor cortices and caudal dorsolateral prefrontal cortex[105,106]
		70	[27, 35, − 1]	R anterior thalamic radiation 100% R rostrum of corpus callosum 92.86% R uncinate fasciculus 100%	Ventromedial prefrontal cortex and orbitofrontal cortex[135,136,187]
		32	[19, 22, 28]	R anterior cingulum bundle 100%	Anterior cingulate cortex and ventromedial prefrontal cortex[135,136]
		21	[6, 12, 31]	R ventral superior longitudinal fasciculus 100%	From supramarginal gyrus to ventral premotor cortex and pars opercularis[105,106]
Positive correlation with diffusion maps: PC 3—Short-term approach behavior 1. BFI Extraversion (+) 2. BFI agreeableness (+) 3. BAS fun seeking (+) 4. ERQ Suppression (−)	RD	905	[25, 21, − 5]	R Inferior frontal-occipital fasciculus 86.3% R Uncinate fasciculus	To ventromedial prefrontal cortex, orbitofrontal cortex[188–190]
		196	[− 14, − 23, 31]	L splenium of corpus callosum 100%	Posterior cingulate cortex and precuneus[135,136]
		31	[45, − 18, 37]	R superior longitudinal fasciculus II 96.8%	The premotor cortices, supplementary motor areas, pars opercularis[106]
Negative correlation with diffusion maps: PC 3—Short-term approach behavior 1. BFI Extraversion (+) 2. BFI agreeableness (+) 3. BAS fun seeking (+) 4. ERQ Suppression (−)	FA	7602	[25, 22, − 6]	R Inferior frontal-occipital fasciculus	
		6960	[− 10, − 17, 29]	L splenium of corpus callosum 49.6%	Posterior cingulate cortex[135,187]
		124	[− 32, − 78, − 1]	L splenium of corpus callosum 93.5% L inferior longitudinal fasciculus 100%	Medial parietal, medial occipital[135,187]
		85	[− 13, 16, 51]	L Corpus callosum (body)	Parietal to precentral regions[135,136]
		83	[− 22, − 83, 10]	L splenium of corpus callosum 100% L inferior longitudinal fasciculus 100%	Medial parietal, medial occipital[135,187]
		56	[− 11, − 86, 23]	L splenium of corpus callosum 100% L inferior longitudinal fasciculus 42.9%	Medial parietal, medial occipital[135,187]
		25	[− 36, 23, − 12]	L uncinate fasciculus 36%	Ventromedial prefrontal cortex, orbitofrontal cortex, inferior frontal cortex[188–190]
		20	[− 24, 13, − 13]	L uncinate fasciculus 100%	
		15	[− 19, − 80, 19]	L splenium of corpus callosum 100% L inferior longitudinal fasciculus 100%	Medial parietal, medial occipital[135,187]
Positive correlation with diffusion maps: PC 4—Long-term approach behavior 1. BAS Drive (+) 2. BAS Reward (+) 3. BAS Fun seeking (+) 4. BFI Openness (+)	RD	97	[28, 17, − 2]	R uncinate fasciculus 100% R Inferior frontal-occipital fasciculus	From anterior temporal lobes (via internal and external capsules) to inferior frontal cortex, vnPFC, orbitofrontal cortex, frontal pole[188–190]

Table 2. TBSS randomized results with TFCE at $p < .05$ after 5000 permutations. The correlation results for behavior data with DTI maps for axial diffusivity (AD), radial diffusivity (RD) and fractional anisotropy (FA) are presented along with the cluster size, peak voxel coordinate and tract anatomy of the findings. LOT—Life LOT—Life Orientation Test. SWLS—Satisfaction With Life Scale. COS—Comparative Optimism Scale. BIS—Behavioral Inhibition System. BAS—Behavioral Approach System. BFI—Big Five Inventory. A plus (minus) sign depicts positive (negative) contributions of the behavioral measures to the principal components.

hemisphere has been involved in a variety of integrative phenomena[84–86], including helping the implicit self[87] maintain a positivity bias[88–90]. The implicit self is a highly integrative construct that processes vast amounts of self-relevant information from cognitive (e.g., autobiographical memories), motivational (e.g., values, needs) and affective (e.g., emotions) systems in parallel[87,91]. Because personal experiences are inherently perceived as positive in healthy individuals[92], a functional implicit self is crucial in maintaining a positivity bias by assimilating negative affective experiences within a network of predominantly positive experiences[81,93]. Due to this holistic nature, the implicit self is believed to be a function of the right hemisphere[87,90]. The incapacity to regulate negative affect and display a (somewhat normal) positivity bias underlies emotional disorders such as depression, alexithymia and suicidal ideation, which are characterized both by a lack of optimism bias[53] and a functionally deficient right hemisphere[79,81,94], including decreased integrity of white matter tracts[95]. Our study thus supports previous findings that the right hemisphere is necessary for healthy individuals to express their positivity bias.

Regarding the individual tracts in the right hemisphere underlying "*Optimism*", the CST was the strongest finding in terms of cluster size. The integrity of the CST is associated with a lower baseline excitability threshold, i.e. the minimum intensity at which the motor system can evoke a motor response[96,97]. At the same time, CST excitability indexes the degree of "wanting" a reward[98]; see also[99] and the certainty of upcoming rewards[100,101]. Our finding that dispositional optimism is foremost associated with the integrity of the CST makes it thus tempting to speculate that optimism is more embodied than we may believe. Could optimism predispose us not
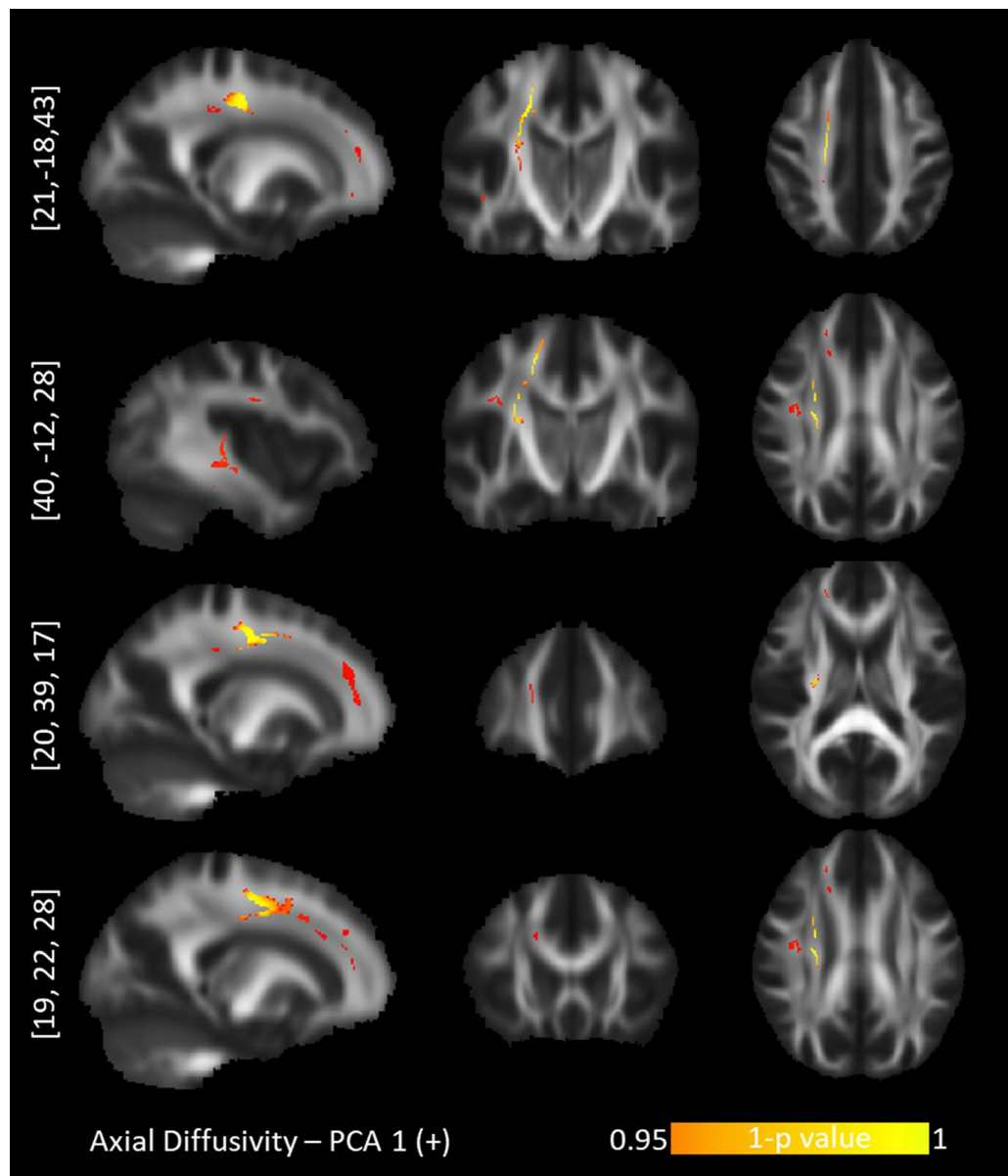
Figure 2. TBSS positive correlations between axial diffusivity and the "Optimism" personality profile. Upper row: corticospinal tract. Second row: dorsal superior longitudinal fasciculus. Third row: anterior corpus callosum. Bottom row: anterior cingulum bundle.

only toward expecting good things to happen but also toward motor readiness to go after these rewards? After all, one of the aspects of dispositional optimism bringing an adaptive advantage in life[102] is its ability to make us effortlessly engage in our goals[103].

Other individual white matter tracts associated with the "*Optimism*" profile were the dorsal SLF, and the anterior CNG, CC and ATR. The dorsal SLF is essential to the dorsal attention pathway[104–106] and its integrity relates to measures of sustained goal-directed visuospatial attention in children[107,108] and adults[109–111]. That optimism and attention deployment are critically linked is demonstrated in various behavioral and neuroimaging studies ([112–115], for a theoretical account, see[116]). Interestingly, the integrity of the right SLF has further been connected to global visual motion sensitivity[117], i.e. the ability to perceive and infer the overall movement trend of a multitude of stimuli (e.g. moving dots) with otherwise random motion. In other words, the right SLF supports seeing the forest and not the trees. This holistic perception ability is likely due to the right-side hemispheric lateralization, as discussed above. The overwhelming evidence suggests that the right SLF is involved in the endogenously controlled capacity to actively detect, follow, and respond to relevant (holistic) stimuli over prolonged periods of time. Although the SLF might not be specific to optimism bias, it might maintain it when other mechanisms are in place to generate it, e.g. by supporting long-term pursuit of desirable outcomes[118].
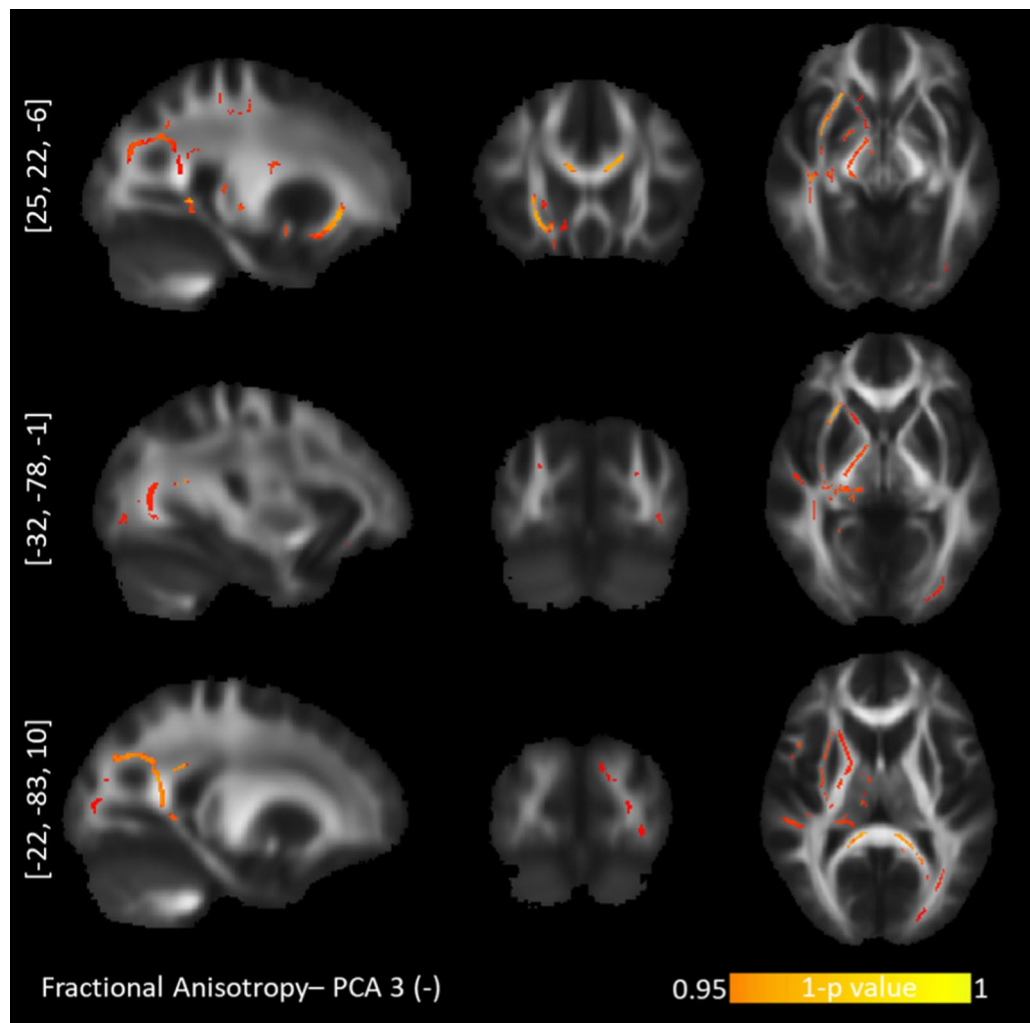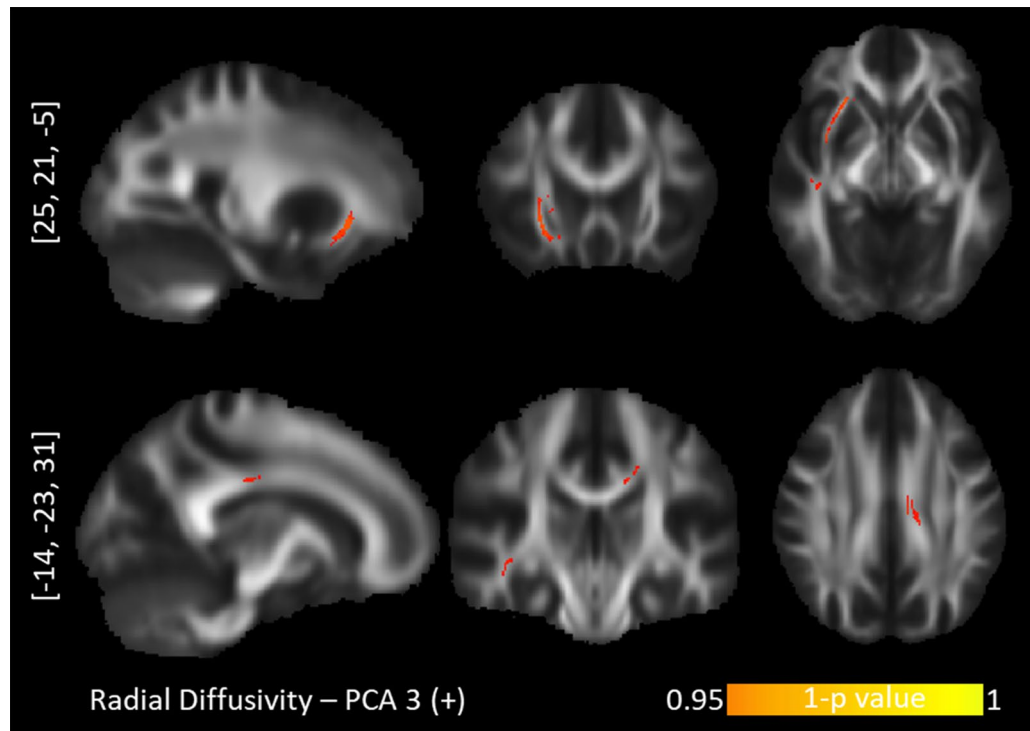
Figure 3. TBSS negative correlations between fractional anisotropy and the "Short-term approach behavior" personality profile. Upper row: inferior fronto-occipital fasciculus. Middle row: inferior longitudinal fasciculus/ posterior corpus callosum. Bottom row: inferior longitudinal fasciculus/posterior corpus callosum.

The remaining white matter tracts whose integrity correlated with the "*Optimism*" component, i.e. the anterior CNG, CC, and ATR, connect brain regions that are part of the anterior midline core of the default mode network (DMN). Notably, the functional connectivity between the core nodes of the DMN positively correlates with the integrity of the CC[119–121], CNG[122–124] and the ATR[122,125]. The anterior midline node of the DMN supports internally directed thought and self-referential processing[126,127], including simulating one's (mostly optimistically biased) future[128–130]. The integrity of the CC, in particular, has been associated with a higher dispositional optimism[131,132] and a higher resistance to updating personal beliefs in a pessimistic direction[133,134]. Furthermore, the gray matter endings of the anterior CC, CNG and ATR all overlap in the ventromedial prefrontal cortex (vmPFC;[135–139]). There is highly converging evidence pointing to the involvement of the vmPFC in optimism bias[53,140–144], and activity in the vmPFC also correlates positively with subjective well-being[145]. Thus, the correlation between the optimism profile and the white matter tracts of vmPFC is not surprising.

In sum, the "*Optimistic*" personality profile correlated with white matter tracts that suggest a motor readiness to act upon the conviction that desired rewards are imminent (CST), a sustained capacity for visually tracking rewards in the environment (SLF) and an intricate network for self-referential processing that helps regulate negative affect and maintain a positive outlook on life (anterior CNG, CC, ATR).

We called the third PCA factor "*Short-term approach behavior*" because impulsivity (indexed by BAS Fun Seeking;[146]), extraversion and agreeableness positively loaded on it. Impulsivity, i.e. the motivation to spontaneously go after novel rewards, is a core part of both extraversion[147,148] and agreeableness[149], so their clustering is not surprising. Furthermore, ERQ Suppression loaded negatively, suggesting an inability to suppress impulsive urges. We note that impulsivity is operationally split into motor impulsivity and cognitive impulsivity[150–153]. Motor impulsivity is similar to motor readiness and correlates with CST integrity and excitability (e.g.[154], see also "Optimism" profile above). By contrast, cognitive impulsivity refers to the inability to compare immediate consequences and the future events with each other and, consequently, the inability to see reasons for delaying immediate satisfaction. The relevant measures on our third PCA factor, namely BAS Fun Seeking[146],

Figure 4. TBSS positive correlations between radial diffusivity and the "Short-term approach behavior". Top row: inferior fronto-occipital fasciculus. Bottom row: posterior corpus callosum.
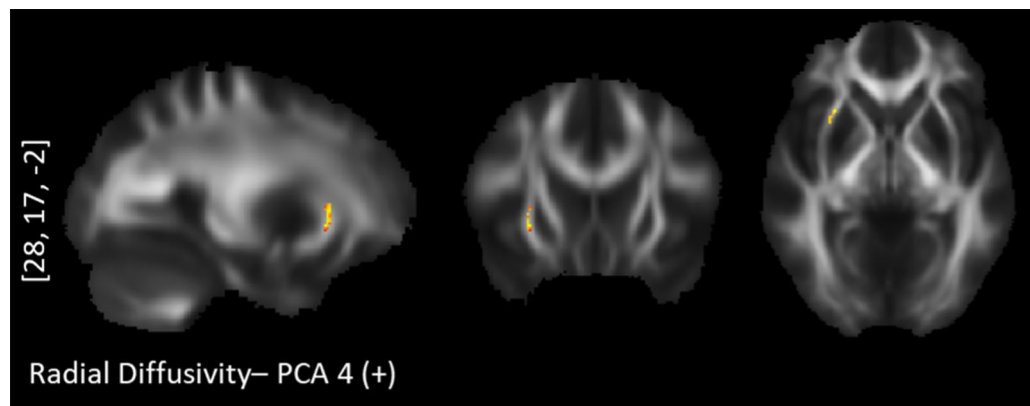
Figure 5. TBSS positive correlations between radial diffusivity and "Long-term approach behavor": right uncinate fasciculus.

extraversion[147,148] and agreeableness[149], measure cognitive impulsivity. Altogether, the "*Short-term approach behavior*" profile correlated negatively with the FA values of the left splenium of CC and left ILF but positively with the RD values of the left splenium and the right UNC/IFOF. FA and RD markers are complementary: low FA and high RD values represent compromised axons (demyelination) while high FA and low RD values represent healthy tracts[77]. Considering this, (impulsive) short-term approach behavior seems to increase as a function of compromised integrity in the left splenium of CC, left ILF and UNC/IFOF. These findings are in line with previous literature on extraversion and compromised posterior CC and IFOF[67,69] as well as with the literature on BAS Fun-Seeking and compromised left IFOF[55]. Interestingly, individuals with either behavioral or substance addiction show more extensive impairments of the integrity of the CC splenium[155–157] and ILF[158,159]. These extensive impairments of both CC and ILF are, in turn, inversely related to the levels of self-reported impulsivity[156]. We thus propose that a minimal loss of integrity in these tracts lifts certain barriers and predisposes individuals to be more outgoing and carefree in approaching people and rewards[160,161], but too extensive a damage to their integrity is a risk factor for addiction and clinical impulsivity.

We termed the fourth PCA factor "*Long-term approach behavior*" due to the high loading of BAS Drive (high-intensity pursuit of desired goals) and BAS Reward Responsiveness (positive affective experience in response to rewards) and, to a lower extent, the contributions of BAS Fun Seeking and Openness. Both BAS Drive and BAS Reward Responsiveness are associated with vigorous pursuit of long-term rewards despite physical or mental challenges[162], while BAS Fun Seeking points to the spontaneous pursuit of novel rewards[146]. Although, taken in isolation, the three BAS components point to different time windows of pursuing rewards, the combined three components are compatible with pursuing long-term goals. A high BAS Drive safeguards the behavioral maintenance of long-term goals despite obstacles while a high BAS Fun Seeking component (combined with the high BFI Openness) ensures the flexibility and readiness to spontaneously seize unexpected alternative ways of attaining the long-term goal. Finally, a high BAS Reward Responsiveness ensures appropriate positive emotional reactions when attaining each milestone on the way to achieving the final behavioral goal, a process that ensures goal pursuit.

In terms of brain structures, the "*Long-term approach behavior*" component correlated positively with RD values in the right UNC/IFOF: the lower the integrity between the anterior temporal lobes and the frontal cortex, particularly the orbitofrontal cortex[163,164], the more prominent the long-term approach behavior. It was proposed that the UNC allows temporal lobe-based stimulus associations (e.g. between the physical properties of a stimulus and the emotions associated with it) to modify behavior via interactions with the orbitofrontal cortex[163,164]. These interactions between the temporal lobe and the orbitofrontal cortex would be instrumental in ensuring that stored stimulus associations reflect up-to-date reward and punishment history. Applied to the present data, one may therefore speculate that the successful behavior of keeping eyes on an end goal depends on not always allowing up to date (and likely transitory) reward and punishment information to interfere with the end goal established much earlier on.

Limitations, strengths and conclusions. We would like to point out that the analyzed sample consisted mostly of females. Given that gender plays a role in brain structure and morphology[165], future studies should include a balanced sample of males and females. We tried to mitigate these confounding influences by taking age, gender, and total intracranial volume as the covariates of no-interest. Our study has the strength of focusing on personality profiles as opposed to isolated constructs and investigating the white matter correlates of the profiles predictive of subjective well-being. The correlates of an "*Optimistim*" personality profile suggest (a) an intricate network for self-referential processing that helps regulate negative affect and maintain a positive outlook on life, (b) a sustained capacity for visually tracking rewards in the environment and (c) a motor readiness to act upon the conviction that desired rewards are imminent. Correlates of a "*Short-term approach behavior*" profile were indicative of minimal loss of integrity in white matter tracts supportive of lifting certain behavioral barriers, possibly allowing individuals to act more outgoing and carefree in approaching people and rewards. Lastly, a "*Long-term approach behavior*" profile's association with white matter tracts suggests lowered sensitivity to transient updates of stimulus-based associations of rewards and setbacks, thus facilitating the successful long-term pursuit of goals.

Given that personality plays a crucial role in subjective well-being, identifying the morphological correlates of personality profiles may provide important information for potential therapeutic interventions. For example, an optimistic personality profile was the strongest predictor of subjective well-being both psychologically in terms of the PCA variance and in terms of structural correlates. Some of the putative mechanisms underlying such a profile are domain-general and not specific to optimism per se, e.g., an intact system for sustained attention to holistic stimuli supported by the right SLF. It will be interesting to investigate whether trainings on targeted activities that tap into the functions of the right SLF might transfer to subjective well-being by increasing optimism. Previously, we showed that an attention bias modification training could successfully enhance optimism bias[118]. Future studies can investigate whether such trainings can also boost subjective well-being.

Methods

Participants.
We recruited 99 healthy candidates with an age criterion between 18 and 40 years (mean age = 24.03 ± 4.39, 62 females). Recruitment was made through emails, flyers and the local participant pool at the University of Bern, Switzerland. Exclusion criteria included self-reported neurological conditions, psychoactive substance usage, left-handedness, and magnetic resonance imaging (MRI) specific problems such as failed image reconstruction and excessive motion artefacts observed on structural scans. For their participation, the students received either course credits or 25 Swiss francs (CHF). Participants gave written informed consent, in accordance with the guidelines of the Declaration of Helsinki. Experimental procedures were approved by the ethics committee of the canton Bern, Switzerland. Five participants were excluded due to incomplete questionnaires. Both DTI and T1-weighted structural scans from all participants qualified visual inspection. Final analysis was conducted on 94 participants.

Psychological assessment.
Using an online portal, all participants completed various psychological questionnaires namely, Comparative Optimism Scale; COS[166], Satisfaction With Life Scale; SWLS[167,168], the revised Life Orientation Test; LOT-R[169,170], Emotion Regulation Questionnaire; ERQ[49,171], the 10-item Big Five Inventory; BFI[172,173], Behavioral Inhibition and Behavioral Activation System Scales; BIS/BAS[146,174]. For each participant, the psychological assessment scales amounted to 16 different variables (refer to Table 1). Using PCA allowed us to reduce the multivariate behavioral dataset into fewer meaningful components, thereby enabling a better interpretation of our psychological scales. The resulting personality profiles were then correlated with MRI-based diffusivity measures of FA, AD and RD. The PCA with varimax rotation was performed with XLSTAT[175]. We included the principal components with an eigenvalue > 1. Only Pearson product moment cor-

relation coefficients exceeding 0.4 with a combined alpha level of 0.05 (Bonferroni corrected for multiple testing) were considered for our analytical interpretations.

Magnetic resonance imaging (MRI) acquisition. MRI measurements were conducted across the study cohort within a 3 T scanner (MAGNETOM Prisma, Siemens, Erlangen, Germany) using a 64-channel head coil, at the Inselspital, University Hospital Bern, Switzerland. The MRI protocol consisted of a 3D magnetization prepared rapid gradient echo (MPRAGE or T1-weighted) sequence with repetition time (TR) = 2300 ms, echo time (TE) = 2.98 ms, inversion time (TI) = 900 ms, flip angle = 9°, matrix size = $160 \times 256 \times 256$ with an isotropic spatial resolution = 1mm³. 2D DTI data were acquired consisting of 12 unweighted (b = 0 s/mm²) and 90 diffusion-weighted (b = 1000 s/mm²) images, with TR/TE = 3200 ms/69 ms, flip angle = 90°, in-plane matrix size = 128×128 with 27 axial slices (thickness = 4 mm, spacing between slices = 5.2 mm) and an in-plane resolution of 1.7×1.7 mm².

Image processing. DICOM images from the MRI were converted to NIfTI format using conversion software; dcm2niix (https://github.com/rordenlab/dcm2niix/releases). Computational image processing included tract-based spatial statistics; TBSS[176] for DTI images. The processes were carried out using FSL6.0.2 (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki) in a MATLAB 2017b environment (developed by The MathWorks, Inc., Natick, United States) utilizing the cluster service UBELIX (https://ubelix.unibe.ch/) from the University of Bern, Switzerland. 'fsleyes' from FSL, served as the viewing software for qualitative assessment of the images.

Tract-based spatial statistics (TBSS). TBSS performed on DTI data is a commonly used voxel-based statistical framework for understanding white matter integrity[76,177]. Frequently used DTI-derived parameters (from diffusivities: parallel component λ_1 and perpendicular components λ_2, λ_3;[77]) include (a) FA: a measure that could explain the directionality strength of local white matter tracts, (b) AD: a diffusion measure of water molecules diffusing parallel to the axonal tracts, (c) RD: a mean diffusion coefficient of water molecules diffusing orthogonal to the axonal tracts. These diffusivity measures independently should provide complementary information about white matter pathology. For example, FA and AD, on one hand, and RD values, on the other hand, represent the degree of water diffusion parallel and perpendicular to the axonal wall, respectively[77]. As such, these markers are complementary: low FA and AD values and high RD values represent compromised axons (demyelination) while high FA and AD values and low RD values represent healthy tracts. TBSS[76], the voxel-based approach used in this paper, utilizes extracted and skeletonized white matter tracts in the FA images of all participants. TBSS has been introduced to overcome the problems associated with the use of standard registration algorithms in other voxel-based approaches[177].

We used the FSL software (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki) for the preprocessing prior to TBSS. First, eddy correction (eddy_correct) was applied on DTI images to address eddy current-induced distortions and motion artefacts. After this step, the DTI images were processed with the FMRIB Software Library's diffusion toolbox (DTIFIT;[178,179]), which fits a diffusion tensor model at each voxel and generates three eigenvalues (λ_1, λ_2, λ_3). Fractional anisotropy (FA = $\sqrt{\frac{1}{2}} \frac{\sqrt{(\lambda 1-\lambda 2)^2+(\lambda 2-\lambda 3)^2+(\lambda 3-\lambda 1)^2}}{(\lambda 1^2+\lambda 3^2+\lambda 3^2)}$), axial diffusivity (AD = λ_1) and radial diffusivity (RD = $\frac{\lambda 1+\lambda 2}{2}$) maps were hence generated.

Details of the underlying processes in the TBSS analysis stream are extensively covered in the literature[180–183]. In brief, for the FA maps, firstly a preprocessing erosion step was applied to remove brain edge artefacts and nullify intensities of end slices, to reduce false positives from tensor fitting. Later, FA maps across the participants were non-linearly registered to a standard template in MNI space (FMRIB58_FA template). Following registration, all FA maps were transformed to the standard MNI space with an isotropic voxel size of 1mm³, by applying the registration warps to individual images. The standardized maps were merged into a single 4D image, mean FA and its subsequent skeletonized version (WM skeleton) were created. The skeleton was restricted to WM with a threshold of FA = 0.2 and standardized FA maps were projected onto the skeleton. Non-FA maps (RD and AD) were also transformed to their respective skeletonized forms by applying the FA-derived registration and projection vectors. Finally, skeletons across the DTI maps were smoothed with an 8 mm FWHM Gaussian kernel. To find the positive and negative associations between the principal components (from PCA) and the DTI maps (FA, AD, and RD), we performed a non-parametric permutation analysis (t-test) using *randomize* (in FSL) with 5000 permutations, with age, gender, and total intracranial volume (TIV) as the covariates of no-interest. Only the clusters surviving a family-wise error (FWE) multiple comparison at $p < 0.05$ are reported.

Ethics approval. All procedures performed in studies involving human participants were approved by the ethical committee of the University of Bern according to the standards of the Declaration of Helsinki.

Consent to participate. All participants provided written consent.

Data availability
Under the Swiss guidelines of data protection (Ordinance HFV Art. 5), the MRI images generated and analyzed during the current study can be made available from the corresponding author on a case-by-case basis.

References

1. Diener, E. *et al.* Findings all psychologists should know from the new science on subjective well-being. *Can. Psychol.* **58**(2), 87 (2017).
2. Potter, S. *et al.* Trajectories of multiple subjective well-being facets across old age: The role of health and personality. *Psychol. Aging* **35**(6), 894 (2020).
3. Cummins, R. A., Gullone, E. & Lau, A. L. *A Model of Subjective Well-Being Homeostasis: The Role of Personality* 7–46 (Springer, 2002).
4. Lucas, R. Exploring the Associations Between Personality and Subjective Well-Being. *Handbook of Well-Being* (DEF Publishers, 2018). https://www.nobascholar.com/chapters/3.
5. Weiss, A., Bates, T. C. & Luciano, M. Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. *Psychol. Sci.* **19**(3), 205–210 (2008).
6. Diener, E., Oishi, S. & Tay, L. Advances in subjective well-being research. *Nat. Hum. Behav.* **2**(4), 253 (2018).
7. Diener, E., Lucas, R. E. & Oishi, S. Advances and open questions in the science of subjective well-being. *Collabra Psychol.* **4**(1), 15 (2018).
8. Chamberlain, K. & Zika, S. Stability and change in subjective well-being over short time periods. *Soc. Indic. Res.* **26**(2), 101–117 (1992).
9. Ugur, Z. B. Does having children bring life satisfaction in Europe?. *J. Happiness Stud.* **21**(4), 1385–1406 (2020).
10. Ahuvia, A. If money doesn't make us happy, why do we act as if it does?. *J. Econ. Psychol.* **29**(4), 491–507 (2008).
11. Ryff, C. D. & Essex, M. J. The interpretation of life experience and well-being: The sample case of relocation. *Psychol. Aging* **7**(4), 507 (1992).
12. Ayton, P., Pott, A. & Elwakili, N. Affective forecasting: Why can't people predict their emotions?. *Think. Reason.* **13**(1), 62–80 (2007).
13. Gilbert, D. T. & Wilson, T. D. Miswanting: Some Problems in the Forecasting of Future Affective States. In *Thinking and Feeling: The Role of Affect in Social Cognition* (ed. Forgas, J. P.) (Cambridge University Press, 2000).
14. Schkade, D. A. & Kahneman, D. Does living in California make people happy? A focusing illusion in judgments of life satisfaction. *Psychol. Sci.* **9**(5), 340–346 (1998).
15. Diener, E., Lucas, R. E. & Scollon, C. N. *Beyond the Hedonic Treadmill: Revising the Adaptation Theory of Well-Being* 103–118 (Springer, 2009).
16. Headey, B. Subjective well-being: Revisions to dynamic equilibrium theory using national panel data and panel regression methods. *Soc. Indic. Res.* **79**(3), 369–403 (2006).
17. Huppert, F. A. The State of Wellbeing Science: Concepts, Measures, Interventions, and Policies. In *Wellbeing: A Complete Reference Guide* (ed. Cooper, C. L.) 1–49 (Wiley, 2014).
18. Veenhoven, R. *Happiness: Also Known as "Life Satisfaction" and "Subjective Well-Being"* 63–77 (Springer, 2012).
19. Coles, E., Cheyne, H. & Daniel, B. Early years interventions to improve child health and wellbeing: What works, for whom and in what circumstances? Protocol for a realist review. *Syst. Rev.* **4**(1), 79 (2015).
20. Daniels, K., Watson, D. & Gedikli, C. Well-being and the social environment of work: A systematic review of intervention studies. *Int. J. Environ. Res. Public Health* **14**(8), 918 (2017).
21. Oishi, S. & Diener, E. *Goals, Culture, and Subjective Well-Being* 93–108 (Springer, 2009).
22. Schwartz, S. H. & Sortheix, F. Values and Subjective Well-Being. In *Handbook of Well-Being* (eds Diener, E. *et al.*) (Noba Scholar, 2018).
23. Carrieri, V. Social comparison and subjective well-being: Does the health of others matter?. *Bull. Econ. Res.* **64**(1), 31–55 (2012).
24. Diener, E. & Fujita, F. Social Comparisons and Subjective Well-Being. In *Health, Coping, and Well-Being: Perspectives from Social Comparison Theory* (eds Buunk, B. P. *et al.*) (Psychology Press, 1997).
25. Fujita, F. The Frequency of Social Comparison and Its Relation to Subjective Well-Being. In *The Science of Subjective Well-Being* (eds Eid, M. & Larsen, R. J.) 239–257 (Guilford Press, 2008).
26. Alarcon, G. M., Bowling, N. A. & Khazon, S. Great expectations: A meta-analytic examination of optimism and hope. *Personal. Individ. Differ.* **54**(7), 821–827 (2013).
27. Scheier, M. F. & Carver, C. S. Effects of optimism on psychological and physical well-being: Theoretical overview and empirical update. *Cogn. Ther. Res.* **16**(2), 201–228 (1992).
28. Scheier, M. F., Carver, C. S. & Bridges, M. W. Optimism, Pessimism, and Psychological Well-Being. In *Optimism & Pessimism: Implications for Theory, Research, and Practice* (ed. Chang, E. C.) (University of Michigan, 2001).
29. Grant, S., Langan-Fox, J. & Anglim, J. The big five traits as predictors of subjective and psychological well-being. *Psychol. Rep.* **105**(1), 205–231 (2009).
30. Gutiérrez, J. L. G., Jiménez, B. M., Hernández, E. G. & Pcn, C. Personality and subjective well-being: Big five correlates and demographic variables. *Personal. Individ. Differ.* **38**(7), 1561–1569 (2005).
31. Haslam, N., Whelan, J. & Bastian, B. Big Five traits mediate associations between values and subjective well-being. *Personal. Individ. Differ.* **46**(1), 40–42 (2009).
32. Shiota, M. N., Keltner, D. & John, O. P. Positive emotion dispositions differentially associated with Big Five personality and attachment style. *J. Posit. Psychol.* **1**(2), 61–71 (2006).
33. Markarian, S. A., Pickett, S. M., Deveson, D. F. & Kanona, B. B. A model of BIS/BAS sensitivity, emotion regulation difficulties, and depression, anxiety, and stress symptoms in relation to sleep quality. *Psychiatry Res.* **210**(1), 281–286 (2013).
34. Sauer, S., Walach, H. & Kohls, N. Gray's behavioural inhibition system as a mediator of mindfulness towards well-being. *Personal. Individ. Differ.* **50**(4), 506–511 (2011).
35. Taubitz, L. E., Pedersen, W. S. & Larson, C. L. BAS Reward Responsiveness: A unique predictor of positive psychological functioning. *Personal. Individ. Differ.* **80**, 107–112 (2015).
36. Updegraff, J. A., Gable, S. L. & Taylor, S. E. What makes experiences satisfying? The interaction of approach-avoidance motivations and emotions in well-being. *J. Personal. Soc. Psychol.* **86**(3), 496 (2004).
37. Brewer, S. K., Zahniser, E. & Conley, C. S. Longitudinal impacts of emotion regulation on emerging adults: Variable-and person-centered approaches. *J. Appl. Dev. Psychol.* **47**, 1–12 (2016).
38. Hu, T. *et al.* Relation between emotion regulation and mental health: A meta-analysis review. *Psychol. Rep.* **114**(2), 341–362 (2014).
39. Penley, J. A. & Tomaka, J. Associations among the Big Five, emotional responses, and coping with acute stress. *Personal. Individ. Differ.* **32**(7), 1215–1228 (2002).
40. Ali, S. & Alea, N. Validating the emotion regulation questionnaire (ERQ) in Trinidad. *Behav Sci.* **1**, 1003 (2018).
41. Balzarotti, S., John, O. P. & Gross, J. J. An Italian adaptation of the emotion regulation questionnaire. *Eur. J. Psychol. Assess.* **26**(1), 61–67 (2010).
42. Gračanin, A., Kardum, I. & Gross, J. J. The Croatian version of the Emotion Regulation Questionnaire: Links with higher-and lower-level personality traits and mood. *Int. J. Psychol.* **55**(4), 609–617 (2020).
43. Gullone, E. & Taffe, J. The Emotion Regulation Questionnaire for Children and Adolescents (ERQ–CA): A psychometric evaluation. *Psychol. Assess.* **24**(2), 409 (2012).

44. Erdle, S. & Rushton, J. P. The general factor of personality, BIS–BAS, expectancies of reward and punishment, self-esteem, and positive and negative affect. *Personal. Individ. Differ.* **48**(6), 762–766 (2010).
45. Rey, L. & Extremera, N. Positive psychological characteristics and interpersonal forgiveness: Identifying the unique contribution of emotional intelligence abilities, Big Five traits, gratitude and optimism. *Personal. Individ. Differ.* **68**, 199–204 (2014).
46. Schuurmans-Stekhoven, J. B. Conviction, character and coping: Religiosity and personality are both uniquely associated with optimism and positive reappraising. *Ment. Health Relig. Cult.* **21**(8), 763–779 (2018).
47. Sharpe, J. P., Martin, N. R. & Roth, K. A. Optimism and the Big Five factors of personality: Beyond neuroticism and extraversion. *Personal. Individ. Differ.* **51**(8), 946–951 (2011).
48. Soto, C. J. Is happiness good for your personality? Concurrent and prospective relations of the big five with subjective well-being. *J. Personal.* **83**(1), 45–55 (2015).
49. Gross, J. J. & John, O. P. Individual differences in two emotion regulation processes: Implications for affect, relationships, and well-being. *J. Personal. Soc. Psychol.* **85**(2), 348–362 (2003).
50. Merchán-Clavellino, A., Alameda-Bailén, J. R., Zayas García, A. & Guil, R. Mediating effect of trait emotional intelligence between the behavioral activation system (BAS)/behavioral inhibition system (BIS) and positive and negative affect. *Front. Psychol.* **10**, 424 (2019).
51. Tull, M. T., Gratz, K. L., Latzman, R. D., Kimbrel, N. A. & Lejuez, C. Reinforcement sensitivity theory and emotion regulation difficulties: A multimodal investigation. *Personal. Individ. Differ.* **49**(8), 989–994 (2010).
52. Buhle, J. T. *et al.* Cognitive reappraisal of emotion: A meta-analysis of human neuroimaging studies. *Cereb. Cortex* **24**(11), 2981–2990 (2014).
53. Dricu, M., Kress, L. & Aue, T. *The Neurophysiological Basis of Optimism Bias. Cognitive Biases in Health and Psychiatric Disorders: Neurophysiological Foundations* (Elsevier, 2020).
54. Privado, J., Roman, F. J., Saenz-Urturi, C., Burgaleta, M. & Colom, R. Gray and white matter correlates of the Big Five personality traits. *Neuroscience* **349**, 174–184 (2017).
55. Xu, J. *et al.* White matter integrity and behavioral activation in healthy subjects. *Hum. Brain Mapp.* **33**(4), 994–1002 (2012).
56. Xu, J. & Potenza, M. N. White matter integrity and five-factor personality measures in healthy adults. *Neuroimage* **59**(1), 800–807 (2012).
57. King, M. L. The neural correlates of well-being: A systematic review of the human neuroimaging and neuropsychological literature. *Cogn. Affect. Behav. Neurosci.* **19**(4), 779–796 (2019).
58. Avinun, R., Israel, S., Knodt, A. R. & Hariri, A. R. Little evidence for associations between the big five personality traits and variability in brain gray or white matter. *Neuroimage* **220**, 117092 (2020).
59. Gerlach, M., Farb, B., Revelle, W. & Amaral, L. A. N. A robust data-driven approach identifies four personality types across four large data sets. *Nat. Hum. Behav.* **2**(10), 735–742 (2018).
60. Kövi, Z. *et al.* Cross-country analysis of alternative five factor personality trait profiles. *Personal. Individ. Differ.* **143**, 7–12 (2019).
61. Kerber, A., Roth, M. & Herzberg, P. Y. Personality types revisited—A literature-informed and data-driven approach to an integration of prototypical and dimensional constructs of personality description. *PLoS ONE* **16**(1), e0244849 (2021).
62. Udayar, S., Urbanaviciute, I., Massoudi, K., Rossier, J. & Fajkowska, M. The role of personality profiles in the longitudinal relationship between work-related well-being and life satisfaction among working adults in Switzerland. *Eur. J. Personal.* **34**(1), 77–92 (2020).
63. Li, Y. *et al.* Linking personality types to depressive symptoms: A prospective typology based on neuroticism, extraversion and conscientiousness. *Neuropsychologia* **136**, 107289 (2020).
64. Madsen, K. S., Jernigan, T. L., Vestergaard, M., Mortensen, E. L. & Baaré, W. F. Neuroticism is linked to microstructural left-right asymmetry of fronto-limbic fibre tracts in adolescents with opposite effects in boys and girls. *Neuropsychologia* **114**, 1–10 (2018).
65. Lewis, G. J. *et al.* Trait conscientiousness and the personality meta-trait stability are associated with regional white matter microstructure. *Soc. Cogn. Affect. Neurosci.* **11**(8), 1255–1261 (2016).
66. Bjørnebekk, A. *et al.* Neuronal correlates of the five factor model (FFM) of human personality: Multimodal imaging in a large healthy sample. *Neuroimage* **65**, 194–208 (2013).
67. Moghaddam, H. S. *et al.* Microstructural white matter alterations and personality traits: A diffusion MRI study. *J. Res. Personal.* **88**, 104010 (2020).
68. Montag, C., Reuter, M., Weber, B., Markett, S. & Schoene-Bake, J.-C. Individual differences in trait anxiety are associated with white matter tract integrity in the left temporal lobe in healthy males but not females. *Neuroscience* **217**, 77–83 (2012).
69. Leshem, R. *et al.* Inward versus reward: White matter pathways in extraversion. *Personal. Neurosci.* **2**, E6 (2019).
70. Liu, W.-Y. *et al.* The Big Five of Personality and structural imaging revisited: A VBM–DARTEL study. *NeuroReport* **24**(7), 375–380 (2013).
71. Boekel, W. *et al.* A purely confirmatory replication study of structural brain-behavior correlations. *Cortex* **66**, 115–133 (2015).
72. Eden, A. S. *et al.* Emotion regulation and trait anxiety are predicted by the microstructure of fibers between amygdala and prefrontal cortex. *J. Neurosci.* **35**(15), 6020–6027 (2015).
73. Pisner, D. A., Smith, R., Alkozei, A., Klimova, A. & Killgore, W. D. Highways of the emotional intellect: White matter microstructural correlates of an ability-based measure of emotional intelligence. *Soc. Neurosci.* **12**(3), 253–267 (2017).
74. d'Arbeloff, T. C. *et al.* Microstructural integrity of a pathway connecting the prefrontal cortex and amygdala moderates the association between cognitive reappraisal and negative emotions. *Emotion* **18**(6), 912 (2018).
75. Zuurbier, L. A., Nikolova, Y. S., Åhs, F. & Hariri, A. R. Uncinate fasciculus fractional anisotropy correlates with typical use of reappraisal in women but not men. *Emotion* **13**(3), 385 (2013).
76. Smith, A. Cognitive empathy and emotional empathy in human behavior and evolution. *Psychol. Record.* **56**(1), 3–21 (2006).
77. Beaulieu, C. The basis of anisotropic water diffusion in the nervous system—A technical review. *NMR Biomed.: Int. J. Devoted Dev. Appl. Magn. Resonance In Vivo* **15**(7–8), 435–455 (2002).
78. Sousa, S. S., Amaro, E., Crego, A., Gonçalves, Ó. F. & Sampaio, A. Developmental trajectory of the prefrontal cortex: A systematic review of diffusion tensor imaging studies. *Brain Imaging Behav.* **12**(4), 1197–1210 (2018).
79. Rotenberg, V. S. Right hemisphere insufficiency and illness in the context of search activity concept. *Dyn. Psychiatry.* **150**(151), 54–63 (1995).
80. Dolcos, F., Rice, H. J. & Cabeza, R. Hemispheric asymmetry and aging: Right hemisphere decline or asymmetry reduction. *Neurosci. Biobehav. Rev.* **26**(7), 819–825 (2002).
81. Rotenberg, V. S. The peculiarity of the right-hemisphere function in depression: Solving the paradoxes. *Prog. Neuropsychopharmacol. Biol. Psychiatry* **28**(1), 1–13 (2004).
82. Rotenberg, V. S. & Weinberg, I. Human memory, cerebral hemispheres, and the limbic system: A new approach. *Genet. Soc. Gen. Psychol. Monogr.* **125**(1), 45–70 (1999).
83. Rotenberg, V. S. An integrative psychophysiological approach to brain hemisphere functions in schizophrenia. *Neurosci. Biobehav. Rev.* **18**(4), 487–495 (1994).
84. Kohn, B. Right-hemisphere speech representation and comprehension of syntax after left cerebral injury. *Brain Lang.* **9**(2), 350–361 (1980).
85. Kane, J. Poetry as right-hemispheric language. *J. Conscious. Stud.* **11**(5–6), 21–59 (2004).

86. Lindell, A. K. In your right mind: Right hemisphere contributions to language processing and production. *Neuropsychol. Rev.* **16**(3), 131–148 (2006).

87. Kuhl, J., Quirin, M. & Koole, S. L. Being someone: The integrated self as a neuropsychological system. *Soc. Personal. Psychol. Compass* **9**(3), 115–132 (2015).

88. Koole, S. L., Schlinkert, C., Maldei, T. & Baumann, N. Becoming who you are: An integrative review of self-determination theory and personality systems interactions theory. *J. Personal.* **87**(1), 15–36 (2019).

89. Quirin, M., Bode, R. C. & Kuhl, J. Recovering from negative events by boosting implicit positive affect. *Cogn. Emot.* **25**(3), 559–570 (2011).

90. Quirin, M., Fröhlich, S. & Kuhl, J. Implicit self and the right hemisphere: Increasing implicit self-esteem and implicit positive affect by left hand contractions. *Eur. J. Soc. Psychol.* **48**(1), 4–16 (2018).

91. Kuhl, J. The volitional basis of Personality Systems Interaction theory: Applications in learning and treatment contexts. *Int. J. Educ. Res.* **33**(7–8), 665–703 (2000).

92. Mezulis, A. H., Abramson, L. Y., Hyde, J. S. & Hankin, B. L. Is there a universal positivity bias in attributions? A meta-analytic review of individual, developmental, and cultural differences in the self-serving attributional bias. *Psychol. Bull.* **130**(5), 711 (2004).

93. Schore, A. N. The experience-dependent maturation of a regulatory system in the orbital prefrontal cortex and the origin of developmental psychopathology. *Dev. Psychopathol.* **8**(1), 59–87 (1996).

94. Weinberg, I. The prisoners of despair: Right hemisphere deficiency and suicide. *Neurosci. Biobehav. Rev.* **24**(8), 799–815 (2000).

95. Liao, Y. *et al.* Is depression a disconnection syndrome? Meta-analysis of diffusion tensor imaging studies in patients with MDD. *J. Psychiatry Neurosci.: JPN* **38**(1), 49 (2013).

96. Klöppel, S. *et al.* The cortical motor threshold reflects microstructural properties of cerebral white matter. *Neuroimage* **40**(4), 1782–1791 (2008).

97. Lepley, A. S., Ly, M. T., Grooms, D. R., Kinsella-Shaw, J. M. & Lepley, L. K. Corticospinal tract structure and excitability in patients with anterior cruciate ligament reconstruction: A DTI and TMS study. *NeuroImage: Clin.* **25**, 102157 (2020).

98. Gupta, N. & Aron, A. R. Urges for food and money spill over into motor system excitability before action is taken. *Eur. J. Neurosci.* **33**(1), 183–188 (2011).

99. Klein, P.-A., Olivier, E. & Duque, J. Influence of reward on corticospinal excitability during movement preparation. *J. Neurosci.* **32**(50), 18124–18136 (2012).

100. Mooshagian, E., Keisler, A., Zimmermann, T., Schweickert, J. M. & Wassermann, E. M. Modulation of corticospinal excitability by reward depends on task framing. *Neuropsychologia* **68**, 31–37 (2015).

101. Bestmann, S. *et al.* Influence of uncertainty and surprise on human corticospinal excitability during preparation for action. *Curr. Biol.* **18**(10), 775–780 (2008).

102. Aspinwall, L. G., Richter, L. & Hoffman, R. R. III. Understanding How Optimism Works: An Examination of Optimists' Adaptive Moderation of Belief and Behavior. In *Optimism & Pessimism: Implications for Theory, Research, and Practice* (ed. Chang, E. C.) (University of Michigan, 2001).

103. Carver, C. S. & Scheier, M. F. Dispositional optimism. *Trends Cogn. Sci.* **18**(6), 293–299 (2014).

104. Nakajima, R. *et al.* Damage of the right dorsal superior longitudinal fascicle by awake surgery for glioma causes persistent visuospatial dysfunction. *Sci. Rep.* **7**(1), 1–10 (2017).

105. Nakajima, R., Kinoshita, M., Shinohara, H. & Nakada, M. The superior longitudinal fascicle: Reconsidering the fronto-parietal neural network based on anatomy and function. *Brain Imaging Behav.* **14**(6), 2817–2830 (2019).

106. Wang, X. *et al.* Subcomponents and connectivity of the superior longitudinal fasciculus in the human brain. *Brain Struct. Funct.* **221**(4), 2075–2092 (2016).

107. Klarborg, B. *et al.* Sustained attention is associated with right superior longitudinal fasciculus and superior parietal white matter microstructure in children. *Hum. Brain Mapp.* **34**(12), 3216–3232 (2013).

108. Cortese, S. *et al.* White matter alterations at 33-year follow-up in adults with childhood attention-deficit/hyperactivity disorder. *Biol. Psychiat.* **74**(8), 591–598 (2013).

109. Chiang, H.-L., Chen, Y.-J., Lo, Y.-C., Tseng, W.-Y.I. & Gau, S.S.-F. Altered white matter tract property related to impaired focused attention, sustained attention, cognitive impulsivity and vigilance in attention-deficit/hyperactivity disorder. *J. Psychiatry Neurosci.: JPN* **40**(5), 325 (2015).

110. Sudre, G. *et al.* Estimating the heritability of structural and functional brain connectivity in families affected by attention-deficit/hyperactivity disorder. *JAMA Psychiat.* **74**(1), 76–84 (2017).

111. Dong, G., Li, H. & Potenza, M. N. Short-term internet-search training is associated with increased fractional anisotropy in the superior longitudinal fasciculus in the parietal lobe. *Front. Neurosci.* **11**, 372 (2017).

112. Kress, L., Bristle, M. & Aue, T. Seeing through rose-colored glasses: How optimistic expectancies guide visual attention. *PLoS ONE* **13**(2), e0193311 (2018).

113. Aue, T., Dricu, M., Singh, L., Moser, D. A. & Raviteja, K. Enhanced sensitivity to optimistic cues is manifested in brain structure: A voxel-based morphometry study. *Soc. Cogn. Affect. Neurosci.* **16**(11), 1170–1181 (2021).

114. Singh, L. *et al.* The effect of optimistic expectancies on attention bias: Neural and behavioral correlates. *Sci. Rep.* **10**(1), 1–13 (2020).

115. Aue, T., Nusbaum, H. C. & Cacioppo, J. T. Neural correlates of wishful thinking. *Soc. Cogn. Affect. Neurosci.* **7**(8), 991–1000 (2012).

116. Kress, L. & Aue, T. The link between optimism bias and attention bias: A neurocognitive perspective. *Neurosci. Biobehav. Rev.* **80**, 688–702 (2017).

117. Braddick, O. *et al.* Individual differences in children's global motion sensitivity correlate with TBSS-based measures of the superior longitudinal fasciculus. *Vis. Res.* **141**, 145–156 (2017).

118. Kress, L. & Aue, T. Learning to look at the bright side of life: Attention bias modification training enhances optimism bias. *Front. Hum. Neurosci.* **13**, 222 (2019).

119. O'Reilly, J. X. *et al.* Causal effect of disconnection lesions on interhemispheric functional connectivity in rhesus monkeys. *Proc. Natl. Acad. Sci.* **110**(34), 13982–13987 (2013).

120. Damoiseaux, J. S. & Greicius, M. D. Greater than the sum of its parts: A review of studies combining structural connectivity and resting-state functional connectivity. *Brain Struct. Funct.* **213**(6), 525–533 (2009).

121. Honey, C. J. *et al.* Predicting human resting-state functional connectivity from structural connectivity. *Proc. Natl. Acad. Sci.* **106**(6), 2035–2040 (2009).

122. Alves, P. N. *et al.* An improved neuroanatomical model of the default-mode network reconciles previous neuroimaging and neuropathological findings. *Commun. Biol.* **2**(1), 1–14 (2019).

123. van den Heuvel, M., Mandl, R., Luijges, J. & Pol, H. H. Microstructural organization of the cingulum tract and the level of default mode functional connectivity. *J. Neurosci.* **28**(43), 10844–10851 (2008).

124. Gordon, E. M. *et al.* Strength of default mode resting-state connectivity relates to white matter integrity in children. *Dev. Sci.* **14**(4), 738–751 (2011).

125. Vidal-Piñeiro, D. *et al.* Decreased default mode network connectivity correlates with age-associated structural and cognitive changes. *Front. Aging Neurosci.* **6**, 256 (2014).

126. Andrews-Hanna, J. R., Smallwood, J. & Spreng, R. N. The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Ann. N. Y. Acad. Sci.* **1316**(1), 29 (2014).
127. Flagan, T. & Beer, J. S. Three ways in which midline regions contribute to self-evaluation. *Front. Hum. Neurosci.* **7**, 450 (2013).
128. Schacter, D. L., Addis, D. R. & Buckner, R. L. Episodic simulation of future events. *Ann. N. Y. Acad. Sci.* **1124**(1), 39–60 (2008).
129. Xu, X., Yuan, H. & Lei, X. Activation and connectivity within the default mode network contribute independently to future-oriented thought. *Sci. Rep.* **6**(1), 1–10 (2016).
130. Schacter, D. L., Benoit, R. G. & Szpunar, K. K. Episodic future thinking: Mechanisms and functions. *Curr. Opin. Behav. Sci.* **17**, 41–50 (2017).
131. Rose, J. P., Jasper, J. D. & Corser, R. Interhemispheric interaction and egocentrism: The role of handedness in social comparative judgement. *Br. J. Soc. Psychol.* **51**(1), 111–129 (2012).
132. Rose, J. P. & Nagel, B. Relation between comparative risk, absolute risk, and worry: The role of handedness strength. *J. Health Psychol.* **18**(7), 866–874 (2013).
133. Lee Niebauer, C., Christman, S., Reid, S. & Garvey, K. Interhemispheric interaction and beliefs on our origin: Degree of handedness predicts beliefs in creationism versus evolution. *Laterality: Asymmetries Body Brain Cogn.* **9**(4), 433–447 (2004).
134. Lee Niebauer, C., Aselage, J. & Schutte, C. Hemispheric interaction and consciousness: Degree of handedness predicts the intensity of a sensory illusion. *Laterality: Asymmetries Body Brain Cogn.* **7**(1), 85–96 (2002).
135. Bubb, E. J., Metzler-Baddeley, C. & Aggleton, J. P. The cingulum bundle: Anatomy, function, and dysfunction. *Neurosci. Biobehav. Rev.* **92**, 104–127 (2018).
136. Wu, Y., Sun, D., Wang, Y., Wang, Y. & Ou, S. Segmentation of the cingulum bundle in the human brain: A new perspective based on DSI tractography and fiber dissection study. *Front. Neuroanat.* **10**, 84 (2016).
137. Wright, N. F., Vann, S. D., Erichsen, J. T., O'Mara, S. M. & Aggleton, J. P. Segregation of parallel inputs to the anteromedial and anteroventral thalamic nuclei of the rat. *J. Comp. Neurol.* **521**(13), 2966–2986 (2013).
138. Grodd, W., Kumar, V. J., Schüz, A., Lindig, T. & Scheffler, K. The anterior and medial thalamic nuclei and the human limbic system: Tracing the structural connectivity using diffusion-weighted imaging. *Sci. Rep.* **10**(1), 1–25 (2020).
139. Jakabek, D. *et al.* Regional structural hypo-and hyperconnectivity of frontal–striatal and frontal–thalamic pathways in behavioral variant frontotemporal dementia. *Hum. Brain Mapp.* **39**(10), 4083–4093 (2018).
140. Blair, K. S. *et al.* Dissociable roles of ventromedial prefrontal cortex (vmPFC) and rostral anterior cingulate cortex (rACC) in value representation and optimistic bias. *Neuroimage* **78**, 103–110 (2013).
141. Dricu, M. *et al.* Group membership dictates the neural correlates of social optimism biases. *Sci. Rep.* **10**(1), 1–17 (2020).
142. Moser, D. A., Dricu, M., Wiest, R., Schüpbach, L. & Aue, T. Social optimism biases are associated with cortical thickness. *Soc. Cogn. Affect. Neurosci.* **15**(7), 745–754 (2020).
143. Sharot, T., Riccardi, A. M., Raio, C. M. & Phelps, E. A. Neural mechanisms mediating optimism bias. *Nature* **450**(7166), 102 (2007).
144. Moser, D. A., Dricu, M., Kotikalapudi, R., Doucet, G. E. & Aue, T. Reduced network integration in default mode and executive networks is associated with social and personal optimism biases. *Hum. Brain Mapp.* **42**, 2893–2906 (2021).
145. Van Reekum, C. M. *et al.* Individual differences in amygdala and ventromedial prefrontal cortex activity are associated with evaluation speed and psychological well-being. *J. Cogn. Neurosci.* **19**(2), 237–248 (2007).
146. Carver, C. S. & White, T. L. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *J. Personal. Soc. Psychol.* **67**(2), 319 (1994).
147. Depue, R. A. & Collins, P. F. Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. *Behav. Brain Sci.* **22**(3), 491–517 (1999).
148. Whiteside, S. P. & Lynam, D. R. The five factor model and impulsivity: Using a structural model of personality to understand impulsivity. *Personal. Individ. Differ.* **30**(4), 669–689 (2001).
149. aan het Rot, M., Moskowitz, D. & Young, S. N. Impulsive behaviour in interpersonal encounters: Associations with quarrelsomeness and agreeableness. *Br. J. Psychol.* **106**(1), 152–161 (2015).
150. Bakhshani, N.-M. Impulsivity: A predisposition toward risky behaviors. *Int. J. High Risk Behav. Addict.* **3**(2), e20428 (2014).
151. Barrat, E. *Impulsiveness and Aggression. Violence and Mental Disorder. Development in Risk Assessment* (University of Chicago, 1995).
152. Chudasama, Y. Animal models of prefrontal-executive function. *Behav. Neurosci.* **125**(3), 327 (2011).
153. Patton, J. H., Stanford, M. S. & Barratt, E. S. Factor structure of the Barratt impulsiveness scale. *J. Clin. Psychol.* **51**(6), 768–774 (1995).
154. Goldwaser, E. L. *et al.* Role of white matter microstructure in impulsive behavior. *J. Neuropsychiatry Clin. Neurosci.* https://doi.org/10.1176/appi.neuropsych.21070167 (2022).
155. Kim, I.-S. *et al.* Reduced corpus callosum white matter microstructural integrity revealed by diffusion tensor eigenvalues in abstinent methamphetamine addicts. *Neurotoxicology* **30**(2), 209–213 (2009).
156. Yip, S. W. *et al.* Shared microstructural features of behavioral and substance addictions revealed in areas of crossing fibers. *Biol. Psychiatry: Cogn. Neurosci. Neuroimaging* **2**(2), 188–195 (2017).
157. Arnone, D., Abou-Saleh, M. T. & Barrick, T. R. Diffusion tensor imaging of the corpus callosum in addiction. *Neuropsychobiology* **54**(2), 107–113 (2006).
158. Bora, E. *et al.* White matter microstructure in opiate addiction. *Addict. Biol.* **17**(1), 141–148 (2012).
159. Joutsa, J., Saunavaara, J., Parkkola, R., Niemelä, S. & Kaasinen, V. Extensive abnormality of brain white matter integrity in pathological gambling. *Psychiatry Res.: Neuroimaging* **194**(3), 340–346 (2011).
160. Hotard, S. R., McFatter, R. M., McWhirter, R. M. & Stegall, M. E. Interactive effects of extraversion, neuroticism, and social relationships on subjective well-being. *J. Personal. Soc. Psychol.* **57**(2), 321 (1989).
161. Chae, H. *et al.* Psychological profile of Sasang typology: A systematic review. *Evid.-Based Complement. Altern. Med.* **6**(S1), 21–29 (2009).
162. Feldman, G., Zayfert, C., Sandoval, L., Dunn, E. & Cartreine, J. A. Reward responsiveness and anxiety predict performance of Mount Everest climbers. *J. Res. Personal.* **47**(1), 111–115 (2013).
163. Olson, I. R., Von Der Heide, R. J., Alm, K. H. & Vyas, G. Development of the uncinate fasciculus: Implications for theory and developmental disorders. *Dev. Cogn. Neurosci.* **14**, 50–61 (2015).
164. Von Der Heide, R. J., Skipper, L. M., Klobusicky, E. & Olson, I. R. Dissecting the uncinate fasciculus: Disorders, controversies and a hypothesis. *Brain* **136**(6), 1692–1707 (2013).
165. Zaidi, Z. F. Gender differences in human brain: A review. *Open Anat. J.* **2**(1), 37–55 (2010).
166. Weinstein, N. D. Unrealistic optimism about future life events. *J. Personal. Soc. Psychol.* **39**(5), 806 (1980).
167. Diener, E., Emmons, R. A., Larsen, R. J. & Griffin, S. The satisfaction with life scale. *J. Personal. Assess.* **49**(1), 71–75 (1985).
168. Schumacher, J. (ed.) *SWLS—Satisfaction with life scale Diagnostische Verfahren zu Lebensqualität und Wohlbefinden* (Hogrefe Goettingen, 2003).
169. Glaesmer, H., Hoyer, J., Klotsche, J. & Herzberg, P. Y. Die deutsche version des Life-Orientation-Tests (LOT-R) zum dispositionellen Optimismus und Pessimismus. *Zeitschrift für Gesundheitspsychologie.* **16**(1), 26–31 (2008).
170. Scheier, M. F., Carver, C. S. & Bridges, M. W. Distinguishing optimism from neuroticism (and trait anxiety, self-mastery, and self-esteem): A reevaluation of the Life Orientation Test. *J. Personal. Soc. Psychol.* **67**(6), 1063–1078 (1994).

171. Abler, B. & Kessler, H. Emotion regulation questionnaire–Eine deutschsprachige Fassung des ERQ von Gross und John. *Diagnostica* **55**(3), 144–152 (2009).
172. Rammstedt, B. & John, O. P. Measuring personality in one minute or less: A 10-item short version of the Big Five Inventory in English and German. *J. Res. Personal.* **41**(1), 203–212 (2007).
173. John, O. P., Donahue, E. M. & Kentle, R. L. *The Big Five Inventory—Versions 4a and 54* (University of California, Berkeley, Institute of Personality and Social Research, 1991).
174. Strobel, A., Beauducel, A., Debener, S. & Brocke, B. A German version of Carver and White's Bis/Bas scales. *Zeitschrift fur Differentielle und Diagnostische Psychologie* **22**(3), 216–227 (2001).
175. Vidal, N. P. *et al.* The use of XLSTAT in conducting principal component analysis (PCA) when evaluating the relationships between sensory and quality attributes in grilled foods. *MethodsX* **7**, 100835 (2020).
176. Smith, S. M. *et al.* Tract-based spatial statistics: Voxelwise analysis of multi-subject diffusion data. *Neuroimage* **31**(4), 1487–1505 (2006).
177. Jones, D. K., Symms, M. R., Cercignani, M. & Howard, R. J. The effect of filter size on VBM analyses of DT-MRI data. *Neuroimage* **26**(2), 546–554 (2005).
178. Behrens, T. E. *et al.* Characterization and propagation of uncertainty in diffusion-weighted MR imaging. *Magn. Reson. Med.: Off. J Int. Soc. Magn. Reson. Med.* **50**(5), 1077–1088 (2003).
179. Feis, R. Image pre-processing. *J. Neurol. Neurosurg. Psychiatry* **0**, 1207–1214. https://doi.org/10.1136/jnnp-2019-320774 (2019).
180. Smith, S. *et al.* Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage* **23**(Suppl 1), S208–S219 (2004).
181. Rueckert, D. *et al.* Nonrigid registration using free-form deformations: Application to breast MR images. *IEEE Trans. Med. Imaging* **18**(8), 712–721 (1999).
182. Smith, S. M. Fast robust automated brain extraction. *Hum. Brain Mapp.* **17**(3), 143–155 (2002).
183. Andersson, J., Jenkinson, M. & Smith, S. *Non-linear optimisation. FMRIB Analysis Group. Technical reports. TR07JA1* (University of Oxford, 2007).
184. Hijaz, T., McComb, E., Badhe, S., Liu, B. & Korutz, A. Diffusion tensor imaging tractography tutorial and introduction to major white matter tract anatomy and function. *Neurographics.* **9**(1), 62–74 (2019).
185. Irish, M. *et al.* Grey and white matter correlates of recent and remote autobiographical memory retrieval–insights from the dementias. *PLoS ONE* **9**(11), e113081 (2014).
186. Niida, R. *et al.* Aberrant anterior thalamic radiation structure in bipolar disorder: A diffusion tensor tractography study. *Front. Psych.* **9**, 522 (2018).
187. Catani, M. & De Schotten, M. T. A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex* **44**(8), 1105–1132 (2008).
188. Hasan, K. M. *et al.* Development and aging of the healthy human brain uncinate fasciculus across the lifespan using diffusion tensor tractography. *Brain Res.* **1276**, 67–76 (2009).
189. Hau, J. *et al.* Revisiting the human uncinate fasciculus, its subcomponents and asymmetries with stem-based tractography and microdissection validation. *Brain Struct. Funct.* **222**(4), 1645–1662 (2017).
190. Kier, E. L., Staib, L. H., Davis, L. M. & Bronen, R. A. MR imaging of the temporal stem: Anatomic dissection tractography of the uncinate fasciculus, inferior occipitofrontal fasciculus, and Meyer's loop of the optic radiation. *Am. J. Neuroradiol.* **25**(5), 677–691 (2004).

Author contributions

M.D. collected the data. R.K. and D.A.M. analyzed the data. M.D., R.K., D.A.M. and T.A. wrote the manuscript. T.A. designed the study.

Funding

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to M.D.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.