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Interindividual differences in intergenerational sustainable behavior are associated with cortical thickness of the dorsomedial and dorsolateral prefrontal cortex

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Abstract

Intergenerational sustainability requires people of the present generation to make sacrifices today to benefit others of future generations (e.g. mitigating climate change, reducing public debt). Individuals vary greatly in their intergenerational sustainability, and the cognitive and neural sources of these interindividual differences are not yet well understood. We here combined neuroscientific and behavioral methods by assessing interindividual differences in cortical thickness and by using a common-pool resource paradigm with intergenerational contingencies. This enabled us to look for objective, stable, and trait-like neural markers of interindividual differences in consequential intergenerational behavior. We found that individuals behaving sustainably (vs. unsustainably) were marked by greater cortical thickness of the dorsomedial and dorsolateral prefrontal cortex. Given that these brain areas are involved in perspective-taking and self-control and supported by mediation analyses, we speculate that greater cortical thickness of these brain areas better enable individuals to take the perspective of future generations and to resist temptations to maximize personal benefits that incur costs for future generations. By meeting recent calls for the contribution of neuroscience to sustainability research, it is our hope that the present study advances the transdisciplinary understanding of interindividual differences in intergenerational sustainability.

Keywords: brain anatomy, intergenerational sustainability, dorsomedial prefrontal cortex, dorsolateral prefrontal cortex, perspective-taking, self-control

Highlights

- In an intergenerational sustainability dilemma with real consequences, successive groups (generations) extract resources from a common pool.

- If the present generation exceeds a certain extraction threshold, this reduces the payoff of the next generation.

- Individual neuroanatomical fingerprints relate to interindividual differences in intergenerational sustainability.

- Sustainable individuals are characterized by greater cortical thickness of the dorsomedial and dorsolateral prefrontal cortex than unsustainable individuals.

- The impact of the structural findings on intergenerational sustainability is mediated by perspective-taking and self-control processes.

1. Introduction

Intergenerational sustainability lies at the heart of societies' and humankind's greatest challenges like public debt, social insurance systems, and global climate change (United Nations, 2021). Even though most people are aware of and concerned about the challenges of social and ecological intergenerational sustainability (European Commission, 2021a; Frank et al., 2020; IPSOS, 2021), individuals vary greatly in taking sustainable actions like supporting policies to raise taxes and the retirement age or engaging in pro-environmental behavior (European Commission, 2021b; Gallup, 2021; Jaime-Castillo, 2013). However, the sources of interindividual differences in *intergenerational* sustainable behavior remain far from being understood.

Behaving in a socially or ecologically sustainable way beyond one's own generation poses unique and challenging dilemmas for humans (e.g. Hauser et al., 2014; Jacquet et al., 2013; Wade-Benzoni, 2008). Such intergenerational sustainability dilemmas arise in situations in which the interests of present decision-makers conflict with the interests of future others because people of the present generation must decide whether to sacrifice (vs. maximize) their own benefits to provide (vs. reduce or destroy) benefits for other people of future generations (Shahen et al., 2021). Crucially, present generations *unidirectionally* affect the outcomes for future generations. Therefore, present generations do not benefit (or suffer) from the long-term consequences of their own behaviors, which distinctively differentiates intergenerational sustainability dilemmas from single-generation social dilemmas. The challenging nature of intergenerational sustainability dilemmas may be traced back to two types of psychological distance and the preferential biases arising from them. First, the social distance between the present generation and future generations speaks to people's preference for greater benefits for themselves or socially close others compared to socially distant others (Jones & Rachlin, 2006), which relates to intergroup bias in single-generation dilemmas (Hewstone et al., 2002). Second, the temporal distance between present behavior and future consequences resonates with people's preference for smaller benefits now over larger benefits later, which relates to temporal discounting in single-generation intertemporal choice dilemmas (e.g. Frederick et al., 2002). However, due to the simultaneous and unique interaction of both dimensions of psychological distance (social and temporal) and their corresponding preferential biases, intergenerational sustainability dilemmas are distinctively more complex than single-generation intergroup situations or intertemporal choice decisions (Wade-Benzoni & Tost, 2009). For instance, while in single-generation intertemporal choice it is the decision-makers *themselves* who profit from being patient, in intergenerational

sustainability dilemmas it is *others* of future generations who profit from sustainable decisions. Therefore, the search for sources of interindividual differences in intergenerational sustainable behavior might be informed by, but cannot be reduced to, research investigating interindividual differences in single-generation dilemmas.

Previous research rarely paid specific attention to interindividual differences in social or ecological *intergenerational* sustainability. More attention has been devoted to investigating interindividual differences in pro-environmental behavior in single-generation contexts. This research mostly focused on values, norms, beliefs, and attitudes (Li et al., 2019; Steg & Vlek, 2009) or on personality traits like the Big Five or the HEXACO (Brick & Lewis, 2016; Kvasova, 2015; Lee et al., 2015; Markowitz et al., 2012). For instance, pro-environmental behavior is positively correlated with biospheric and altruistic values but negatively with hedonic and egoistic values (e.g. Bouman et al., 2021; Steg et al., 2014; Tolppanen & Kang, 2021), and the personality trait of openness to experience positively relates to pro-environmental actions (e.g. Brick & Lewis, 2016; Klein et al., 2019; Markowitz et al., 2012). However, research on the green gap consistently shows that values and attitudes are often only weakly associated with actual green behavior (ElHaffar et al., 2020), and predictions of pro-environmental behaviors based on personality traits reveal heterogenous effects that are small or moderate in size (Soutter et al., 2020).

In the present study, we combined neuroscientific and behavioral economic methods to assess trait-like interindividual differences in intergenerational sustainability. We applied a neural trait approach, which leverages research showing that interindividual differences in brain structural properties like cortical thickness or resting-state activation can provide objective trait-like markers (for reviews see Nash et al., 2015; Wyss & Knoch, 2022). Such neural traits are relatively stable over time in healthy adults (Cannon et al., 2012; Gregory et al., 2020), are individually specific (Näpflin et al., 2007; Valizadeh et al., 2018), and can explain interindividual differences in behaviors by allowing for inferences about the processes underlying behavioral heterogeneity (Baumgartner et al., 2013, 2021; Gianotti et al., 2019; Morishima et al., 2012; Yamagishi et al., 2016). Crucially, neural traits are objective brain-based measures that, unlike self-reports, cannot be adulterated by response biases or demand characteristics. Moreover, we measured intergenerational sustainable behavior by using a behavioral paradigm that modeled critical contingencies characterizing intergenerational dilemmas and elicited consequential behavior in a well-controlled setting. Thus, in line with recent calls for combining behavioral paradigms with neuroscientific methods for intergenerational sustainability research (Aoki et al., 2020; Eyring et al., 2021;

Sawe, 2019; Sawe & Chawla, 2021), we investigated whether interindividual differences in cortical thickness were associated with behavioral differences in a costly played intergenerational sustainability dilemma game.

To assess intergenerational sustainability, we focused directly on the social consequences for future generations and built on a game established by Hauser et al. (2014). In this intergenerational sustainability dilemma game, four study participants partaking on the same day formed the present generation, whereas four other participants partaking one week later formed the future generation. Participants of the present generation neither knew each other nor the participants of future generations. Over several independent rounds, each participant could extract points from a common pool shared with the other participants of the present generation. Importantly, if the present generation's collective extraction exceeded a certain threshold, the payoff of every participant of the next generation was reduced considerably. By using this game, we could model the characteristic features and contingencies of intergenerational sustainable behavior. Participants had to cooperate with anonymous others of the present generation by incurring real costs to benefit other unknown participants of future generations rather than themselves. Additionally, participants of future generations would experience the consequences of participants' behavior with temporal delay and could not reciprocate (or retaliate).

Because of the lack of studies investigating neuroanatomical sources of interindividual differences in intergenerational sustainable behavior, it is difficult to propose hypotheses regarding brain structures that explain these interindividual differences. Nevertheless, previous research on single-generation social dilemmas, intergroup situations, and intertemporal choice allowed for tentative hypotheses, even though intergenerational sustainable behavior cannot be reduced to these phenomena.

First, taking the perspective of future others may be a pivotal mechanism by which individuals can overcome the social distance from future generations and can cooperate to benefit future generations. In fact, research has shown that taking the perspective of others can reduce intergroup bias (Todd & Galinsky, 2014), is associated with cooperation in social dilemmas (Ramsøy et al., 2015; Rumble et al., 2009), and can promote sustainable behavior in intergenerational sustainability dilemmas in general (Langenbach et al., 2022; Shahen et al., 2021; Wade-Benzoni, 2008), and in pro-environmental behavior in particular (e.g. Pfattheicher et al., 2016; for review see Heinz & Koessler, 2021). On the neural level, perspective-taking is known to be supported by the dorsomedial prefrontal cortex (DMPFC) and the temporoparietal junction (TPJ) (Adolphs, 2003; Frith & Frith, 2006, 2021; Healey &

Grossman, 2018; van Overwalle, 2009). Moreover, interindividual differences in the morphology and interconnectivity of these brain regions were found to explain differences in the capacity to overcome social distance in single-generation intergroup situations (Baumgartner et al., 2013, 2015). We therefore hypothesized that participants who can be categorized behaviorally as intergenerational sustainable (vs. unsustainable) would be more inclined to take the perspective of future others and would be marked by greater cortical thickness of the DMPFC and/or TPJ.

Second, engaging in self-control may be an additional mechanism by which individuals can overcome the social and temporal distance from future generations. Self-control enables an individual to advance one goal over a second goal when the two are perceived to be in conflict (Inzlicht et al., 2021). The two conflicting goals may be maximizing benefits of oneself or close others vs. maximizing collective benefits irrespective of the social distance to beneficiaries or receiving a smaller-sooner vs. a larger-later reward (temporal discounting). In both cases, these conflicts manifest in temptations, which require self-control capacity to resist (Hofmann et al., 2009, 2012; Hofmann & van Dillen, 2012; Kotabe & Hofmann, 2015). Ample neuroscientific evidence suggests that the capacity to engage in self-control critically depends on the structure and function of the lateral prefrontal cortex (PFC) for social (for reviews see Nash et al., 2015; Wyss & Knoch, 2022) and temporal decision-making (Figner et al., 2010; Frost & McNaughton, 2017; Peters & Büchel, 2011). Moreover, studies applying a neural trait approach found that interindividual differences in baseline activity of the lateral PFC explained differences in daily pro-environmental behavior (Baumgartner et al., 2019) and temporal discounting (Gianotti et al., 2012) in single-generation contexts. Thus, we hypothesized that intergenerationally sustainable (vs. unsustainable) participants would be better able to engage in self-control and would be marked by greater cortical thickness of the lateral PFC.

2. Method

2.1 Participants

We acquired behavioral and brain data of 77 students from the University of Bern. Of these, 14 had to be excluded due to artifacts in the anatomical brain data or because they failed comprehension check (see game-specific questions). Therefore, we finally analyzed a sample of 63 participants (33 female, 30 male, mean age ± SD = 21.79 ± 2.82). All participants were right-handed, reported no history of neurological or cardiovascular disease or psychological disorders, and gave written informed consent before participation. The study was conducted according to the principles expressed in the Declaration of Helsinki and was approved by the ethics committee of the canton of Bern (no. 2020-00302).

2.2 Procedure

The present study is part of a larger project, in which participants' behavioral as well as structural and functional brain data was acquired. In the present study, we were interested in the sources of individual differences in intergenerational sustainable behavior. Thus, we applied a neural trait approach by focussing on the analysis of task-independent brain structure. Note that the functional brain data will be reported in a separate article investigating the mental processes during intergenerational sustainable decision-making. After first reading the instructions for the intergenerational sustainability game outside of the scanner, participants completed the game inside the scanner. Directly after the game, participants answered game-specific questions probing engagement in perspective-taking and self-control during the game and the comprehension check. After that, participants underwent structural magnetic resonance imaging. At the end of the session, participants received a fixed show-up fee of 40 CHF. Two weeks after the session, participants received a link to an online questionnaire (see trait questionnaire) and received their additional payment, which depended on their own and others' behavior (see intergenerational sustainability dilemma game).

2.3 Intergenerational sustainability dilemma game

We aimed for assessing intergenerational sustainable behavior irrespective of the context of pro-environmental behavior. To this end, we focused directly on social consequences on future generations and designed a game inspired by the seminal study of Hauser et al. (2014) (see Figure 1). To model the succession of different generations separated by a temporal delay, four participants who completed their session on the same day formed the present generation, while four other participants who would partake about 7 days later constituted the next generation. Participants were informed about this real

implementation of a sequence of temporally separated generations and the real monetary consequences for both the present and next generation in detail during the instructions.

In each of 16 independent trials, participants could extract between 0 and 20 points (in increments of 2 points) from a pool shared with the other three participants of the present generation. Each point was worth 1 CHF. Extraction of points took place under two conditions, which were equally distributed over the 16 trials in a pseudo-randomized order. In eight trials, participants of the present generation were informed that if they collectively extracted more than 40 points, every participant's payoff of the present generation was reduced by 80% for that trial. In the other eight trials, participants were informed that if the present generation's collective extraction exceeded 40 points, the payoff of every participant of the next generation would be reduced by 80% in that trial, while the payoffs of the participants of the present generation were not affected. Hence, trials differed in whether the present or the next generation's payoff was affected if the present generation exceed the threshold of 40 points. Accordingly, we will name the experimentally manipulated factor *Affected Generation (Gen)* and refer to its two conditions as Gen_{pres} for trials affecting the present generation and as Gen_{next} for trials affecting the next generation.

In each trial, participants were informed about the current condition via a decision screen. In the top half of the screen, they saw which generation (present vs. next) would be affected by their decision, and they were reminded of the collective extraction threshold of 40 points and on the payoff reduction consequences if the threshold was exceeded. In the bottom half of the screen, participants saw the question "How many points would you like to extract?" and a visual scale with the numbers from 0 to 20 in increments of 2. They could input their decision by using two navigation buttons and one confirmation button.

After all participants of the present generation had completed their sessions, two trials were selected randomly to be paid out (taking into account potential payoff reductions). Participants were then given feedback on their generation's collective behavior and its consequences for the present and next generation and received their payment.

2.4 Categorization of behavioral types

We categorized participants as sustainable or unsustainable according to their behavior in the intergenerational sustainability dilemma game. We named this between-subject factor *Behavioral Type* and refer to its two levels using $Type_{sus}$ for sustainable and $Type_{unsus}$ for unsustainable participants. We categorized participants as sustainable if their median extraction *in trials affecting the next generation* was lower than or equal to 10 points.

Otherwise, we categorized participants as unsustainable. Please note that this procedure is not the same as a median split but a categorization based on an a priori defined threshold set to a participant's individual *median extraction* of 10 points in trials affecting the next generation. We chose a median extraction of 10 points as critical threshold for categorization due to the following reasons. In every trial affecting the next generation, each of the four participants of the present generation could extract up to 10 points without risking to collectively extract more than 40 points, which would reduce the payoff of the next generation. Therefore, 10 points represent a reasonable sustainability threshold. Moreover, we calculated median instead of mean behavior over trials because the mean is overly sensitive to small behavioral heterogeneity between trials. For instance, if participants extracted 10 points in seven trials but 12 points in one trial, they would be categorized as unsustainable according to mean behavior (mean extraction of 10.25 points), even though this behavior would more reasonably be categorized as sustainable, which is the case if one aggregates trials by median behavior (median extraction of 10 points).

2.5 Game-specific questions

After game completion, we asked participants to indicate their agreement to specific statements on a scale from 1 ("do not agree at all") to 11 ("completely agree"). In a first block, participants indicated their agreement to the statements that (1) putting themselves in the shoes of members of the next generation and (2) putting themselves in the shoes of members of the present generation influenced their decision in trials affecting the next generation's payoff. Additionally, participants indicated their agreement to the statement that (1) they were tempted to extract more than 10 points and that (2) they tried to resist this temptation in Gen_{next} trials. These two statements were designed to reflect that behavior resulting from (failed) self-control processes involves (1) a desire conflicting with a higher-order goal (a *temptation*) and (2) a (lack of) effort to control this desire (effort to *resist* the temptation) (Hofmann et al., 2009, 2012; Hofmann & van Dillen, 2012; Kotabe & Hofmann, 2015). In a second block, participants answered the same statements as in the first block but now concerning trials affecting the present generation. However, they were not asked to indicate the extent to which they took the perspective of members of the next generation because this statement was not sensible in Gen_{pres} trials.

We calculated participants' differential engagement in perspective-taking in Gen_{next} trials by subtracting perspective-taking with members of the next generation (Target of Perspective-Taking: TP_{next}) from perspective-taking with members of the present generation

(TP_{pres}). To quantify participants' differential engagement in self-control, we calculated two difference scores. We (1) subtracted participants' temptation in Gen_{next} from Gen_{pres} trials ($\Delta temptation$) and we (2) subtracted participants' effort to resist the temptation in Gen_{next} from Gen_{pres} trials ($\Delta resist_{temptation}$). In statistical analyses (see mediation results, Supplementary Analysis S1, and Supplementary Figure S1B), we focused on $\Delta resist_{temptation}$ while entering $\Delta temptation$ as a covariate. Because we statistically adjusted for $\Delta temptation$, we considered effects regarding $\Delta resist_{temptation}$ as representing effects concerning differential engagement in self-control (Hofmann et al., 2009, 2012; Hofmann & van Dillen, 2012; Kotabe & Hofmann, 2015).

As a comprehension check, participants had to indicate the average amount of points each member of the present generation could extract without reducing the payoff of the next generation. Hence, this question allowed us to ensure that participants did not accidentally behave unsustainably while believing they were behaving sustainably (or vice versa).

2.6 Trait questionnaire (Schwartz Value Scale)

We asked participants to fill out the Schwartz Value Scale (Steg et al., 2014) online after the experimental session. Participants rated how important 16 values were for them as leading principles in life (1: "not at all important", 6: "very important"). The SVS is divided into four subscales, which assess altruistic, egoistic, hedonic, and biospheric values. These values have been argued to play crucial roles in pro-environmental (Steg et al., 2014) and intergenerational behavior (Wade-Benzoni & Tost, 2009). Therefore, we checked whether brain anatomy was associated with intergenerational sustainability independently of the SVS (for details, see Supplementary Analysis S2 and Supplementary Table S1).

2.7 Acquisition of anatomical brain data

Anatomical brain data was acquired on a Siemens MAGNETOM Prisma 3.0 Tesla whole-body scanner using a 64-channel head coil. T1-weighted 3D-modified driven equilibrium Fourier transformation (MDEFT) images were acquired from each subject (176 slices, field of view: $256 \times 256 \times 176$, slice thickness: 1 mm, no gap, repetition time: 7.93 ms, echo time: 2.49 ms, flip angle: 16°).

2.8 Preprocessing of anatomical brain data

We used the computational anatomy toolbox (CAT12, version r1742, http://www.neuro.uni-jena.de/cat/, Dahnke et al., 2013) implemented in the statistical parametric mapping software (SPM 12, version v7771, http://www.fil.ion.ucl.ac.uk/spm/software/spm12/) for preprocessing, which consisted of the

following steps: We (1) classified brain tissue into grey matter (GM), white matter (WM), and cerebrospinal fluid (CSF) by using an adaptive maximum a posterior technique, which does not necessitate a priori information on tissue probabilites, and by applying a partial volume segmentation approach, which estimates a simplified mixed model of a maximum of two tissue types (Tohka et al., 2004). Based on this tissue segmentation, we (2) estimated for each GM voxel its distance from the WM/GM boundary. This resulted in a WM distance map whose values at the outer GM/CSF boundary represent the GM thickness. Then, we (3) projected these distances' local maxima to other GM voxels by using a neighbor relationship described by the WM distance. By using this projection-based method, cortical thickness is corrected for partial volume effects, sulcal blurring, and sulcal asymmetries. Next, we (4) corrected topological defects like handles or holes by using spherical harmonics (Yotter, Dahnke, et al., 2011). We (5) created a spherical map of the cortical surface by using an algorithm that reduces area distortion (Yotter, Thompson, et al., 2011). This spherical mapping allows for reparameterizing the surface mesh into a common coordinate system for inter-subject analysis. Finally, we (6) applied spherical registration to MNI standard space by using the volume-based diffeomorphic DARTEL algorithm (Ashburner, 2007), which was adapted to work with spherical maps. To prepare the surface data for statistical analysis, we used the defaults suggested by CAT12 for cortical thickness analyses: We resampled the surface data by using the supplied 32k surface mesh, which has an average vertex spacing of about 2 mm, and smoothed the data with a full width at half maximum smoothing kernel of 12 mm.

2.9 Statistical analyses of anatomical brain data

We conducted two-sample t-tests on the smoothed cortical thickness measures in CAT12. We additionally included sex and age as covariates of no interest in the design matrix because these variables have been found to affect cortical thickness (e.g. Gennatas et al., 2017). We looked for cortical thickness differences between behavioral types across the whole brain as well as across a priori defined regions of interest involved in perspective-taking (DMPFC and TPJ) and self-control (lateral PFC). For this purpose, we created a mask consisting of the DMPFC, bilateral TPJ and bilateral lateral PFC. For the DMPFC and TPJ, we used a meta-analysis on social cognition (van Overwalle, 2009) to define peaks in the left TPJ ($x = -49$, $y = -58$, $z = 22$), the right TPJ ($x = 53$, $y = -54$, $z = 22$), and the DMPFC ($x = -3$, $y = 48$, $z = 30$), which consisted of the average coordinates of areas that had consistently been found activated in perspective-taking tasks (including goal, intention, and trait inferences as well as morality judgments). Then, we created 20 mm spheres centred on these coordinates

by using the WFU Pickatlas toolbox in SPM 12 (Maldjian et al., 2003). Finally, we mapped these volumes to the 32k surface mesh as implemented in the surface tools in CAT12. For the lateral PFC, we used the Desikan-Killiany surface atlas as provided in CAT12 (Desikan et al., 2006), of which we combined the bilateral rostral and caudal parcellations of the middle frontal gyrus and pars orbitalis and triangularis of the inferior frontal gyrus.

We considered findings significant if they survived family-wise error (FWE) correction on peak- or cluster-level at p < 0.05 across the whole brain (whole brain FWE corrected) or across the small surface mask defined above (small surface FWE corrected). We used a cluster-defining threshold of $t(59) = 3.23$ (corresponding to $p_{uncor.} < 0.001$). For significant findings, we extracted cortical thickness values of the corresponding cluster, which we subsequently adjusted for the covariates of no interest by regressing out sex and age. We used these values for further plotting of the discovered anatomical differences as well as for mediation and logistic regression analyses by using the statistical software R version 4.1.3 (R Core Team, 2021). To report effect sizes of cortical thickness differences between sustainable and unsustainable participants, we calculated Cohen's d, with $d > 0.2$ representing a small, $d > 0.5$ a medium, and $d > 0.8$ a large effect size (Cohen, 1988). Additionally, we calculated η^2 as an effect size measure indexing the percentage of variance in cortical thickness that can be explained by participants' *Behavioral Type* ($Type_{unsus}$ vs. $Type_{sus}$). We considered $\eta_p^2 > 0.01$ as representing a small, $\eta_p^2 > 0.06$ a medium, and $\eta_p^2 > 0.14$ a large effect (Cohen, 1988).

2.10 Statistical analyses of behavioral and psychometric data

We conducted two-way mixed between-within-subjects analyses of variance (ANOVAs) in R by using the package afex (version 1.0-1, Singmann et al., 2021). We used *Behavioral Type* ($Type_{unsus}$ vs. $Type_{sus}$) as between-subject factor and *Affected Generation* (Gen_{pres} vs. Gen_{next}) as within-subject factor. We used R's stats package's function *t.test()* for two-sample t-tests for comparisons of levels of between-subjects factors and paired t-tests for comparisons of levels of within-subjects factors. We conducted linear regression and binary logistic regression analyses by using R's stats package's functions *lm()* and *glm()*, and we calculated Pearson correlation coefficients by using the package correlation (version 0.8.0, Makowski et al., 2020).

2.11 Mediation analyses

We conducted mediation analyses by using the PROCESS R code (version 4.0.1), which is available online (http://www.processmacro.org/download.html) and documented in

Hayes (2018). PROCESS is a tool that models ordinary least squares and logistic regression path analyses and allows for estimating direct and indirect effects in mediation analyses. We reasoned that participants' cortical thickness as neural trait would affect perspective-taking and self-control processes, which in turn would impact whether participants would behave intergenerationally sustainably or not. We therefore investigated whether an independent variable X (participants' extracted and adjusted cortical thickness values of significant brain clusters) affected the binary dependent variable Y (whether participants were behaviorally categorized as sustainable or unsustainable) through a mediating variable M (participants' differential engagement in perspective-taking and self-control). To test whether the mediated, indirect effect through M was statistically significant, we used 5'000 bootstrap samples to generate 95% bootstrap confidence intervals ($95\%\text{-}CI_{boot}$) for the indirect effect (with the value zero not contained in the interval indicating a significant indirect effect).

3. Results

3.1 Behavioral Results

We categorized participants as unsustainable if their median extraction in trials affecting the next generation exceeded 10 points and as sustainable otherwise (see methods for details). We found 30 sustainable and 33 unsustainable participants. There were no differences between these behavioral types regarding trait altruistic, egoistic, hedonic, and biospheric values or the distribution of sex (see Supplementary Table S2). To describe the extraction behavior of these types, we conducted an ANOVA on the median of extracted points with the between-subject factor *Behavioral Type* (unsustainable vs. sustainable, abbreviated with $Type_{unsus}$ vs. $Type_{sus}$) and within-subject factor *Affected Generation* (trials affecting the present generation vs. trials affecting the next generation, abbreviated with Gen_{pres} vs. Gen_{next}) (Figure 2). Sustainable and unsustainable participants differed in their extraction behavior depending on which generation was affected by their decisions (ANOVA interaction effect: $F(1,61) = 98.78$, $p < 0.001$, $\eta_p^2 = 0.618$). By necessity of the chosen categorization, in Gen_{next} trials, sustainable participants extracted less points than unsustainable participants (μ's represent cell means: $\mu_{Unsus} = 16.30$, $\mu_{Sus} = 9.10$, $t(61) = -9.94$, $p < 0.001$, $d = -2.51$). However, and not necessarily implied by the categorization, the two types did not differ in extracted points in Gen_{pres} trials ($\mu_{Unsus} = 9.09$, $\mu_{Sus} = 8.93$, $t(61) = -0.36$, $p = 0.721$, $d = -0.09$).

3.2 Cortical thickness differences between the two types

Compared to unsustainable participants, sustainable participants were marked by greater cortical thickness (at $p < 0.05$, small surface FWE corrected) in two brain areas, including the left DMPFC (x = -8, y = 43, z = 20, peak t-value: 4.26, cluster extent: 26 vertices, peak-level corrected, Figure 3A) and the left DLPFC (x = -45, y = 15, z = 40, peak t-value: 3.91, cluster extent: 59 vertices, cluster-level corrected, Figure 4A). Effect sizes suggested that cortical thickness differences between sustainable and unsustainable participants were large according to Cohen's d (DMPFC: $d = 1.011$, $\eta^2 = 0.208$; DLPFC: $d = 0.963$, $\eta^2 = 0.193$), and that 20.8% of variance in cortical thickness of the DMPFC and 19.3% of variance in cortical thickness of the DLPFC were explained by whether a participant was sustainable or unsustainable. Please note that the effect of Behavioral Type (sustainable > unsustainable) on cortical thickness was independent of participant's sex (no Behavioral Type × sex interaction, see Supplementary Table S3 and S4).

Results hold when including the SVS subscales (altruistic, egoistic, hedonic, and biospheric values) as covariates (see hierarchical binary logistic regression analyses in Supplementary Analysis S2 and Supplementary Table S1). Moreover, brain structural differences had unique explanatory power to discriminate between sustainable and unsustainable participants over and above the SVS subscales: While the SVS subscales alone were insignificant predictors of *Behavioral Type* (βs of all subscales $p \geq 0.113$) and only achieved a rather weak discriminative ability ($R^2_{Tjur} = 0.060$), adding cortical thickness of DMPFC and DLPFC increased the discriminative ability by a factor of 4.84 ($R^2_{Tjur} = 0.288$, comparison of models: $\Delta\chi^2(2) = 16.95$, $p < 0.001$).

Whole brain corrected analyses revealed no additional brain regions in which sustainable participants showed greater cortical thickness than unsustainable participants (at FWE corrected $p < 0.05$). In the inverse contrast (unsustainable participants > sustainable participants), no findings emerged (at $p < 0.05$, whole brain or small surface FWE corrected).

3.3 Mediators between brain structure and sustainability

As stated in our hypotheses, we expected that interindividual differences in intergenerational sustainability would be associated with corresponding differences in how individuals engage in perspective-taking and self-control. In our brain anatomical analyses, we found that cortical thickness of two key areas known to be involved in perspective-taking (DMPFC, Frith & Frith, 2006, 2021; Healey & Grossman, 2018; van Overwalle, 2009, 2011) and self-control (DLPFC, Frost & McNaughton, 2017; Peters & Büchel, 2011; Wyss & Knoch, 2022) explained interindividual differences in intergenerational sustainable behavior.

We conducted mediation analyses to test whether cortical thickness of these brain areas indeed affected intergenerational sustainability by influencing how participants differentially engaged in these two socio-cognitive processes (Figure 3B and 4B).

Participants indicated to what extent taking the perspective of others of the next (Target of Perspective-Taking: TP_{next}) and of the present (TP_{pres}) generation affected their decisions *in trials affecting the next generation*, and we calculated participants' differential engagement in perspective-taking in Gen_{next} trials (TP_{next} - TP_{pres}). Hence, higher positive values indicated that participants more strongly engaged in taking the perspective of others of the next generation, whereas lower negative values indicated that participants more strongly engaged in taking the perspective of others of the present generation, and values around zero represented that participants engaged in taking the perspective of others of both generations in a balanced way. In trials affecting the next generation , sustainable participants equally engaged in perspective-taking with members of the next and present generation, with a slight preference for taking the perspective of members of the next generation (μ_{next} = 8.37, μ_{pres} = 6.40, $\Delta\mu_{next-pres}$ = 1.97, $t(29)$ = 2.60, $p < 0.05$, d = 0.47). In contrast, unsustainable participants strongly took the perspective of members of the present generation, but much less of members of the next generation (μ_{next} = 4.82, μ_{pres} = 8.42, $\Delta\mu_{next-pres}$ = -3.61, $t(32)$ = -5.52, $p < 0.001$, d = -0.96) (for detailed analysis, see Supplementary Analysis S1 and Supplementary Figure S1A). We tested whether this differential engagement in perspective-taking mediated the effect of cortical thickness of the DMPFC on participants' sustainability. Higher cortical thickness of the DMPFC predicted more balanced or next generation oriented perspective-taking (unstandardized linear regression coefficient: a = 10.61, SE = 3.51, $p < 0.01$), which in turn increased the odds of being of the sustainable behavioral type (unstandardized binary logistic regression coefficient: b = 0.35, SE = 0.10, $p < 0.001$). Crucially, the indirect effect of cortical thickness on *Behavioral Type* was significant (product of regression coefficients: ab = 3.68, 95%-CI_{boot} = [1.229; 10.273]). Therefore, the effect of cortical thickness of the DMPFC on participants' sustainability was mediated by differential engagement in taking the perspective of others of the next or present generation.

Participants additionally indicated to what extent they were tempted to extract more than 10 points and to what extent they tried to resist this temptation in Gen_{next} and Gen_{pres} trials, and we calculated participants' differential temptation and differential effort to resist this temptation (Gen_{next} - Gen_{pres}). Higher positive values in differential effort to resist temptation indicated that participants more strongly tried to resist the temptation in Gen_{next}

trials, whereas lower negative values indicated that participants more strongly tried to resist the temptation in Gen_{pres} trials, and values near zero represented equal efforts to resist temptations irrespective of which generation was affected. Sustainable participants tried to resist temptation to an equal extent in Gen_{pres} and Gen_{next} trials ($\mu_{next} = 7.04$, $\mu_{pres} = 6.69$, $\Delta\mu_{next-pres} = 0.35$, $t(29) = 0.67$, $p = 0.509$, $d = 0.12$), whereas unsustainable participants put less effort into resisting temptations in Gen_{next} than Gen_{pres} trials ($\mu_{next} = 3.70$, $\mu_{pres} = 8.16$, $\Delta\mu_{next-pres} = -4.47$, $t(32) = -6.87$, $p < 0.001$, $d = -1.20$) (for detailed analysis, see Supplementary Analysis S1 and Supplementary Figure S1B). We then used differential effort to resist temptation as a mediator of the effect of cortical thickness of the DLPFC on *Behavioral Type* while also including differential temptation as a covariate (these two variables were not correlated: $Pearson\ r = 0.02$, $t(61) = 0.12$, $p = 0.902$). We included differential temptation as a covariate of no interest to take into account that behavior resulting from (failed) self-control processes depends on the experience of temptation in the first place, which is why researchers should control for the degree to which participants are actually tempted by certain stimuli (Hofmann et al., 2009; Hofmann & van Dillen, 2012). Higher cortical thickness of the DLPFC predicted more equal or greater ($aGen_{next} > aGen_{pres}$) efforts to resist temptation ($a = 7.34$, $SE = 2.39$, $p < 0.01$), which in turn increased the odds of being of the sustainable behavioral type ($b = 0.45$, $SE = 0.15$, $p < 0.01$). Importantly, the indirect effect of cortical thickness on *Behavioral Type* was significant ($ab = 3.32$, 95%-$CI_{boot} = [1.131; 9.697]$). Thus, the effect of cortical thickness of the DLPFC on participants' sustainability was mediated by differential efforts to resist temptations (independent of potential differences in differential temptation). Please note that mediation results hold if effort to resist temptation only in trials affecting the next generation is used as mediator and if mediations are run without differential temptation as covariate (see Supplementary Table S5).

4. Discussion

What are the sources of interindividual differences in intergenerational sustainable behavior? Previous research mostly focused on ecological aspects of sustainability in single-generation contexts and relied on self-reports. In the present study, we assessed consequential behavior and used objective measures of brain anatomical interindividual differences by combining a behavioral paradigm with a neural trait approach. Based on extraction behavior in a common-pool resource paradigm with intergenerational contingencies (intergenerational sustainability dilemma game), we categorized participants as sustainable (n = 30) or unsustainable (n = 33) and tested whether these two types were characterized by brain anatomical differences in cortical thickness. Sustainable (vs. unsustainable) participants were marked by greater cortical thickness of the DMPFC and DLPFC.

The DMPFC, as a central node of the mentalizing system, is a key brain area involved in perspective-taking (Arioli et al., 2021; Fehlbaum et al., 2021; Frith & Frith, 2006, 2021; Healey & Grossman, 2018; Jamali et al., 2021; van Overwalle, 2009, 2011). More specifically, the DMPFC seems especially involved in taking the perspective of socially distant, dissimilar others (Denny et al., 2012; Frith & Frith, 2021; van Overwalle, 2009). For instance, cortical thickness and grey matter volume in the DMPFC was found to predict more equal (less biased) engagement in taking the perspective of socially distant outgroup and socially close ingroup members, which in turn was associated with less biased (i.e. less outgroup disadvantaging) behavior affecting these targets of mentalizing (Baumgartner et al., 2013). The present study transfers and extends these findings regarding single-generation intergroup situations to intergenerational sustainable behavior, which resonates with accounts comparing future generations to outgroups relative to the present generation as ingroup (Meleady & Crisp, 2017; Pearson & Schuldt, 2018). Our mediation analysis corroborated that greater cortical thickness of the DMPFC predicted less biased (i.e. less next generation disadvantaging) engagement in perspective-taking, which in turn increased the probability of being of the intergenerational sustainable type. We therefore speculate that greater cortical thickness of the DMPFC reflects a greater capacity to take the perspective of others, even if they are socially and temporally distant from the self. This enables perspective-taking with future others, which in turn motivates individuals to not only care about their own and the present generations' outcomes but also about future other generations' outcomes and to behave intergenerationally sustainably.

This reasoning is in line with a recent study arguing that insufficient intergenerational mentalizing might be the source of unsustainable behavior (Langenbach et al., 2022). The

authors showed that enhancing cortical excitability of the TPJ by applying high-definition transcranial direct current stimulation (HD-tDCS) increased sustainable behavior. While we did not find cortical thickness differences between sustainable and unsustainable participants in the TPJ, one might speculate that in Langenbach et al. (2022), stimulation of the TPJ in part affected behavior by indirectly stimulating the DMPFC. The TPJ and DMPFC are highly interconnected as shown by structural and functional connectivity analyses (Fehlbaum et al., 2021; Wang et al., 2021), and studies using transcranial magnetic stimulation (TMS) and tDCS have recognized and capitalized on the fact that these brain stimulation techniques not only cause local but also distributed network effects (Bergmannet al., 2021; Chang et al., 2021; Ghobadi-Azbari et al., 2021; Ruff et al., 2009). For instance, inhibiting the right TPJ by continuous theta-burst TMS was not only found to reduce the TPJ's activity, but also its functional connectivity with the medial PFC during a behavioral task relying on mentalizing processes (Hill et al., 2017). Interestingly, the effects of stimulation on behavior were not due to changes in the TPJ's activity but could be attributed to changes in its functional connectivity with the medial PFC. Thus, future research applying brain stimulation directly to the DMPFC in combination with simultaneous functional brain imaging might provide causal evidence and further insights regarding this brain area's role for intergenerational sustainable behavior.

Sustainable (vs. unsustainable) participants were not only marked by greater cortical thickness of the DMPFC but also of the DLPFC. The DLPFC is a central brain region involved in self-control, which is needed for the advancement of a higher-order goal over a current desire with which it is perceived to be in conflict, as is typically the case in social and intertemporal decision-making (Baumgartner et al., 2011; Fehr & Krajbich, 2014; Figner et al., 2010; Frost & McNaughton, 2017; Hare et al., 2009; Peters & Büchel, 2011; Wyss & Knoch, 2022). Brain anatomical studies repeatedly showed that greater cortical thickness or grey matter volume of the DLPFC is associated with less impulsive, more strategic and goal-directed behavior, which might be interpreted as reflecting a greater capacity for self-control (Baumgartner et al., 2021; Bjork et al., 2009; Pan et al., 2021; Schilling et al., 2012; Schmidt et al., 2018; Steinbeis et al., 2012; Yamagishi et al., 2016). Although in a single-generation context only, a recent study applying a neural trait approach provided evidence for the involvement of the lateral PFC in a form of ecological sustainable behavior (Baumgartner et al., 2019). In this resting-state EEG study, greater task-independent cortical baseline activity in the lateral PFC predicted more frequent everyday pro-environmental behavior, which was interpreted as a neural marker for self-control capacities. Importantly, in the present study we

found that the effect of greater cortical thickness of the DLPFC on increased probability of intergenerational sustainable behavior was mediated by greater efforts to resist temptations to benefit the present generation at the cost of future generations. Thus, we conjecture that sustainable (vs. unsustainable) participants' greater cortical thickness of the DLPFC is indicative of a greater capacity for self-control benefitting future others.

Taken together, the present study demonstrates that brain structural differences in DMPFC and DLPFC can explain interindividual differences in intergenerational sustainable behavior. We interpret these findings as providing evidence for the involvement of perspective-taking and self-control processes as sources of behavioral heterogeneity in sustainability. Regarding the interplay of these two socio-cognitive processes, we speculate that taking the perspective of future others might deliver the initial motivation to behave intergenerationally sustainably. Once activated, the goal to maximize delayed collective outcomes benefitting others in the future conflicts with the desire to maximize immediate personal benefit. It then requires self-control to resist this egoistic and immediate temptation resulting from the social distance between benefactors and beneficiaries and the temporal distance between immediate and future benefits, which interactively characterize the unique and challenging nature of intergenerational sustainability dilemmas. Hence, we conjecture that perspective-taking and self-control help reduce the discounting of the future of others that hinders intergenerational sustainability. This reasoning resonates with theoretical considerations and empirical findings attributing a role to perspective-taking (e.g. Pahl & Bauer, 2013; Pfattheicher et al., 2016; Uhl-Haedicke et al., 2019) and cognitive- or self-control (Bamberg, 2013; Langenbach et al., 2020; Nielsen, 2017; Redondo & Puelles, 2017; Weber, 2017; Wyss et al., 2022) for pro-environmental behavior in the realm of ecological sustainability. With the present study, we complement and extend previous research by showing that structural differences in brain areas involved in these socio-cognitive processes explain interindividual differences in intergenerational sustainable behavior irrespective of the context of pro-environmental behavior.

Like in any experimental design, one needs to consider whether our behavioral game adequately represented the complexity of real intergenerational sustainable behavior. It is challenging (if not practically impossible) to measure intergenerational behavior between real generations separated by several decades in a well-controlled setting. However, intergenerational behavior can be modeled by approximating its characteristic features and contingencies. This approach was pioneered in a seminal study by Hauser et al. (2014) and has successfully been implemented by numerous studies since then (e.g. Kamijo et al., 2016;

Shahen et al., 2021; Shahrier et al., 2017; Timilsina et al., 2022). Like these studies, we used a behavioral economic game modelling key features of intergenerational sustainability dilemmas (social and temporal distance between benefactors and beneficiaries, temporal delay between actions and consequences, unidirectionality, and non-reciprocity). We therefore believe that our game reasonably mimics intergenerational contingencies within the possibilities of a well-controlled laboratory setting.

The present study explicitly investigated the interaction of social and temporal aspects in intergenerational sustainability. Considered individually, these aspects also apply to single-generation social dilemmas and intertemporal choice tasks. It is a different and open question whether and to what extent behavior in these classic single-generation paradigms also relates to intergenerational sustainability. We would encourage future studies to investigate these potential relationships by using different designs optimized for these questions. Further, as is the case for many brain studies, our sample consisted of students. It would be interesting to investigate a more diverse population.

In conclusion, the present study identified cortical thickness of the DMPFC and DLPFC as neural traits capable of explaining interindividual differences in intergenerational sustainable behavior. These neural traits might complement more commonly used self-report trait questionnaires by providing a unique and incremental ability to explain differences in intergenerational sustainability while simultaneously hinting at the involvement of specific socio-cognitive processes (perspective-taking and self-control) as potential drivers of individual heterogeneity. Thus, the present study lends further support to the neural trait approach (Nash et al., 2015) and to recent calls for the contribution of neuroscience to sustainability research (Aoki et al., 2020; Eyring et al., 2021; Sawe, 2019; Sawe & Chawla, 2021). Importantly, we are not claiming that our results have policy relevance. In our view, these results provide first evidence in basic research. Of course, neuroscience alone cannot solve the challenge of overcoming intergenerational dilemmas. However, a neuroscientific approach can provide an additional method of analysis and therefore play a unique role in advancing transdisciplinary research and the understanding of intergenerational sustainability.

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Data and code availability statement

The dataset analyzed in the present study as well as scripting and plotting code are available from the corresponding authors via email on request.

Credit Author Statement
Emmanuel Guizar Rosales: Conceptualization, Investigation, Software, Formal analysis, Writing – Original Draft, Writing – Review & Editing, Visualization

Thomas Baumgartner: Conceptualization, Investigation, Software, Formal analysis, Writing – Review & Editing, Visualization, Supervision

Daria Knoch: Conceptualization, Writing – Review & Editing, Funding acquisition, Resources, Supervision

Figure captions

A trials affecting the present generation (Gen_{pres})

individual decisions

consequences for

present generation | next generation

10 | 10
20 | 50 | 10

Reduction of each participant's payoff by **80%** | none

10 | 10
10 | 40 | 10

No reduction of payoff | none

B trials affecting the next generation (Gen_{next})

individual decisions

consequences for

present generation | next generation

10 | 10
20 | 50 | 10

No reduction of payoff | **Reduction** of each participant's payoff by **80%**

10 | 10
10 | 40 | 10

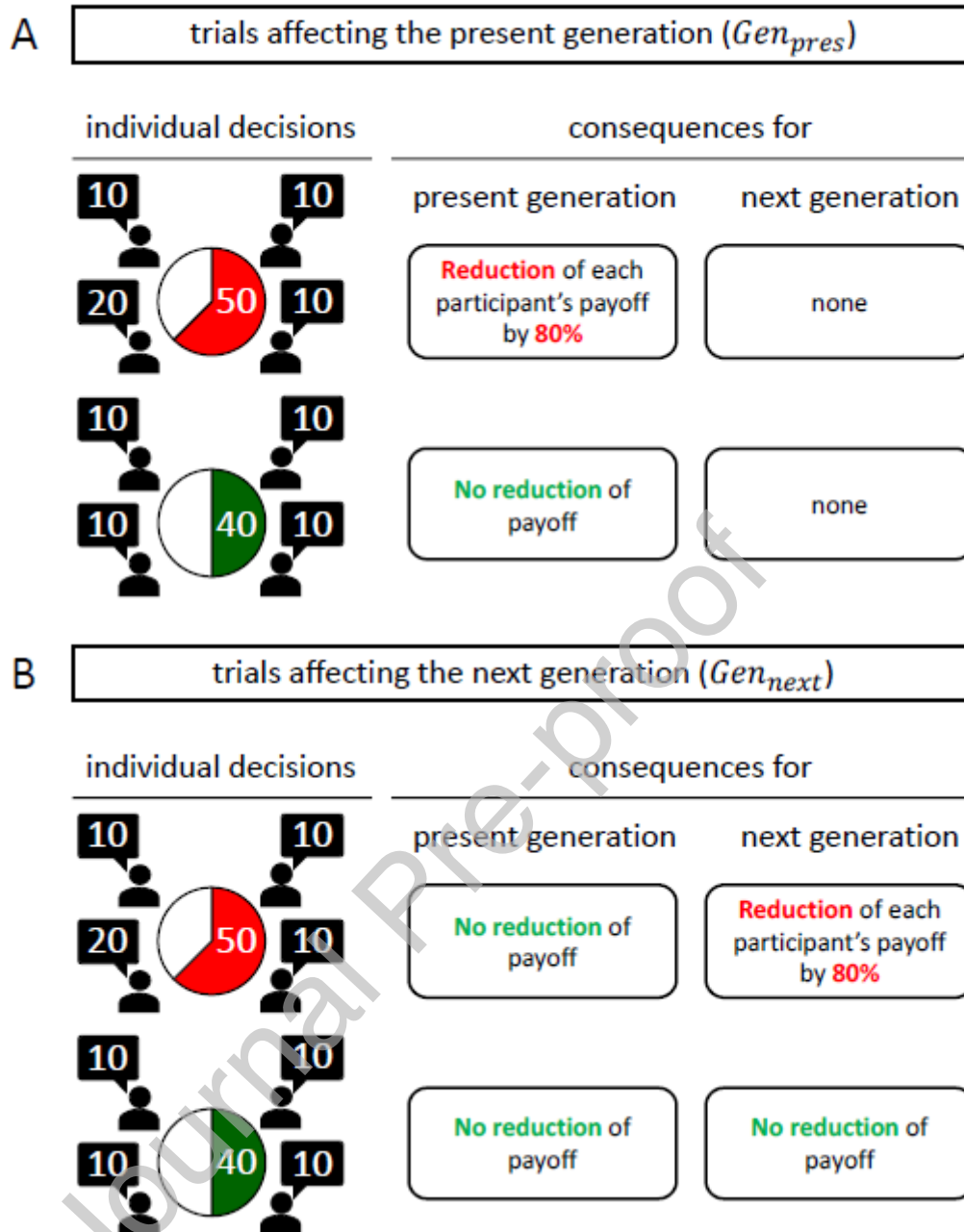**No reduction** of payoff | **No reduction** of payoff

Figure 1. Schematic display of the intergenerational sustainability dilemma game. Over 16 trials, the four participants forming the present generation could each extract between 0 and 20 points of a pool shared with the other three participants of the present generation (80 points in the pool in total). At the start of each trial, participants were informed under which condition of the factor *Affected Generation (Gen)* they had to make their decision. Panel **(A)** illustrates the game mechanics for trials affecting the present generation (Gen_{pres}). If participants of the present generation collectively extracted more than 40 points, their payoff was reduced by 80% in that trial. If participants collectively extracted less or equal to 40 points, their payoff was not reduced. Panel **(B)** displays the game mechanics for trials affecting the next generation (Gen_{next}). If participants

of the present generation collectively extracted more than 40 points, the payoff of the present generation remained unaffected, but the payoff of the other participants of the next generation would be reduced by 80%. If participants of the present generation extracted less or equal to 40 points, neither the present nor the next generation's payoff was reduced. After the present generation had completed the game, two trials were selected at random to determine payoffs with a conversation rate of 1 point = 1 CHF.
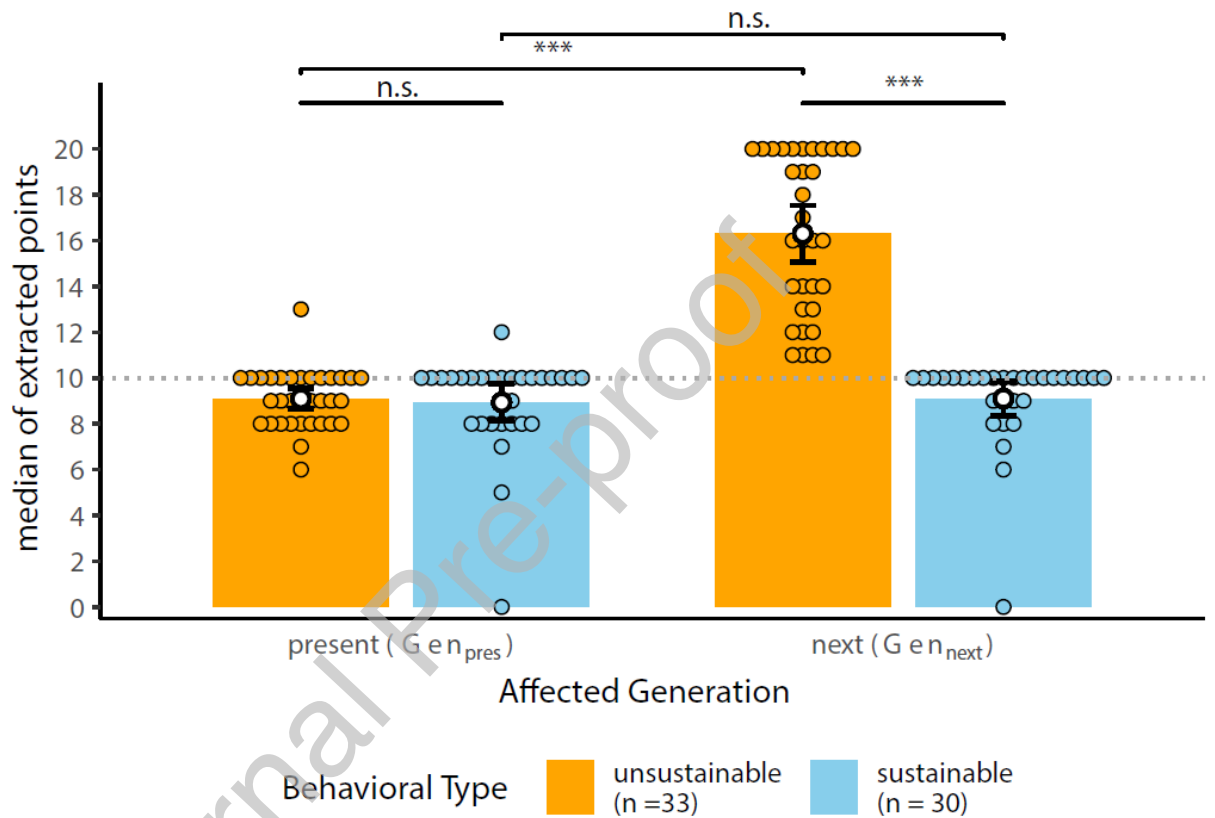

Figure 2. Extraction behavior by *Behavioral Type* (unsustainable participants in orange and sustainable participants in blue, see legend). The bar graph illustrates that sustainable and unsustainable participants showed a different median extraction behavior in trials affecting the next generation (Gen_{next}) but not in trials affecting the present generation (Gen_{pres}). The dotted line represents the 10 points that each participant of the present generation could extract on average without reducing payoffs for the present (in Gen_{pres} trials) or next (in Gen_{next} trials) generation. Error bars represent 95% confidence intervals of cell means. n.s.: $p > 0.05$, ***$p < 0.001$.
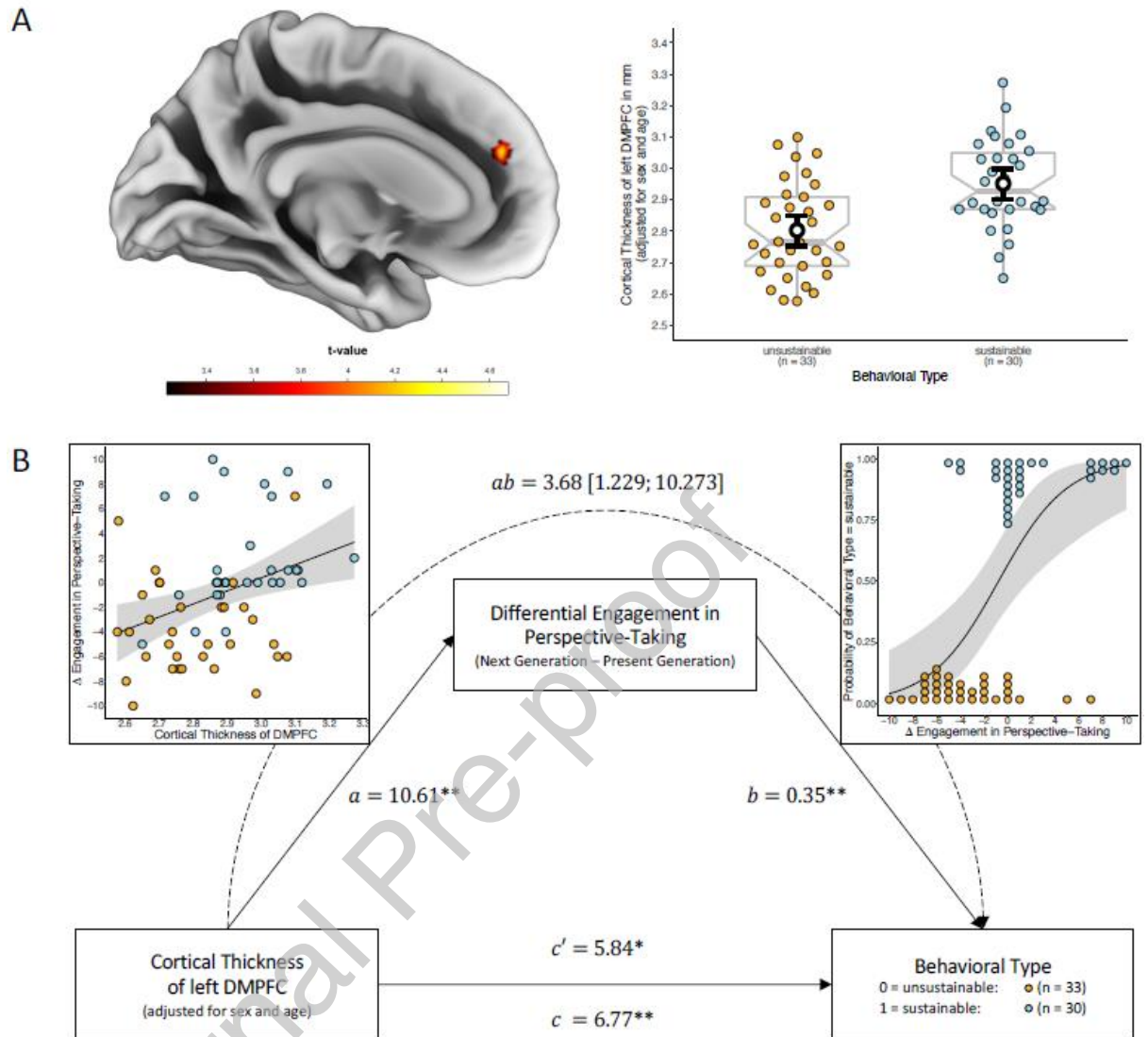
Figure 3. Interindividual differences in structural brain characteristics of the left DMPFC were

associated with differences in intergenerational sustainability via differential engagement in perspective-taking.

Depicted in **(A)** are the structural differences in the left DMPFC ($p < 0.05$, small surface FWE peak-level

corrected), which were qualified by greater cortical thickness in sustainable compared to unsustainable

participants. Findings are depicted at $p_{uncorr.} < 0.001$ using t-maps. Box plots illustrate cortical thickness values

(adjusted for sex and age) based on the depicted region. In the box plots, the horizontal line represents the

median and the notch indicates the 95% confidence interval around the median. The white circles on top of the

box plots represent the group mean, and error bars represent the 95% confidence interval of the mean. Each

point represents the cortical thickness value of one participant. As displayed in panel **(B)**, greater cortical

thickness of the left DMPFC predicted more equal or next generation oriented perspective-taking, which in turn

increased participants' odds of behaving intergenerationally sustainably. Path coefficient a represents an

unstandardized linear regression coefficient, whereas coefficients b, c, and c' represent unstandardized binary logistic regression coefficients in log-odds metric (c = total effect, c' = direct effect). The interval accompanying the indirect effect ab represents a 95% bootstrap confidence interval calculated using 5'000 bootstrap samples. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Subplots visualize regression path a (scatter plot for linear regression) and b (dot plot for logistic regression) with lines of best fit surrounded by their corresponding 95% confidence intervals.
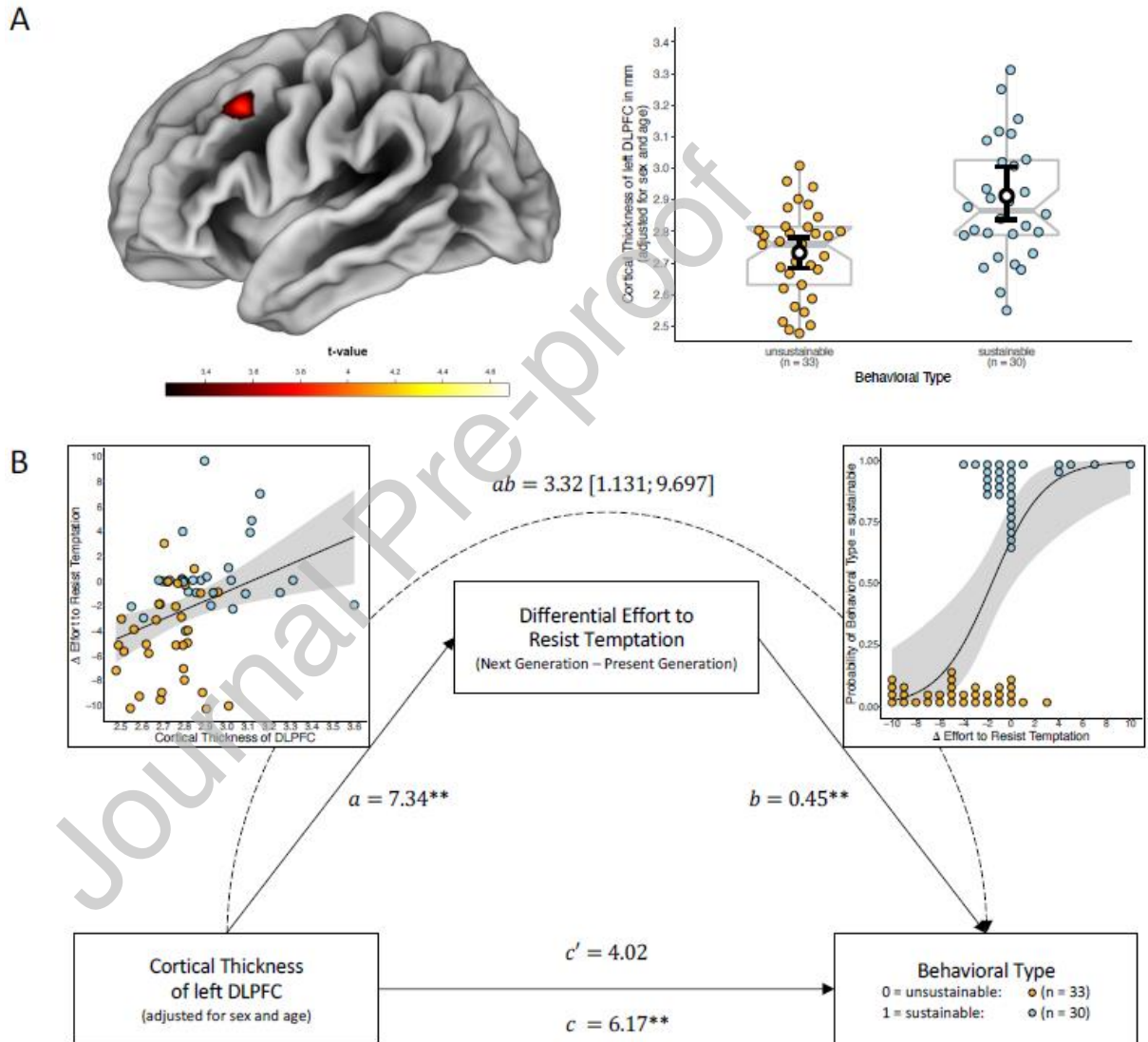

Figure 4. Interindividual differences in structural brain characteristics of the left DLPFC were associated with differences in intergenerational sustainability via differential effort to resist temptation. Depicted in **(A)** are the structural differences in the left DLPFC ($p < 0.05$, small surface FWE cluster-level corrected), which were qualified by greater cortical thickness in sustainable compared to unsustainable participants. Findings are depicted at $p_{uncorr.} < 0.001$ using t-maps. As displayed in panel **(B)**, greater cortical thickness of

the left DLPFC predicted more equal or greater ($Gen_{next} > Gen_{pres}$) efforts to resist temptation, which in turn increased participants' odds of behaving intergenerationally sustainably. Regression paths and corresponding subplots are based on models in which differential temptation ($Gen_{next} - Gen_{pres}$) was entered as an additional covariate. For further explanations, see Figure 3, which follows the same logic regarding statistical annotations.

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