Cerebellum anatomy predicts individual risk-taking behavior and risk tolerance

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Abstract

Human risk tolerance is highly idiosyncratic and individuals often show distinctive preferences when faced with similar risky situations. However, the neural underpinnings of individual differences in risk-taking remain unclear. Here we combined structural and perfusion MRI and examined the associations between brain anatomy and individual risk-taking behavior/risk tolerance in a sample of 115 healthy participants during the Balloon Analogue Risk Task, a well-established sequential risky decision paradigm. Both whole brain and region-of-interest analyses showed that the left cerebellum gray matter volume (GMV) has a strong association with individual risk-taking behavior and risk tolerance, outperforming the previously reported...
associations with the amygdala and right posterior parietal cortex (PPC) GMV. Left cerebellum GMV also accounted for risk tolerance and risk-taking behavior changes with aging. However, regional cerebral blood flow (CBF) provided no additional predictive power. These findings suggest a novel cerebellar anatomical contribution to individual differences in risk tolerance. Further studies are necessary to elucidate the underestimated important role of cerebellum in risk-taking.

**Keywords**
Risk tolerance; Balloon analogue risk task; Cerebellum; Hierarchical Bayesian modeling

1. **Introduction**

On a daily basis, humans are faced with making numerous decisions under risk or uncertainty. It can be as mundane as whether to try a new restaurant or as consequential as whether to wear a face mask amid an infectious disease outbreak. Individual differences in risk-taking are one of the most critical factors in explaining a range of real-life behaviors, such as financial choices (Noussair et al., 2014), alcohol consumption (Abbey et al., 2006), and gambling (Wiehler and Peters, 2015).

Risk tolerance is defined as the willingness to take risks for some reward (Karlsson Linnér et al., 2019). For decades, decision researchers have been investigating how our brain responds to risk and what neural mechanisms underlie individual differences in risk tolerance (Bechara et al., 1997; Hsu et al., 2005) and the advent of neuroimaging techniques such as functional magnetic resonance imaging (fMRI) has increased understanding of the neurobiological underpinnings of human risk taking (Quartz, 2009; Schonberg et al., 2011). Neural activity in multiple brain regions, including the striatum, amygdala, anterior cingulate cortex (ACC), and ventromedial prefrontal cortex (vmPFC) has been associated with risk-taking and decision-making behavior (Tom et al., 2007). In addition, gray matter volume (GMV) in the right posterior parietal cortex (PPC) (Gilaie-Dotan et al., 2014; Grubb et al., 2016) and bilateral amygdala (Jung et al., 2018) have also been linked to risk tolerance in decision-making tasks. These findings suggest that individuals’ risk tolerance is, at least partly, shaped by neuroanatomic features in the brain.

Most laboratory studies investigate risk taking behavior with one-shot gamble choice tasks, in which participants were typically asked to choose between two monetary gambles with given probabilities. For example, participants may choose between an option offering an 80% chance of $50, and a 20% chance of $0, versus an option offering $40 for sure. Typically, these tasks directly depict the probabilities of each decision outcome in numeric or graphic formats (Gilaie-Dotan et al., 2014; Grubb et al., 2016; Jung et al., 2018). The limited ecological validity and scope of these tasks, however, may undermine the replicability and generalizability of the intriguing findings. Specifically, risk tolerance is likely a multifaceted psychological construct rather than a unidimensional psychological trait (Erev et al., 2017; Frey et al., 2017). Previous studies suggested that while most people are risk-averse in choosing between prospects in which probabilities are explicitly given,
they may become risk-seeking when probabilities have to be inferred from past experiences (Hertwig et al., 2004; Kahneman and Tversky, 1979). Neuroimaging studies also suggest that risky decisions with ambiguous risks may activate additional brain regions than risky decisions with risk information given (Huettel et al., 2006). Therefore, decision tasks which provide more ecological validity of risk-taking assessment are needed to better understand the neuroanatomic underpinnings of the multidimensional risk tolerance.

In this study, we employed a well validated and more ecologic paradigm – the Balloon Analogue Risk Task (BART) (Lejuez et al., 2003) to assess individual risk-taking behavior and risk tolerance. In this task, participants are required to pump a virtual balloon to earn rewards. The more pumps participants made, the higher rewards they could collect, and the greater risk that the balloon might burst after each pump. If the balloon burst, participants lost all the rewards they accumulated for the balloon. The BART resembles risky decision making in real life, where the exact probability distribution of the outcomes is unknown. Unlike the one-shot gamble choice, the BART is a sequential decision task, in which the final reward is the outcome of a series of decisions. Moreover, because of its sequential nature of balloon-pumping, optimal decision making in BART requires multiple cognitive functions including optimal stopping and behavior planning (Wallsten et al., 2005). These unique features of the BART provide an opportunity to study risk tolerance beyond the scope of the standard risky gamble choices, such as learning from past experiences, planning, and stopping functions, which are rarely examined in studies of risky gamble choices.

We used the extended Expectancy Valence model (Busemeyer and Stout, 2002; Wallsten et al., 2005) to model the behavioral data and characterize individual risk tolerance $\gamma$ during the BART. This model has four free parameters including risk tolerance parameter $\gamma$, prior belief of balloon not bursting parameter $\phi$, updating rate parameter $\eta$, and inverse temperature parameter $\tau$. Previous studies suggest that this model outperforms other models and provide a good description of risk-taking data in the BART (e.g., Wallsten et al., 2005). Moreover, in order to further evaluate the association between neurobiological features and risk tolerance, we modified the Expectancy Valence model using neurobiological features as the predictors of risk tolerance parameter $\gamma$ in a manner analogous to linear regression (Boehm et al., 2018). In these models, risk tolerance became an intermediate variable and was not directly estimated. Instead, the coefficients of the neurobiological features as a function of risk tolerance across individuals were estimated, representing the extent to which the neurobiological features determine risk tolerance in the BART. In so doing, we not only replicated previous findings on the predictive power of neuroanatomic features in risk tolerance, including the right PPC and bilateral amygdala GMV, but also uncovered a strong and cerebellar anatomical contribution to risk tolerance in the BART. Furthermore, because VBM analysis only assesses variability in brain structure, we also used arterial spin labeling (ASL) perfusion fMRI to quantify regional CBF as a biomarker of brain function to determine if it would provide additional explanatory power for individual risk-taking behavior and risk tolerance.

Aging has a well-documented effect on risky decision making, and people typically become less risk-tolerant and more cautious when they grow older (Deakin et al., 2004; Heckhausen et al., 1989; Vroom and Pahl, 1971). Prior work suggests that neuroanatomical changes
in the right PPC may underlie age-related changes in risk tolerance using risky gamble choice tasks (Grubb et al., 2016). Moreover, there is some evidence suggesting that risk tolerance may vary with gender. For example, a previous study reported that men were more risk tolerant than women in decision-making (Bollen and Posavac, 2018). Therefore, in this study we investigated the effects of aging and gender on risk tolerance in the BART and the neuroanatomic changes underlying such effects, to unpack the co-evolution of neurobiological features and risk tolerance.

2. Materials and methods

2.1. Sample characteristics

All participants were right-handed, had a normal or corrected-to-normal vision, and neurologically and psychiatrically healthy. A total of 115 healthy adults (age range 21–50 years, 59 male) were included in the final analysis, including 39 White, 37 African American, 18 Asian, and 21 with more than one races. The study procedure was approved by the University of Pennsylvania institutional review board. Written informed consent was obtained from all participants.

2.2. Procedure

The MRI-compatible BART paradigm (Rao et al., 2008) was designed to measure individual risk-taking behavior within the MRI scan chamber. During the task, participants were asked to inflate a virtual balloon that could either grow larger or explode. For each balloon, participants had the option to continue or discontinue inflating the balloon by pressing two buttons. Larger balloons were always associated with greater risk of explosion and increased monetary rewards. The probability of explosion was set to monotonically increase from 0 to 89.6%, and the wager to increase from 0 to 5.15 dollars, from the smallest balloon to the largest balloon. The maximum number of inflations participants could make for each balloon was 12 and unknown to the participants. Participants were instructed to make multiple inflation attempts for the balloons and maximize their monetary rewards. If participants continued to inflate the balloon and the balloon exploded, they lost the wager of the current balloon which was subtracted from their total winnings. If participants stopped inflating the balloon, they could cash out and collect the wager for the current balloon. The timing of inflation was controlled by a cue and participants could press a button to continue or discontinue inflation only when the color of the cue was green. The outcome for each trial was immediately provided to participants once they collected the wager or the balloon exploded.

2.3. Image acquisition

MRI scans were performed using a 3T Siemens Trio scanner (Siemens Medical Systems, Erlangen, Germany). High-resolution anatomic images were obtained using a T1-weighted 3D Magnetization Prepared Rapid Acquisition Gradient Echo (MPRAGE) sequence with repetition time (TR) = 1620 ms, echo time (TE) = 3.09 ms, flip angle (FA) = 15°, 176 contiguous slices, matrix size = 192 × 256, voxel size = 0.98 × 0.98 × 1.0 mm³. ASL perfusion images were acquired by using a pseudo-continuous ASL (pCASL) sequence with a 2D echoplanar imaging readout (EPI) with the following parameters: TR = 4 s, TE = 18
ms, labeling time = 1.5 s, delay time = 1.0 s, FOV = 220 × 220 mm, matrix = 64 × 64, slice thickness = 5 mm, interslice gap = 1 mm, number of slices= 20, 60 acquisitions. During the scan, the participants were instructed to keep their eyes open and fixate on a cross mark in the center of the screen.

2.4. Behavior modeling

The current study applied hierarchical Bayesian modeling to study behavioral BART performance. We modeled the BART performance using the Expectancy Valence model (Busemeyer and Stout, 2002; van Ravenzwaaij et al., 2011; Wallsten et al., 2005). According to this model, a participant develops a belief of the balloon bursting probability for each trial $k$. This belief, $p_{k}^{burst} = 1 - \frac{\phi + \eta \sum_{K=0}^{K-1} n_{K}^{success}}{1 + \eta \sum_{K=0}^{K-1} n_{K}^{pumps}}$, is a function of her/his prior belief of balloon not bursting $\phi$ and is updated based on one’s experience with the task throughout the trials, with $\eta$ representing the updating rate, $n_{K}^{pumps}$ representing the total number of pumps in trial $K$ and $n_{K}^{success}$ representing the number of successful pumps in trial $K$. Participants may display different levels of risk tolerance in our task. Following Wallsten et al. (2005), we defined risk tolerance $\gamma$ as the risk aversion parameter in the prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), where $\gamma = 1$ means risk-neutral, $0 < \gamma < 1$ means risk-aversion and $\gamma > 1$ means risk-seeking. With a given burst belief $p_{k}^{burst}$ and risk tolerance $\gamma$, we can derive the desirable number of pumps $o_{k} = \frac{-\gamma}{\log(1 - p_{k}^{burst})}$ for each trial $k$. The probability of making the $l$th pump in trial $k$ (if the balloon does not burst after the $(l-1)$th pump) is written as

$$p_{kl}^{pump} = \frac{1}{1 + \exp(-\gamma \times (o_{k} - l))}$$

In summary, the mathematical model used in the current study is described by four free parameters (Wallsten et al., 2005). We estimated the model parameters at the individual level with the hierarchical Bayesian analysis implemented in the hBayesDM (version 1.0.2) R package (ccs-lab.github.io/hBayesDM/) for computational modeling of BART data (Ahn et al., 2017; Wallsten et al., 2005). Hierarchical Bayesian analysis can provide individual-level parameter estimation and can be interpreted with more confidence compared to maximum likelihood estimation methods (Ahn et al., 2011). We used Ahn et al. (2017) default specification of prior distributions and initialized four Markov Chain Monte Carlo (MCMC) chains randomly and in each chain collected 10,000 formal samples after 1000 burn-in samples.

We then ran ten additional hierarchical Bayesian models to directly evaluate the neurobiological features’ predictive ability for risk tolerance in the BART. All hierarchical Bayesian analysis was carried out in Stan (StanDevelopmentTeam, 2019). In these models, the risk tolerance parameter $\gamma$ was written as a linear function of a set of neurobiological features across participants, in a manner analogous to linear regression. The predicted $\gamma$ was in turn imputed into a hierarchical Bayesian version of the extended Expectancy Valence...
model that was fitted on the behavioral BART data. Note that all the neurobiological features were normalized before entering the hierarchical Bayesian models. We used the standard normal distribution as the prior distribution for the neurobiological features coefficients. For convergence check, we ran four independent MCMC chains of 10,000 formal samples after 5000 burn-in samples each. The convergence of the MCMC chains were accessed using the Gelman–Rubin statistic ($\hat{R} < 1.1$ for all parameters) (Gelman and Rubin, 1992).

### 2.5. VBM analysis

Voxel-based morphometry was performed using CAT12 (Jena University Hospital, Departments of Psychiatry and Neurology, Jena, Germany, www.neuro.uni-jena.de) and SPM12 toolbox (Wellcome Department of Cognitive Neurology, London www.fil.ion.ucl.ac.uk), implemented in MATLAB 2016 (Mathworks Inc., Sherborn, MA, USA). All images were visually inspected for artifacts and passed homogeneity control implemented in the CAT12 toolbox. The structural images were normalized to Montreal Neurological Institute (MNI) stereotactic space, spatially smoothed with a Gaussian kernel (FWHM = 8 mm), and then entered a voxel-wise whole-brain multiple regression analysis with gender, age, and total GMV included as covariates. This analysis revealed a cluster in the left cerebellum where the anatomy significantly correlated with risk tolerance. To provide better localization of the observed cerebellar cluster, the Spatially Unbiased Infratentorial Toolbox (SUIT, version 3.4, github.com/jdiedrichsen/suit/) was used to isolate the cerebellum from the rest of brain (Diedrichsen, 2006; Diedrichsen and Zotow, 2015). Brain tissues outside the cerebellum were manually removed and excluded by MRICron software and the cerebellum images were then normalized to MNI space using a diffeomorphic spatial deformation (DARTEL) algorithm (Ashburner, 2007).

### 2.6. ASL analysis

ASL imaging data were processed using SPM12 (www.fil.ion.ucl.ac.uk/spm/) and ASLtbx (cfn.upenn.edu/perfusion/software.htm) (Wang et al., 2008). The functional image is realigned to correct head motion and co-register with the anatomical image. A series of perfusion-weighted images is then generated by subtracting the label from the control images. These images were then converted to absolute total CBF images based on a single compartment continuous arterial spin labeling (CASL) perfusion model (Wang et al., 2005). The mean CBF images were normalized to MNI space and spatially smoothed with a Gaussian kernel (FWHM = 8 mm). Regional CBF was sampled using the MarsBaR toolbox.

### 2.7. Mediation analysis

We performed multiple mediation analyses using PROCESS to investigate the role of GMV in multiple brain regions between age and risk-taking behavior/risk tolerance. PROCESS is an ordinary least squares path analysis modeling tool based on SPSS (www.processmacro.org), which can estimate indirect effects and direct effects in mediation models. Here we used the 95% bootstrap confidence intervals (95% CI) from 5000 bootstraps to assess the significance of effects. If a 95% CI doesn’t include zero, the $p$-value would be < 0.05, which is the conventional level of statistical significance.
3. Results

3.1. Hierarchical Bayesian modeling of behavior

On group level, the mean estimation of $\gamma$ is 0.458 (90% high-density interval is [0.445, 0.472]), indicating that participants were risk averse on the BART. This is consistent with previous findings from the modeling of BART data (e.g. Wallsten et al., 2005; Zhou, 2017). On the individual level, all participants $\gamma$ values are below 1. Importantly, this suggests that participants tended to under-pump the balloon as risk neutrality ($\gamma = 1$) corresponds to expected value maximization and is typically regarded as optimal in the context of repeated decision making. Thus, in this experiment, participants with higher $\gamma$ (i.e., closer to 1) can be regarded making more optimal decisions.

In many previous studies, BART performance was usually quantified by adjusted BART scores ($\text{BART}_{adj}$), i.e., the average number of pumps on the unexploded balloons (Lejuez et al., 2003). A higher $\text{BART}_{adj}$ score reflects higher risk-seeking behavior propensity. In the following analyses, we used $\text{BART}_{adj}$ to index risk-taking behavior, and $\gamma$ to index risk tolerance. As shown in Fig. 1, the correlation between $\text{BART}_{adj}$ and $\gamma$ was highly significant, indicating that $\gamma$ plays a key role in risk-taking behavior in the BART. There was also a significant negative correlation between age and $\text{BART}_{adj}$, and a trend towards a negative correlation between age and $\gamma$.

3.2. Associations between right PPC/amygdala anatomy and risk-taking

We first examined the associations between right PPC, bilateral amygdala GMV, and risk-taking behavior/risk tolerance (Gilaie-Dotan et al., 2014; Grubb et al., 2016; Jung et al., 2018). The right PPC was defined as a cluster from the literature (Gilaie-Dotan et al., 2014) and bilateral amygdala were defined from the automated anatomical labeling atlas (Rolls et al., 2015).

As shown in Fig. 2, both right PPC GMV and bilateral amygdala GMV showed significant positive correlations with the risk tolerance $\gamma$ and risk-taking behavior $\text{BART}_{adj}$. These results replicated findings from previous studies (Gilaie-Dotan et al., 2014; Jung et al., 2018). However, after controlling for gender, age, and total GMV, the correlations between the right PPC GMV or bilateral amygdala GMV and individual risk tolerance $\gamma$ or risk-taking behavior $\text{BART}_{adj}$ were not significant (all $p > 0.1$).

3.3. Associations between cerebellum anatomy and risk-taking

We conducted a voxel-wise whole-brain multiple regression analysis with gender, age, and total GMV included as covariates. The results were displayed in Fig. 3a. This analysis found a cluster in the left cerebellar Crus I (extended to VI) where the anatomy significantly correlated with risk tolerance $\gamma$ (peak MNI coordinates = $[-11, -75, -27]$), cluster-level FWE corrected $p < 0.05$). However, no regions in the right PPC or bilateral amygdala were detected even with a liberal threshold of uncorrected $p < 0.005$.

To validate cerebellum findings from the whole brain analysis, we further performed an independent region of interest (ROI) analysis based on a literature defined cerebellum ROI.
from a PET imaging study of risky decision making (Ernst et al., 2002). As shown in Fig. 3b and c, the independent ROI analyses confirmed significant positive correlations between the left cerebellum GMV and individual risk tolerance $\gamma (r = 0.37, p < 0.001)$ as well as that between the left cerebellum GMV and individual risk-taking behavior BART$\text{adj} (r = 0.29, p = 0.002)$. After controlling for gender, age, and total GMV, these correlations remained significant (both $p < 0.01$).

### 3.4. The mediating role of cerebellum anatomy between age/gender and risk-taking

To examine the mediating roles of above mentioned GMVs in the relationships between age and risk-taking behavior/risk tolerance, we conducted mediation analyses similar to the previous study (Grubb et al., 2016). As shown in Fig. 4, there was a significant indirect effect ($p < 0.05$) between age and $\gamma$ only through the left cerebellum GMV, but not through right PPC GMV or bilateral amygdala GMV. Similarly, there was a significant indirect effect ($p < 0.05$) between age and BART$\text{adj}$ only through the left cerebellum GMV. The direct effect between age and $\gamma$ was not significant, suggesting that left cerebellum GMV played a full mediation role between age and $\gamma$/BART$\text{adj}$. We also calculated the mediating effects between gender and risk-taking behavior/risk tolerance. As shown in Fig. S1, left cerebellum GMV played a full mediation role between gender and $\gamma$/BART$\text{adj}$.

### 3.5. Associations between regional CBF and risk-taking

We conducted a series of correlation analyses to examine the associations between $\gamma$/BART$\text{adj}$ and regional CBFs in the right PPC, bilateral amygdala, and left cerebellum. As shown in Fig. 5, there were significant negative correlations between bilateral amygdala CBF and $\gamma$ and BART$\text{adj}$ (both $p < 0.05$), and trend towards significant negative correlations between right PPC CBF and $\gamma$ ($p = 0.07$) and between left cerebellum CBF and BART$\text{adj}$ ($p = 0.05$). However, none of these correlations were significant after controlling for gender, age, and whole brain mean CBF (all $p > 0.1$).

To examine whether regional CBF would provide additional predictive power to the BART risk-taking behavior and risk tolerance, we further carried out a stepwise regression analysis with all the neurobiological features, including GMVs and regional CBFs in the target brain areas, as well as gender and age, as potential predictors. Only left cerebellum GMV entered the final model, and accounting for 22.2% of the variation in $\gamma$, while no regional CBF provided additional predictive power to the risk-taking behavior and risk tolerance.

### 3.6. Hierarchical Bayesian modeling including neurobiological features

To further validate the neurobiological features underlying risk tolerance in BART, we directly modeled the choice data using various neurobiological features as predictors of the risk tolerance parameter $\gamma$ in hierarchical Bayesian models. Specifically, we regressed $\gamma$ as a function of the neurobiological features. The predicted $\gamma$ was in turn imputed into the extended Expectancy Valence model to fit participants’ choice data. We tested ten such models with different neurobiological covariates and estimated the models marginal likelihoods (Gronau et al., 2017). The higher the marginal log-likelihood (MLL), the better the model performance. We can calculate a Bayes factor between each pair of models as...
\[ BF_{1,2} = e^{MLL_1 - MLL_2}, \] where \( MLL_1 \) and \( MLL_2 \) are the marginal log-likelihoods of the two models, respectively. The marginal likelihoods and the corresponding Bayes factors are appropriate measures of model performance as they automatically achieve a balance between the goodness of fit and model complexity.

As shown in the middle column of Table 1, modeling risk tolerance on the GMVs of right PPC and bilateral amygdala improved the marginal log-likelihood, relative to the baseline model without neurobiological covariates, suggesting that both the GMVs of right PPC and bilateral amygdala have predictive power for risk tolerance in the BART. By contrast, the inclusion of regional CBF values in right PPC, bilateral amygdala, and left cerebellum as covariates did not improve model performance. The left cerebellum GMV proved the most powerful predictor of risk tolerance in the BART. As shown in each row of Table 1, including left cerebellum GMV as a covariate improved model performance with Bayes factors at an order of magnitude of 10 (i.e. \( BF > 10^{10} \)), no matter what other covariates were involved. Furthermore, the model that included only left cerebellum GMV provided the best model performance. The Bayes factor between that model and the second-best model, the one including both left cerebellum GMV and bilateral amygdala GMV as the predictors, was 61, which provides substantial evidence for the winning model.

The posterior estimation of the coefficient associated with the left cerebellum GMV in the models also revealed a robust effect of left cerebellum GMV on risk tolerance. As in the right column of Table 1 and Fig. 6, the posterior estimation of left cerebellum GMV coefficient in the various hierarchical Bayesian models with neurobiological covariates was higher than zero, while the prior distribution was set at zero with a unit deviation. Overall, both Bayesian model selection and Bayesian estimation of the coefficient suggest that a larger left cerebellum GMV leads to greater risk tolerance in the BART.

### 4. Discussion

In the present study, we examined how well multi-modal neural markers explain and predict individual risk-taking behavior and risk tolerance in the BART, an ecological decision task in which the probabilities are not explicitly given. We replicated previous findings from risky gamble choice tasks that greater GMVs in the right PPC and bilateral amygdala are associated with higher risk tolerance. We further found that left cerebellum GMV was a strong predictor of risk tolerance, with much stronger predictive power than the right PPC and bilateral amygdala. We also found that left cerebellum GMV fully mediated the relationship between age/gender and risk tolerance, suggesting that changes in the left cerebellum microstructure can account for risk tolerance changes with aging or gender.

Using the BART to measure risk tolerance, we replicated the key findings from the literature that right PPC GMV and bilateral amygdala GMV are associated with risk tolerance (Gilaie-Dotan et al., 2014; Grubb et al., 2016; Jung et al., 2018). While Grubb et al. (2016) reported that the right PPC GMV is highly predictive of risk tolerance in choices between a certain payoff and a risky gamble, Jung et al. (2018) observed a trending relationship between the right PPC GMV and risk tolerance and further showed that the GMV in bilateral amygdala is highly predictive of risk tolerance in a similar task. These different findings may arise...
from some differences in the experimental procedure. For example, while Grubb et al. (2016) used a graphic format to present probabilities (together with numeric digits), Jung et al. (2018) used purely numeric percentages. It may also arise from the heterogeneity among participants. Nonetheless, we replicated both findings using a sequential balloon analogue risk taking paradigm which is different from the one-shot risky gamble tasks, suggesting that the rich microstructure of the decision process in the BART may offer an ideal test-bed for uncovering the biological underpinnings of risk tolerance.

A novel finding in our study was the strong association between left cerebellum GMV and risk tolerance. This may reflect specific features of the BART. In particular, sequential balloon-pumping may capture cognitive functions involved in risk tolerance for everyday decision making, such as optimal planning and stopping. The cerebellum is widely known to contribute to these executive functions (Barton, 2012; Gao et al., 2018). Our finding that the higher left cerebellum GMV leads to higher risk tolerance and more advantageous decision making is consistent with those previous findings.

The predictive power of left cerebellum GMV may also be uniquely associated with decisions in which the probabilities are not explicitly given, such as the BART. Instead, participants must derive a sense of risk probabilities from their experience with the game. The BART also requires participants to make decisions sequentially with outcome feedback after each decision making. Accordingly, participants update the riskiness of their decisions, in stark contrast with the one-shot risky gamble choice where learning from past experiences is absent. With these features, the BART provides a good resemblance to how people interact with a capricious environment in typical everyday decision-making.

A recent study with a very large sample size found that GMV in multiple brain regions, including the cerebellum, was negatively correlated with the tendency to engage in everyday risky behaviors (Aydogan et al., 2021). Although our results appear to be contradictory to theirs, both our and their studies are consistent with the role of the cerebellum in optimal stopping and behavior planning. Since almost all participants in our study showed some degree of risk aversion, participants with higher risk tolerance (with $\gamma$ closer to 1) were more likely to engage in optimal decision making and ended up earning more rewards (Wallsten et al., 2005; Zhou, 2017). By contrast, in Aydogan et al. (2021), risky behavior was defined as behaviors with negative consequences such as smoking and drinking. Thus, Aydogan et al. (2021) results also suggest that higher cerebellum GMV may lead to optimal decision making by reducing the tendencies of suboptimal risky behavior. Congruently, both our study and Aydogan et al. (2021) study suggest that cerebellar anatomy may be a reliable predictor of risk preference, although the relationship between cerebellum GMV and risk attitude may not be monotonic. Rather, the cerebellum anatomy may represent the optimality of risky decision making, which needs to be examined in future studies.

Forward internal models of cerebellar function that can mimic the input and output characteristics of the motor apparatus and external objects or their inverse transformations may also explain cerebellar influence on BART performance (Kawato et al., 2003). The cerebellar forward internal model helps predict future outcomes in decision making (Blackwood et al., 2004; Ernst et al., 2002; Vorhold et al., 2007). It provides an estimate
of the new state or outcome for specific inputs (Sokolov et al., 2017). In motion control, the forward internal model transforms a motor command into a prediction of the sensory consequences of a motor act (Ishikawa et al., 2016). It generates sensory prediction which can be used to coordinate motor output (Ebner et al., 2011), predicts the consequences of a motor act (Wolpert and Kawato, 1998), and updates the state estimation of the motor system (Frens and Donchin, 2009). Decision making is a complex process that involves calculating both the potential rewards and the associated negative consequences of different choices. The role of the cerebellum in decision making may be similar to that in motion control, which includes two elementary components, prediction and error-based learning. From a computational viewpoint, the cerebellum is specialized for supervised learning, which is guided by the error signal encoded in the climbing fiber input from the inferior olive (Doya, 2000). The cerebellum processes error signals that could be used for improving performance (Ernst et al., 2002), monitors and adjusts input from cortical systems (Bower, 1997; Harrington et al., 2004), process error signals that can be used to improve performance (Doya, 2000). In the BART, participants must code the potential gains and losses on each balloon and choose between inflating the balloon and cashing out. The role of the cerebellum in the BART may be to monitor feedback (i.e. whether a balloon explodes) and to optimize the reaction on each balloon.

Since greater risk-taking behavior is associated with larger number of pumps participants made for the balloons, motor actions (i.e., button presses) may be a potential confounding factor in our study. To provide insights into the cerebellar contribution to risk tolerance during the BART, we compared our cerebellar findings with two existing functional cerebellar atlases (Buckner et al., 2011; King et al., 2019). These atlases summarized several functional regions within cerebellum based on wide-ranging task domains. With the “Buckner_7Networks” atlas, most of our cerebellar ROI overlaps with region 6, which is the representation of the frontoparietal network (Buckner et al., 2011). The structure and function of the frontoparietal network are known to support working memory, attention, and executive functions (Coull et al., 1996; Veldsman et al., 2020). With the “MDTB_10Regions” atlas, most of our cerebellar ROI overlaps with region 5, which is also associated with attention- and working memory-related features (King et al., 2019). In addition, we did a multiple regression analysis on the independent ROI data by including BART$_{adj}$ (average number of pumps participants made for the unexploded balloons) as a covariate to control for the confounding factor of motor actions. The correlation between the left cerebellar GMV and individual risk tolerance remained significant after controlling for BART$_{adj}$ ($p = 0.007$), suggesting that motor actions cannot explain the associations between cerebellar anatomy and risk tolerance. Taken together, these findings suggest that the observed cerebellar association with risk tolerance may reflect cognitive-related features rather than motor-related features.

Abnormal cerebellum morphometry is also associated with several neuropsychiatric disorders characterized by risky behaviors (impulsivity), including schizophrenia (Courchesne et al., 1988), autistic spectrum disorders (D’Mello and Stoodley, 2015), and marijuana use (Medina et al., 2010). Moreover, alcohol abuse is one of the most commonplace risk-taking behaviors and abnormal cerebellar morphometry has been associated with the age at first drinking but is independent of the duration and the amount

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of alcohol intake (Chanraud et al., 2007). It suggests that cerebellar morphometry may contribute to risky behaviors in early adolescence, instead of vice versa, alcohol exposure cause alterations of cerebellar morphometry. Our findings are also consistent with a previous study showing that amphetamine may reduce cerebellar hyperactivity which is associated with impulsive behavior (Majdak et al., 2016). Taken together, these studies support the important role of the cerebellum in risk tolerance and impulsive action.

In contrast to the cerebellum anatomy, regional CBF in the cerebellum, right PPC, and amygdala did not provide additional predictive power for individual risk tolerance. A possible limitation for ASL perfusion imaging is that the 2D pCASL sequence used in this study did not have good coverage on the cerebellum, which is on the edge of imaging volume and sensitive to motion artifacts. In addition, unlike the GMV which is more a like latent trait-like biomarker, CBF may reflect not only latent traits, but also phasic situational effects (Hermes et al., 2009). These factors may attenuate the associations between regional CBF and individual risk tolerance. Nevertheless, our findings suggest that brain morphometry outperforms regional CBF for predicting the trait-like individual risk tolerance.

Not surprisingly, left cerebellum GMV fully mediated the relationship between age and risk tolerance. Moreover, left cerebellum GMV also mediated the relationship between gender and risk tolerance. Left cerebellum GMV seems to be a valuable indicator of risk tolerance, whether the changes in the risk tolerance vary together with age or gender. There is a widespread view that women may be more risk-averse than men (Bollen and Posavac, 2018; Duell et al., 2018). In our study, we only observed a trend for gender difference in risk tolerance ($p = 0.07$). Previous studies suggest that gender difference in the willingness to take risk may be context sensitive (Maxfield et al., 2010) and culture-specific (Friedl et al., 2020). A more recent study reported that men do not necessarily make more risky choices than women (Baeckström et al., 2021). Nevertheless, more studies are needed to further examine gender differences in risk tolerance and cerebellar anatomy.

In summary, findings from this study demonstrate a novel cerebellar anatomical contribution to risk tolerance during the BART. This study extends prior research showing a link between risk tolerance and structural neurobiological features. Further studies are necessary to elucidate the underestimated important role of the cerebellum in multidimensional risk-taking and real-world risky behaviors.

**Supplementary Material**

Refer to Web version on PubMed Central for supplementary material.

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Data availability statement

The data that support the findings of this study are available from the corresponding author, Dr. Hengyi Rao, with the need for a formal data sharing agreement and a formal project outline.

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Fig. 1.
Correlations between risk tolerance ($\gamma$), risk-taking behavior (BART$_{adj}$), and age.
Fig. 2.
Correlations between GMV in the previously reported right PPC/bilateral amygdala regions and risk tolerance/ risk-taking behavior. (a) A priori defined region of interest: right PPC (left) and bilateral amygdala (right) (b) Risk tolerance ($\gamma$) plotted as a function of right PPC GMV. (c) Risk-taking behavior (BART$_{adj}$) plotted as a function of right PPC GMV. (d) Risk tolerance ($\gamma$) plotted as a function of bilateral amygdala GMV. (e) Risk-taking behavior (BART$_{adj}$) plotted as a function of bilateral amygdala GMV.
Correlations between the left cerebellum GMV and risk tolerance/risk-taking behavior. (a) VBM map showing significant correlations between risk tolerance ($\gamma$) and GMV in the left cerebellar Crus I (extended to VI). Gender, age, and total GMV were included in the design matrix as covariates. The statistical significance threshold was set at cluster-level FWE-corrected $p < 0.05$ (cluster size $> 100$) and at voxel-level uncorrected $p < 0.001$. (b) Risk tolerance ($\gamma$) plotted as a function of left cerebellum GMV (independent ROI). (c) Risk behavior (BART<sub>adj</sub>) plotted as a function of left cerebellum GMV (independent ROI).
Fig. 4.
Mediating roles of the GMVs in the relationships between age and risk tolerance/risk-taking behavior. (a) mediating role of bilateral amygdala GMV between age and risk tolerance; (b) mediating role of bilateral amygdala GMV between age and risk behavior; (c) mediating role of right PPC GMV between age and risk tolerance; (d) mediating role of right PPC GMV between age and risk behavior; (e) mediating role of left cerebellum GMV between age and risk tolerance; (f) mediating role of left cerebellum GMV between age and risk behavior; (g) mediating role of bilateral amygdala GMV, right PPC GMV and left cerebellum GMV between age and risk tolerance; (h) mediating role of bilateral amygdala GMV, right PPC GMV and left cerebellum GMV between age and risk behavior. Note. The solid and dashed lines indicate the significant/non-significant relationship between each variable, respectively. The hypothetical causations are indicated by a one-way arrow. Indirect effect = a × b; direct effect = c'. Unstandardized regression coefficients are presented.
Fig. 5.
Correlations between regional CBFs and risk tolerance/risk-taking behavior. (a) Risk tolerance ($\gamma$) plotted as a function of right PPC CBF. (b) Risk-taking behavior ($\text{BART}_{\text{adj}}$) plotted as a function of right PPC CBF. (c) Risk tolerance ($\gamma$) plotted as a function of bilateral amygdala CBF. (d) Risk-taking behavior ($\text{BART}_{\text{adj}}$) plotted as a function of bilateral amygdala CBF. (e) Risk tolerance ($\gamma$) plotted as a function of left cerebellum CBF. (f) Risk-taking behavior ($\text{BART}_{\text{adj}}$) plotted as a function of left cerebellum CBF.
Fig. 6.
Prior and posterior distributions of left cerebellum GMV’s coefficient in the hierarchical Bayesian models with neurobiological covariates. The prior distribution of the coefficient is the standard normal distribution (i.e. zero mean with unit standard deviation). GMV = grey matter volume; lCB = left cerebellum; rPPC = right posterior parietal cortex; bAMY = bilateral amygdala; rCBF = regional cerebral blood flow.
### Table 1

The marginal log-likelihoods of Bayesian hierarchical models with neurobiological covariates and Bayesian estimation of the coefficient of left cerebellum GMV.

| Covariates other than left cerebellum GMV | Marginal log-likelihood | Bayesian estimation of left cerebellum GMV’s coefficient |
|------------------------------------------|-------------------------|--------------------------------------------------------|
|                                          | Left cerebellum GMV     | Left cerebellum GMV                                  | Mean [90% HDI]                           |
|                                          | excluded                | included                                              |                                          |
| None                                     | –3905                   | –3868                                                 | 0.35 [0.01, 0.90]                        |
| Right PPC GMV                            | –3897                   | –3873                                                 | 0.81 [0.03, 1.62]                        |
| Bilateral amygdala GMV                   | –3893                   | –3872                                                 | 0.81 [0.03, 1.61]                        |
| Right PPC GMV+ bilateral amygdala GMV    | –3896                   | –3875                                                 | 1.19 [0.15, 2.06]                        |
| rCBFs                                    | –3911                   | –3871                                                 | 0.24 [–0.09, 0.64]                       |

Note. The right column reports the posterior mean and 90% high density interval of the left cerebellum GMV’s coefficient from the model involving left cerebellum GMV in each row. The rCBFs include the regional CBFs in right PPC, bilateral amygdala, and left cerebellum. Values in square brackets indicate the 90% HDI for the posterior parameter distribution. HDI = high density interval.