

© 2025 American Psychological Association ISSN: 2325-9965

2025, Vol. 12, No. 3, 216-245 https://doi.org/10.1037/dec0000261

Reassessing the Gut-Cognition Link: Exploring Psychophysiological Mechanisms of Risky Decision-Making

Lisa Musculus¹, Laura Broeker¹, Jose Walter Tolentino-Castro¹, Sven Hoffmann², Ismael Pedraza-Ramirez¹, Sylvain Laborde¹, Babett Lobinger¹, Uirassu Borges¹, Roman Liepelt², Alexandra Pizzera¹, Andreas Schwiertz³, and Markus Raab^{1, 4}

¹ Department of Performance Psychology, Institute of Psychology, German Sport University Cologne ² Department General Psychology: Judgement, Decision Making, Action, Faculty of Psychology, FernUniversität Hagen

³ Medizinisches Versorgungszentrum Institute of Microecology GmbH, Herborn, Germany ⁴ School of Applied Sciences, London South Bank University

In a 6-week randomized, triple-blind, placebo-controlled trial, we investigated the impact of a probiotic intervention on risky choices in healthy adults as well as a potential link between gut microbiota and risky decision-making. Our study explored whether the gut-brain interaction was mediated by gut bacteria or cardiac vagal activity, representing the vagal pathway in the gut-brain axis. Additionally, we examined whether these potential mediations would be moderated by interoceptive accuracy. To assess risky decision-making, the Iowa Gambling Task (IGT; Bechara et al., 1994) and the Balloon Analogue Risk Task (BART; Lejuez et al., 2002) were employed. Interoceptive accuracy was captured with the heartbeat perception task (Dunn et al., 2012; Schandry, 1981). Neither the probiotic intervention nor many of the tested bacteria and cardiac vagal activity predicted risky decision-making. Our data suggest a potential gut-cognition link in healthy adults predominantly via Faecalibacterium prausnitzii and Lactobacillaceae that merits further investigation. This connection was found for risky decision-making in the BART and IGT tasks and was moderated by interoceptive accuracy. Participants with high accuracy in perceiving internal bodily signals while also exhibiting higher numbers of specific bacteria (i.e., F. prausnitzii, Lactobacillaceae) were less inclined to make risky choices. While our results warrant further research concerning the role of Bacillota family of gut bacteria, other recent studies have brought neurotransmitters into play. Future research should consider these possible factors together, scrutinizing psychophysiological mechanisms in risky decision-making.

Keywords: somatic marker hypothesis, gut-cognition link, gut-brain axis, probiotic intervention, microbiome

Supplemental materials: https://doi.org/10.1037/dec0000261.supp

Tim Rakow served as action editor.

Lisa Musculus https://orcid.org/0000-0003-1350-7903 Lisa Musculus and Laura Broeker share first authorship. Andreas Schwiertz and Markus Raab share senior authorship. All data and code for reproducing the analyses are available at the Open Science Framework of Lisa Musculus at https://osf.io/ fq4p7/. The study protocol and procedure were approved by the local ethics committee of the German Sport University

The authors declare that they have no conflicts of interest with respect to their authorship or the publication of this

article. They thank Kathrin Engel, Alina Graw, Alexander vom Dorp, and Daniel Wins for their help in participant recruitment and data collection. They thank Medizinisches Versorgungszentrum Institut für Mikroökologie GmbH for the stoolanalysis kits and the quantitative polymerase chain reaction analyses, and also thank Winclove for the provision of the probiotic/placebo powder, randomization procedure, as well as sequencing analyses to ensure data quality.

Lisa Musculus played a lead role in conceptualization, formal analysis, investigation, methodology, project administration, visualization, supervision, writing-original draft, and writing-review and editing. Laura Broeker played a lead

What if the human gut microbiota impacts not only physical health but risky decisions such as whether to invest money or cross a busy street? Risky decisions involve some element of uncertainty in terms of expected outcome, even though explicit descriptions of probabilities and associated costs may exist (Buelow & Suhr, 2009; Rosenbaum et al., 2018). In advance of such risky decision options, physiological signals may warn individuals and guide them when navigating risks (e.g., Carter & Pasqualini, 2004), especially in time-sensitive situations and environments with incomplete information. These physiological signals include changes with regard to muscle tone, heart rate, posture, or endocrine activity, and Bechara and Damasio (2005) suggested that also an overall positive or negative state can form a "gut feeling" that guides an individual's risky decision-making. Damasio (1996; Damasio et al., 1991), being among the first researchers suggesting this connection between the bodily, somatic system and the brain, proposed that visceral responses are integrated in higher brain regions and strongly influence subsequent decisionmaking ("somatic marker hypothesis"). For instance, a study using skin conductance during the Iowa gambling task (IGT) compared patients with ventromedial prefrontal cortex damage to controls. Controls, but not patients, showed stronger anticipatory skin conductance responses when planning to pick from a "bad deck" associated with lower rewards, compared with "good decks" (Bechara et al., 1996; for skin conductance in the BART, see also Wright & Rakow, 2017). The anticipatory skin conductance responses have been equated with "gut feelings" (e.g., Bechara, 2011, p. 80) without testing whether the gut was

actually the source of that signaling. Yet, a growing body of research suggests that the gutbrain axis (Cryan & Dinan, 2012; Forsythe et al., 2012; Rhee et al., 2009) plays a modulatory role in behavior, with the gut microbiota exhibiting multiple effects on emotions, motivation, and also higher cognitive functions like decisionmaking (Falkenstein et al., 2024; Mayer, 2011; Montiel-Castro et al., 2013; Sarkar et al., 2018). Concerning decision-making, recent work showed that participants exhibit decreased risktaking behavior as compared with a placebo group on the Maastricht Gambling Task after a 28-day probiotic intervention (Dantas et al., 2022; see Table 1). However, no stool samples were analyzed that could have identified differences in gut microbiota after the probiotic intervention. By contrast, this was ensured in a later study by Falkenstein et al. (2024) who examined changes in microbiota composition through a synbiotic (i.e., pro- and prebiotics) intervention and possible impacts on decisionmaking in the ultimatum game. They also examined potential mechanisms taking into account dopamine and serotonin precursors, which have been previously linked to decisionmaking behavior. After their intervention, decision-making was less rational and increasingly sensitive to social considerations and the synbiotic-induced decrease in tyrosine (i.e., dopamine precursor) led to an increase in rejection rates of unfair offers. Sharing the interest in a potential functional connection between gut microbiota and decision-making, but risky decision-making in particular, we also used an approach combining a probiotic intervention and microbiome composition

role in conceptualization, formal analysis, investigation, methodology, project administration, visualization, supervision, writing-original draft, and writing-review and editing. Jose Walter Tolentino-Castro played a lead role in project administration, supervision, and investigation, and a supporting role in writing-review and editing. Sven Hoffmann played a supporting role in conceptualization, formal analysis, investigation, methodology, and writing-review and editing. Ismael Pedraza-Ramirez played a supporting role in conceptualization, investigation, methodology, and writingreview and editing. Sylvain Laborde played a supporting role in conceptualization, methodology, and writing-review and editing. Babett Lobinger played a supporting role in conceptualization, visualization, and writing-review and editing. Uirassu Borges played a supporting role in conceptualization, methodology, and writing-review and editing. Roman Liepelt

played a supporting role in conceptualization, methodology, and writing–review and editing. Alexandra Pizzera played a supporting role in conceptualization, visualization, and writing–review and editing. Andreas Schwiertz played a lead role in conceptualization, formal analysis, and providing resources, and played a supporting role in writing–review and editing. Markus Raab played a lead role in conceptualization and providing resources, and a supporting role in formal analysis, methodology, supervision, writing–original draft, and writing–review and editing.

Correspondence concerning this article should be addressed to Lisa Musculus, Department of Performance Psychology, Institute of Psychology, German Sport University Cologne, Am Sportpark Müngersdorf 6, 50933 Cologne, Germany. Email: l.musuculus@dshs-koeln.de

This article is intended solely for the personal use of the individual user and is not to be disseminated broadly. This document is copyrighted by the American Psychological Association or one of its allied publishers.

Overview of Intervention Studies Examining Probiotic-Intervention Effects on Cognition (Intervention Studies) in Healthy Adults Table 1

			Intervention studies		:	
Publication	Design	Probiotic composition	Cognitive task	Main effects on cognitive outcome	Main effects on microbiota	Mechanism proposed and/or tested
Falkenstein et al. (2024)	7-week, randomized, double-blind, placebo-controlled N = 101 male adults (M = 32.05 ± 10.6)	B. lactis, L. animalis, L. casei, L. salivarius, L. lactis, inulin 2 × 10° CFU/dose	Ultimatum game	Probiotic group rejected a higher proportion of offers	Probiotic effect dependent on baseline gut composition (the more unbalanced the F/B ratio, the bigger the intervention effect)	Tested mechanism: whether intervention changed plasma levels of dopamine-precursor tyrosine and serotonin precursor tryptophan probosed mechanism: in probiotic group participants with higher F/B ratio at baseline (a) had stronger gut changes and (b) had a reduction in tyrosine which resulted in a higher increase in rejection of unfair offers
ct al. (2024)	Ruiz-Gonzalez 10-week, randomized, B. lactis, L. rhan et al. (2024) double-blind, placebo- Daily: 3.3×10^9 controlled, crossover CFU/capsule $N = 33$ healthy older adults $(M = 65.94 \pm 6.2)^a$	B. lactis, L. rhannosus Daily: 3.3 × 10 ⁹ CFU/capsule	MMSE, Color-Word Stroop, Corsi Task, Digit Span Test, Go/No-Go Task, Iowa Gambling Task, Tower of London, Trail Making Task, WCST Beck Depression Inventory, State-Trait Anxiety Inventory	Noticeable enhancements after intervention observed in cognitive function, memory (MMSE), digit span test, and depressive symptoms. Significant improvements observed in planning and problem-solving skills, selective attention, cognitive flexibility, impulsivity, and inhibitory ability.	Not tested	Tested mechanism: NA Proposed mechanism: Significant improvement in cognitive function following multispecies probiotic administration experienced by participants may be explained by existence of several gut- brain interaction pathways

This document is copyrighted by the American Psychological Association or one of its allied publishers. This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Table 1 (continued)

, k, k, st.	Intervention studies Main effects on Machanism proposed and/or	e microbiota	Participants in probiotics Relative abundances aroup significantly of bacteria like Proposed mechanism: greater changes in Lachnospira, Bifdobacterium longum total score and almost Bifdobacterium, BB68S improves cognitive all domains (except Dorea, and function by reshaping gut for language domain) Cellulosilyticum microbiota, reducing (associated with placebo group positive health placebo group effects, including along gut-brain axis improved gut health and potentially cognitive function) increased after probiotic intervention; significant decrease in abundance of bacteria associated with cognitive impairment (e.g., Collinsella, Bilanhila) Respective decrease in abundance of bacteria associated with cognitive impairment (e.g., Collinsella, Bilanhila)	Probiotic group Significantly reduced risk-taking compared with placebo group. Despite a general nover time, probiotics group less likely to engage in risky decisions by the end decisions by the end decisions by the end significantly reductions in inflammation of the cardy reduction of the cardy reductions in inflammation of the cardy reduction of the cardy reduc
		Probiotic composition	Be longum BB68S Repeatable Battery for the Assessment of CFU/sachet Status: Attention Task, Coding Task, Delayed Memory Task, Digit Span Te Figure Copyl Task, Immediate Memory Task, List Learning Task, List Learning Task, List Recall Task, Picture Naming Task, Picture Naming Task, Picture Naming Task, Story Memory Task, Story Memory Task, Story Memory Task, Story Recall Task, Sto	Ecologic Barrier: B. Maastricht Gambling bifdum W23, B. lactis Task, Maastricht W52, L. acidophilus Choice Game W37, L. brevis W63, L. casei W56, L. salivarius W24, Lactococcus lactis (W19, W58) Daily: NA
SS SS SS SS SP SS		Design	8-week, randomized, double-blind, placebo-controlled N = 60 healthy elderly adults (placebo: M = 64.5 ± 3.8, probiotics: M = 64.1 ± 3.4)	4-week, randomized, double-blind, placebo- controlled N = 57 healthy adults $(M = 23.4 \pm 4.0)^a$
Probiotic composition B. longum BB68S Daily: 5 × 10 ¹⁰ CFU/sachet CFU/sachet Ecologic Barrier: B. Ecologic Barrier: B. W52, L. acidophilus W37, L. brevis W63, L. case! W56, L. salivarius W24, Lactococcus lactis (W19, W58) Daily: NA		Publication	Shi et al. (2022)	Dantas et al. (2022)

This document is copyrighted by the American Psychological Association or one of its allied publishers. This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Table 1 (continued)

	Mechanism proposed and/or tested		Tested mechanism: NA Proposed mechanism: NA	Tested mechanism: Ruminococaceae_UCG-003 associated with increased working memory performance in probiotic group Proposed mechanism: Probiotics may exert effects on cognition via increased stress resilience	Tested mechanism: NA Proposed mechanism: Production of neurotransmitters (e.g., GABA, dopamine, acetylcholine, serotonin), by commensal bacteria, and neurochemicals including blood BDNF, may directly or indirectly modulate cognition (table continues)
	Main effects on microbiota		Not tested	Significant change in microbial beta diversity in both groups	Significant changes at genus level in gut microbial composition in probiotics group, no changes in the control group. Relative abundances of Eubacterium,
dies	Main effects on cognitive outcome	group exhibited significant increase in future-oriented decisions, were more likely to prioritize future rewards over immediate ones, and placed more value on future rewards compared with placebo eroun	Overall improvement in cognitive performance for both groups; only probiotic group showed improvement in WCST	Scores of digit span backward improved after stress-inducing cold pressor test, but effect was not observed in placebo group	Probiotics group greater improvement in mental flexibility test and stress score compared with placebo group
Intervention studies	Cognitive task		Color-Word Stroop, Lexical Decision Task, Rey's Auditory Verbal Learning Test, Verbal Fluency Test, WCST	Digit Span Test (backward and forward), fMRI tasks, Socially Evaluated Cold Pressor Test Beck Depression Inventory	Boston Naming Test, Constructional Praxis Recall, Constructional Praxis, Trail Making Task (A and B), Digit Span Test, Fluency Task, Mental Flexibility Task, Verbal Word List
	Probiotic composition		B. lactis BS01; L. acidophilus LA02 Daily: B. lactis BS01: 2 × 10 ⁹ CFU; L. acidophilus LA0: 2 × 10 ⁹ CFU	B. bifidum W23, B. lactis W51; B. lactis W52; L. acidophilus W37, L. brevis W63; L. casei W56, L. salivarius W24, Lactococcus lactis W19, L. lactis W58 Daily: 5 × 109 CFIVAose	B. bifidum BGN4 B. longum BORI Daily: 1×10^9 CFU/capsule
	Design		6-week, randomized, single-blind, placebo- controlled $N = 38$ healthy females $(M = 23.9 \pm 4.0)^a$	4-week, randomized, single-blind, placebo-controlled N = 56 healthy females (placebo: M = 22.4 ± 0.5 [SEM]), probiotic: M = 21.8 ± 0.5 [SEM])	12-week, randomized, B. double-blind, placebo- B. controlled N = 53 healthy elderly adults (placebo: M = 72.0 ± 3.4, probiotics: M = 71.1 ± 5.0)
	Publication		Czajeczny et al. (2021)	Bloemendaal et al. (2021)	Kim et al. (2021)

This document is copyrighted by the American Psychological Association or one of its allied publishers. This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Table 1 (continued)

			Intervention studies			
Publication	Design	Probiotic composition	Cognitive task	Main effects on cognitive outcome	Main effects on microbiota	Mechanism proposed and/or tested
			Encoding, Word List Recall, Word List Recognition, Word List Savings Satisfaction With Life Scale, Stress Questionnaire, Geriatric Depression Scale, Positive Affect and Negative Affect Schedule		Allisonella, Clostridiales, Prevotellaceae gradually changed during intervention and significantly decreased at week 12 in probiotics group	and mood status; mitigation of inflammation in older adults with probiotic intervention might positively impact cognitive and mental functions via modulation of BDNF signaling.
(2019)	4-week, randomized, double-blind, placebo- controlled N = 58 healthy females (placebo: M = 22.0 ± 0.5 [SEM], probiotics: M = 21.0 ± 0.4 [SEM])	B. bifidum W23, B. lactis W51; B. lactis W52, L. acidophilus W37, L. brevis W63, L. casei W56, L. salivarius W24, Lactococcus lactis W19, L. lactis W58 Daily: 5 × 10° CFU/dose	Digit Span Test (backward and forward), Color-Word Stroop, Emotional Face-Matching Paradigm, Emotional Face-Word Stroop, Socially Evaluated Cold Pressor Test Beck Depression Inventory	Probiotics improved working memory performance only after stress induction; no effects without prior stress induction	Not tested	Tested mechanism: NA Proposed mechanism: Probiotics may exert effects on cognition via increased stress resilience
(2019)	12-week, randomized, double-blind, placebo-controlled N = 103 mildly stressed adults (placebo: M = 32.1 ± 11.4, probiotics: M = 31.3 ± 10.8)	L. plantarum P8 Daily: 2×10^{10} CFU/2 g	Cognitive State Britet Battery: Detection Identification Task, One Card Learning Task, One Card Back Task, Groton Maze Chase, Groton Maze Final Recall, Social Emotional Task, Continuous Paired International Shopping List Depression, Anxiety and Stress Scale Perresison Anxiety and Paresis Scale	Social emotional speed response plus verbal and memory learning improved	Not tested	Tested mechanism: <i>L. plantarum P8</i> reduced stress and anxiety symptoms via anti- inflammatory properties, followed by enhanced memory and cognitive abilities Proposed mechanism: see above

This document is copyrighted by the American Psychological Association or one of its allied publishers. This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Table 1 (continued)

	Mechanism proposed and/or tested	Tested mechanism: NA Proposed mechanism: NA	Tested mechanism: Nicotinate and nicotinamide metabolism significantly lower after probiotic intake Proposed mechanism: Potential link between specific Bacteroides, memory and recognition	Tested mechanism: NA Proposed mechanism: NA
	Main effects on microbiota	Not tested T	Subtle changes in gut T microbial community in probiotics group (no significant intervention effect on microbial diversity)	Not tested T
lies	Main effects on cognitive outcome	Probiotic group significantly improved on coding and figure recall specifically, and in overall score	Probiotic administration associated with less decision change for unpleasant stimuli compared with placebo and no intervention; probiotic administration significantly increased response accuracy for unpleasant stimuli compared with placebo and no intervention	No improvement in cognitive parameters
Intervention studies	Cognitive task	Digit Span Test, Figure Copy and Line Orientation, Figure Recall, List Learning, List Recall, List Recognition, Picture Naming and Semantic Fluency Story Memory, Story Recall Profile of Mood States	₽	Cambridge Neuropsychological Test Automated Battery: Attention Switching Task, Emotion Recognition Task, Emotional Stroop, Motor Screening Test, Paired Associate Learning, Rapid Visual Information- Processing
	Probiotic composition	L. helveticus CM4 (fermented milk) Daily: NA	B. bifidum W23, B. lactis W51, B. lactis W52, L. acidophilus W22, L. casei W56, L. paracasei W20, L. salivarius W24, Lactococcus lactis W19, L. plantarum W62 Daily: 7.5 × 10° CFU/3 g	L. rhamnosus Daily: 1×10^9 CFU/capsule
	Design	8-week, randomized, double-blind, placebo- controlled N = 61 healthy adults (placebo: $M = 57.8 \pm$ 5.9, probiotics: $M =$ 58.5 ± 6.5)	4-week, randomized, double-blind, placebo- controlled plus control group N = 45 healthy adults $(M = 26.2 \pm 4.8)^a$	4-week, randomized, placebo-controlled, crossover (blinding NA) N = 29 healthy males (placebo: M = 23.6 ± 1.0, probiotics: M = 25.6 ± 1.1)
	Publication	Ohsawa et al. (2018)	Bagga et al. (2018)	(2017)

This document is copyrighted by the American Psychological Association or one of its allied publishers. This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Table 1 (continued)

	Mechanism proposed and/or tested	Tested mechanism: NA Proposed mechanism: NA	Tested mechanism: NA Probiotics improve epithelial barrier function and decrease permeability, eventually affecting cognitive function Proposed mechanism: see above	Tested mechanism: NA Proposed mechanism: As L. helveticus IDCC3801 does not appear to have a GABA- producing ability, mechanisms for cognitive- enhancing effects of fermented milk in cognitive fatigue tests might be related to unknown ingredients produced in fermented milk by L. helveticus IDCC3801.
	Main effects on microbiota	Not tested	Not tested	Not tested
tudies	Main effects on cognitive outcome	Mild improvement in visuospatial memory; EEG profile consistent with improved memory	Significantly reduced cognitive reactivity to depression in probiotics group	Improvement on information processing task and color-word Stroop in fermented milk-treated groups compared with placebo group
Intervention studies	Cognitive task	Cambridge Neuropsychological Test Automated Battery: Emotional Face-Word Stroop, Paired Associate Learning Test, Processing Task, Rapid Visual Information- Processing Task Emotion Recognition Task	Leiden Index of Depression Sensitivity-Revised, Beck Depression Inventory II	Digit Span Test, Story Recall Test, Verbal- Learning Test Rapid Visual Information Processing task, Color-Word Stroop, Serial 3s/7s.
	Probiotic composition	B. longum 1,714 strain Daily: 1 × 10 ⁹ CFU/stick	B. bifidum W23, B. lactis W52; L. acidophilus W37, L. brevis W63, L. casei W56, L. salivarius W54, Lactococcus lactis (W19, W58) Daily: 2,5 × 10.9 CFU/g	L. helveticus (fermented milk) L. helveticus IDCC3801 (0.5% glucose, 10% skim milk) Daily: NA
	Design	4-week, within-subjects, placebo-controlled (blinding NA) $N = 22 \text{ healthy males}$ $(M = 25.5 \pm 1.2)^{a}$	Steenbergen et 4-week, randomized, al. (2015) triple-blind, placebo- controlled $N=40$ healthy adults (placebo: $M=19.7 \pm 1.7$ probiotics: $M=20.2 \pm 2.4$)	12-week, randomized, double-blind, placebo-controlled $N=36$ healthy elderly adults (placebo: $M=65.0\pm4.1$, probiotics [500 mg]: $M=64.5\pm2.2$, probiotics [1,000 mg]: $M=64.4\pm4.5$, probiotics [2,000]: $M=66.6\pm5.0$)
	Publication	Allen et al. (2016)	Steenbergen et al. (2015)	Chung et al. (2014)

 Fable 1
 (continued)

	Mechanism proposed and/or tested	No significant change Tested mechanism: NA in fecal microbiota Proposed mechanism: NA composition after intervention between groups
	Main effects on microbiota	
studies	Main effects on cognitive outcome	Affected activity of brain areas controlling central processing (emotion and sensation)
Intervention studies	Cognitive task	Emotional Faces Attention Task
	Probiotic composition	B. animalis subsp lactis Emotional Faces (strain number 1-2494); Attention Task L. bulgaricus; Streptococcus thermophilus Daily, lactis = 1.25 × 10 ¹⁰ CFU, bulgaricus + thermophilus = 1.2 × 10 ⁹ CFU/cup
	Design	(2013) 4-week, randomized, (2013) double-blind, placebo- controlled $N = 27$ healthy females $(M = 30.0 \pm 10.4)$ years) ^a
	Publication	Tillisch et al. (2013)

reported; NA = not available; EEG = electroencephalogram; fMRI = functional magnetic resonance imaging; CFU = colony-forming unit; MMSE = Mini-Mental State Examination; WCST = Wisconsin Card Sorting Task; BDNF = brain-derived neurotrophic factor; GABA = gamma-Aminobutyric acid; F/B = Firmicutes/Bacteroidetes; SEM = B = Bijdobacterium; L = Lactobacillus; for reasons of completeness, all tests/tasks used in the studies are mentioned, however, only results for the cognitive tasks are standard error of the mean; BORI = Bifidobacterium Original Rotavirus Inhibition ¹No group-specific demographics are given. Last update: January 2025.

MUSCULUS ET AL.

analyses. We further used a triple-blind (vs. double-blind) design and theoretically derived potential psychophysiological mechanisms of risky decisions.

Background: Gut-Cognition Link in Humans

While most research focused on the effects of gut microbiota on affective states, primarily on mood (e.g., Jenkins et al., 2016) or depression (Pennisi, 2019), less evidence for the influence of the gut microbiota on cognition in general, and decision-making in particular, has been established (cf. Tooley, 2020). Yet, some studies in humans suggest a gut bacteria-cognition link (Sarkar et al., 2018; Tooley, 2020) which is functionally established through the gut-brain axis (for a recent perspective and summary, see Castells-Nobau et al., 2024; Cryan & Dinan, 2015; Cryan et al., 2019). Experimental probiotic intervention studies showed reductions in rumination and aggressive cognition (Steenbergen et al., 2015), improved verbal and visuospatial memory (Allen et al., 2016; Lew et al., 2019), and cognitive performance under acute stress circumstances (Bloemendaal et al., 2021; Papalini et al., 2019). However, other studies with human participants found no benefits of a diverse microbiota composition or its experimental manipulation through probiotics, diet, infection, or exercise for cognition (Kelly et al., 2017; Novotný et al., 2019). Importantly, if effects are established, they often occur in groups of patients suffering from a disease like Alzheimer's (e.g., effects on memory, Akbari et al., 2016; fibromyalgia, Roman et al., 2018; or hepatic encephalopathy, Bajaj et al., 2012). Only a few studies directly tested causal effects of probiotic interventions on cognition in healthy humans (see Table 1, for an overview). Although we included exclusively placebo-controlled studies in the overview, among those only one employed a triple-blind design (Steenbergen et al., 2015). The latter 4-week study focused on probiotic effects on information processing in healthy participants. Results suggested a reduction in selfreported cognitive reactivity (i.e., dysfunctional thoughts leading to sad mood) through probiotic intervention. Most critically, Steenbergen et al.'s (2015) study and eight other intervention studies (i.e., 9 of 14 studies) did not quantify the probiotic effect on microbiota composition, making it difficult to infer underlying mechanisms. Most similar with regard to cognitive

outcome measures were the studies by Ruiz-Gonzalez et al. (2024) and Dantas et al. (2022), that demonstrated changes in decision-making (i.e., performance on the IGT as proxy of cognitive decline, yet no specific interest in risky decision-making discussed by Ruiz-Gonzalez et al., 2024) and reduced risky decision-making after the probiotic intervention (Dantas et al., 2022), yet neither study examined microbiota pre- or postintervention and therefore only speculated about potential mechanisms (see Table 1). In our study, we aimed at testing (a) whether probiotics can exert an effect on risky decisionmaking as part of higher cognition in healthy humans and (b) one potential underlying physiological mechanism.

The impact of probiotics on cognition and its psychophysiological mechanisms in healthy humans are not thoroughly explored. Lactic acid bacteria have been suggested to have a direct effect on neurotransmitters like gamma-Aminobutyric acid (GABA) as one of the main inhibitory neurotransmitters significantly involved in physiological and psychological regulation (Del Toro-Barbosa et al., 2020; Wall et al., 2014). However, most existing studies do not fulfill strict experimental criteria to rigorously test causal relationships, such as a triple-blind, placebo-controlled design with both female and male participants, to thoroughly examine microbiota-induced "purely" cognitive outcomes. Addressing this gap, we conducted a methodologically rigorous intervention study, employing a triple-blind, placebocontrolled pre-post design assessing risky decision-making as the main cognitive outcome and potential psychophysiological mediators. Fecal analyses and standardized cognitive tasks were used to investigate possible psychophysiological mechanisms in risky decision-making, elucidating the gut-cognition relationship.

Psychophysiological Mechanisms Underlying the Gut-Cognition Link

Different research fields have proposed several mechanisms for how the gut microbiota may impact human cognition (e.g., neuroscience, gastroenterology, and psychology; Critchley & Harrison, 2013; Cryan & O'Mahony, 2011; Mayer, 2011; Sarkar et al., 2016, 2018) and are likely to account for risky decision-making in particular. Most relevant for the present study

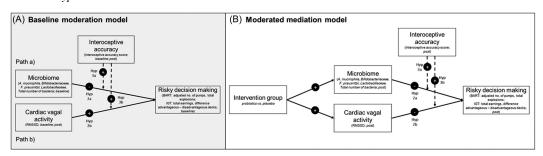
may be the bidirectional communication between the gut and the brain, the neural pathway via the vagus nerve (Bonaz et al., 2018; Bravo et al., 2011; Forsythe et al., 2012; Mayer, 2011; Sarkar et al., 2016). The vagal innervation of the gastrointestinal tract contributes to gut proprioception (González-Arancibia et al., 2019), with distinct vagal afferents ending in immediate proximity to enteroendocrine cells (Mayer, 2011). Primary vagal and spinal afferents from the gastrointestinal tract project to the vagal nucleus tractus solitarius and the lamina I of the dorsal horn, respectively. Both directly signal to the ventromedial thalamic nuclei and activate the anterior cingulate cortex via thalamocortical pathways (Foster et al., 2017; Mayer, 2011). These brain areas are integral components of the central autonomic network, an internal regulation system that governs visceromotor, neuroendocrine, and behavioral responses crucial for goal-directed behavior (Benarroch, 1993).

In the present study, we focused on risky decision-making. Relevant dimensions for risky decision-making are risk appraisals (balancing losses against gains) and short- versus long-term rewards. Studies have shown that risk avoidance is associated with the activation of brain regions that are related to behavioral adaptation, that is, inferior frontal gyrus/anterior insula and the anterior cingulate cortex, as shown by brain imaging studies (Brown & Braver, 2007; Krawitz et al., 2010; Magno et al., 2006). It has also been demonstrated that higher risk-taking ending in losses may elicit stronger physiological responses (e.g., skin conductance, Wright & Rakow, 2017). Risk aversion and, more specifically, inhibited risk taking after failure, have been found in studies using the Balloon Analogue Risk Task (BART; Fukunaga et al., 2012; Lejuez et al., 2002; Wright & Rakow, 2017). In this task, participants inflate a virtual balloon to earn rewards for each pump while balancing the risk of bursting and so gaining no reward. For instance, Telzer et al. (2015) found that individuals with stronger activation in the ventral striatum, a brain region linked to rewards and intuitive decisionmaking, were more likely to take risks by inflating the balloon further instead of cashing out. Schonberg et al. (2011) also found that participants with stronger activation in brain regions associated with intuition (i.e., insula and orbitofrontal cortex) were more likely to engage in risky behavior during the BART. The dimension of short- versus

long-term rewards has also shown to involve the activation of the amygdala-striatal and prefrontal (i.e., ventromedial and orbito-prefrontal cortex) networks, representing affective impulsive processing and more reflective processing, respectively (Aydogan et al., 2021; Brevers et al., 2013). These networks are linked to each other through the right vagal sensory ganglion, activating dopamine release in the substantia nigra pars compacta (Yu et al., 2020; see also results by Falkenstein et al., 2024). Therefore, the vagal pathway also seems to be involved in risky decision-making (and other cognitive functions; Farmer et al., 2021; Laborde & Raab, 2013; Sie et al., 2019; Thayer et al., 2009: neurovisceral integration model). As one example, by using the IGT, Forte et al. (2021) showed that higher vagally mediated heart rate variability, that is the variation in time intervals between consecutive heartbeats mediated by cardiac vagal activity, is related to decision-making. Based on the assumption that higher vagally mediated heart rate variability reflects better inhibitory functioning, the study showed that good decision makers had a higher vagal tone in the resting state HRV than bad decision makers. HRV seems therefore to be related to decision-making performance. Furthermore, studies demonstrating that a severance of the vagus nerve reverses probiotic effects (Sarkar et al., 2016) suggest vagal activity to be a mediator in the gutcognition link, which we targeted in the present study (see Figure 1, path b). Together, we propose gut bacteria and vagal activity as potential psychophysiological mechanisms to underlie the gut-cognition link conveyed through the gut-brain axis (see, for a recent special issue, Hassouna et al., 2024). These mechanisms coexist, and possibly describe the gut-cognition link at different levels rather than being independent or in competition.

It has been suggested that afferent vagal activity might contribute to decision-making particularly when individuals exhibit high levels of interoceptive accuracy (Dunn et al., 2012; Garfinkel et al., 2015; Preuschoff et al., 2008). Interoception is the perception and sensation of internal bodily signals. The most widely used and validated paradigm to measure interoception is heartbeat perception task (Murphy et al., 2017) and studies show that sensitivity for interoceptive processes may be generalized across cardiovascular and gastric domains (Herbert et al., 2012; Whitehead & Drescher, 1980). Accurate perception of subliminal, interoceptive signals not only matters for affective responses (Berntson et al., 2003; Critchley & Harrison, 2013; Mayer, 2011) but may also affect risky decision-making (Berntson et al., 2003; Dunn et al., 2010; Werner et al., 2009, 2013). This relationship is evidenced by the overlapping brain anatomy for interoception and the tendency to risky decisionmaking in the anterior insula (Aydogan et al., 2021; Zaki et al., 2012). A study by Kandasamy et al. (2016) showed that participants who were

Figure 1 *A-Priori Hypotheses*



Note. (A) The baseline regression models tested whether there is a link between the human gut microbiota (path a) or cardiac vagal activity (path b) and risky decision-making, as well as whether this link is moderated by interoceptive accuracy. (B) The moderated mediation models aimed at testing whether the potential causal intervention effect is mediated by the baseline human gut microbiota (path a) or cardiac vagal activity (path b) as well as whether either path is moderated by interoceptive accuracy. The "plus" and "minus" represent the direction of the hypothesized relation. BART = Balloon Analogue Risk Task; IGT = Iowa Gambling Task; RMSSD = root-mean-square of successive differences; Hyp = hypothesis.

more sensitive to their bodily signals (high in interoception with regard to perceiving their own heartbeats) generated greater profits and survived longer as traders in the financial market. We therefore expect interoceptive accuracy to enhance the link between bodily changes, such as altered gut bacteria or vagal activity, and subsequent risky choices. Thus, we judge that interoceptive accuracy qualifies as a potential moderator in the proposed psychophysiological mechanism underlying risky decision-making (Boem et al., 2024).

The Present Study

First, this study aimed to experimentally assess the causal impact of a probiotic gut microbiota intervention on decision-making, specifically focusing on risky decisions (Hyp1; see Figure 1). As outlined earlier, we hypothesize somatic signaling to be especially important for guiding risky decision-making, which are therefore often colloquially termed "gut decisions." We therefore focus on the direct influence of the gut microbiota and propose a psychophysiological mechanism underlying risky decisions in particular, for which almost no empirical investigations exist. We used validated, complementary tasks for risky decision-making: the IGT (Bechara et al., 1994) together with the BART (Lejuez et al., 2002). We chose these tasks, as there is evidence that the neurophysiological mechanisms involved in these tasks share networks that are assumed to play a role in the gut-brain axis via the vagal pathway (e.g., prefrontal, cognitive control networks, Wang et al., 2022; somatic maker, Bechara et al., 2005; skin conductance/somatic marker, Wright & Rakow, 2017; emotion-based learning, Turnbull et al., 2005).

Second, we investigated the proposed psychophysiological mechanisms underlying the gut—decision-making link further (for a-priori hypotheses, see Figure 1). This involved testing whether gut bacteria (Hyp2a; see Figure 1, path a) or efferent cardiac vagal activity (Hyp2b; see Figure 1, path b) compose the link to risky decision-making in both a baseline (Figure 1A) and a potential mediation model (Figure 1B). To assess gut microbiota, bacteria were selected based on their relevance for vagal pathway signaling (e.g., Cawthon & de La Serre, 2018), but we had no specific predictions for the effects of each of the bacteria.

Additionally, we explore whether the links are moderated by interoceptive accuracy (Garfinkel et al., 2015; Mayer, 2011; Preuschoff et al., 2008).

We hypothesized that individuals with higher interoceptive accuracy (moderator), i.e., better at perceiving internal signals from their gut or their heart, are more likely to exhibit a stronger connection between these psychophysiological mediators, microbiome (path a) or cardiac vagal activity (path b), and risky decision-making (see Figure 1). This implies a more robust link between changes in the gut microbiota or cardiac vagal activity and risky decision-making when these changes are well perceived.

Method

Intervention Design

We tested two experimental groups, a probiotic intervention and a placebo group, with a tripleblind, randomized intervention design with preand posttest. The 6-week intervention required participants to take one dose of probiotics/placebo every day (see Table 1). The study was preregistered on Deutscher Register Klinischer Studien (German Registry of Clinical Studies; DRKS00017667 at https://drks.de/search/de/tria I/DRKS00017667) before data collection began. The data analysis plan was not preregistered. Data collection started in June 2019 and stopped in March 2020 due to the COVID-19 pandemic. The study conformed to the 2008 Declaration of Helsinki (World Medical Association, 2024) and was approved by the local ethics committee (German Sport University Cologne No. 180/2018).

Participants

As of the time of our data collection (2019–2020), only one study was comparable in design (i.e., triple-blind) but did not examine potential psychophysiological mechanisms, no referential effect sizes for an a-priori sample size estimation existed. Our power calculation for sample size was based on the triple-blind study by Steenbergen et al. (2015), f = 0.374, $\alpha = .05$, power = 0.8, which yielded a required sample size of N = 59 participants. One hundred participants were recruited on campus and via leaflets and different social

media channels. During the recruitment process, prospective participants were instructed that they could take part only if they met the following inclusion criteria: age (18-40 years), no medication (no acute medication, no antibiotics the previous 6 months, no psychotropic drugs the previous 4 weeks), no medical condition (no psychological or neurological disorders; no cardionephric, hepatoenteric, cardiovascular, or pulmonary diseases; no diabetes type I or II), and no intolerances (no acute or chronic food allergies). Ninety participants were eligible. Of these, only n = 67 completed the posttest, because data collection was aborted by the pandemic lockdown. Including only participants with a complete data set in the data analyses (i.e., including all dependent variables) yielded a final sample size of n = 55 participants ($M_{age} = 26.8 \pm 5.1$ years, 38 women). This sample size was deemed appropriate considering the sample size estimation based on Steenbergen et al. (2015) and because it was in the range of sample sizes of most other studies controlling microbiota and showing effects on cognition (see Table 1).

The probiotics manufacturer numbered and randomized all intervention kits beforehand (coding lists were blinded) using a randomization plan generator, making sure that each four consecutive kits contained two probiotics and two placebo kits. The participant number assigned to participants in the order of registration for the study determined whether participants received a probiotics or placebo kit (probiotics group: n = 28, $M_{\rm age} = 27.2 \pm 5.4$ years, 17 women; placebo group: n = 27, $M_{\rm age} = 26.4 \pm 4.8$ years, 21 women). All participants were remunerated with their individual gut microbiota analysis, a 20-min hydro jet massage, or a free canteen meal and course credit (if applicable).

Materials and Measures

Probiotics and Placebo

Members of the *Lactobacillaceae* and *Bifidobacteriaceae* families have been shown to increase vagal signaling in the brain (Cawthon & de La Serre, 2018), which may be due to their ability to produce GABA (Del Toro-Barbosa et al., 2020; Diez-Gutiérrez et al., 2020) and acetylcholine (Wall et al., 2014). This is why the probiotic used was a multispecies blend. Each 4-g sachet of probiotic powder

contained probiotic bacteria, namely B. bifidum W23, B. lactis W51, B. lactis W52, L. acidophilus W37, Levilactobacillus brevis W63, Lacticaseibacillus casei W56, Ligilactobacillus salivarius W24, Lactococcus lactis W19, and Lactococcus lactis W58; $\geq 2.5 \times 10^9$ colony-forming units per gram and cornstarch, maltodextrin, vegetable protein, potassium chloride, magnesium sulfate, and manganese sulfate. The 4-g sachet of placebo powder contained cornstarch, maltodextrin, vegetable protein, potassium chloride, magnesium sulfate, and manganese sulfate. Probiotic and placebo kits had the same label. Probiotic and a matching placebo powder were kindly provided by Winclove B.V. Participants dissolved the powder in warm water for at least 1 min and were instructed to drink the solution on an empty stomach prior to breakfast or bedtime consistently over the 6-week period.

Screening Questionnaire

A Screening Questionnaire included demographic information (age, profession, mother tongue, height, weight), information regarding any event or substance consumption during the previous 24 hr potentially influencing heart rate (wake-up time, sleep duration, sleep quality, food intake in the past 16 hr, water intake, number of caffeinated drinks, being in a rush, smoking, alcohol), and medication (contraception). Participants also provided health data (date of last period, whether they had been delivered by natural birth or cesarean, and whether they had been breastfed), current dietary behaviors (forms of nutrition, e.g., ketogenic, vegan, low-carb, fasting, current diets), and information on physical activity (last active session, type of sports, amount of training per week, experience in years, highest division in which they had participated).

Risky Decision-Making

The Iowa Gambling Task. The IGT assesses real-world risky decision-making in a laboratory context (Bechara et al., 1994, 1997; Buelow & Suhr, 2009; available at https://www.millisecond.com/download/library/iowagamblingtask). The task has been found to be a valid measure of risky decision-making (Buelow & Suhr, 2009; Clark et al., 2008). Bechara et al. (1994) found that individuals with ventromedial prefrontal cortex damage, compared with controls, show

impairment on the IGT, which indicates the involvement of this brain area in the regulation of decision-making.

Participants received a virtual beginning balance of \$2,000 and were instructed to maximize their profit through selecting cards from four card decks. When selecting from Deck A, participants received \$100 on every trial, but in five out of ten trials, they lost between \$35 and \$150. Similarly, choosing from Deck B also yielded a \$100 win, but participants lost \$1,250 in one out of ten trials. Decks A and B were therefore considered "disadvantageous" and selection from these decks was deemed risky. The remaining two decks, C and D, were more advantageous in the long run, offering smaller immediate rewards but ultimately a net benefit. Deck C provided a smaller win of \$50, with losses ranging from \$25 to \$75 in five out of ten trials. Deck D also gave an immediate win of \$50, but participants lost \$250 in one out of ten trials. In total, participants selected 100 cards. Dependent variables of interest were the total of advantageous minus disadvantageous selections and participants' total earnings. Individuals with lower scores on advantageous minus disadvantageous selections were considered to be higher in risk tendency (Steingroever et al., 2013).

The Balloon Analogue Risk Task. The BART was created to assess risky decision-making (Lejuez et al., 2003, available at https://www.milli second.com/download/library/bart). Participants pump up a virtual balloon on a computer screen by mouse clicks. Each click is accompanied by an inflation sound and an optically growing balloon. Participants were instructed that the gain for every pump would be 5 cents, saved in a temporary reserve, and that the sum could be collected by clicking a "collect" button. An exploding balloon made participants lose the temporary reserve. Every balloon had an individual explosion point (randomized, ranging from 1 to 128 pumps; unbeknownst to participants). After each explosion or money collection, a new balloon appeared until a total of 20 balloons had been completed. The dependent variables were the so-called adjusted number of pumps (i.e., total number of nonexploded balloons across all trials only, i.e., sum score) and the number of total explosions across trials (i.e., sum score). Individuals with higher scores on adjusted number of pumps and explosions were considered to be higher in risk tendency (Lejuez et al., 2003).

Collection and Analyses of Fecal Samples

All participants were provided with sterile containers and instructed on how to collect the fecal samples at home and how to send the samples to the Medizinisches Versorgungszentrum Institute of Microecology. The stool samples were immediately frozen at -35 °C and analyzed within a few days.

Sample Preparation, DNA Extraction, and **Quantification of Target Bacteria by Real-Time Quantitative Polymerase** Chain Reaction (qPCR). Members of the Lactobacillaceae and Bifidobacteriaceae families have been shown to increase vagal signaling in the brain (Cawthon & de La Serre, 2018), which is why target bacteria specifically selected for this study were Akkermansia muciniphila (Akk.mucF + Akk.mucR, A. muciniphila), Faecalibacterium prausnitzii (Praus F480 + Praus R631, F. prausnitzii), Lactobacilli/Enterococci (LabF362 + LabR677, L. acidophilus), and Bifidobacterium sp. (F_Bifid09c + R_Bifid06, B. adolescentis). Microbial DNA was extracted using the QIAsymphony DSP Virus/Pathogen Mini-Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instructions. Automated isolation and pipetting of 96-well plates (Micro Amp Optical 96-Well Reaction Plate, Applied Biosystems) were performed with the QIAsymphony SP/AS instrument (QIAGEN, Hilden, Germany) using the QIAsymphony DSP Virus/Pathogen Mini-Kit. Primers and the qPCR procedure were performed as described elsewhere (see Unger et al., 2016). The target bacteria were analyzed in copies/g stool.

Sequencing Analyses for Validation. In addition to the qPCR analysis, the stool samples were also analyzed through sequencing, that is, through amplification of the 16S ribosomal ribonucleic acid gene, targeting the variable regions V1-V2 (27F-338R; see Supplemental Material A, for further details), to ensure data quality. In summary, sequencing results clearly demonstrated sufficient quality for bacterial community analysis in the present sample.

Cardiac Vagal Activity (Mediator)

Cardiac vagal activity represents the contribution of the vagus nerve to cardiac regulation and is acknowledged to index self-regulation on, for instance, the cognitive and health levels (Laborde et al., 2017; Thayer et al., 2009). According to the recommendations of the manufacturer (Brain Products), three electrocardiogram (ECG) electrodes were attached. To maximize the R-peak amplitude, one electrode was positioned at the right clavicle lateral to the midclavicular line (-) and the second at the left anterior axillary line (+). The third—the ground electrode—was attached to the outer right ankle. The ECG was recorded using an ActiChamp amplifier (Brain Products) with a sampling rate of 1,000 Hz. Following the importing of raw ECG data into Matlab and EEGLAB (Delorme & Makeig, 2004), the ECG was high-pass filtered (0.1 Hz) via a nonphase-shifting finite impulse response filter. Following this, line noise was removed using the cleanline plug-in in EEGLAB. R peaks were detected via custom Matlab scripts using a Pan-Tompkins algorithm (Hamilton & Tompkins, 1986; Pan & Tompkins, 1985). Artefactual interbeat intervals (IBIs) were automatically detected and removed (i.e., IBIs >2 SD and IBIs <2 SD). Per subject, only <5% were allowed, and if the rejection rate was higher, data were manually rechecked and selection was corrected or the whole data set was rejected. From these IBIs, the root-mean-square of successive differences was analyzed. Both measures are core indicators of cardiac vagal activity (Laborde et al., 2017).

Interoceptive Accuracy (Moderator): Heartbeat Perception Task

The Heartbeat perception task (Dunn et al., 2012; Schandry, 1981) required participants to count heartbeats during epochs of 45 s, 60 s, and 100 s (Schandry, 1981), which were compared with the quantity of heartbeats simultaneously measured on the ECG trace. The three ECG electrodes (anode, cathode, ground) measured participants' heart rate while they sat upright on a chair with both knees and hips at a 90° angle and with palms resting on the table (neutral seating position) in front of a computer monitor. The software visually signaled the onset of rest and perception periods. Participants were instructed to follow the visual signals on screen and write down the counted number of heartbeats on article once a brief tone signaled the end of the perception period. The counting periods of 45 s, 60 s, and 100 s were randomized and unknown to the participants. They were further instructed not to use their pulse or any other physical manipulation that might facilitate the perception of heartbeats. The interoceptive accuracy score (IACC) was based on the comparison between the total number of perceived and actual heartbeats across all three epochs, calculated as an estimation error ratio, IACC = $1 - [(N_{\text{actual heartbeats}} - N_{\text{counted heartbeats}})/N_{\text{actual heartbeats}}]$. Perfect detection would yield an IACC of 1, completely failing would yield an IACC of 0. The IACC was used for the hypothesis-testing analyses.

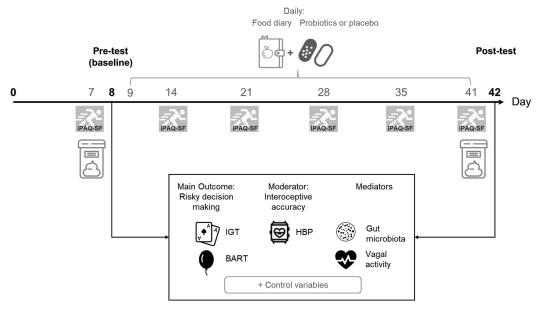
Control Variables

The pretest included several measures to gather potential control variables that aimed at controlling for group differences between placebo and probiotic groups at baseline. We added a list of control variables related to the general health status of participants, personality, and preference for intuitive decisions in order to control for these variables in case of potential interactions with our main variables of interest. The control variables include the 1-min-estimation task, personality traits (NEO-Five Factor Inventory [FFI]), preference for intuition versus deliberation (PID-scale), and health status, assessed through the physical activity questionnaire (International Physical Activity Questionnaire-Short Form [IPAQ-SF]), food intake, mental health (World Health Organization-5), and physical health (body mass index). A detailed description of each control variable with citations for sources can be found in Supplemental Material B, with the corresponding analysis of variance results and Bayes factor in Supplemental Table B1.

Procedure

The procedure is depicted in Figure 2. Eight days prior to the laboratory pretest session, participants received an instructional video and the first stool sample kit. They were instructed to continue their usual dietary and physical activities and to track their diet in a daily diary, which was administered via smartphone app (FatSecret) for the next 7 days. Physical activity was assessed electronically with the IPAQ-SF on the past day of the week. Participants were further instructed to collect a stool sample on the seventh

Figure 2
Procedure Overview



Note. BART = Balloon Analogue Risk Task; HBP = heartbeat perception task; IGT = Iowa Gambling Task; IPAQ-SF = International Physical Activity Questionnaire (Short Form).

day, which was the day prior to cognitive testing in the lab. On the 8th day, participants visited the lab for baseline measures (i.e., pretests). Participants were welcomed, signed informed consent, and were asked to confirm the dispatch of the stool sample and the completion of the first IPAQ-SF. Participants were then seated in front of the test computer monitor and the three ECG electrodes were attached. Four experimental blocks followed. Participants first completed the heartbeat perception task, followed by a 5-min inactive phase in a neutral seating position. They then completed the BART and the IGT (or vice versa, counterbalanced across participants), followed by another 5-min inactive phase in the neutral seating position. In the third block, participants performed the 1-min-estimation task, followed by a 5-min inactive phase. In the last experimental block, participants filled in the electronic screening questionnaire and the trait questionnaires NEO-FFI and PID, which took approximately 20 min to complete. After that the ECG was detached, and participants were thanked and given the probiotics/placebo powder for the

following 6 weeks as well as the second stool sample kit.

Every 7 days during the intervention period, participants were reminded via email to fill in the IPAQ-SF via smartphone app.

The second stool sample was collected on the 41st day, which was the day prior to cognitive testing at posttest. On the 42nd day, participants visited the lab for posttests at the same time of day as for pretests. The experimental protocol followed the same procedure as the pretests except for the trait questionnaires. The NEO-FFI and PID were replaced by the World Health Organization-5 at posttest.

Data Analysis

The statistical analyses were conducted with RStudio (Version 1.4.1717) and JASP for Bayesian statistics (JASP 0.18.3.0; Wagenmakers, Love, et al., 2018). Data and code are publicly available under "files" at the Open Science Framework (https://osf.io/xrh9g/?view_only=None).

Preanalyses

Before the main analyses were conducted, all dependent, moderator, and mediator variables were checked for normality, missing values, and outliers ("DataExplorer" package). Outliers were identified and removed based on Rosner's generalized extreme Studentized deviate test ("EnvStats" package), yielding a total of 11 outliers removed. Following these analyses, the dependent, mediator, and moderator variables were transformed before the hypothesis-testing analyses were conducted. All variables were z transformed except for the microbiota data and the root-mean-square of successive differences of the heart rate variability (HRV) data, which were log transformed (Jian et al., 2018; see Supplemental Material C1, for descriptive statistics).

We further tested a priori whether the probiotics versus placebo group differed in the relevant control variables by a one-factorial (between-subjects: probiotics, placebo) analysis of variance. Results can be taken from Supplemental Material B1.

Main Hypothesis-Testing Analyses

For the first hypothesis on the intervention effect, we used a 2 (within-subject: pre, post) \times 2 (between-subjects: probiotics, placebo) mixed analysis of variance (analyses of variance; function "anova_test" of the "rstatix" package). For testing, hypotheses 2a, b and 3a, b moderated mediation models were computed (see Figure 1). In the first step, the assumptions were checked using the "gvlma" package and function. Then, the "mediation" package (V.4.5.0, Tingley et al., 2014) was used to fit linear regression models for each outcome and mediator using the "lm" function (see Formulas 1 and 2). Next, the outcome and mediation models were statistically compared using the "mediate" function of the same package (see Formulas 3–5). Thereby, direct and indirect effects as well as interactions with the moderator were estimated. The moderator was added using an interaction term and the $M \pm SD$ was used to denote high versus low levels of the moderator when reporting interaction effects.

Baseline regression models (see Figure 1):

 The linear regression models tested if the respective risky decision-making outcome (BART: adjusted no. of pumps, total no. of

- explosions; IGT: total earnings, difference advantageous—disadvantageous decks) could be predicted by gut bacteria (A. muciniphila, Bifidobacteriaceae, F. prausnitzii, Lactobacillaceae, total number of bacteria) or by cardiac vagal activity (HRV: root-mean-square of successive differences; code: regr.mf — lm[decision_making ~ microbiota + cardiac vagal activity])
- In the moderated regression models, the moderator interoceptive accuracy was added (code: mod_regr.mf ← lm[decision_making ~ microbiota + cardiac vagal_activity + interoceptive_accuracy + microbiota: interoceptive_accuracy + cardiac vagal_activity:interoceptive_accuracy]).

Moderated mediation models (see Figure 1):

3. The full moderated mediation models tested if the respective risky decisionmaking outcome could be predicted by the interaction between the experimental group (probiotics vs. placebo group) and gut bacteria or cardiac vagal activity as well as by the interaction between the mediator and the moderator interoceptive accuracy (code: step 1: outcome.mf ← lm[decision_making ~ intervention_group × microbiota OR cardiac vagal activity × interoceptive_accuracy]; step 2: mediator.mf ← lm[microbiota OR cardiac vagal activity ~ intervention_group × interoceptive_accuracy]; step 3: moderated_mediation.mf ← mediation::mediate [outcome.mf, mediator.mf, treat = "intervention group", mediator = "microbiota OR cardiac vagal_activity," moderator = "interoceptive_accuracy"]).

In the last step, we conducted Bayesian analyses using the default priors in JASP (cf. Wagenmakers, Love, et al., 2018; Wagenmakers, Marsman, et al., 2018) accompanying the frequentist analyses.

Results

Control Variable Analyses

The ANOVA revealed no significant group differences in the control variables 1-min estimation, physical activity, age, sex, body mass index, personality NEO-FFI, personality PID, mode of

delivery, breastfeeding, wellbeing, or fibers, carbohydrates, (saturated) fat, sugar, cholesterol, protein, and potassium as reported in the food diary app. Group differences only appeared for mean calorie consumption (kilocalories), $F(1, 51) = 4.36, p = .042, \eta^2 = .078, BF_{10} = 0.63, BF_{01} = 1.60,$ and sodium consumption (grams), $F(1, 49) = 15.31, p < .001 \eta^2 = .024, BF_{10} = 1.00, BF_{01} = 1.00$. Calorie and sodium consumption were higher in the placebo as compared with the probiotics group. However, the Bayes factors suggest that the evidence for the H1 stating that the intervention groups differ is weak (van Doorn et al., 2021).

Main Hypothesis-Testing Analyses

Intervention Effect (Hyp1)

We found no significant intervention effects in any of our tasks (BF₀₁ = [3.57–8.06], indicating the Bayes factor in favor of H0 over H1): In the IGT, there was neither an intervention effect (2: pre, post × 2: placebo, probiotic) for the total of advantageous minus disadvantageous selections, $F(1,61) = 1.63, p = .207, \eta^2 = .026, BF_{01} = 3.57,$ nor for participants' total earnings, $F(1,61) = 0.06, p = .804, \eta^2 = .0001, BF_{01} = 7.81.$ In the BART, likewise there was neither an intervention effect for the adjusted number of pumps, $F(1,60) < 1, p = .984, \eta^2 = .001, BF_{01} = 8.06,$ nor the number of total explosions, $F(1,60) = 0.27, p = .608, \eta^2 = .004, BF_{01} = 7.05.$

As there were no baseline differences between the two experimental groups (probiotics vs. placebo), IGT: advantageous minus disadvantageous selections, F(1, 65) = 0.28, p = .602, $\eta^2 = .004$, $BF_{01} = 4.45$, total earnings, F(1, 65) = 1.11, p = .297, $\eta^2 = .017$, $BF_{01} = 3.68$; BART: adjusted number of pumps, F(1, 64) = 0.88, p = .351, $\eta^2 = .014$, $BF_{01} = 3.66$, total explosions, F(1, 65) = 0.39, p = .536, $\eta^2 = .006$, $BF_{01} = 3.10$, data from pretests were pooled for the baseline regression models testing hypotheses 2a and 2b.

Baseline Regression Models: Relation Between Microbiota (Hyp2a)/Cardiac Vagal Activity (Hyp2b) and Risky Decision-Making

For the BART task, 1/10 models and for the IGT 1/10 models yielded a significant model fit and had a BF₁₀ > 3 indicating moderate evidence

(van Doorn et al., 2021; see Table 2). All model fit statistics and Bayes factors for all models are reported in Supplemental Material D3, while in the main text, only significant results will be reported. Significant relations to risky decision-making were obtained for *F. prausnitzii*, but not for the other bacteria tested (*A. muciniphila*, *Bifidobacteriaceae*, *Lactobacillaceae*, *total number of bacteria*).

For the BART total explosions, the results of the significant regression models provide moderate evidence (BF₁₀ = 8.63) supporting the alternative hypothesis regarding the Microbiota (i.e., F. prausnitzii) \times Interoception mechanism (path a). Within this overall model, none of the significant effects obtained were supported by the Bayesian analyses. Thus, the following results should be considered as trends and preliminary rather than conclusive: The results showed an effect of interoceptive accuracy (moderator) on total explosions (see Table 2: model 1 corresponds to #8 in the R code; assumption checks can be found in Supplemental Materials D1 and D2). Results further hint at an interaction effect of the microbiota bacteria (predictor: F. prausnitzii) and interoceptive accuracy (moderator) on BART total explosions (see model 1, Table 2). In particular, for people with rather good (M + 1 SD) interoceptive accuracy, the relation between F. prausnitzii and the number of total explosions was negative, whereas for people with worse interoceptive accuracy, these relations were positive. This suggests that people who were better at perceiving internal bodily signals and had a higher amount of F. prausnitzii were less likely to make risky choices in the BART task, whereas people who were less able to perceive bodily signals and had a higher amount of F. prausnitzii were more likely to make risky choices in the BART task. This descriptive pattern of results is what we had hypothesized (path a).

For the IGT total earnings, the results of the significant regression models provide moderate evidence (BF₁₀ = 3.74) supporting the alternative hypothesis regarding the Microbiota (i.e., $F.\ prausnitzii$) × Interoception mechanism (path a). Within this overall model, none of the significant effects obtained were supported by the Bayesian analyses. Thus, as for the BART, the following IGT-results should be considered as trends and preliminary rather than conclusive: For total earnings, the regression models

This article is intended solely for the personal use of the individual user and is not to be disseminated broadly. This document is copyrighted by the American Psychological Association or one of its allied publishers.

 Table 2

 Overview of the Regression Effects (Baseline and Post Data)

$ m BF_{10}$	8.63	3.74	7.42	3.39
\mathbf{BF}_{01}	0.12	0.27	0.14	0.30
Model fit BF ₀₁ BF ₁₀	$p = .015 \ 0.12 \ 8.63$	p = .019 0.27 3.74	p = .008	p = .018 0.30 3.39
Cardiac Vagal Activity × Interoceptive Accuracy	$^{\rm n.s.}_{\rm BF_{01}}=0.41,{\rm BF_{10}}=2.45$	$^{\rm n.s.}_{\rm BF_{01}}=1.91,{\rm BF_{10}}=0.52$	$^{\text{n.s.}}_{\text{DF}_{01}} = 0.23, \text{BF}_{10} = 4.32$	$^{\rm n.s.}_{\rm PF_{01}}=0.34,~{ m BF_{10}}=2.98$
Microbiota × Interoceptive Accuracy	b = -0.58 (SE = 0.19), $p = .005BF01 = 0.56, BF10 = 1.77$	b = 0.38 (SE = 0.18), p = .045 BF ₀₁ = 2.40, BF ₁₀ = 0.42	$b = 0.26 \ (SE = 0.13),$ p = .050 $BF_{01} = 0.33, BF_{10} = 3.02$	$BF_{01} = 0.48, BF_{10} = 2.11$
Interoceptive accuracy (moderator)	b = 12.92 (SE = 4.41), p = .006 BF ₀₁ = 0.45, BF ₁₀ = 2.21	$BF_{01} = 2.31, BF_{10} = 0.43$	$^{\text{n.s.}}_{\text{BF}_{01}} = ^{\text{n.s.}}_{0.18, \text{ BF}_{10}} = ^{\text{b}}_{10} = ^{\text{c}}_{10} = ^{c$	$BF_{01} = 0.29, BF_{10} = 3.48$
Microbiota parameter Cardiac vagal activity Interoceptive accuracy (predictor 1) (predictor 2) (moderator)	RMSSD n.s. $BF_{01} = 1.51, BF_{10} = 0.66$	RMSSD n.s. BF ₀₁ = 2.87 , BF ₁₀ = 0.35	RMSSD n.s. $BF_{01} = 1.67, BF_{10} = 0.60$	RMSSD n.s. $BF_{01} = 0.97, BF_{10} = 1.03$
Microbiota parameter (predictor 1)	F. prausnitzü n.s. $BF_{01} = 3.20, BF_{10} = 0.31$	F. prausnitzii, $b = 0.40$ (SE = 0.14), $p = 0.07$ BF ₀₁ = 0.67, BF ₁₀ =	Lactobacillaceae n.s. $BF_{01} = 2.28, BF_{10} = 0.44$	Lactobacillaceae n.s. $BF_{01} = 2.48, BF_{10} = 0.40$
Time point Model Outcome	Baseline 1 (#8) BART total explosions	IGT total earnings	1 (#14) IGT total earnings	2 (#19) IGT diff. decks
Model	1 (#8)	2 (#13)	1 (#14)	2 (#19)
Time point	Baseline	Baseline 2 (#13) IGT total earnings	Post	Post

predictor heart rate variability (RMSSD) out of a total of 40 models (20 models baseline data, 20 models post data) are provided. The first two rows include data from pretests (day 42) collapsed across both groups. "#" indicate the corresponding model in the R code; BART = Balloon Analogue Risk Task; IGT = Iowa Gambling Task; RMSSD = root-mean-square of successive differences; n.s. = not significant according to inference statistics; SE = standard error; BF = Bayes Note. Significant regression models for the predictor 1 = microbiota (A. muciniphila, Bifidobacteriaceae, F. prausnitzii, Lactobacillaceae, or total number of bacteria) and the

indicated that the gut bacteria *F. prausnitzii* predicted the total earnings (see Table 2, model 2 corresponds to #13 in the R code).

The results also yielded an effect of interoceptive accuracy (moderator) and an interaction effect of F. prausnitzii and interoceptive accuracy (moderator) on the total earnings (model 2). This indicates, as for the BART, that for people with rather good $(M+1\ SD)$ interoceptive accuracy, the relation between F. prausnitzii and their total earnings was positive, whereas there was no significant relation for people with worse interoceptive accuracy $(M-1\ SD)$. That is, people who were better at perceiving internal bodily signals and had a high amount of F. prausnitzii were less likely to make risky choices that resulted in losing money in the IGT.

In sum, only two models (of 20) supported the alternative hypothesis regarding the Microbiota × Interoception mechanism (path a) for risky decision-making, which for the BART and the IGT was constituted by *F. prausnitzii*.

Postdata Regression Models as Control: Relation Between Microbiota (Hyp2a)/Cardiac Vagal Activity (Hyp2b) and Risky Decision-Making

In order to infer the stability of our results, data from day 42 after the intervention were taken to repeat all analyses reported in the previous section. These analyses were conducted post hoc and the results need to be interpreted with caution because participants had taken probiotics for 42 days. Although no statistically significant intervention effect was obtained, probiotics might still have affected the gut microbiota.

No differences between the two experimental groups (probiotics vs. placebo) were apparent in the post data, IGT: total earnings, F(1, 61) = 0.79, p = .379, $\eta^2 = .013$, BF₀₁ = 2.79, advantageous minus disadvantageous selections F(1, 61) = 1.22, p = .274, $\eta^2 = .020$, BF₀₁ = 3.00; BART: adjusted number of pumps, F(1, 60) = 0.60, p = .441, $\eta^2 = .010$, BF₀₁ = 3.00, total explosions, F(1, 60) = 0.002, p = .968, $\eta^2 = .001$, BF₀₁ = 3.86. Data were pooled across groups accordingly to conduct postdata regression models providing additional evidence concerning hypotheses 2a and 2b.

For the BART task, 1/10 models and for the IGT 1/10 models yielded a significant model fit

and had a BF₁₀ greater than 3 indicating moderate evidence (van Doorn et al., 2021; see Table 2). All model fit statistics and Bayes factors for all models are reported in Supplemental Material D6 (for assumption checks path a/path b, see also Supplemental Materials D4 and D5), while in the main text, only significant results will be reported. Significant relations to risky decision-making were only obtained for *Lactobacillaceae*, but not for the other bacteria tested (*A. muciniphila*, *Bifidobacteriaceae*, *F. prausnitzii*, *total number of bacteria*).

For the IGT total earnings and the difference between advantageous-disadvantageous decks, the results of the significant regression models both provide moderate evidence (total earnings: $BF_{10} =$ 7.42; difference of advantageous–disadvantageous decks: $BF_{10} = 3.39$) in favor of the alternative hypothesis regarding the Microbiota × Interoception mechanism (path a). In detail, within the significant overall model, only one significant effect was obtained which was supported by the Bayesian analyses: the interaction effect of Lactobacillaceae with interoceptive accuracy on total earnings (BF_{10} = 3.02). The results also yielded an interaction effect of Lactobacillaceae and interoceptive accuracy (moderator) on the IGT variable total earnings (post model 2). The interaction at the post test was similar to the way that interoceptive accuracy interacted with F. prausnitzii at baseline: For participants with rather good interoceptive accuracy, the relation between *Lactobacillaceae* and their total earnings was positive, whereas there was no significant relation for people with worse interoceptive accuracy. That is, people who were better at perceiving internal bodily signals and had a high amount of Lactobacillaceae were less likely to make risky choices that resulted in losing money in the IGT.

Moderated Mediation Models: Causal Probiotics Versus Placebo Effect on Decision-Making via Microbiota/Cardiac Vagal Activity Moderated by Interoceptive Accuracy (Hyp3a,b)

The moderated mediation analyses revealed neither a significant intervention effect (probiotics vs. placebo) nor significant changes from pre to post in the BART or IGT. Therefore, as absent effects do not allow continuing with the analysis of a moderated mediation in the post data this part was dropped.

Discussion

After reviewing literature on the gut-cognition link, uncertainties persisted regarding the effects of probiotic interventions on cognition in healthy humans and particularly the constituting psychophysiological mechanisms. To address this gap, our study aimed to deepen the understanding of the psychophysiological mechanisms constituting the gut-cognition link by focusing on risky decision-making and psychophysiological mediators. Using a triple-blind, placebo-controlled pre-post design, we followed the gold standard of intervention studies, employing validated measures to assess gut microbiota and risky decision-making.

In healthy adults of both sexes, our 6-week probiotic intervention neither elicited a direct effect on risky decision-making nor an indirect effect on mediators, namely cardiac vagal activity and gut bacteria. It should be noted that for this study and its design, nonsignificance of these effects should be interpreted as inconclusive rather than absent evidence. At the time when the study was designed, most studies targeting cognition in healthy humans (see Table 1, studies 2014–2018) were conducted over 4 weeks. Despite our longer intervention duration (6 weeks), and the specific targeting of bacteria known to activate GABA and acetylcholine in vitro (Del Toro-Barbosa et al., 2020; Wall et al., 2014), no discernible effects were observed. The absence of clear evidence for a probiotic intervention effect aligns with a systematic review, suggesting no convincing effects of probiotic interventions in healthy participants (Kristensen et al., 2016). Kristensen et al. (2016) criticized, for instance, statistical power due to small sample sizes or variations in the habitual diet of participants. Even if changes are detected, they often involve the functioning of single microbes rather than a comprehensive alteration in microbiota composition or general functioning (Bagga et al., 2018; Sanders, 2016). Subtle changes in some bacteria were observed between the two intervention groups (see, e.g., A. muciniphila and F. prausnitzii; Supplemental Material C1), but these were not indicative of an overall intervention effect. Bagga et al. (2018) proposed that indirect effects (e.g., provision of important nutrients) can account for absent intervention effects, yet in our control analyses we found no associations between nutrition (habitual diet), assessed through daily

diaries, and microbiota. Recent evidence also suggests that even daily variations in microbiome composition, with some reporting up to 100-fold changes in bacterial abundance within short timeframes, can occur (Procházková et al., 2024; Vandeputte et al., 2021).

Probiotic administration varies greatly among studies, including colony-forming units per gram per dosage (see probiotic composition, Table 1) and bacterial composition. Currently, there is no standardized recommendation for optimizing psychobiotic potential. Future studies should establish gold standards for probiotics administration in healthy humans and systematically explore dose—response relations. Importantly, evaluating changes in microbiota creates an added value and future studies must remedy the disregard of stool samples in probiotic intervention studies (Del Toro-Barbosa et al., 2020).

In our study, we tested healthy, young adults (max. age = 41 years) of both sexes (important to close the female data gap) of whom a majority led a healthy lifestyle and can be described as having an above-average fitness level. Our sample should therefore be considered representative of a limited yet not insignificant population of young adults (in line with Simons et al., 2017, for constraints on generality). Regarding the risk measures applied, the IGT has been criticized in terms of validity, not being suited for the assessment of individual differences in risky decision-making (see e.g., Schmitz et al., 2020), but rather tapping into broader decision-making processes beyond pure risk/reward sensitivity. Using the BART in addition was a first step to counteract this shortcoming, as both tasks have a differentiated view of the relationship between risk and reward. In our study, we used the outcome of the risky decision in both the IGT and the BART which are unsuited to provide insights on single decision processes. As an alternative, cognitive modeling approaches and rigorous parameter estimation (Coon & Lee, 2022) could provide a more differentiated picture of people's risky decision-making. In detail, differentiated cognitive models for the IGT (e.g., Steingroever et al., 2013; Haines et al., 2018) and the BART (e.g., van Ravenzwaaij et al., 2011) have been developed to reflect decision-making processes. Future studies interested in decisionmaking processes, could relate them to acute, momentary psychophysiological assessment (e.g., time-sensitive electroencephalogram, cardiac activity together with trial-by-trial analysis of decision-making), and apply additional paradigms of risky decision-making in order to enrich the understanding of risky decision-making. We believe that the triple-blind design of our study results in similar outcomes in other studies, yet replication studies should adhere to the study protocol, especially with regard to probiotic administration, probiotic composition, the analyzed target bacteria, intervention duration, and electrode application.

Although we did not find evidence for intervention effects, our baseline data, and additionally cross-checks with the post data, can contribute possible insights into the gut-cognition link in healthy humans, particularly in risky decisionmaking. Before, we interpret the results, we want to explicate that in light of the many models tested and the corresponding risk of type 1 error, the evidence reported and interpreted here needs to be treated with caution. Including Bayesian analyses, even though we had no prior belief about the influence of specific bacteria, was important to draw probabilistic conclusions about the results. Future studies would do well to preplan Bayesian analyses when the gut-cognition link is examined and multiple bacteria are involved. Our results provide preliminary, moderate evidence that interoceptive accuracy moderates the relationship between microbiota and risky decision-making, lending preliminary support for the hypothesized psychophysiological mechanism of risky decision-making. Specifically, for IGT total earnings in the postintervention data (BF₁₀ > 3), Lactobacillaceae were positively associated with better decision-making only in individuals with high interoceptive accuracy, whereas no significant relationship was observed in those with lower interoceptive accuracy. This pattern suggests that interoceptive sensitivity may play a role in determining whether gut-derived signals contribute to risky decision-making processes. Notably, similar interaction trend emerged for F. prausnitzii in the baseline data for both the BART and the IGT, though the evidence remained inconclusive (BF₁₀ < 3). These findings align with theoretical perspectives suggesting that the integration of bodily signals—potentially mediated by interoception-can shape cognitiveaffective processes such as risk-taking (e.g., Kandasamy et al., 2016). However, given the complexity of the gut-brain axis and the exploratory nature of our study, further research is needed to clarify whether interoceptive accuracy

functions as a moderator and which specific bacteria play a role in gut-derived influences on decision-making. Other studies demonstrated meaningful relations in other samples like children, unhealthy adults, or elderly cohorts and to other cognitive functions (for an overview, see Castells-Nobau et al., 2024). Future studies could explore, contrary to healthy populations, how specific clinical gut conditions, such as leaky gut syndrome or inflammatory bowel disease, manifest in bacterial diversity and microbiota composition and are linked to risky decision-making or other cognitive outcomes.

To post hoc reason about the results obtained for the specific bacteria and to guide future research, we discuss current literature on the role of F. prausnitzii and Lactobacillaceae for cognition. F. prausnitzii has recently been found to be a prominent bacteria in a 4-week intervention study in children (Sagbasan et al., 2024). The study aimed at enhancing gut microbiome diversity through insulin administration and demonstrated cognitive improvements, particularly in memory processes, which were associated with significant increases in F. prausnitzii (Sagbasan et al., 2024). The results by Bagga et al. (2018) also fit in here. They indicated a potential link between specific Bacteroides species and brain memory and recognition, among others, Faecalibacteria (see Bagga et al., 2018, Supplemental Material). F. prausnitzii is a predominant bacterial species in the healthy human large intestine and is recognized as a major butyric acid producer (Ferreira-Halder et al., 2017; Miguel et al., 2013). It plays a key role in colonocyte fueling, exerts potent neuropharmacological effects, and prevents "leaky gut" (Camilleri, 2019; Kondrashina et al., 2021; Stilling et al., 2016). Our results can add to the current evidence that F. prausnitzii might be not only associated with memory performance but possibly also with decision-making (i.e., fewer risk taking).

The inclusion of *Lactobacillaceae* in probiotics (e.g., fermented milk) has been previously associated with significant improvements in intervention groups for attention and memory (Ohsawa et al., 2018) and reduced risk-taking (Dantas et al., 2022). However, while *Lactobacillaceae* were part of the probiotic composition (see Table 1), they were often not directly examined in the microbiota composition, making it more

difficult to reason about its role in cognitive function in healthy adults. Bringing our findings together, it is, however, interesting to note that the Lactobacillaceae family and Faecalibacterium prausnitzii belong to the same phylum, Bacillota (formerly known as Firmicutes, e.g., Duncan et al., 2002), which is why future research could explore the role of Bacillota for decision-making further. To better understand the psychophysiological connection between the gut and risky decision-making—or cognitive performance more broadly, future studies should assess gut microbiota composition and bacterial diversity (e.g., Castells-Nobau et al., 2024) alongside specific bacterial strains. Building on these findings, research should further investigate the mechanisms underlying the gut-brain link in decision-making, with a particular focus on how interoceptive accuracy shapes the integration of microbiota-derived signals into cognitive and affective processes. As we hypothesized, the vagus nerve, as a primary bidirectional communication channel between the gut and the brain, may facilitate this interaction by modulating autonomic regulation and prefrontal cortex activity. An intriguing future direction would be to investigate whether prefrontal networks, previously associated with reflective processing and risk avoidance, serve as functional neural basis for this gut-derived influence (for a meta-analysis, see Wang et al., 2022; for IGT, see also Brevers et al., 2013). To directly test the involvement of the prefrontal network (Brevers et al., 2013) or the neurotransmitter signaling eliciting the functional gut-cognition link (e.g., Del Toro-Barbosa et al., 2020; Kim et al., 2021; Wall et al., 2014; Yu et al., 2020), more studies using functional magnetic resonance imaging or positron emission tomography are needed in the future.

Considering that the neural networks involved in risky decision-making are also shared with the vagus nerve via the vagal sensory ganglion (Yu et al., 2020), and recognizing the vagal pathway as a significant mechanism in the gut-cognition link (see e.g., Dantas et al., 2022), we also investigated whether cardiac vagal activity was a relevant mediator. Our data did not support the proposed mediation via vagally mediated HRV, as inferred from baseline tests of cardiac vagal activity.

One possible explanation for not finding direct effects on HRV may be that the probiotics employed may not have generated sufficient GABA or acetylcholine (e.g., Del Toro-Barbosa et al., 2020; Wall et al., 2014). While all the employed bacteria could produce lactic or acetic acid, the probiotics primarily targeted GABA release. Future studies could explore other potential indicators of vagal tone using different probiotics as suggested by Tillisch et al. (2013). They propose that potential mediators of probiotic effects include signaling molecules (e.g., tryptophan; Cryan & Dinan, 2012; Rhee et al., 2009). Consistent with this, Falkenstein et al. (2024)—a study conducted well after ours-suggested that tryptophan and tyrosine influence risky decisionmaking. They found that reducing tyrosine led to a greater increase in rejection of unfair offers in the ultimatum game compared with participants with probiotic-modulated gut microbiota. However, they did not assess interoception or vagal activity. Notably, cardiac vagal activity remains one of the most reliable, noninvasive measures of efferent vagal activity from the brainstem in humans. Ideally, future approaches would therefore look at multiple possible factors constituting psychophysiological mechanisms in different risky decision tasks. Given that we assessed the efferent brain-heart connection as a proxy for the vagal pathway, not finding a meaningful relation between HRV and risky decision-making does not mean that the vagus nerve was not involved. In addition to the efferent signaling, in future research, the afferent connection of the vagus nerve should be examined (e.g., via heart-beat-evoked-potentials, Richter et al., 2021) to scrutinize the gut-brain axis.

Conclusion

In summary, our study provides preliminary results on a psychophysiological link between microbiota and decision-making, particularly in the context of risky choices. Specifically, *F. prausnitzii* was associated with risky decision-making behavior, moderated by interoceptive accuracy. Higher levels of *F. prausnitzii* (baseline) and higher levels of *Lactobacillaceae* (post data) in healthy individuals in combination with a more accurate perception of internal bodily signals was related to higher earnings (IGT). This suggests that candidate bacteria in the human gut, coupled with the ability to perceive internal bodily signals, may shape real decisions under risk. We encourage future studies to replicate our

preliminary results and interdisciplinary research to explore the impact of the human gut microbiota on other pertinent real-life risky decisions, such as financial investments or pedestrian crossings on busy streets.

References

- Akbari, E., Asemi, Z., Daneshvar Kakhaki, R., Bahmani, F., Kouchaki, E., Tamtaji, O. R., Hamidi, G. A., & Salami, M. (2016). Effect of probiotic supplementation on cognitive function and metabolic status in Alzheimer's disease: A randomized, double-blind and controlled trial. Frontiers in Aging Neuroscience, 8, Article 256. https://doi.org/10.3389/fnagi.2016.00256
- Allen, A. P., Hutch, W., Borre, Y. E., Kennedy, P. J., Temko, A., Boylan, G., Murphy, E., Cryan, J. F., Dinan, T. G., & Clarke, G. (2016). Bifidobacterium longum 1714 as a translational psychobiotic: Modulation of stress, electrophysiology and neurocognition in healthy volunteers. *Translational Psychiatry*, 6(11), Article e939. https://doi.org/10 .1038/tp.2016.191
- Aydogan, G., Daviet, R., Karlsson Linnér, R., Hare, T. A., Kable, J. W., Kranzler, H. R., Wetherill, R. R., Ruff, C. C., Koellinger, P. D., Nave, G., & the BIG BEAR Consortium. (2021). Genetic underpinnings of risky behaviour relate to altered neuroanatomy. *Nature Human Behaviour*, 5(6), 787–794. https://doi.org/10.1038/s41562-020-01027-y
- Bagga, D., Reichert, J. L., Koschutnig, K., Aigner, C. S., Holzer, P., Koskinen, K., Moissl-Eichinger, C., & Schöpf, V. (2018). Probiotics drive gut microbiome triggering emotional brain signatures. *Gut Microbes*, 9(6), 486–496. https://doi.org/10.1080/19490976 .2018.1460015
- Bajaj, J. S., Hylemon, P. B., Ridlon, J. M., Heuman, D. M., Daita, K., White, M. B., Monteith, P., Noble, N. A., Sikaroodi, M., & Gillevet, P. M. (2012). Colonic mucosal microbiome differs from stool microbiome in cirrhosis and hepatic encephalopathy and is linked to cognition and inflammation. *American Journal of Physiology-Gastrointestinal and Liver Physiology*, 303(6), G675–G685. https://doi.org/10.1152/ajpgi.00152.2012
- Bechara, A. (2011). Human emotions in decision making: Are they useful or disruptive? In O. Vartanian & D. R. Mandel (Eds.), *Neuroscience of decision making* (pp. 73–95). Psychology Press.
- Bechara, A., & Damasio, A. R. (2005). The somatic marker hypothesis: A neural theory of economic decision. *Games and Economic Behavior*, 52(2), 336–372. https://doi.org/10.1016/j.geb.2004.06.010
- Bechara, A., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future

- consequences following damage to human prefrontal cortex. *Cognition*, 50(1–3), 7–15. https:// doi.org/10.1016/0010-0277(94)90018-3
- Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science*, 275(5304), 1293–1295. https://doi.org/10.1126/ science.275.5304.1293
- Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (2005). The Iowa Gambling Task and the somatic marker hypothesis: Some questions and answers. *Trends in Cognitive Sciences*, 9(4), 159– 162. https://doi.org/10.1016/j.tics.2005.02.002
- Bechara, A., Tranel, D., Damasio, H., & Damasio, A. R. (1996). Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cerebral Cortex*, 6(2), 215–225. https://doi.org/10.1093/cercor/6.2.215
- Benarroch, E. E. (1993). The central autonomic network: Functional organization, dysfunction, and perspective. *Mayo Clinic Proceedings*, *68*(10), 988–1001. https://doi.org/10.1016/S0025-6196(12)62272-1
- Berntson, G. G., Sarter, M., & Cacioppo, J. T. (2003). Ascending visceral regulation of cortical affective information processing. *The European Journal of Neuroscience*, 18(8), 2103–2109. https://doi.org/10.1046/j.1460-9568.2003.02967.x
- Bloemendaal, M., Szopinska-Tokov, J., Belzer, C., Boverhoff, D., Papalini, S., Michels, F., van Hemert, S., Arias Vasquez, A., & Aarts, E. (2021). Probioticsinduced changes in gut microbial composition and its effects on cognitive performance after stress: Exploratory analyses. *Translational Psychiatry*, 11(1), Article 300. https://doi.org/10.1038/s41398-021-01404-9
- Boem, F., Greslehner, G. P., Konsman, J. P., & Chiu, L. (2024). Minding the gut: Extending embodied cognition and perception to the gut complex. Frontiers in Neuroscience, 17, Article 1172783. https://doi.org/10 .3389/fnins.2023.1172783
- Bonaz, B., Bazin, T., & Pellissier, S. (2018). The vagus nerve at the interface of the microbiota-gut-brain axis. *Frontiers in Neuroscience*, *12*, Article 49. https://doi.org/10.3389/fnins.2018.00049
- Bravo, J. A., Forsythe, P., Chew, M. V., Escaravage, E., Savignac, H. M., Dinan, T. G., Bienenstock, J., & Cryan, J. F. (2011). Ingestion of Lactobacillus strain regulates emotional behavior and central GABA receptor expression in a mouse via the vagus nerve. Proceedings of the National Academy of Sciences of the United States of America, 108(38), 16050–16055. https://doi.org/10.1073/pnas.1102999108
- Brevers, D., Bechara, A., Cleeremans, A., & Noël, X. (2013). Iowa Gambling Task (IGT): Twenty years after—gambling disorder and IGT. Frontiers in Psychology, 4, Article 665. https://doi.org/10.3389/fpsyg.2013.00665

- Brown, J. W., & Braver, T. S. (2007). Risk prediction and aversion by anterior cingulate cortex. *Cognitive, Affective & Behavioral Neuroscience*, 7(4), 266–277. https://doi.org/10.3758/CABN.7.4.266
- Buelow, M. T., & Suhr, J. A. (2009). Construct validity of the Iowa Gambling Task. *Neuropsychology Review*, 19(1), 102–114. https://doi.org/10.1007/s11 065-009-9083-4
- Camilleri, M. (2019). Leaky gut: Mechanisms, measurement and clinical implications in humans. *Gut*, 68(8), 1516–1526. https://doi.org/10.1136/gutjnl-2019-318427
- Carter, S., & Pasqualini, M. S. (2004). Stronger autonomic response accompanies better learning: A test of Damasio's somatic marker hypothesis. *Cognition & Emotion*, 18(7), 901–911. https://doi.org/ 10.1080/02699930341000338
- Castells-Nobau, A., Mayneris-Perxachs, J., & Fernández-Real, J. M. (2024). Unlocking the mindgut connection: Impact of human microbiome on cognition. *Cell Host & Microbe*, 32(8), 1248–1263. https://doi.org/10.1016/j.chom.2024.07.019
- Cawthon, C. R., & de La Serre, C. B. (2018). Gut bacteria interaction with vagal afferents. *Brain Research*, 1693, 134–139. https://doi.org/10.1016/j .brainres.2018.01.012
- Chung, Y., Jin, H., Cui, Y., Kim, D. S., Jung, J. M., Park, J., Jung, E., Choi, E., & Chae, S. (2014). Fermented milk of Lactobacillus helveticus IDCC3801 improves cognitive functioning during cognitive fatigue tests in healthy older adults. *Journal of Functional Foods*, 10, 465–474. https://doi.org/10.1016/j.jff.2014.07.007
- Clark, L., Bechara, A., Damasio, H., Aitken, M. R., Sahakian, B. J., & Robbins, T. W. (2008). Differential effects of insular and ventromedial prefrontal cortex lesions on risky decision-making. *Brain: A Journal* of Neurology, 131(5), 1311–1322. https://doi.org/10 .1093/brain/awn066
- Coon, J., & Lee, M. D. (2022). A Bayesian method for measuring risk propensity in the balloon analogue risk task. *Behavior Research Methods*, 54(2), 1010–1026. https://doi.org/10.3758/s13428-021-01634-1
- Critchley, H. D., & Harrison, N. A. (2013). Visceral influences on brain and behavior. *Neuron*, 77(4), 624– 638. https://doi.org/10.1016/j.neuron.2013.02.008
- Cryan, J. F., & Dinan, T. G. (2012). Mind-altering microorganisms: The impact of the gut microbiota on brain and behaviour. *Nature Reviews Neuroscience*, *13*(10), 701–712. https://doi.org/10.1038/nrn3346
- Cryan, J. F., & Dinan, T. G. (2015). More than a gut feeling: The microbiota regulates neurodevelopment and behavior. *Neuropsychopharmacology*, 40(1), 241–242. https://doi.org/10.1038/npp.2014.224
- Cryan, J. F., & O'Mahony, S. M. (2011). The microbiome-gut-brain axis: From bowel to behavior. Neurogastroenterology and Motility, 23(3), 187–192. https://doi.org/10.1111/j.1365-2982.2010.01664.x

- Cryan, J. F., O'Riordan, K. J., Cowan, C. S. M., Sandhu, K. V., Bastiaanssen, T. F. S., Boehme, M., Codagnone, M. G., Cussotto, S., Fulling, C., Golubeva, A. V., Guzzetta, K. E., Jaggar, M., Long-Smith, C. M., Lyte, J. M., Martin, J. A., Molinero-Perez, A., Moloney, G., Morelli, E., Morillas, E., ... Dinan, T. G. (2019). The microbiota-gut-brain axis. *Physiological Reviews*, *99*(4), 1877–2013. https://doi.org/10.1152/physrev.00018.2018
- Czajeczny, D., Kabzińska, K., & Wójciak, R. W. (2021). Effects of Bifidobacterium Lactis BS01 and Lactobacillus Acidophilus LA02 on cognitive functioning in healthy women. *Applied Neuropsychology Adult*, 30(5), 552–560. https://doi.org/10.1080/23279095.2021.1967155
- Damasio, A. R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 351(1346), 1413–1420. https://doi.org/10.1098/rstb.1996.0125
- Damasio, A. R., Tranel, D., & Damasio, H. (1991).
 Somatic markers and the guidance of behaviour:
 Theory and preliminary testing. In H. S. Levin,
 H. M. Eisenberg, & A. L. Benton (Eds.), Frontal lobe function and dysfunction (pp. 217–229).
 Oxford University Press. https://doi.org/10.1093/oso/9780195062847.003.0011
- Dantas, A. M., Sack, A. T., Bruggen, E., Jiao, P., & Schuhmann, T. (2022). The effects of probiotics on risk and time preferences. *Scientific Reports*, 12(1), Article 12152. https://doi.org/10.1038/s41598-022-16251-x
- Del Toro-Barbosa, M., Hurtado-Romero, A., Garcia-Amezquita, L. E., & García-Cayuela, T. (2020). Psychobiotics: Mechanisms of action, evaluation methods and effectiveness in applications with food products. *Nutrients*, 12(12), Article 3896. https://doi.org/10.3390/nu12123896
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009
- Diez-Gutiérrez, L., San Vicente, L., Luis, L. J., Villarán, M. D. C., & Chávarri, M. (2020). Gammaaminobutyric acid and probiotics: Multiple health benefits and their future in the global functional food and nutraceuticals market. *Journal of Functional Foods*, 64, Article 103669. https://doi.org/10.1016/j .jff.2019.103669
- Duncan, S. H., Hold, G. L., Harmsen, H. J. M., Stewart, C. S., & Flint, H. J. (2002). Growth requirements and fermentation products of Fusobacterium prausnitzii, and a proposal to reclassify it as Faecalibacterium prausnitzii gen. nov., comb. nov. *International Journal of Systematic and Evolutionary Microbiology*, 52(6), 2141–2146. https://doi.org/10.1099/00207713-52-6-2141

- Dunn, B. D., Evans, D., Makarova, D., White, J., & Clark, L. (2012). Gut feelings and the reaction to perceived inequity: The interplay between bodily responses, regulation, and perception shapes the rejection of unfair offers on the ultimatum game. Cognitive, Affective & Behavioral Neuroscience, 12(3), 419–429. https://doi.org/10.3758/s13415-012-0092-7.
- Dunn, B. D., Galton, H. C., Morgan, R., Evans, D., Oliver, C., Meyer, M., Cusack, R., Lawrence, A. D., & Dalgleish, T. (2010). Listening to your heart. How interoception shapes emotion experience and intuitive decision making. *Psychological Science*, 21(12), 1835–1844. https://doi.org/10 .1177/0956797610389191
- Falkenstein, M., Simon, M. C., Mantri, A., Weber, B., Koban, L., & Plassmann, H. (2024). Impact of the gut microbiome composition on social decisionmaking. *PNAS Nexus*, 3(5), Article pgae166. https:// doi.org/10.1093/pnasnexus/pgae166
- Farmer, A. D., Strzelczyk, A., Finisguerra, A., Gourine, A. V., Gharabaghi, A., Hasan, A., Burger, A. M., Jaramillo, A. M., Mertens, A., Majid, A., Verkuil, B., Badran, B. W., Ventura-Bort, C., Gaul, C., Beste, C., Warren, C. M., Quintana, D. S., Hämmerer, D., Freri, E., ... Koenig, J. (2021). International consensus based review and recommendations for minimum reporting standards in research on transcutaneous vagus nerve stimulation (version 2020). Frontiers in Human Neuroscience, 14, Article 568051. https://doi.org/10.3389/fnhum.2020.568051
- Ferreira-Halder, C. V., Faria, A. V. S., & Andrade, S. S. (2017). Action and function of Faecalibacterium prausnitzii in health and disease. *Best Practice & Research. Clinical Gastroenterology*, *31*(6), 643–648. https://doi.org/10.1016/j.bpg.2017.09.011
- Forsythe, P., Kunze, W. A., & Bienenstock, J. (2012). On communication between gut microbes and the brain. *Current Opinion in Gastroenterology*, 28(6), 557–562. https://doi.org/10.1097/MOG.0b01 3e3283572ffa
- Forte, G., Morelli, M., & Casagrande, M. (2021). Heart rate variability and decision-making: Autonomic responses in making decisions. *Brain Sciences*, 11(2), Article 243. https://doi.org/10.3390/brainsci 11020243
- Foster, J. A., Rinaman, L., & Cryan, J. F. (2017). Stress & the gut-brain axis: Regulation by the microbiome. *Neurobiology of Stress*, 7, 124–136. https://doi.org/10.1016/j.ynstr.2017.03.001
- Fukunaga, R., Brown, J. W., & Bogg, T. (2012). Decision making in the Balloon Analogue Risk Task (BART): Anterior cingulate cortex signals loss aversion but not the infrequency of risky choices. *Cognitive, Affective, & Behavioral Neuroscience*, 12(3), 479–490. https://doi.org/10.3758/s13415-012-0102-1

- Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., & Critchley, H. D. (2015). Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness. *Biological Psychology*, 104, 65–74. https://doi.org/10.1016/j.biopsycho .2014.11.004
- González-Arancibia, C., Urrutia-Piñones, J., Illanes-González, J., Martinez-Pinto, J., Sotomayor-Zárate, R., Julio-Pieper, M., & Bravo, J. A. (2019).
 Do your gut microbes affect your brain dopamine? *Psychopharmacology*, 236(5), 1611–1622. https://doi.org/10.1007/s00213-019-05265-5
- Haines, N., Vassileva, J., & Ahn, W. Y. (2018). The outcome-representation learning model: A novel reinforcement learning model of the iowa gambling task. *Cognitive Science*, 42(8), 2534–2561. https:// doi.org/10.1111/cogs.12688
- Hamilton, P. S., & Tompkins, W. J. (1986). Quantitative investigation of QRS detection rules using the MIT/BIH arrhythmia database. *IEEE Transactions* on *Biomedical Engineering*, 33(12), 1157–1165. https://doi.org/10.1109/TBME.1986.325695
- Hassouna, R., Van Oudenhove, L., Le Nevé, B., & Barwich, A. S. (2024). Editorial: The organs of sensibility: Multimodal sensing within the microbiota-gut-brain axis and how it drives physiology, behavior and perception. *Frontiers in Neuroscience*, 18, Article 1380039. https://doi.org/10.3389/fnins.2024.1380039
- Herbert, B. M., Muth, E. R., Pollatos, O., & Herbert, C. (2012). Interoception across modalities: On the relationship between cardiac awareness and the sensitivity for gastric functions. *PLOS ONE*, 7(5), Article e36646. https://doi.org/10.1371/journal.po ne.0036646
- Jenkins, T. A., Nguyen, J. C. D., Polglaze, K. E., & Bertrand, P. P. (2016). Influence of tryptophan and serotonin on mood and cognition with a possible role of the gut–brain axis. *Nutrients*, 8(1), Article 56. https://doi.org/10.3390/nu8010056
- Jian, C., Luukkonen, P., Yki-Järvinen, H., Salonen, A., & Korpela, K. (2018). Quantitative PCR provides a simple and accessible method for quantitative microbiome profiling. BioRxiv. https:// doi.org/10.1101/478685
- Kandasamy, N., Garfinkel, S. N., Page, L., Hardy, B., Critchley, H. D., Gurnell, M., & Coates, J. M. (2016). Interoceptive ability predicts survival on a London trading floor. *Scientific Reports*, 6(1), Article 32986. https://doi.org/10.1038/srep32986
- Kelly, J. R., Allen, A. P., Temko, A., Hutch, W., Kennedy, P. J., Farid, N., Murphy, E., Boylan, G., Bienenstock, J., Cryan, J. F., Clarke, G., & Dinan, T. G. (2017). Lost in translation? The potential psychobiotic Lactobacillus rhamnosus (JB-1) fails to modulate stress or cognitive performance in healthy male subjects. *Brain, Behavior, and Immunity*, 61, 50–59. https://doi.org/10.1016/j.bbi.2016.11.018

- Kim, C. S., Cha, L., Sim, M., Jung, S., Chun, W. Y., Baik, H. W., & Shin, D. M. (2021). Probiotic supplementation improves cognitive function and mood with changes in gut microbiota in community-dwelling older adults: A randomized, double-blind, placebo-controlled, multicenter trial. The Journals of Gerontology: Series A, Biological Sciences and Medical Sciences, 76(1), 32–40. https://doi.org/10.1093/gerona/glaa090
- Kondrashina, A., Brodkorb, A., & Giblin, L. (2021). Sodium butyrate converts Caco-2 monolayers into a leaky but healthy intestinal barrier resembling that of a newborn infant. *Food & Function*, *12*(11), 5066–5076. https://doi.org/10.1039/D1FO00519G
- Krawitz, A., Fukunaga, R., & Brown, J. W. (2010). Anterior insula activity predicts the influence of positively framed messages on decision making. *Cognitive, Affective & Behavioral Neuroscience*, 10(3), 392–405. https://doi.org/10.3758/CABN.10.3.392
- Kristensen, N. B., Bryrup, T., Allin, K. H., Nielsen, T., Hansen, T. H., & Pedersen, O. (2016). Alterations in fecal microbiota composition by probiotic supplementation in healthy adults: A systematic review of randomized controlled trials. *Genome Medicine*, 8(1), Article 52. https://doi.org/10.1186/s13073-016-0300-5
- Laborde, S., Mosley, E., & Thayer, J. F. (2017). Heart rate variability and cardiac vagal tone in psychophysiological research—Recommendations for experiment planning, data analysis, and data reporting. *Frontiers* in *Psychology*, 8, Article 213. https://doi.org/10.3389/ fpsyg.2017.00213
- Laborde, S., & Raab, M. (2013). The tale of hearts and reason: The influence of mood on decision making. *Journal of Sport & Exercise Psychology*, 35(4), 339–357. https://doi.org/10.1123/jsep.35.4.339
- Lejuez, C. W., Aklin, W. M., Jones, H. A., Richards, J. B., Strong, D. R., Kahler, C. W., & Read, J. P. (2003). The Balloon Analogue Risk Task (BART) differentiates smokers and nonsmokers. *Experimental and Clinical Psychopharmacology*, *11*(1), 26–33. https://doi.org/10.1037/1064-1297.11.1.26
- Lejuez, C. W., Read, J. P., Kahler, C. W., Richards, J. B., Ramsey, S. E., Stuart, G. L., Strong, D. R., & Brown, R. A. (2002). Evaluation of a behavioral measure of risk taking: The Balloon Analogue Risk Task (BART). *Journal of Experimental Psychology: Applied*, 8(2), 75–84. https://doi.org/10.1037/1076-898X.8.2.75
- Lew, L. C., Hor, Y. Y., Yusoff, N. A. A., Choi, S. B., Yusoff, M. S. B., Roslan, N. S., Ahmad, A., Mohammad, J. A. M., Abdullah, M. F. I. L., Zakaria, N., Wahid, N., Sun, Z., Kwok, L. Y., Zhang, H., & Liong, M. T. (2019). Probiotic Lactobacillus plantarum P8 alleviated stress and anxiety while enhancing memory and cognition in stressed adults: A randomised, double-blind, placebo-controlled

- study. *Clinical Nutrition*, *38*(5), 2053–2064. https://doi.org/10.1016/j.clnu.2018.09.010
- Magno, E., Foxe, J. J., Molholm, S., Robertson, I. H., & Garavan, H. (2006). The anterior cingulate and error avoidance. *The Journal of Neuroscience*, 26(18), 4769–4773. https://doi.org/10.1523/JNEU ROSCI.0369-06.2006
- Mayer, E. A. (2011). Gut feelings: The emerging biology of gut–brain communication. *Nature Reviews Neuroscience*, *12*(8), 453–466. https://doi.org/10.1038/nrn3071
- Miquel, S., Martín, R., Rossi, O., Bermúdez-Humarán, L. G., Chatel, J. M., Sokol, H., Thomas, M., Wells, J. M., & Langella, P. (2013). Faecalibacterium prausnitzii and human intestinal health. *Current Opinion in Microbiology*, 16(3), 255–261. https://doi.org/10.1016/j.mib.2013.06.003
- Montiel-Castro, A. J., González-Cervantes, R. M., Bravo-Ruiseco, G., & Pacheco-López, G. (2013). The microbiota-gut-brain axis: Neurobehavioral correlates, health and sociality. Frontiers in Integrative Neuroscience, 7, Article 70. https://doi.org/10.3389/ fnint.2013.00070
- Murphy, J., Brewer, R., Catmur, C., & Bird, G. (2017). Interoception and psychopathology: A developmental neuroscience perspective. *Developmental Cognitive Neuroscience*, 23, 45–56. https://doi.org/10.1016/j.dcn.2016.12.006
- Novotný, M., Klimova, B., & Valis, M. (2019). Microbiome and cognitive impairment: Can any diets influence learning processes in a positive way? Frontiers in Aging Neuroscience, 11, Article 170. https://doi.org/10.3389/fnagi.2019.00170
- Ohsawa, K., Nakamura, F., Uchida, N., Mizuno, S., & Yokogoshi, H. (2018). Lactobacillus helveticus-fermented milk containing lactononadecapeptide (NIPPLTQTPVVVPPFLQPE) improves cognitive function in healthy middle-aged adults: A randomised, double-blind, placebo-controlled trial. *International Journal of Food Sciences and Nutrition*, 69(3), 369–376. https://doi.org/10.1080/09637486.2017.1365824
- Pan, J., & Tompkins, W. J. (1985). A real-time QRS detection algorithm. *IEEE Transactions on Biomedical Engineering*, 32(3), 230–236. https://doi.org/10.1109/TBME.1985.325532
- Papalini, S., Michels, F., Kohn, N., Wegman, J., van Hemert, S., Roelofs, K., Arias-Vasquez, A., & Aarts, E. (2019). Stress matters: Randomized controlled trial on the effect of probiotics on neurocognition. *Neurobiology of Stress*, 10, Article 100141. https:// doi.org/10.1016/j.ynstr.2018.100141
- Pennisi, E. (2019). Gut bacteria linked to mental wellbeing and depression. *Science*, 363(6427), Article 569. https://doi.org/10.1126/science.363.6427.569
- Preuschoff, K., Quartz, S. R., & Bossaerts, P. (2008). Human insula activation reflects risk prediction errors as well as risk. *The Journal of Neuroscience*,

- 28(11), 2745–2752. https://doi.org/10.1523/JNEUR OSCI.4286-07.2008
- Procházková, N., Laursen, M. F., La Barbera, G., Tsekitsidi, E., Jørgensen, M. S., Rasmussen, M. A., Raes, J., Licht, T. R., Dragsted, L. O., & Roager, H. M. (2024). Gut physiology and environment explain variations in human gut microbiome composition and metabolism. *Nature Microbiology*, 9(12), 3210–3225. https://doi.org/10.1038/s41564-024-01856-x
- Rhee, S. H., Pothoulakis, C., & Mayer, E. A. (2009). Principles and clinical implications of the braingut-enteric microbiota axis. *Nature Reviews. Gastroenterology & Hepatology*, 6(5), 306–314. https://doi.org/10.1038/nrgastro.2009.35
- Richter, F., García, A. M., Rodriguez Arriagada, N., Yoris, A., Birba, A., Huepe, D., Zimmer, H., Ibáñez, A., & Sedeño, L. (2021). Behavioral and neurophysiological signatures of interoceptive enhancements following vagus nerve stimulation. *Human Brain Mapping*, 42(5), 1227–1242. https://doi.org/ 10.1002/hbm.25288
- Roman, P., Estévez, A. F., Miras, A., Sánchez-Labraca, N., Cañadas, F., Vivas, A. B., & Cardona, D. (2018). A pilot randomized controlled trial to explore cognitive and emotional effects of probiotics in fibromyalgia. *Scientific Reports*, 8(1), Article 10965. https://doi.org/10.1038/s41598-018-29388-5
- Rosenbaum, G. M., Venkatraman, V., Steinberg, L., & Chein, J. M. (2018). The influences of described and experienced information on adolescent risky decision making. *Developmental Review*, 47, 23–43. https://doi.org/10.1016/j.dr.2017.09.003
- Ruiz-Gonzalez, C., Cardona, D., Rueda-Ruzafa, L., Rodriguez-Arrastia, M., Ropero-Padilla, C., & Roman, P. (2024). Cognitive and emotional effect of a multi-species probiotic containing Lactobacillus rhamnosus and Bifidobacterium lactis in healthy older adults: A double-blind randomized placebo-controlled crossover trial. *Probiotics and Antimicrobial Proteins*. Advance online publication. https://doi.org/10.1007/ s12602-024-10315-2
- Sagbasan, B. H., Williams, C. M., Bell, L., Barfoot, K. L., Poveda, C., & Walton, G. E. (2024). Inulin and freeze-dried blueberry intervention lead to changes in the microbiota and metabolites within in vitro studies and in cognitive function within a small pilot trial on healthy children. *Microorganisms*, 12(7), Article 1501. https://doi.org/10.3390/microorganisms12071501
- Sanders, M. E. (2016). Probiotics and microbiota composition. *BMC Medicine*, 14(1), Article 82. https://doi.org/10.1186/s12916-016-0629-z
- Sarkar, A., Harty, S., Lehto, S. M., Moeller, A. H., Dinan, T. G., Dunbar, R. I. M., Cryan, J. F., & Burnet, P. W. J. (2018). The microbiome in psychology and cognitive neuroscience. *Trends in*

- Cognitive Sciences, 22(7), 611–636. https://doi.org/10.1016/j.tics.2018.04.006
- Sarkar, A., Lehto, S. M., Harty, S., Dinan, T. G., Cryan, J. F., & Burnet, P. W. J. (2016). Psychobiotics and the manipulation of bacteria-gut-brain signals. *Trends in Neurosciences*, 39(11), 763–781. https://doi.org/10.1016/j.tins.2016.09.002
- Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology*, 18(4), 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486.x
- Schmitz, F., Kunina-Habenicht, O., Hildebrandt, A., Oberauer, K., & Wilhelm, O. (2020). Psychometrics of the Iowa and Berlin gambling tasks: Unresolved issues with reliability and validity for risk taking. *Assessment*, 27(2), 232–245. https://doi.org/10 .1177/1073191117750470
- Schonberg, T., Fox, C. R., & Poldrack, R. A. (2011). Mind the gap: Bridging economic and naturalistic risk-taking with cognitive neuroscience. *Trends in Cognitive Sciences*, 15(1), 11–19. https://doi.org/10 .1016/j.tics.2010.10.002
- Shi, S., Zhang, Q., Sang, Y., Ge, S., Wang, Q., Wang, R., & He, J. (2022). Probiotic Bifidobacterium longum BB68S improves cognitive functions in healthy older adults: A randomized, double-blind, placebo-controlled trial. *Nutrients*, 15(1), Article 51. https://doi.org/10.3390/nu15010051
- Sie, J. H., Chen, Y. H., Chang, C. Y., Yen, N. S., Chu, W. C., & Shiau, Y. H. (2019). Altered central autonomic network in baseball players: A restingstate fMRI study. *Scientific Reports*, 9(1), Article 110. https://doi.org/10.1038/s41598-018-36329-9
- Simons, D. J., Shoda, Y., & Lindsay, D. S. (2017). Constraints on Generality (COG): A proposed addition to all empirical papers. *Perspectives on Psychological Science*, 12(6), 1123–1128. https://doi.org/10.1177/1745691617708630
- Steenbergen, L., Sellaro, R., van Hemert, S., Bosch, J. A., & Colzato, L. S. (2015). A randomized controlled trial to test the effect of multispecies probiotics on cognitive reactivity to sad mood. *Brain, Behavior, and Immunity*, 48, 258–264. https://doi.org/10.1016/j.bbi.2015.04.003
- Steingroever, H., Wetzels, R., Horstmann, A., Neumann, J., & Wagenmakers, E. J. (2013). Performance of healthy participants on the iowa gambling task. *Psychological Assessment*, 25(1), 180–193. https://doi.org/10.1037/a0029929
- Stilling, R. M., van de Wouw, M., Clarke, G., Stanton, C., Dinan, T. G., & Cryan, J. F. (2016). The neuropharmacology of butyrate: The bread and butter of the microbiota-gut-brain axis? *Neurochemistry International*, 99, 110–132. https://doi.org/10.1016/j.neuint.2016.06.011
- Telzer, E. H., Fuligni, A. J., Lieberman, M. D., Miernicki, M. E., & Galván, A. (2015). The quality of adolescents' peer relationships modulates neural sensitivity to risk taking. Social Cognitive and

- Affective Neuroscience, 10(3), 389–398. https://doi.org/10.1093/scan/nsu064
- Thayer, J. F., Hansen, A. L., Saus-Rose, E., & Johnsen, B. H. (2009). Heart rate variability, prefrontal neural function, and cognitive performance: The neurovisceral integration perspective on self-regulation, adaptation, and health. *Annals of Behavioral Medicine*, 37(2), 141–153. https://doi.org/10.1007/s12160-009-9101-z
- Tillisch, K., Labus, J., Kilpatrick, L., Jiang, Z., Stains, J., Ebrat, B., Guyonnet, D., Legrain-Raspaud, S., Trotin, B., Naliboff, B., & Mayer, E. A. (2013). Consumption of fermented milk product with probiotic modulates brain activity. *Gastroenterology*, 144(7), 1394–1401. https://doi.org/10.1053/j.gastro.2013.02.043
- Tingley, D., Yamamoto, T., Hirose, K., Keele, L., & Imai, K. (2014). mediation: R package for causal mediation analysis. *Journal of Statistical Software*, 59(5), 1–38. https://doi.org/10.18637/jss.v059.i05
- Tooley, K. L. (2020). Effects of the human gut microbiota on cognitive performance, brain structure and function: A narrative review. *Nutrients*, 12(10), Article 3009. https://doi.org/10.3390/nu12103009
- Turnbull, O. H., Evans, C. E., Bunce, A., Carzolio, B., & O'connor, J. (2005). Emotion-based learning and central executive resources: An investigation of intuition and the Iowa Gambling Task. *Brain and Cognition*, 57(3), 244–247. https://doi.org/10.1016/ j.bandc.2004.08.053
- Unger, M. M., Spiegel, J., Dillmann, K. U., Grundmann, D., Philippeit, H., Bürmann, J., Faßbender, K., Schwiertz, A., & Schäfer, K. H. (2016). Short chain fatty acids and gut microbiota differ between patients with Parkinson's disease and age-matched controls. *Parkinsonism & Related Disorders*, 32, 66–72. https://doi.org/10.1016/j.pa rkreldis.2016.08.019
- van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N. J., Gronau, Q. F., Haaf, J. M., Hinne, M., Kucharský, Š., Ly, A., Marsman, M., Matzke, D., Gupta, A. R. K. N., Sarafoglou, A., Stefan, A., Voelkel, J. G., ... Wagenmakers, E. J. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin & Review*, 28(3), 813–826. https://doi.org/10.3758/s13423-020-01798-5
- van Ravenzwaaij, D., Dutilh, G., & Wagenmakers, E.-J. (2011). Cognitive model decomposition of the BART: Assessment and application. *Journal of Mathematical Psychology*, 55(1), 94–105. https:// doi.org/10.1016/j.jmp.2010.08.010
- Vandeputte, D., De Commer, L., Tito, R. Y., Kathagen, G., Sabino, J., Vermeire, S., Faust, K., & Raes, J. (2021). Temporal variability in quantitative

- human gut microbiome profiles and implications for clinical research. *Nature Communications*, 12(1), Article 6740. https://doi.org/10.1038/s41467-021-27098-7
- Wagenmakers, E. J., Love, J., Marsman, M., Jamil, T.,
 Ly, A., Verhagen, J., Selker, R., Gronau, Q. F.,
 Dropmann, D., Boutin, B., Meerhoff, F., Knight, P.,
 Raj, A., van Kesteren, E. J., van Doorn, J., Šmíra,
 M., Epskamp, S., Etz, A., Matzke, D., ... Morey,
 R. D. (2018). Bayesian inference for psychology.
 Part II: Example applications with JASP.
 Psychonomic Bulletin & Review, 25(1), 58–76.
 https://doi.org/10.3758/s13423-017-1323-7
- Wagenmakers, E. J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Love, J., Selker, R., Gronau, Q. F., Šmíra, M., Epskamp, S., Matzke, D., Rouder, J. N., & Morey, R. D. (2018). Bayesian inference for psychology. Part I: Theoretical advantages and practical ramifications. *Psychonomic Bulletin & Review*, 25(1), 35–57. https://doi.org/10.3758/s13423-017-1343-3
- Wall, R., Cryan, J. F., Ross, P., Fitzgerald, G. F., Dinan, T. G., & Stanton, C. (2014). Bacterial neuroactive compounds produced by psychobiotics. In M. Lyte & J. F. Cryan (Eds.), Microbial endocrinology: The microbiota-gut-brain axis in health and disease (pp. 221–239). Springer. https://doi.org/ 10.1007/978-1-4939-0897-4_10
- Wang, M., Zhang, S., Suo, T., Mao, T., Wang, F., Deng, Y., Eickhoff, S., Pan, Y., Jiang, C., & Rao, H. (2022). Risk-taking in the human brain: An activation likelihood estimation meta-analysis of the balloon analog risk task (BART). *Human Brain Mapping*, 43(18), 5643–5657. https://doi.org/10 .1002/hbm.26041
- Werner, N. S., Jung, K., Duschek, S., & Schandry, R. (2009). Enhanced cardiac perception is associated with benefits in decision-making. *Psychophysiology*, 46(6), 1123–1129. https://doi.org/10.1111/j.1469-8986.2009.00855.x
- Werner, N. S., Schweitzer, N., Meindl, T., Duschek, S., Kambeitz, J., & Schandry, R. (2013). Interoceptive awareness moderates neural activity during decision-making. *Biological Psychology*, 94(3), 498–506. https://doi.org/10.1016/j.biopsycho. 2013.09.002
- Whitehead, W. E., & Drescher, V. M. (1980). Perception of gastric contractions and self-control of gastric motility. *Psychophysiology*, *17*(6), 552–558. https://doi.org/10.1111/j.1469-8986.1980.tb0 2296.x
- World Medical Association. (2024). The World Medical Association-Declaration of Helsinki. https://www.wma.net/what-we-do/medical-ethics/declaration-of-helsinki/
- Wright, R. J., & Rakow, T. (2017). Don't sweat it: Re-examining the somatic marker hypothesis using variants of the Balloon Analogue Risk Task.

Decision, 4(1), 52–65. https://doi.org/10.1037/dec0000055

Yu, C. D., Xu, Q. J., & Chang, R. B. (2020). Vagal sensory neurons and gut-brain signaling. *Current Opinion in Neurobiology*, 62, 133–140. https://doi.org/10.1016/j.conb.2020.03.006

Zaki, J., Davis, J. I., & Ochsner, K. N. (2012). Overlapping activity in anterior insula during interoception and emotional experience. *NeuroImage*, 62(1), 493–499. https://doi.org/10.1016/j.neuroima ge.2012.05.012

Received April 22, 2024
Revision received March 18, 2025
Accepted March 21, 2025

E-Mail Notification of Your Latest Issue Online!

Would you like to know when the next issue of your favorite APA journal will be available online? This service is now available to you. Sign up at https://my.apa.org/portal/alerts/ and you will be notified by e-mail when issues of interest to you become available!