

Neurocognitive predictors of food memory in healthy adults – A preregistered analysis

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ABSTRACT

Memory processes have long been known to determine food choices (Rozin & Zellner, 1985) but recognition memory of food and its cognitive, homeostatic and neuroanatomical predictors are still largely understudied.

60 healthy, overweight, non-restrictive eating adults (20 females) took part in a food wanting and subsequent food recognition and lure discrimination task at four time points after a standardized breakfast shake. With advanced tractography of 3 T diffusion-weighted imaging data, we investigated the influence of the uncinate fasciculus' (UF) brain microstructure on the interplay of food wanting and memory processes. The analysis was preregistered in detail and conducted with Bayesian multilevel regression modeling.

Target recognition (d') and lure discrimination (LDI) performance of food tended to be higher than of art images while single image food memory accuracy evidently dominated art memory. On this single item level, wanting enhanced recognition accuracy and caloric content enhanced food memory accuracy. The enhancement by reward anticipation was most pronounced during memory encoding. Subjective hunger level did not predict performance on the memory task. The microstructure of the UF did neither evidently affect memory performance outcomes nor moderate the wanting enhancement of the recognition accuracy. Interestingly, female participants outperformed males on the memory task, and individuals with stronger neuroticism showed poorer memory performance.

We shed light on to date understudied processes in food decision-making: reward anticipation influenced recognition accuracy and food memory was enhanced by higher caloric content, both effects might shape food decisions. Our findings indicate that brain microstructure does not affect food decision processes in adult populations with overweight. We suggest extending investigation of this interplay to brain activity as well as to populations with eating behaviour disorders.

1. Introduction

In a world overloaded with food stimuli, cognitive processes contributing to food choices move into focus, especially considering public health strategies to address the overnutrition pandemic (Berthoud, 2012). The complexity of food choices reflects in current debates around food desires (wanting) (García-García et al., 2020) and food memory (Seitz et al., 2021). Well-known memory processes crucial for food choices represent previously learned preferences (Rozin & Zellner, 1985). Recently, memory of eating (Higgs & Spetter, 2018; Seitz, Blaisdell, & Tomiyama, 2021;), working memory (Spetter et al., 2020)

and spatial food memory (de Vries et al., 2020) have been established as modifiers of food intake. Largely understudied though is the role of recognition memory in food choices. Both, food recognition memory and food choices are constantly manipulated by the daily overload of food stimuli. Additionally, metabolic hunger impacts food choices, namely food wanting (Berthoud, 2007), and food memory (Morris & Dolan, 2001). We aim to shed light on how food wanting and hunger determine food memory and how the underlying neural anatomy contributes to this interplay.

The importance of the hippocampus in memory (Wixted & Squire, 2010) and the regulation of human food intake has been extensively

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studied, e.g. its inhibitory output to hypothalamic feeding centers (see review by [Stevenson & Francis, 2017](#)). However, modulation of food memory through cognitive processes and associated neural pathways providing input to the hippocampus are mostly understudied. This modulation of memory and the respective input to the hippocampus is provided by the amygdala, directly as well as indirectly through the entorhinal cortex ([Kensinger & Schacter, 2006](#); [Roesler & McGaugh, 2022](#)). The amygdala and the orbito-frontal cortex (OFC) are implicated in the encoding of (food) value ([Canli et al., 2000](#); [Richardson et al., 2004](#); [Warlow & Berridge, 2021](#)) and in hunger enhanced recognition memory ([Morris & Dolan, 2001](#)). Nevertheless, the influence of subjective food value, namely food wanting, on recognition memory as well as the contribution of the underlying neural pathways remain unclear.

The neural pathway connecting the OFC with the amygdala and entorhinal cortex is the uncinate fasciculus (UF) ([Thiebaut de Schotten et al., 2012](#); [Von Der Heide et al., 2013](#)). The microstructural coherence of the UF correlates with emotional memory ([Yau et al., 2009](#)) and emotion management ([Pisner et al., 2017](#)) as well as with activation of the hippocampus during an emotional memory task ([Granger et al., 2021](#)). As emotions and subjective value are processed in the same brain areas (OFC ([Gottfried et al., 2003](#)) and amygdala ([Murray, 2007](#))), we hypothesized a putative top-down modulatory control by microstructural properties of the UF in memory processes which integrate food wanting and hunger.

Besides recognition of food items, the ability to detect differences in visual details (lure discrimination) form crucial parts of food memory and might influence food choices. Previous studies have revealed effects of emotion on both recognition and lure discrimination performance ([Kensinger, 2007](#); [Chainay et al., 2012](#); [Leal et al., 2014](#)) endorsing our assumption that parallelly processed reward reflected in food wanting might also affect food memory. To study the influence of reward on memory, we contrasted art to food images as art images can elicit similar desire and reward patterns in the brain ([Berridge & Kringelbach, 2008](#)).

Based on previous findings and our assumptions, we formulated and preregistered in more detail the following hypotheses:

1. We hypothesize that recognition performance for food items would be better than for non-food (art) items.
2. We believe that subjective hunger level might modulate recognition performance for food items.
3. We suppose that recognition performance for food items (or in general) could be enhanced by subjective incentive value (wanting).
4. We suggest that the coherence of the UF could influence food recognition performance as well as the above mentioned correlations and modulations by subjective hunger or wanting. We find it also possible that only the coherence of a sub-bundle of the uncinate fasciculus might be relevant for the information transmission.
5. We think that discrimination of visual details is also better for food than non-food but could be differentially affected by subjective hunger level, wanting or the UF's microstructure.

To this end, we analyzed food wanting and memory performance, brain microstructure using diffusion-weighted magnetic resonance imaging (MRI), and subjective hunger level assessed during MRI in a well-characterized adult sample following a detailed preregistration at <https://osf.io/2z4dn>.

2. Methodology

2.1. Experimental design and participants

The over-arching study was designed as a double-blind randomized controlled cross-over (within-subject) intervention trial and preregistered at <https://osf.io/f6qz5>. The detailed analysis for the present investigation on whether wanting, subjective hunger and UF microstructure predict recognition performance and lure discrimination of

food items was preregistered at <https://osf.io/2z4dn>. For this preregistered analysis, we evaluated data from all four time points cross-sectionally by controlling for possible intervention effects, so that we were able to feed $n = 181$ data sets into the behavioural analysis and $n = 176$ data sets into the neuroimaging analysis.

Each participant was invited four times to undergo extensive testing following identical procedures each time: fasted overnight, blood sampling (i.a. fasted ghrelin), anthropometric measurements (body mass index (BMI), percentage fat mass (%FM), Waist-to-Hip ratio (WHR)), standardized breakfast shake (10% of gender-individual calorie need based on [Harris & Benedict, 1918](#)), MR scanning including two fMRI tasks (with different picture sets for each visit), structural and diffusion-weighted imaging, and post-MRI computer tasks. All participants were reimbursed for participation and gave written informed consent. The study was approved by the Research Ethics Committee of the University of Leipzig and was conducted in accordance with the Declaration of Helsinki. Inclusion and exclusion criteria were predefined and registered at <https://clinicaltrials.gov/ct2/show/NCT03829189>. The study population consisted of 60 healthy adults (20 females), aged 19 to 45 years, with a BMI of 25 to 30 kg/m² at baseline visits. Female participants were required to take contraceptives to minimize hormonal variations induced by the menstrual cycle. Participants were excluded if they suffered from a neurological, psychiatric, or metabolic disorder or if they took any medication acting on the central nervous system. Deviating from the preregistration, we additionally had to exclude one participant who was diagnosed with diabetes. Also, pregnancy or lactation and any type of dietary restrictions or antibiotic treatment in the last 3 months led to exclusion. For more details see the [clinicaltrials.gov-preregistration](https://clinicaltrials.gov/preregistration). The study population can be described as young, healthy and overweight. At the beginning of each testing day, participants' BMI and WHR were measured and with bioelectric impedance analysis, we assessed their percentage fat mass (%FM). In addition, we evaluated participants' eating behaviour with the German versions of the TFEQ ([Pudel & Westenhöfer, 1989](#)) and EDEQ ([Hilbert et al., 2007](#)), socio-economic status ([Lampert et al., 2013](#)), personality traits with the NEO-Five-Factor-Inventory by Costa and McCrae ([Borkenau & Ostendorf, 2008](#)) and attention network performance ([Fan et al., 2002](#)).

2.2. Imaging data collection

Magnetic resonance imaging (MRI) was conducted at a 3 Tesla Prisma Fit Magnetom (Siemens, Erlangen, Germany). Anatomical MRI was acquired using a T1-weighted MPRAGE sequence using the ADNI protocol with the following parameters: TR = 2300 ms; TE = 2.98 ms; flip angle = 9°; FOV: (256 mm)²; voxel size: (1.0 mm)³; 176 slices. Diffusion-weighted MRI data was acquired using the following parameters: TR = 5200 ms; TE = 75 ms; flip angle = 90°; FOV: (220 mm)²; voxel size: (1.7 mm)³; 88 slices; max. b = 1000 s/mm² in 60 diffusion directions (+7 b0-images); partial Fourier = 7/8; GRAPPA-factor = 2; interpolation = OFF. Ap/pa-encoded b0-images were acquired for distortion correction.

DWI data were preprocessed following a high standard pipeline which includes denoising, removal of Gibbs-ringing artefact to increase image quality ([Thieleking et al., 2021](#)), correction for susceptibility distortions as well as correction for head motion and eddy currents. Quality control led to exclusion of four data sets as can be followed up on in the preregistration (<https://osf.io/2z4dn>). After quality assurance, we used model-free fiber reconstruction based on generalized q-sampling (GQI) ([Yeh et al., 2010](#)) to create in-vivo whole-brain normalized quantitative anisotropy (nQA) maps. This model-free method, in comparison to a tensor-based approach, calculates spin distribution functions which presumably improve the modeling of crossing fibers and resolve partial volume effects and thereby result in more accurate deterministic tractography ([Yeh et al., 2013](#)). Next, we conducted deterministic diffusion tractography with DSI Studio (version 2022.01.11) ([Yeh, 2021](#)) and extracted mean normalized quantitative

anisotropy values (nQA) of the UF as well as of a sub-bundle. Normalization of QA was performed by scaling the subject-wise maximum QA value to 1. All (pre)processing steps, tractography settings and regions of interest can be accessed in detail via GitLab (https://gitlab.gwdg.de/gut_brain_study/analysis_dsistudio_tractography).

2.3. Behavioural assessment

Participants took part in a food wanting and subsequent food memory task. In both tasks, food was contrasted to art images. Food pictures, including nutrient values such as calorie content, were taken from the food-pics database (Blechert et al., 2014; Medawar et al., 2022); the art.pics database (Thieleking et al., 2020) served as source for the art images. The wanting task included 80 food (20 per calorie quartile) and 80 art images (12 animals, 56 objects and 12 plants). Food and art served as image category in the analysis. Participants indicated food and art wanting on an 8-point-Likert scale (see Fig. 1) and, in order to stimulate reward anticipation, they received the highest-rated food item to eat and the highest-rated art image as print-out after scanning. For the statistical analysis, images were categorized into “unwanted”, “neutral” and “wanted” images based on the participants’ ratings. The wanting task represented the memory encoding phase and was followed by the memory task after a break of about 20mins with structural scans. The memory task also consisted of 80 food and 80 art images with 30 old (targets), 30 similar (lures) and 20 new images (novels) in each image category. The memory task was a combined recognition and lure discrimination task with corrected target recognition d' , lure discrimination index LDI and response accuracy as outcome measures. This task was adapted from the mnemonic similarity task (MST) originally developed in the Stark Lab (Kirwan & Stark, 2007; Stark Lab;) and has

been continuously refined by Stark, Yassa and colleagues (Bakker et al., 2008; Yassa et al., 2010, 2011; Stark et al., 2015). In parallel to the previously published version of the emotional MST by Leal, Granger and colleagues (Leal et al., 2014; Granger et al., 2021), we included the two-choice version of the MST and replaced emotional with desire ratings during the encoding phase. In the recognition phase, participants had to indicate as quickly as possible if they had seen the presented food or art image in the previous task (“old”) or if they had not seen it before (“new”) which also included similar images (see Fig. 1). No feedback on performance was provided. Wanting ratings for new and similar images were obtained after the MRI scan, meaning not during memory encoding. Nevertheless, wanting attribution occurred before the reward hand-out and was therefore similarly reward-anticipatory as for the old images. In accordance with the two-choice version of the MST, we measured target recognition d' as the difference of correct recognition of targets and false recognition of lures and novels, and lure discrimination LDI as rate of correct attribution of “new” to lures compared to targets. Detailed calculation of the memory outcome measures d' , LDI and response accuracy as well as the creation of the wanting categories in accordance with emotional categories from previous tasks (Leal et al., 2014; Granger et al., 2021) can be followed up in the ReadMe under https://gitlab.gwdg.de/gut_brain_study/analysis_r_memory.

Before and after each of the fMRI tasks, participants were asked to indicate their hunger level on an 8-point-Likert scale (‘How hungry are you right now?’ - ‘not at all’ to ‘extremely hungry’). After the MR scanning, participants filled out an 8-point visual analogue scale to indicate their well-being regarding anxiety, nausea, exhaustion by and difficulty of the tasks. At the end of the study, participants additionally indicated liking ratings on all images that had been presented during the fMRI tasks. In order to assess general preference and not wanting,

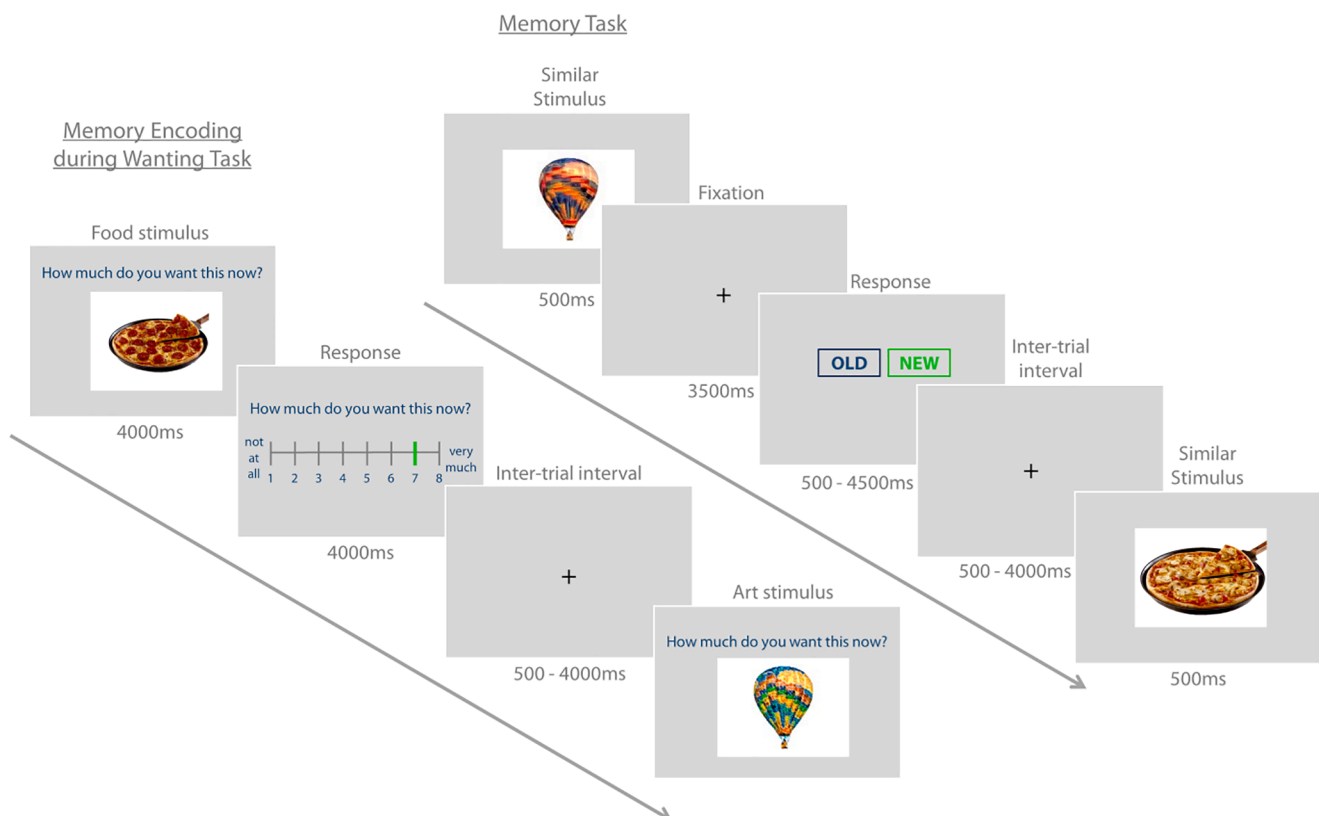


Fig. 1. Wanting task and subsequent Memory task. Left: **Memory Encoding during Wanting Task:** Participants were asked to indicate on an 8-point-Likert scale how much they want to have the depicted food or art image. They were previously told that they would be rewarded with the highest-rated food and art image after the MRI scan. Right: **Memory task including target recognition and lure discrimination:** Participants had to indicate as quickly as possible if they had seen the presented food or art image in the previous task (“old”) or if they had not seen it before (“new”) which also included similar images. Depicted are two exemplary similar (but not identical) food (pizza) and art (hot-air balloon) stimuli.

participants did not receive rewards after completion of the liking task.

2.4. Statistical analysis

We applied Bayesian multilevel regression modeling as test statistic with R (version 4.1.1 (R Core Team, 2021)). To assess the predictive accuracy of a Bayesian regression model (BRM), Vehtari, Gelman, and Gabry proposed the expected log pointwise predictive density (elpd) (Vehtari et al., 2017) which can be estimated by leave-one-out (loo) cross-validation. The higher the predictive accuracy of a model, the higher is its elpd. We previously tested for random intercepts and random slopes present in the data, set up full models with these random effects and subsequently defined null models to test for fixed effects (van Doorn et al., 2021). As Bayesian inference testing is more conservative than classical comparison procedures that are based on Type I error, there is no need for multiple comparison testing (Gelman & Tuerlinckx, 2000).

In the result section, I present which Bayesian multilevel regression models (BRMs) predict the collected data most accurately and which effects we can therefore assume to exist in our study population. During Bayesian regression modeling, posterior distributions of the predictor variables are calculated. The mean estimate or the odds ratio and their 95%-credible interval (CI) of the posterior distributions result from this modeling. If the credible interval does not include Zero, we can infer that the effect is probably present in the study population. Through comparison of the predictive accuracy (elpd) of the full and null models, we can additionally find out which model predicts the data best. To follow-up on the model estimates of the predictors and random effects, tables were linked to the respective figures.

2.5. Code accessibility

We version-controlled and published the tractography of white matter and the statistical analysis including details on software, functions and options via GitLab. Regarding the tractography, all (pre)processing steps, settings and regions of interest can be accessed in detail here: (https://gitlab.gwdg.de/gut_brain_study/analysis_dsistudio_tractography). The code for the statistical analysis and all model results can be accessed here: https://gitlab.gwdg.de/gut_brain_study/analysis_r_memory.

The code was checked for validity by a researcher who is independent of the study and the group and who has experience in using R.

3. Results

3.1. Is the recognition performance for food items better than for non-food (art) items?

The corrected target recognition d' and the lure discrimination LDI are both higher for food compared to art (non-food = NF) images. The difference in memory indices between image categories (food = yellow, non-food = blue) is highly probable as the posterior distributions of the estimates revealed; the credible intervals do not include Zero (Fig. 2). Even though the difference in predictive accuracy (expected log pointwise predictive density = Δelpd) in the model comparison (Table 1, Eq. 1 & 2) is inconclusive, due to the large standard errors, the superiority of food over art memory accuracy seemed to be evident. The estimates in the d' and LDI models as well as the model comparison regarding response accuracy of single images (Table 1, Eq. 3 & 4) support the superiority of food over art memory accuracy. Response accuracy of a single image equaled 1 when an old image was correctly recognized as “old” (hit) and a new or similar image was correctly dismissed as “new” (correct rejection); otherwise response accuracy for incorrect categorization was 0. Estimates of all predictors and covariates can be followed up in (Fig. 2-1, Fig. 2-2, Tables 2-1, 2-2 & 2-3).

3.1.1. Do image characteristics interfere with single image response accuracy? (exploratory)

The normed complexity of the food (F) images (yellow) was lower compared to art (NF) images (blue; Fig. 3 A) while object size was not different between food and art images (Fig. 3 B). The subjective characteristics arousal, recognizability and valence were z-scored as food and art images were evaluated by two independent populations and on different rating scales. The model comparison regarding normed complexity (Table 1, Eq. 5–7) was inconclusive ($\Delta\text{elpd} < \text{se}$), however, we detected an evident interaction effect with image category (Fig. 3 C & Fig. 3-1). Therefore, we conducted post-hoc tests on the role of normed complexity on food and art memory accuracy separately. These post-hoc tests confirmed what can be inferred from Fig. 3 C, namely, that normed complexity predicts response accuracy of food images (Fig. 3-2 A) but not of art images (Fig. 3-2 B). Odds ratios of predictors and covariates of all models are listed in Tables 3-1, 3-2 and 3-3. The effect of object size on food and art memory accuracy was also differential (Fig. 3 D) and, again, post-hoc tests revealed that object size evidently predicted food (Fig. 3-3 A, Table 3-4) but not art response accuracy (Fig. 3-3 B, Table 3-5). The subjective arousal (violet) and valence (orange) did

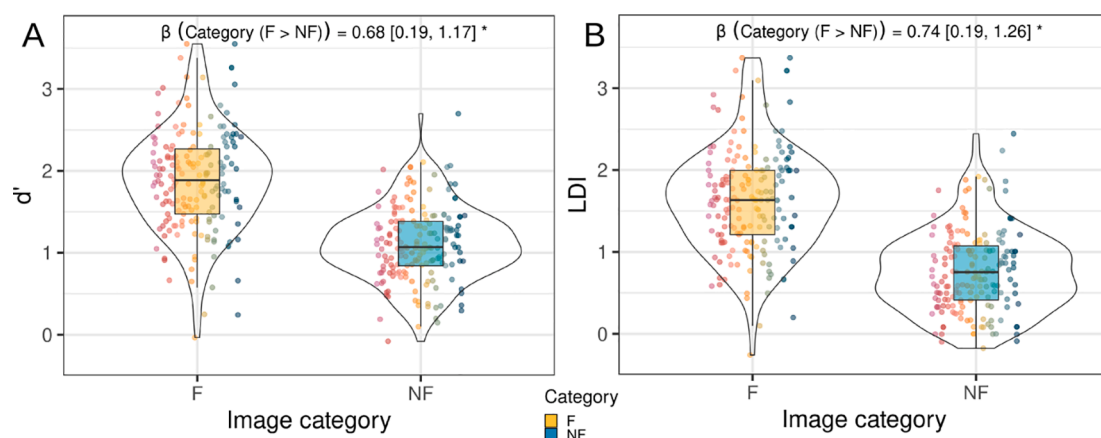


Fig. 2. Memory performance per Image Category. A) The target recognition d' and B) the lure discrimination LDI of food (F) items (yellow) is probably better than of non-food (NF)/art items (blue). Violin plots present the distribution of the two memory indices per image category (F/NF) over the color-coded single subjects' performance in the respective category. The estimate's CI did not include 0 which indicated an evident difference between image categories regarding d' and LDI but the model including image category as predictor did not present an evidently higher predictive accuracy than the null model (Table 1, Eq. 1 & 2). Estimates of all predictors and covariates are listed in Fig. 2-1 and Tables 2-1 & 2-2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Model equations of full and null models and the difference in predictive accuracy with standard errors ($\Delta\text{elpd} \pm \text{se}$). Each model comparison delivers either evident, highly probable or inconclusive results that one of the models predicts the memory performance (d' , LDI or response accuracy) better than the other models. A model predicts memory performance evidently better than the other models if $\Delta\text{elpd} > \text{se}$. If $\Delta\text{elpd} < \text{se}$ but the predictors' posterior distributions show an evident effect, we can assume that the predictive effect is highly probable. The comparison is inconclusive if $\Delta\text{elpd} < \text{se}$ and the predictors' posterior distributions do not show an evident effect. The evidently highest elpds / best models are marked with * and the models with highly probable predictive effects are marked with (*).

Eq. No.	Model Title	Model type	Model Equation dependent variable ~ predictors & covariates (without random effects for visual clarity)	Difference in Predictive Accuracy ($\Delta\text{elpd} \pm \text{se}$)
1	Category	full model (*)	$d' / \text{LDI} \sim \text{Image Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : probably highest elpd; LDI : probably highest elpd
2	Category	null model	$d' / \text{LDI} \sim \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -0.2 ± 0.5 ; LDI : -0.5 ± 0.5
3	Category	full model *	Response accuracy ~ Image Category + normed Complexity + Wanting + Image Status + Gender + Age + Intervention + Timepoint + Intervention*Timepoint	response accuracy: * evidently highest elpd
4	Category	null model	Response accuracy ~ normed Complexity + Wanting + Image Status + Gender + Age + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -2.9 ± 2.5
5	Complexity	full model (*)	Response accuracy ~ Image Category + normed Complexity + Image Category*normed Complexity + Wanting + Image Status + Gender + Age + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -0.5 ± 1.1
6	Complexity	null model	Response accuracy ~ Image Category + normed Complexity + Wanting + Image Status + Gender + Age + Intervention + Timepoint + Intervention*Timepoint	response accuracy: reference elpd
7	Complexity	null model 2	Response accuracy ~ Image Category + Wanting + Image Status + Gender + Age + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -1.2 ± 1.3
8	Hunger	full model	$d' / \text{LDI} \sim \text{Image Category} + \text{Subj Hunger Level} + \text{Image Category} * \text{Subj Hunger Level} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -1.6 ± 0.6 ; LDI : -1.2 ± 0.5
9	Hunger	null model 1	$d' / \text{LDI} \sim \text{Image Category} + \text{Subj Hunger Level} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -1.4 ± 0.5 ; LDI : -0.3 ± 0.4
10	Hunger	null model 2 *	$d' / \text{LDI} \sim \text{Image Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : * evidently highest elpd; LDI : probably highest elpd

Table 1 (continued)

Eq. No.	Model Title	Model type	Model Equation dependent variable ~ predictors & covariates (without random effects for visual clarity)	Difference in Predictive Accuracy ($\Delta\text{elpd} \pm \text{se}$)
11	Wanting	full model	$d' / \text{LDI} \sim \text{Image Category} + \text{Wanting Category} + \text{Image Category} * \text{Wanting Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -0.4 ± 1.2 ; LDI : -2.0 ± 1.5
12	Wanting	null model 1	$d' / \text{LDI} \sim \text{Image Category} + \text{Wanting Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : reference elpd; LDI : -1.4 ± 0.9
13	Wanting	null model 2 *	$d' / \text{LDI} \sim \text{Image Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -0.8 ± 2.1 ; LDI : * evidently highest elpd
14	Single item wanting	full model	Response accuracy ~ Image Category + Wanting + Image Category*Wanting + Image Status + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: reference elpd
15	Single item wanting	null model 1 (*)	Response accuracy ~ Image Category + Wanting + Image Status + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -1.4 ± 1.9
16	Single item wanting	null model 2	Response accuracy ~ Image Category + Image Status + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -6.8 ± 3.8
17	Image Status	full model (*)	Response accuracy ~ Image Category + Wanting + Image Status + Image Category*Wanting + Image Status*Wanting + Image Status*Image Category + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: probably highest elpd
18	Image Status	null model 1	Response accuracy ~ Image Category + Wanting + Image Status + Image Category*Wanting + Image Status*Wanting + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -0.8 ± 1.5
19	Image Status	null model 2	Response accuracy ~ Image Category + Wanting + Image Status + Image Category*Wanting + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -9.4 ± 4.5
20	Image Status	null model 3	Response accuracy ~ Image Category + Wanting + Image Status + normed Complexity + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	response accuracy: -10.7 ± 4.9
21	UF	full model	$d' / \text{LDI} \sim \text{Image Category} + \text{Wanting Category} + \text{Subj Hunger Level} + \text{nQA}(\text{UF}) + \text{Image Category} * \text{nQA}(\text{UF}) + \text{Wanting Category} * \text{nQA}(\text{UF})$	d' : -2.5 ± 2.7 ; LDI : -4.3 ± 2.0

(continued on next page)

Table 1 (continued)

Eq. No.	Model Title	Model type	Model Equation dependent variable ~ predictors & covariates (without random effects for visual clarity)	Difference in Predictive Accuracy ($\Delta\text{elpd} \pm \text{se}$)
22	UF	null model 7	+ Subj Hunger Level*nQA (UF) + Age + Gender + Intervention + Timepoint + Intervention*Timepoint d' / LDI ~ Image Category + Wanting Category + Subj Hunger Level + nQA(UF) + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	d': -1.3 ± 0.5; LDI: -3.1 ± 1.1
23	UF	null model 11	d' / LDI ~ Image Category + nQA(UF) + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	d': -2.3 ± 2.1; LDI: -1.2 ± 0.6
24	UF	null model 13	d' / LDI ~ Image Category + Wanting Category + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	d': reference elpd; LDI: -1.6 ± 1.0
25	UF	null model 14 (*)	d' / LDI ~ Image Category + Age + Gender + Intervention + Timepoint + Intervention*Timepoint	d': -1.3 ± 2.1; LDI: probably highest elpd

not predict response accuracy (Fig. 4 A & B), the perceived

recognizability (red) of the food (yellow) and art (blue) images, though, seemed to negatively influence response accuracy independent of image category (Fig. 4 C & D). Odds ratios of predictors and covariates of all models are listed in Tables 4-1, 4-2 and 4-3.

3.2. Does subjective hunger level moderate recognition or lure discrimination performance for food items?

The mean subjective hunger level averaged per MRI session did not influence food recognition (Fig. 5 A, yellow) nor lure discrimination performance (Fig. 5 B, yellow). Subjective hunger level neither had an effect on art (NF) memory performance (Fig. 5, blue) nor independently of image category (Fig. 5-1). The lack of an effect of subjective hunger could also be inferred from the model comparison as the null model 2 without subjective hunger as predictor showed the highest predictive accuracy for d' and LDI (Table 1, Eq. 8–10; Tables 5-1 & 5-2). The irrelevance of subjective hunger is also visualized in the posterior distributions of the mean estimates (Fig. 5-2). As preregistered, we investigated if task-specific subjective hunger level, i.e. during the wanting or memory task respectively, predicted (food) memory performance measures (Fig. 5-3). None of these task-specific hunger levels did influence target recognition or lure discrimination performance.

We additionally evaluated if fasted ghrelin serum levels as metabolic measure of hunger might predict target recognition or lure discrimination. However, neither food recognition nor lure discrimination performance were influenced by ghrelin levels nor did we detect an influence independent of image category (exploratory analysis, Fig. 5-4). Estimates of the predictors and random effects of all models in the

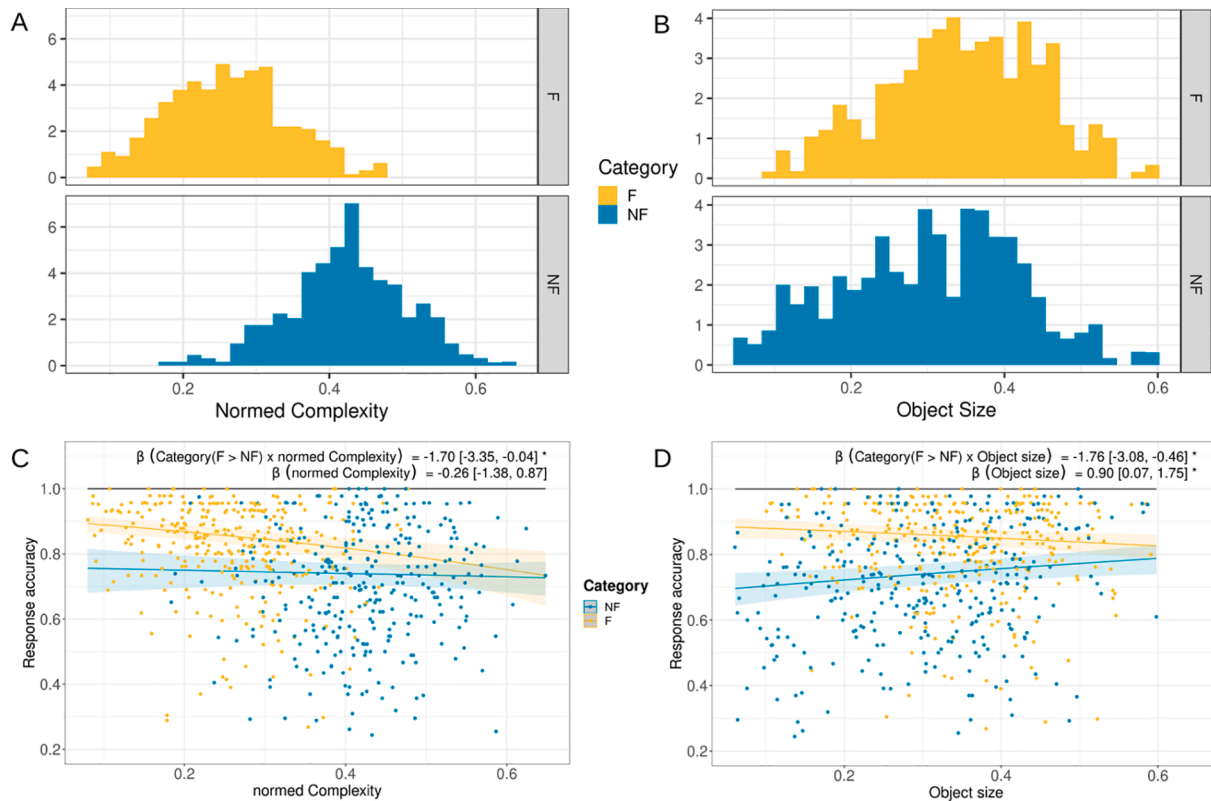


Fig. 3. Normed complexity and object size of visual stimuli. A) The distribution of normed complexity values differs between the two image categories. Non-Food (art) images have on average a higher normed complexity than food images. B) The object size of the centrally depicted food and non-food items does not differ between the image categories. C) Predicted response accuracy depending on normed complexity of the images. Points show the actual data and lines with 95%-CI depict predictions based on full model. Image complexity might predict response accuracy of food items. The interaction estimate of the full model (Table 1, Eq. 5) indicated that response accuracy of the two image categories was differently affected by normed complexity. Post-hoc tests confirmed that higher normed complexity predicted lower food memory accuracy while art memory accuracy was not affected. D) Predicted response accuracy depending on object size of the items. Points show the actual data and lines with 95%-CI depict predictions based on full model. Object size affected food and art memory accuracy differently. Post-hoc tests confirmed that larger object size predicted lower food memory accuracy while art memory accuracy was not affected.

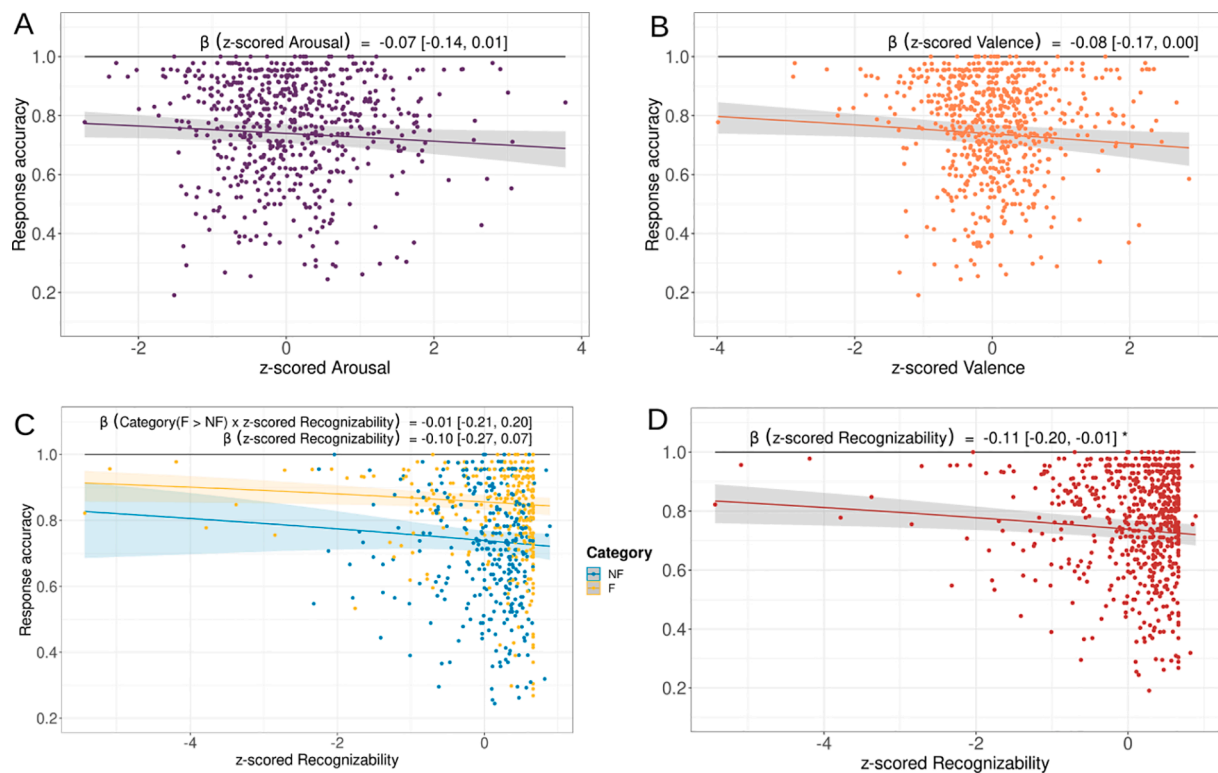


Fig. 4. Predicted and actual response accuracy depending on subjective arousal, valence and recognizability of visual stimuli. Points show averaged response accuracy of each image against their z-scored characteristic and lines with 95%-CI depict predictions based on null (A, B, D) or full (C) model. A) Arousal and B) valence did not evidently influence response accuracy neither of food nor of art images. C&D) Recognizability, however, seemed to evidently predict lower response accuracy of food and art images.

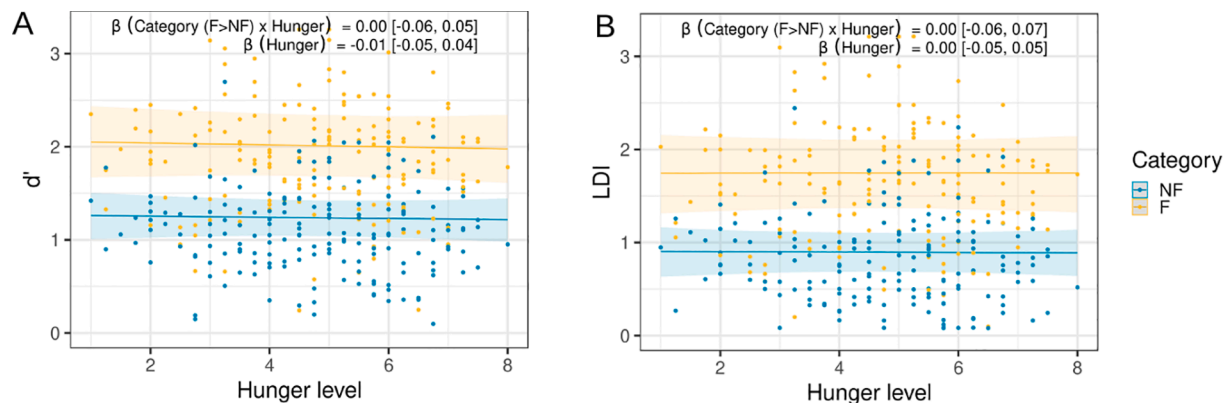


Fig. 5. Memory performance depending on subjective hunger per image category. Actual and predicted A) target recognition d' and B) lure discrimination LDI depending on subjective hunger level per image category. Points show the actual data and lines with 95%-CI depict predictions based on full model. **Neither d' nor LDI were affected by the subjective hunger level.** The estimates of the interaction of the full model (Table 1, Eq. 8, Tables 5-1 & 5-2) indicated that the image categories were not differently influenced by hunger and the estimates of the main effect of the null model (Table 1, Eq. 9, Fig. 5-1, Tables 5-1 & 5-2) suggested that the subjective hunger level did not affect memory performance in general. Neither task-specific hunger level (Fig. 5-3) nor ghrelin serum levels as a proxy for objective hunger (Fig. 5-4, Tables 5-3 & 5-4) predicted memory performance.

model comparison are listed in the [supplementary material](#) (Tables 5-3 & 5-4).

3.3. Could the memory performance for food items (or in general) be enhanced by wanting?

Wanting defined as categories “unwanted” (red), “neutral” (blue) and “wanted” (green) did not influence neither recognition nor lure discrimination performance in general (Fig. 6) nor food memory in specific (see predictions in Fig. 6-1). Both, the model comparison

(Table 1, Eq. 11–13) and model estimates, emphasized that wanting categories did not predict neither d' nor LDI (Fig. 6-2; Tables 6-1 & 6-2).

3.3.1. Does single item wanting influence response accuracy? (exploratory)

Wanting ratings of the single images predicted response accuracy. In addition to the pre-registered hypotheses regarding the wanting enhancement of the memory indices d' and LDI, we exploratorily investigated the wanting rating of every image as opposed to categorized wanting ratings. We found an evident enhancement by higher wanting which is slightly stronger for art (Fig. 7, blue) compared to food

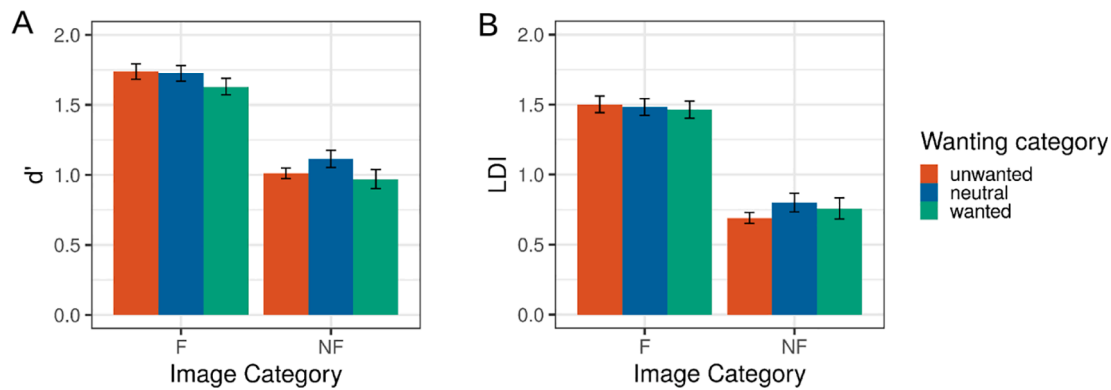


Fig. 6. Memory performance depending on wanting and image category. A) Target recognition d' and B) lure discrimination LDI depending on wanting and image category. Depicted are mean d' (LDI) \pm standard error. Predictions by the full model are depicted in Fig. 6-1. **Neither d' nor LDI were predicted by wanting category.** Estimates of all predictors and covariates are listed in Fig. 6-2 and Tables 6-1 & 6-2.

images (Fig. 7, yellow). Even though the predictive accuracy of the full model (Table 1, Eq. 14) was supposedly higher compared to the null models (Table 1, Eq. 15 & 16), the estimate of the interaction effect of image category and wanting did not support evident differences between the wanting effect on food and art as the credible interval included Zero (for all model estimates see Table 7-1). Therefore, we conducted post-hoc analyses in which we detected wanting enhancement for food and art separately (model estimates see Tables 7-1 & 7-2). Notably, neither normed image complexity nor depicted object size did influence the wanting enhancement of the response accuracy. In sum, the wanting main effect's mean estimate (Fig. 7) as well as its odds ratio in the full model (Fig. 7-1A) and the null model without interaction (Fig. 7-1B) confirm a general enhancement of response accuracy by single item wanting.

3.3.2. Is the effect of single item wanting on response accuracy stronger during memory encoding? (exploratory)

The enhancement of response accuracy by higher single item wanting was strongest for the old images (dark-blue) across food and art images, i.e. during memory encoding, while the enhancement was less for new images (red) and irrelevant for similar images (light-violet; Fig. 8; also see predictions in Fig. 8-1). The main effects of image status also suggest that the response accuracy for new images was clearly higher than for old images and lowest for similar images (Fig. 8). Similar images were evidently worse discriminated among the art images compared to the food images (Fig. 8-2; also see predictions in Fig. 8-3).

All results were independent of normed image complexity. Odds ratios of predictors and covariates of all models in the comparison (Table 1, Eq. 17–20) are listed in Table 8-1.

3.4. Does the coherence of the entire uncinate fasciculus (UF) or a sub-bundle of the UF influence food memory performance?

We derived the tracts of the UF from deterministic tractography. The microstructural coherence of the UF reflects in the average normalized quantitative anisotropy (nQA) of the whole tract. The nQA of the entire UF was higher compared to the nQA of the sub-bundle of the UF which we traced as a proxy for a direct communication pathway from OFC to MTL (Table 3). nQA values of the UF ranged from about 0.21 to 0.33 and were comparable for both hemispheres (paired Bayesian ttest: BF = 0.09). nQA values of the sub-bundle ranged from about 0.10 to 0.23 and were evidently different between hemispheres (paired Bayesian ttest: BF > 5*10⁴). The magnitude of nQA values of the UF was comparable to whole brain nQA. Fig. 9 displays exemplary fiber tracts of the entire UF and its sub-bundle. We tested for the role of the microstructural properties of the UF and its sub-bundle in (food) memory processes but our hypotheses were not hemisphere-specific. Therefore, we used the average nQA value of the UF and the sub-bundle of the UF per participant per session for statistical analyses. Microstructural coherence of the UF did not predict neither food (yellow) nor art (blue) target recognition or lure discrimination performance (Fig. 10 A&B) nor independently of image category (Fig. 10-1 A&B). Neither did the sub-bundle of the UF

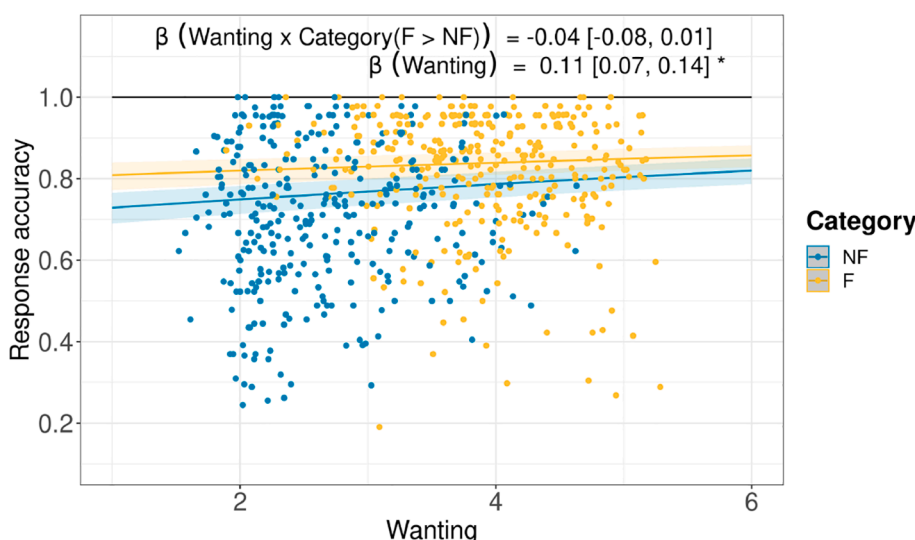


Fig. 7. Predicted response accuracy by single image wanting rating per image category. Points show averaged response accuracy and averaged wanting of each image and predictions are based on full model (Table 1, Eq. 14). The estimate of the interaction suggests that the two image categories are slightly but not evidently differently influenced by wanting rating. **Higher wanting enhances response accuracy** as the estimate of the main effect of the full model reveals but wanting might play a more important role for the art/non-food (NF) images. Odds ratios of all predictors and covariates are listed in Fig. 7-1 and Table 7-1. Odds ratios of the wanting effect per image category (F/NF) are listed separately in Tables 7-2 & 7-3.

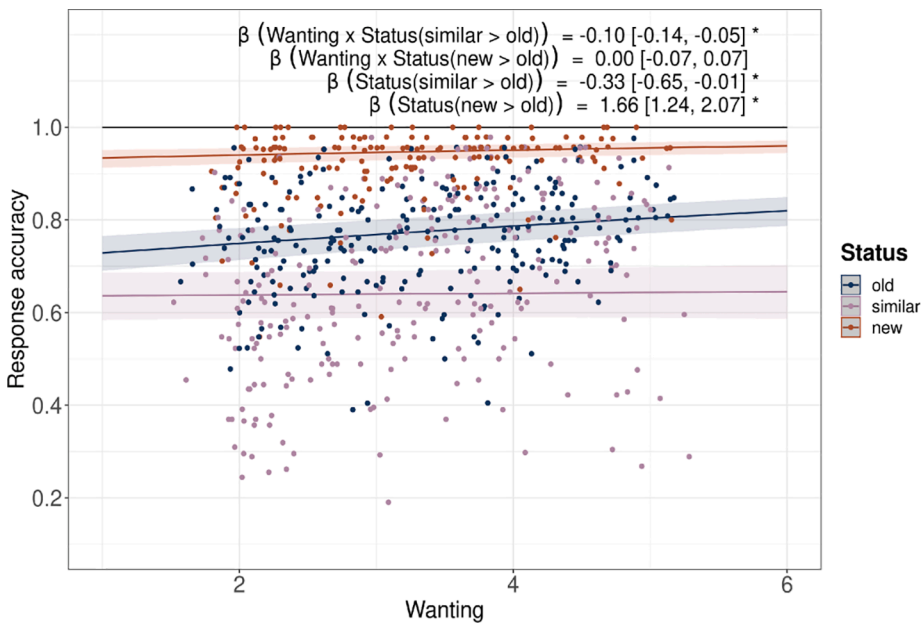


Fig. 8. Predicted response accuracy by single image wanting rating for old (dark-blue), similar (light-violet) and new (red) images respectively. Points show averaged response accuracy and averaged wanting of each image and predictions are based on full model (Table 1, Eq. 17). The estimates of the interactions endorse the visually evident effect that the wanting enhancement of the response accuracy was strongest for the old images, namely during memory encoding. Response accuracy for new images was higher than for old images and lowest for similar images. Odds ratios of all predictors and covariates are listed in Fig. 8-2 and Table 8-1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

predict category-specific memory performance (Fig. 10 C&D) nor independently of image category (Fig. 10-1 C&D). In both cases, the full-null model comparisons (Table 1, Eq. 21–25 and Table 2, Eq. 26–30) as well as the posterior distributions of the main effects of nQA emphasized a lack of memory accuracy modulation by microstructural coherence. Based on the interaction estimates, we could additionally infer that neither the UF nor its sub-bundle moderated the evident effect of image category (Figs. 10-2 & 10-3). Estimates of all models in the comparison are listed in the supplementary material (Tables 10-1 to 10-4). Due to the evident difference in average nQA between left and right sub-bundles of the UF, we reran the models for left and right sub-bundles respectively. However, these exploratory analyses did not reveal a hemisphere-specific role of the sub-bundle of the UF in memory processes (Fig. 10-4).

3.4.1. Is the compactness of the individuals white matter relevant when investigating microstructural effects? (exploratory)

In order to exclude an influence of inter-individual differences in whole brain white matter density, we re-ran all models, addressing the effect of microstructural coherence on memory performance measures, taking whole brain nQA values into account. We corrected the nQA(UF) and nQA(sub-UF) for global white matter density. Thereto, we calculated relative nQA values by division through nQA(whole brain). We could not find an evident effect of these relative microstructural coherence measures on target recognition or lure discrimination performance – neither by relative nQA(UF) nor by relative nQA(sub-UF) (Fig. 10-5).

3.4.2. Is the detected positive wanting effect on response accuracy moderated by the microstructural coherence of the UF? (exploratory)

We hypothesized that the UF might have a modulatory role on the interplay of wanting and memory. As the wanting categories did not evidently differ regarding memory performance measures, we extended the analysis to a possible moderation of single item wanting enhancement of response accuracy by microstructural properties of the UF. However, we did not detect a moderation neither for all images (Fig. 11 A) nor for old images (Fig. 11 B), for which the wanting enhancement was most pronounced. The mean estimates (Fig. 11) and median odds ratios (Fig. 11-1) of the posterior distributions of the nQA(UF)*wanting interaction supported this lack of modulatory top-down control. Odds ratios of the predictors and random effects of all models in the model

comparison are listed in Table 11-1. In summary, the positive wanting effect on response accuracy was not evidently moderated by the microstructural coherence of the UF.

3.5. Further behavioural analyses

In order to discuss the enhanced response accuracy by wanting during memory encoding, we additionally considered the effects of general preference (i.e. liking). The enhancement by wanting compared to liking during memory encoding is slightly stronger which is supported by the slight difference in mean estimates of the main effects (Fig. 12 A & B). The estimate of the interaction of liking with image category suggested that enhancement during memory encoding by liking is similar for food (yellow) and art (blue) images (Fig. 12 A, Table 12-1). The same can be concluded for the enhancement by wanting (Fig. 12 B, Table 12-2). Even though the model comparison (Table 2, Eq. 35–37) supported the enhanced response accuracy through liking.

As preregistered, we investigated if body composition measures, namely BMI, gender-standardized waist-to-hip ratio and gender-standardized fat mass, affect food memory performance. Neither target recognition nor lure discrimination were predicted by body composition measures nor did we find differences between food and art memory performance. We investigated if possible effects of nausea, anxiety, difficulty of the tasks or exhaustion by the tasks affected memory performance. None of these well-being measures influenced the participants' performance on the memory task (see [GitLab repository](#)).

Higher calorie content of the food images was related to higher response accuracy. The estimates of the main effects (Fig. 13, Fig. 13-1 A) showed that food memory accuracy was evidently better in the highest calorie quartile compared to the lowest calorie quartile. The model comparison (Table 2, Eq. 38–40) additionally showed that the wanting enhancement of response accuracy did not depend on calorie content of the depicted food (Fig. 13-1 B, Table 13-1).

Female participants ($n = 20$; dark-red) outperformed male participants ($n = 40$; dark-yellow) in the memory task. Target recognition, lure discrimination and memory accuracy were predicted by gender which was included as covariate in all Bayesian regression models (see Fig. 14). With additional exploratory analyses, we aimed to understand this gender difference. The analyses included interactions of gender with socio-economic status, attention network performance, personality traits and eating behaviour traits, as well as their main effects. Gender

Table 2

Model equations of full and null models and the difference in predictive accuracy with standard errors ($\Delta\text{elpd} \pm \text{se}$). Each model comparison delivers either evident, highly probable or inconclusive results that one of the models predicts the memory performance (d' , LDI or response accuracy) better than the other models. A model predicts memory performance evidently better than the other models if $\Delta\text{elpd} > \text{se}$. If $\Delta\text{elpd} < \text{se}$ but the predictors' posterior distributions show an evident effect, we can assume that the predictive effect is highly probable. The comparison is inconclusive if $\Delta\text{elpd} < \text{se}$ and the predictors' posterior distributions do not show an evident effect. The evidently highest elpds / best models are marked with * and the models with highly probable predictive effects are marked with (*).

Eq. No.	Model Title	Model type	Model Equation dependent variable ~ predictors & covariates (without random effects for visual clarity)	Difference in Predictive Accuracy ($\Delta\text{elpd} \pm \text{se}$)
26	sub-UF	full model	$d' / \text{LDI} \sim \text{Image Category} + \text{Wanting Category} + \text{Subj Hunger Level} + \text{nQA}(\text{sub-UF}) + \text{Image Category} * \text{nQA}(\text{sub-UF}) + \text{Wanting Category} * \text{nQA}(\text{sub-UF}) + \text{Subj Hunger Level} * \text{nQA}(\text{sub-UF}) + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -4.1 ± 1.6 ; LDI : -4.8 ± 2.1
27	sub-UF	null model 7	$d' / \text{LDI} \sim \text{Image Category} + \text{Wanting Category} + \text{Subj Hunger Level} + \text{nQA}(\text{sub-UF}) + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -1.6 ± 0.5 ; LDI : -2.5 ± 1.0
28	sub-UF	null model 11	$d' / \text{LDI} \sim \text{Image Category} + \text{nQA}(\text{sub-UF}) + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -2.0 ± 2.0 ; LDI : -1.0 ± 0.4
29	sub-UF	null model 13	$d' / \text{LDI} \sim \text{Image Category} + \text{Wanting Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : reference elpd; LDI : -1.4 ± 1.0
30	sub-UF	null model 14 *	$d' / \text{LDI} \sim \text{Image Category} + \text{Age} + \text{Gender} + \text{Intervention} + \text{Timepoint} + \text{Intervention} * \text{Timepoint}$	d' : -1.1 ± 2.0 ; LDI : * evidently highest elpd
31	Wanting/UF	full model	Response accuracy ~ Image Category + Subj Hunger Level + Wanting + nQA(UF) + Image Category * nQA(UF) + Subj Hunger Level * nQA(UF) + Wanting * nQA(UF) + Age + Gender + Intervention + Timepoint + Intervention * Timepoint	response accuracy: -3.6 ± 1.1
32	Wanting/UF	null model 2 *	Response accuracy ~ Image Category + Subj Hunger Level + Wanting + nQA(UF) + Image Category * nQA(UF) + Age + Gender + Intervention + Timepoint + Intervention * Timepoint	response accuracy: * evidently highest elpd
33	Wanting/UF	null model 3	Response accuracy ~ Image Category + Subj Hunger Level + Wanting + nQA(UF) + Age + Gender + Intervention +	response accuracy: -0.8 ± 0.5

Table 2 (continued)

Eq. No.	Model Title	Model type	Model Equation dependent variable ~ predictors & covariates (without random effects for visual clarity)	Difference in Predictive Accuracy ($\Delta\text{elpd} \pm \text{se}$)
34	Wanting/UF	null model 6	Timepoint + Intervention * Timepoint Response accuracy ~ Image Category + Age + Gender + Intervention + Timepoint + Intervention * Timepoint	response accuracy: -4.2 ± 3.0
35	Single item liking (old images)	full model	Response accuracy ~ Image Category + Liking + Age + Gender + Intervention + Timepoint + Intervention * Timepoint	response accuracy: reference elpd
36	Single item liking (old images)	null model 1 (*)	Response accuracy ~ Image Category + Liking + Age + Gender + Intervention + Timepoint + Intervention * Timepoint	response accuracy: 0.0 ± 0.8
37	Single item liking (old images)	null model 2	Response accuracy ~ Image Category + Age + Gender + Intervention + Timepoint + Intervention * Timepoint	response accuracy: -2.9 ± 2.6
38	Calorie content (food images)	full model	Response accuracy ~ Wanting + Calorie Content + Wanting * Calorie Content + Image Status + Age + Gender + Timepoint + Intervention + Timepoint * Intervention	response accuracy: -1.9 ± 1.5
39	Calorie content (food images)	null model 1 (*)	Response accuracy ~ Wanting + Calorie Content + Image Status + Age + Gender + Timepoint + Intervention + Timepoint * Intervention	response accuracy: -0.7 ± 1.2
40	Calorie content (food images)	null model 2	Response accuracy ~ Wanting + Image Status + Age + Gender + Timepoint + Intervention + Timepoint * Intervention	response accuracy: probably highest elpd
41	Neuroticism	full model	$d' / \text{LDI} \sim \text{Neuroticism} + \text{Neuroticism} * \text{Gender} + \text{Neuroticism} * \text{Age} + \text{Gender} + \text{Age}$	d' : -1.6 ± 1.1 ; LDI : -1.5 ± 0.7
42	Neuroticism	null model 1	$d' / \text{LDI} \sim \text{Neuroticism} + \text{Neuroticism} * \text{Gender} + \text{Gender} + \text{Age}$	d' : -0.8 ± 1.1 ; LDI : -0.7 ± 0.7
43	Neuroticism	null model 2 (*)	$d' / \text{LDI} \sim \text{Neuroticism} + \text{Gender} + \text{Age}$	d' : probably highest elpd LDI : probably highest elpd
44	Neuroticism	null model 3	$d' / \text{LDI} \sim \text{Gender} + \text{Age}$	d' : -2.1 ± 1.6 ; LDI : -1.6 ± 1.5
45	Microstructural coherence	full model	nQA(UF) ~ Gender + Age + Gender * Age + Timepoint * Intervention + Timepoint + Intervention	nQA(UF): -1.9 ± 2.5
46	Microstructural coherence	null model 1	nQA(UF) ~ Gender + Age + Gender * Age + Timepoint + Intervention	nQA(UF): reference elpd
47	Microstructural coherence	null model 2	nQA(UF) ~ Gender + Age + Timepoint + Intervention	nQA(UF): -3.3 ± 3.4

(continued on next page)

Table 2 (continued)

Eq. No.	Model Title	Model type	Model Equation dependent variable ~ predictors & covariates (without random effects for visual clarity)	Difference in Predictive Accuracy ($\Delta\text{elpd} \pm \text{se}$)
48	Microstructural coherence	null model 3	nQA(UF) ~ Gender + Timepoint + Intervention	nQA(UF): -1.9 ± 1.9
49	Microstructural coherence	null model 4	nQA(UF) ~ Timepoint + Intervention	nQA(UF): -1.4 ± 2.1

interaction effects on target recognition or lure discrimination

Table 3

Mean, standard deviation and range of normalized quantitative anisotropy values (nQA) of the uncinate fasciculus (UF) and its sub-bundle as well as the whole brain.

nQA	left UF	right UF	average UF	left sub-bundle of UF	right sub-bundle of UF	average sub-bundle of UF	whole brain
Mean(SD)	0.271 (0.021)	0.271 (0.023)	0.271 (0.022)	0.183 (0.024)	0.171 (0.028)	0.177 (0.022)	0.274 (0.021)
Range	0.211 - 0.318	0.208 - 0.326	0.213 - 0.320	0.111 - 0.243	0.100 - 0.264	0.105 - 0.234	0.209 - 0.329

performance could not be confirmed. However, the personality trait “neuroticism” predicted target recognition and lure discrimination performance. We found that the more neurotic the participants the worse their memory performance (Fig. 15). This effect was independent of their gender and age (Tables 15-1 & 15-2).

3.6. Further DWI analyses

Microstructural coherence of the UF was neither evidently decreased by age (Fig. 16 A) nor evidently different between females (dark-red) and males (dark-yellow; Fig. 16 B). The model comparison (Table 2, Eq. 45–49) did not allow for confident inferences about possible effects on UF microstructure. Nevertheless, the model estimates indicated a lack of an age and/or gender effect (see Table 16-1). An impact of the individuals’ body composition reflected in BMI, WHR (gender-

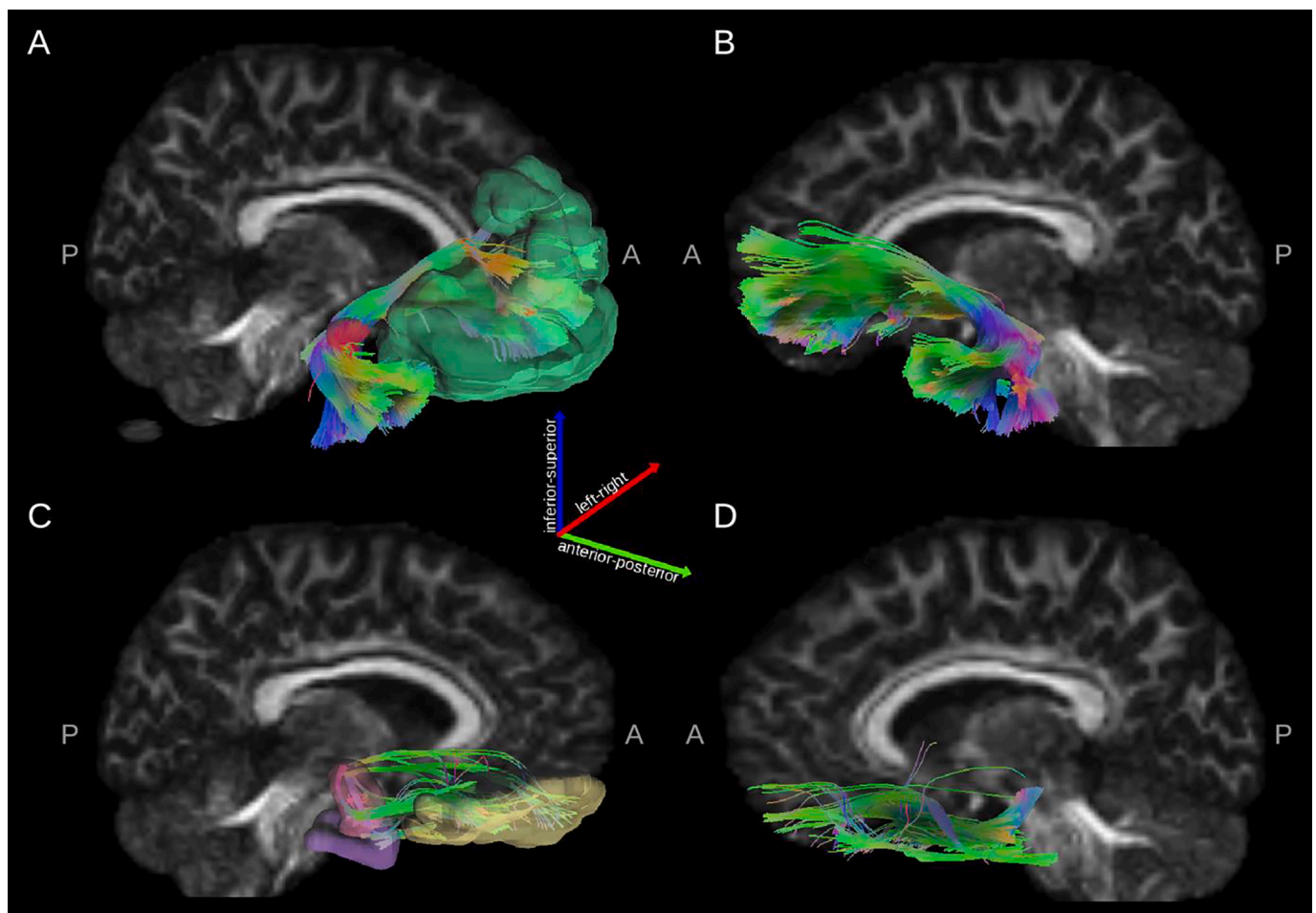


Fig. 9. Exemplary tracing results of in-vivo uncinate fasciculi (UF) and sub-bundles of the UF. A: right UF with ROIs, B: left UF, C: right sub-bundle with ROIs, D: left sub-bundle. Fiber tracts are derived from deterministic tractography conducted in DSI studio (version 2022.01.11) overlaid on a subject’s whole brain normalized quantitative anisotropy map. A) Regions-of-interest for tractography of the entire UF, exemplary for the right hemisphere: red: UF seed region from John Hopkins university (JHU) labels atlas (1 mm), merged end region (green) consisting of Brodman Areas 11 and 47 identical to Granger et al. (2021) and Brodman area 10 from Brodman atlas (within DSI studio). C) Regions-of-interest for tractography of sub-bundle of the UF, exemplary for the right hemisphere: yellow: seed orbitofrontal cortex regions from the AAL2 atlas (within DSI studio), pink amygdala from the FreeSurferDKT subcortical atlas and violet: the entorhinal cortex from the FreeSurferDKT cortical atlas. Orientations: A: anterior, P: posterior. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

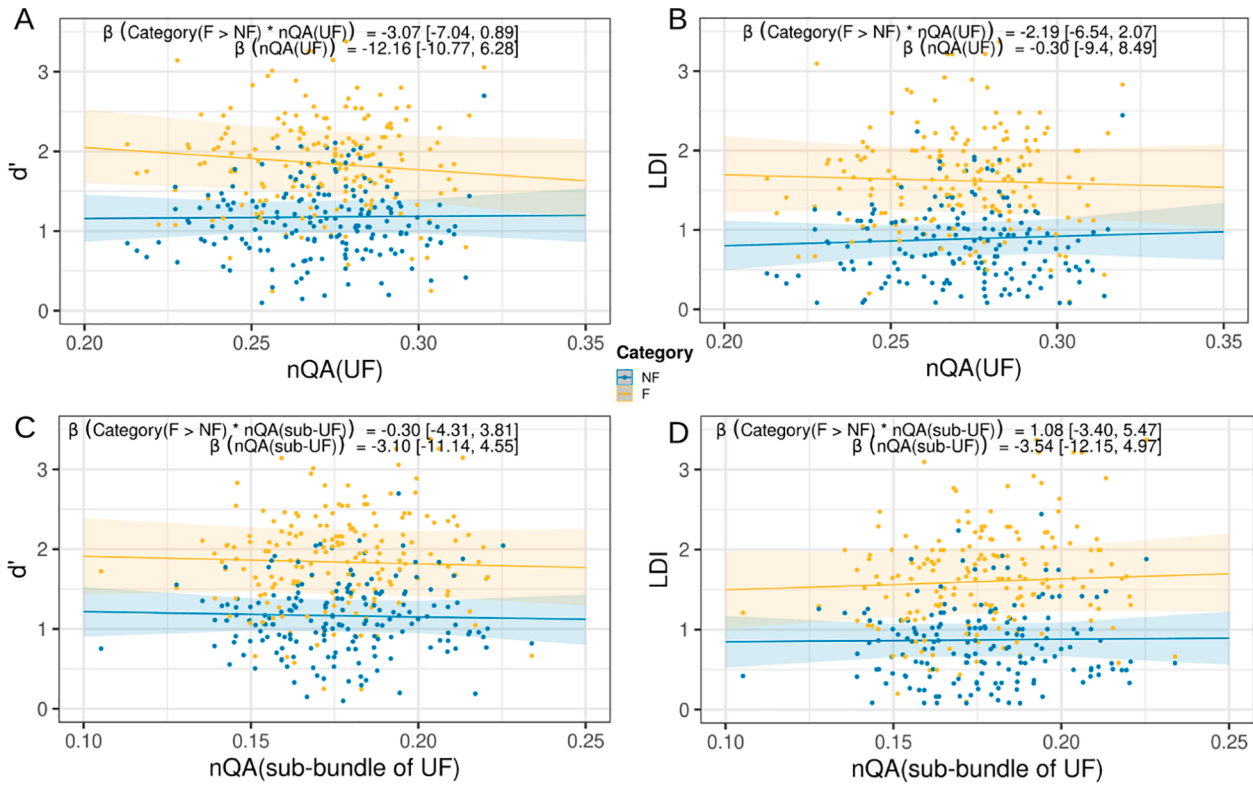


Fig. 10. Memory performance depending on microstructural coherence of UF and its sub-bundle per category. Actual and predicted A + C) target recognition d' and B + D) lure discrimination LDI depending on normalized quantitative anisotropy (nQA) of the uncinate fasciculus (UF, A&B) and its sub-bundle (C&D). Points show the actual data and lines with 95%-CI depict predictions based on full models (Table 1, Eq. 21 & Table 2, Eq. 26). **Neither d' nor LDI were affected by the microstructural coherence of the UF, reflected in nQA, or by its sub-bundle.** The estimates of the interaction of the full model indicated that the image categories were not differently influenced by the UF's microstructural coherence. The estimates of the main effect neither support an effect of microstructural coherence on memory performance (Fig. 10-1). Estimates of all predictors and covariates are visualized in Figs. 10-2 & 10-3 and listed in Tables 10-1 – 10-4. A hemisphere-specific role of the sub-bundle of the UF could not be confirmed (Fig. 10-4).

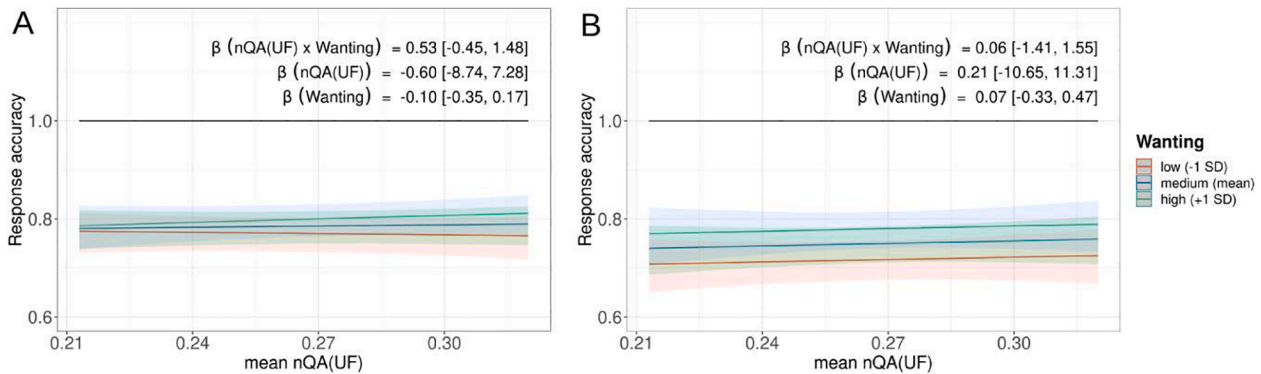


Fig. 11. Predicted response accuracy by wanting depending on the microstructural integrity of the UF. Predictions are based on the full model (Table 2, Eq. 31) A) for all images and B) for old images only. The estimates of the interactions endorsed the visually evident lack of a moderation effect of nQA(UF) on the wanting enhancement of the response accuracy. Odds ratios of all predictors and covariates are visualized in Fig. 10-1 and listed in Table 11-1.

standardized) and %FM (gender-standardized) was equally undetectable. In summary, neither the microstructural coherence of the UF (Fig. 16) nor of the whole brain (Fig. 16-1) was affected by gender, age or body composition.

4. Discussion

In this preregistered study combining in-depth behavioural, physiological and advanced neuroimaging data from 60 adults (20 females) of up to four time points, we find that desire to eat (i.e. food wanting)

predicted recognition of food items and desire to have (i.e. art wanting) predicted recognition of art prints. Additionally, food was better memorized than art images and high caloric content increased memorability of food items. In contrast, we could not detect a moderating effect of microstructural measures of the uncinate fasciculus on memory performance, extracted from diffusion imaging, in this homogeneous cohort of 20 to 41 year old adults. Exploratory results indicated effects of gender and personality traits on memory performance.

Food images tended to be better recognized and discriminated than art images. Evolutionary seen, the ability to recognize and discriminate

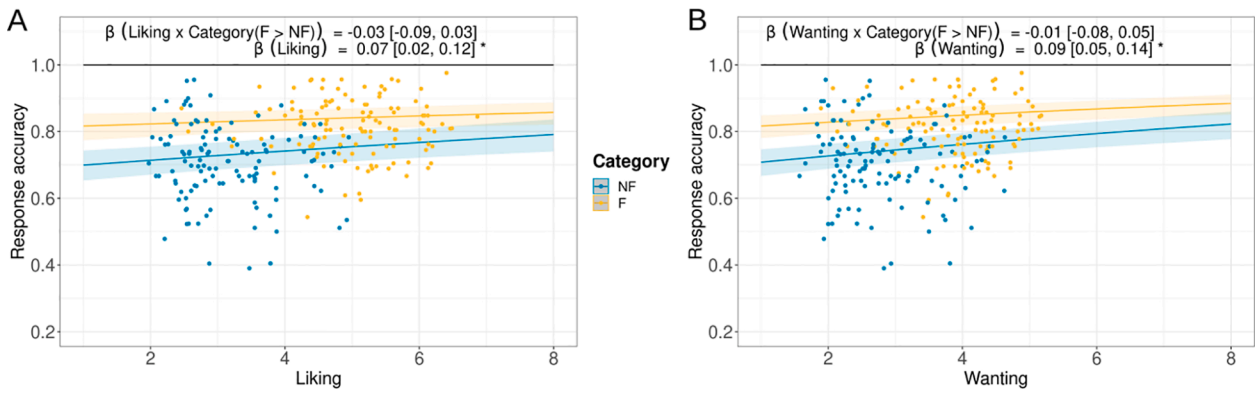


Fig. 12. Recognition accuracy of old images predicted by A) liking and B) wanting. Depicted are points reflecting averaged response accuracy and averaged liking/wanting of each image as well as predictions and their 95%-CI based on full models (Table 2, Eq. 35). The estimates of the interaction of the full model indicate that wanting and liking affect both image categories similarly. The enhancement by wanting during memory encoding is slightly stronger than by general liking. Odds ratios of the corresponding models are listed in Tables 12-1 – 12-2.

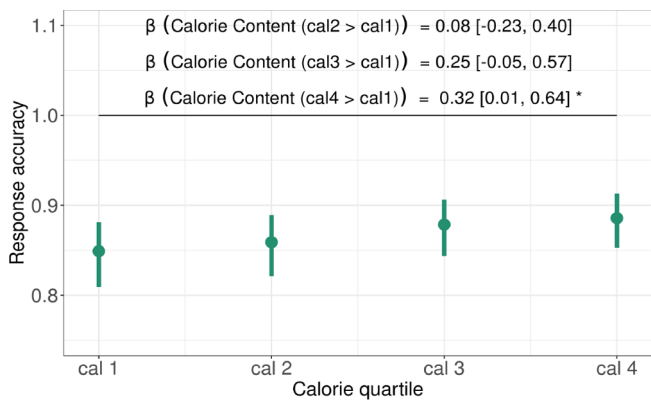


Fig. 13. Response accuracy predicted by calorie content of the food items. Predictions are based on the null model 1 (Table 2, Eq. 39). Mean predictions and their 95%-CI are depicted. **Very high calorie content compared to very low calorie content evidently influenced response accuracy of the food images.** Odds ratios of all predictors and covariates are visualized in Fig. 13-1 and listed in Table 13-1.

visual details of food items has been important to differentiate between edible and potentially toxic food items, e.g. berries or mushrooms. This bias of greater attention to food stimuli (Kumar et al., 2016; Kirsten

et al., 2019) might explain increased recognition and discrimination performance (Humphreys et al., 2010). In our study, we confirmed that food tended to be better recognized and discriminated than art images. Evidently, single image memory accuracy was better for food than art images. Despite differences in edge-based image complexity, the lower complexity of food images could not entirely explain the superiority of food memory accuracy. The visual stimuli were initially matched for composition/scene complexity which could have otherwise biased memory performance (Gomez et al., 2020). We reduced scene complexity of art images as we created the art.pics out of animal, object and plant photos by applying art styles with a deep learning algorithm (Thieleking et al., 2020). Therefore, the art.pics consist of centrally shown items which do not differ in object size from the food images. Differences in normed complexity, though, are inherent to the nature of food and art imaged as this measure reflects the amount of contrast edges per item size (e.g. low regarding single tomatoes or lemons; high considering images based on e.g. Klimt's style or the Portuguese tile pattern (Azulejos)). We recommend for future experiments to additionally add, for example, uni-coloured shapes to the art images in order to match the food images with low complexity, and to reduce the ratio of highly complex art images. Even though food and art stimuli did not differ in object sizes, the size of the food items seemed to have negatively affected food memory accuracy. Despite the visual approximation of food and art memory accuracy with higher complexity and with increasing object size, however, the superiority of food over art memory

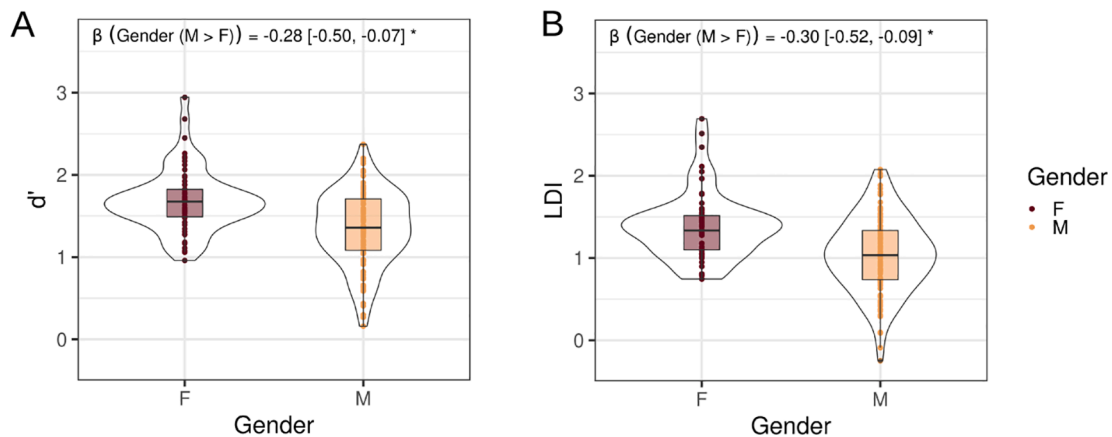


Fig. 14. Memory performance per gender group. A) The target recognition d' and B) the lure discrimination LDI of female (F) participants (bordeaux) is better than of male participants (M) (orange). Violin plots present the distribution of the two indices per gender. The estimate's CI did not include 0 which indicated an evident difference in memory performance between gender groups. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

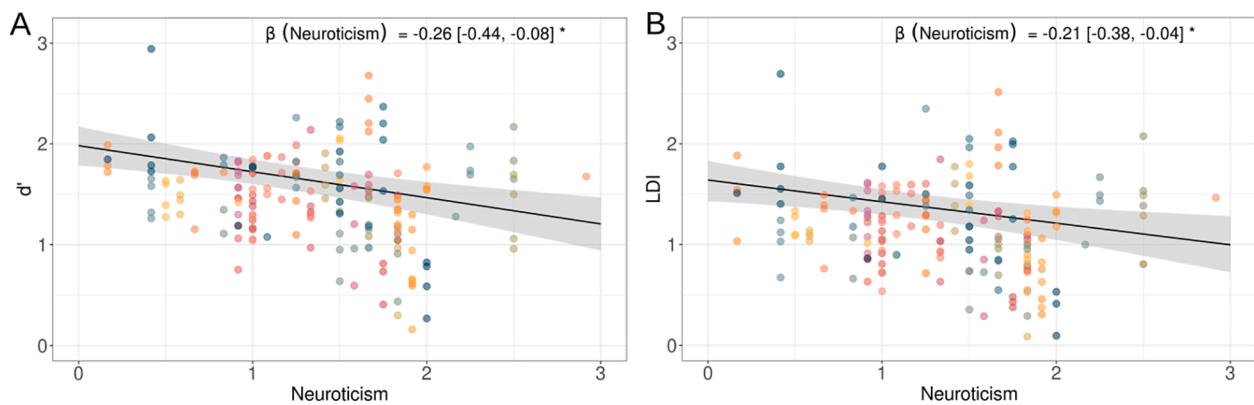


Fig. 15. Memory performance depending on personality trait neuroticism. Actual and predicted A) target recognition d' and B) lure discrimination LDI depending on neuroticism assessed with the NEO-FFI. Points show the actual data and lines with 95%-CI depict predictions based on null model 2 (Table 2, Eq. 43). d' and LDI were evidently predicted by neuroticism. **The more neurotic the participants, the worse their memory performance.** Estimates of the corresponding models are listed in Tables 15-1 & 15-2.

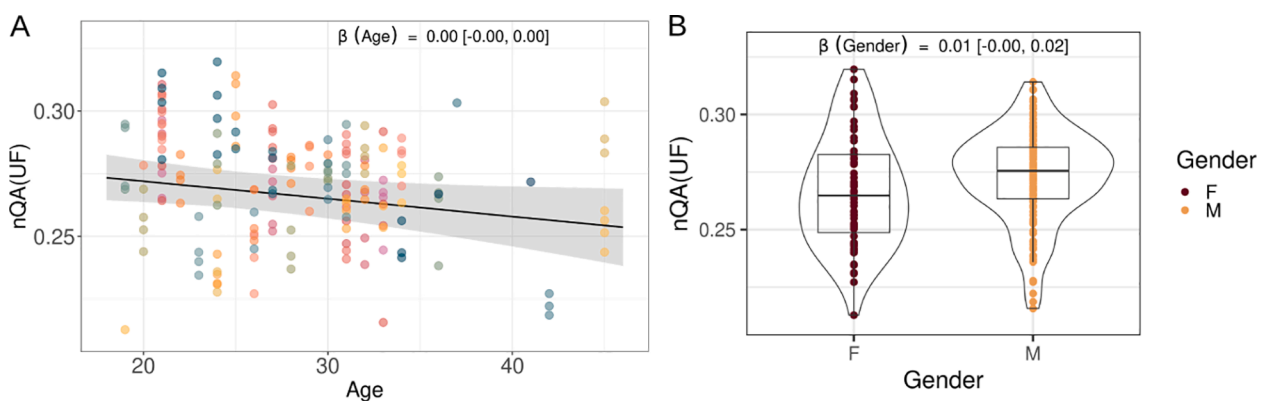


Fig. 16. Microstructural coherence of UF depending on age and gender. Actual and predicted microstructural coherence of the UF, reflected in its nQA value, A) by age and B) by gender. Points show actual data of the color-coded subjects. A) Prediction line with 95%-CI is based on null model 2 (Table 2, Eq. 47). B) Violin and boxplots present the distribution of the nQA values over both genders. **Neither age nor gender predicted the microstructural coherence of the UF.** Odds ratios of the corresponding models are listed in Table 16-1. The effects of age and gender on the whole brain's microstructural coherence is shown in Fig. 16-1.

accuracy remained statistically evident when accounting for complexity and object size. Marin and Leder (2013) have additionally shown that the influence of image complexity might relate to arousal and pleasantness. In our study, though, arousal and pleasantness (valence) did not affect memory performance. Unexpectedly, though, higher subjective recognizability was associated with lower memory accuracy but the superiority of food over art memory subsisted. Therefore, we conclude that the stronger evolutionary and hedonic relevance of food compared to art might be determining the superiority of food over art memory performance.

Subjective hunger level varied largely but did not predict memory performance in our population. Several previous studies (Morris & Dolan, 2001; Talmi et al., 2013; Montagnin et al., 2021) found an enhancing effect of hunger on food memory performance when hunger was contrasted to satiety. In our study though, participants received a standardized breakfast-shake. Thus, the difference in perceived hunger states might not have been large enough to explain variance in food memory performance. Additionally, fasted ghrelin serum levels, as a proxy for "physiological hunger", neither predicted subsequent memory performance. However, ghrelin serum levels were not measured immediately before the task which may explain a lack of correlation with food memory compared to previous studies (Carlini et al., 2010).

The stronger the wanting to eat a certain food during memory encoding the better was the food recognition accuracy in the subsequent task in our study. This finding suggests that not only *wanting* alone determines if a certain food is chosen to eat but that food choices might

also be influenced by recognition memory which, in turn, is reinforced by previous rewarding experiences. Besides the enhancement of food recognition accuracy through food wanting, we also detected this wanting enhancement could for the art images. Hence, recognition of single items in general seems to be fortified through desire. Hereby, we add on previous studies showing that future food choices might be moderated by episodic memory of previous eating experiences (Higgs, 2016; Higgs & Spetter, 2018). This study of Higgs and colleagues replicated the observations made much earlier with famous patient H.M. (Scoville & Milner, 1957; Hebben et al., 1985). Our study adds to the field that not only actual eating episodes modulate future food choices but that the anticipation of the reward through eating already enhances memory accuracy of the desired food. Outside of the experimental context, desire to eat and reward value of certain food is constantly manipulated by an overload of especially high-caloric and high-energy food stimuli in our environment (Powell et al., 2007; Duraisingam et al., 2021). This often repetitious exposure to high-caloric and high-energy food might additionally enhance their memorability (Stang, 1975) and thereby fortify overnutrition. Overnutrition could also be mediated by a calorie bias in humans' recognition memory. Recently, de Vries and colleagues (de Vries et al., 2022) have already shown that humans' spatial recognition memory is biased towards high-caloric compared to low-caloric food items independent of desire to eat. In our study, this calorie bias in food recognition memory accuracy was also evident and independent of desire to eat. However meaningful for our ancestors, this calorie bias in recognition memory in combination

with an increased desire to eat high-caloric food which in turn enhances recognition might be nowadays detrimental for a healthy, intuitive food decision-making.

Considering the close link of reward and emotion (Baxter et al., 2000; Murray, 2007) and previous studies showing effects of emotion on target recognition *d'* and lure discrimination LDI (Kensinger et al., 2006; Leal et al., 2014; Szöllösi & Racsomány, 2020), we hypothesized an effect of wanting on these memory indices. However, we could not confirm this effect, possibly due to power reduction after categorizing into “unwanted”, “neutral” and “wanted” images. We suppose that individualized picture sets of more intensely desired or despised food images could elicit food wanting effects on different memory sub-processes.

As wanting is distinct to liking (Berridge, 2009), we compared the effect of wanting during memory encoding to the participants' general liking of these encoded images. The enhancement by liking was also evident but weaker than by wanting. This finding confirms the previously claimed enhanced recognition accuracy by preference (Brooks & Watkins, 1989; Newell & Shanks, 2007; Wang & Chang, 2004) and furthers the field by adding a slightly stronger memory enhancement through wanting. Unclear is though, if liking and wanting determine recognition accuracy or if recognition enhances liking and wanting through the mere exposure effect. The direction of this relation has been previously questioned (Brooks & Watkins, 1989; Wang & Chang, 2004). In the case of a “cross-talk” between wanting and memory, the danger of a vicious cycle regarding food-decision making could arise. While speculative, this vicious cycle could consist of food choices of high-caloric, highly wanted food items and an increased recognition memory of these, which then in turn leads to a more frequent choice of these food items due to the remembered desire and positive experience.

In our study, we could not find an association between food recognition or lure discrimination performance and participants' eating behaviour. This result endorsed our screening attempt that the participants scored low on food restrictions and eating restraint. Therefore, populations with aberrant eating traits may behave differently. Previous studies showed that restrained eaters present more extreme cravings than unrestrained eaters (Fedoroff et al., 2003). Besides higher cravings, higher calorie content has been shown to enhance spatial memory of food items and memory of eating (Seitz et al., 2021). Therefore, studying the influence of food wanting and calorie content on food memory in restrained eaters might be insightful regarding their food decision-making.

On the neuronal level, we hypothesized a putative top-down modulatory control by microstructural properties of the uncinate fasciculus (UF) in memory processes which integrate (food) wanting and hunger. The UF connects brain areas which process wanting (Berridge, 2009; Lebreton et al., 2009), hunger (Morris & Dolan, 2001; Malik et al., 2008), emotion (Gao et al., 2021) and memory (Bakker et al., 2008; Yassa & Stark, 2011). In detail, the reward anticipation and evaluation of food and art activate, among others, neurons in the OFC (O'Doherty et al., 2001; Berridge, 2009; Sescousse et al., 2013). Even though viewing and evaluation of food pictures might activate parts of the OFC stronger than non-food/art pictures (van der Laan et al., 2011), value information should be transmitted for both stimulus types through the UF to amygdala and hippocampus. These two brain areas are not only active during reward anticipation (Schott et al., 2008) as well as encoding and retrieval of emotional memories (Murty et al., 2010; Dolcos et al., 2012) but are also crucial in the regulation of food intake (Davidson et al., 2009; Higgs, 2005; Izadi & Radahmadi, 2022; Zhang, Li, & Guo, 2011). Previously, the UF has already been shown to play a role in emotional memory processes (Yau et al., 2009; Granger et al., 2021). Due to the shared neuronal correlates of (food) reward and emotion processing, we expected a similar influence of the UF's microstructure on reward enhanced memory processes, especially regarding food as a primary reward. However, we could not transfer and confirm the UF's role in wanting enhanced (food) memory, neither for the UF nor for a sub-bundle of the UF. We selected this sub-bundle based on fibers which

terminate in the MTL and might carry directly relevant information for wanting enhanced recognition. Alerted by differences in the average microstructural coherence of the right and left sub-bundle, we found some evidence in the literature for a possibly hemisphere-specific role of the UF's sub-bundle in wanting enhanced recognition (Canli et al., 2000; Dolcos et al., 2004). However, we could not detect that neither left nor right hemispheric OFC-MTL communication, respectively, might be important for wanting enhanced recognition. Another possible explanation for the lack of microstructural modulation of memory in general might be that in this relatively young and healthy study population, white matter properties might not (yet) be relevant in the interaction of cognitive functions. Previous studies showed that variations or changes in white matter microstructure correlate with memory performance, but these correlations concern mainly elderly populations (Cremers et al., 2016) and populations with neuropsychological disorders (Alves et al., 2018; Subramaniam et al., 2018).

Female participants in our study outperformed male participants regarding target recognition, lure discrimination and memory accuracy but none of the assessed anthropometric, cognitive or personality measures could explain this gender difference. However, we detected a negative influence of neuroticism on memory indices. Higher cognitive load due to neurotic behaviour might lead to reduced memory capacities. This assumption is supported by associations of neuroticism with reduced retrospective memory (Buchanan, 2017) and working memory performance (Studer-Luethi et al., 2012). Our gender-unbalanced study design does not allow for definite conclusions but in line with previous studies (Levy, Astur, & Frick, 2005; Wang, 2013), gender differences in memory performance might be evident. Overall, through conscientious definition of our study population, advanced tractography of white matter and conservative Bayesian regression modeling (Gelman & Tuerlinckx, 2000), we are confident presented results are reliable and that the detected effects are not false positives.

In conclusion, we showed that food recognition memory is influenced by food desires. In contrast, the microstructure of implicated neural pathways, namely the UF, was not of importance for memory performance in this sample of healthy, overweight adults. We suggest that transferring the memory encoding, namely the reward evaluation, as well as the recognition assessment into virtual reality (e.g. supermarket or cafeteria buffet) to increase ecological validity of the two tasks. Thereby, brain responses and relevant information transmission between implicated brain areas through the UF might be fortified. Furthermore, comparing vulnerable populations with potentially deteriorated white matter, such as elderly (Westlye et al., 2010) or obese (Zhang et al., 2018) individuals, with our relatively healthy study population could shed light on whether UF microstructural coherence indeed determines cognitive functions related to food memory. Regarding the overnutrition pandemic, cognitive behavioural therapies could be improved by strategies that connect food desires and subsequent food recognition. The interlacing of food desires and food memory could also be considered in the development of public health campaigns and regulations.

CRediT authorship contribution statement

Ronja Thieleking: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Evelyn Medawar:** Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – review & editing, Project administration. **Arno Villringer:** Conceptualization, Resources, Writing – review & editing, Funding acquisition. **Frauke Beyer:** Methodology, Software, Resources, Writing – review & editing. **A. Veronica Witte:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared my data processing and analysis code in GitLab repositories listed in the manuscript's methodology section.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.nlm.2023.107813>.

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