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The ascending arousal system and its impact on cognition

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Appendix A

Supplementary Figures for Chapter 2

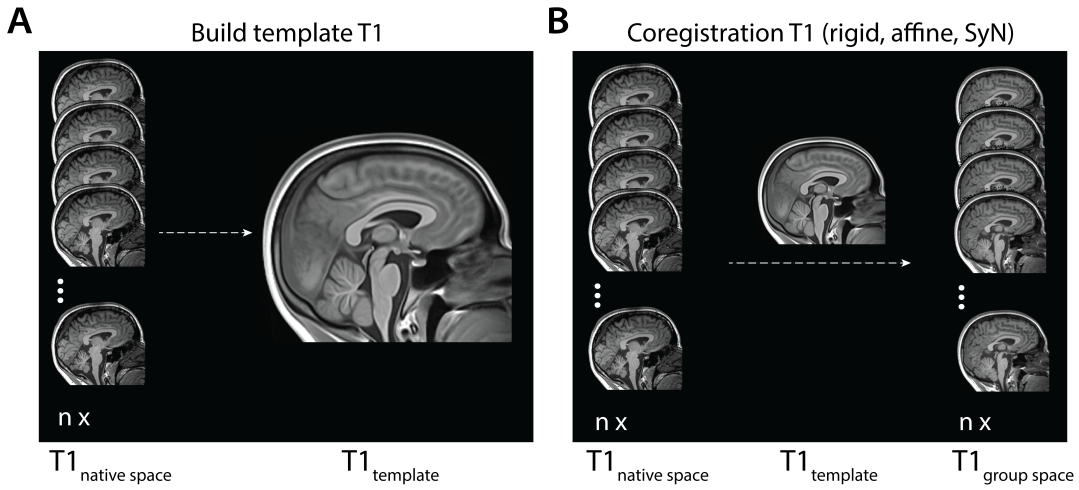


Figure A.1: Overview of template building and coregistration steps performed in ANTs. (a) Individual T1 images ($T1_{\text{native space}}$) were submitted to a template building algorithm where they were aligned and used to generate a group average ($T1_{\text{template}}$). (b) Individual T1 images ($T1_{\text{native space}}$) were coregistered to the T1 template in a separate coregistration step, generating individual T1 images in group space ($T1_{\text{group space}}$). Abbreviations: SyN - symmetric normalization.

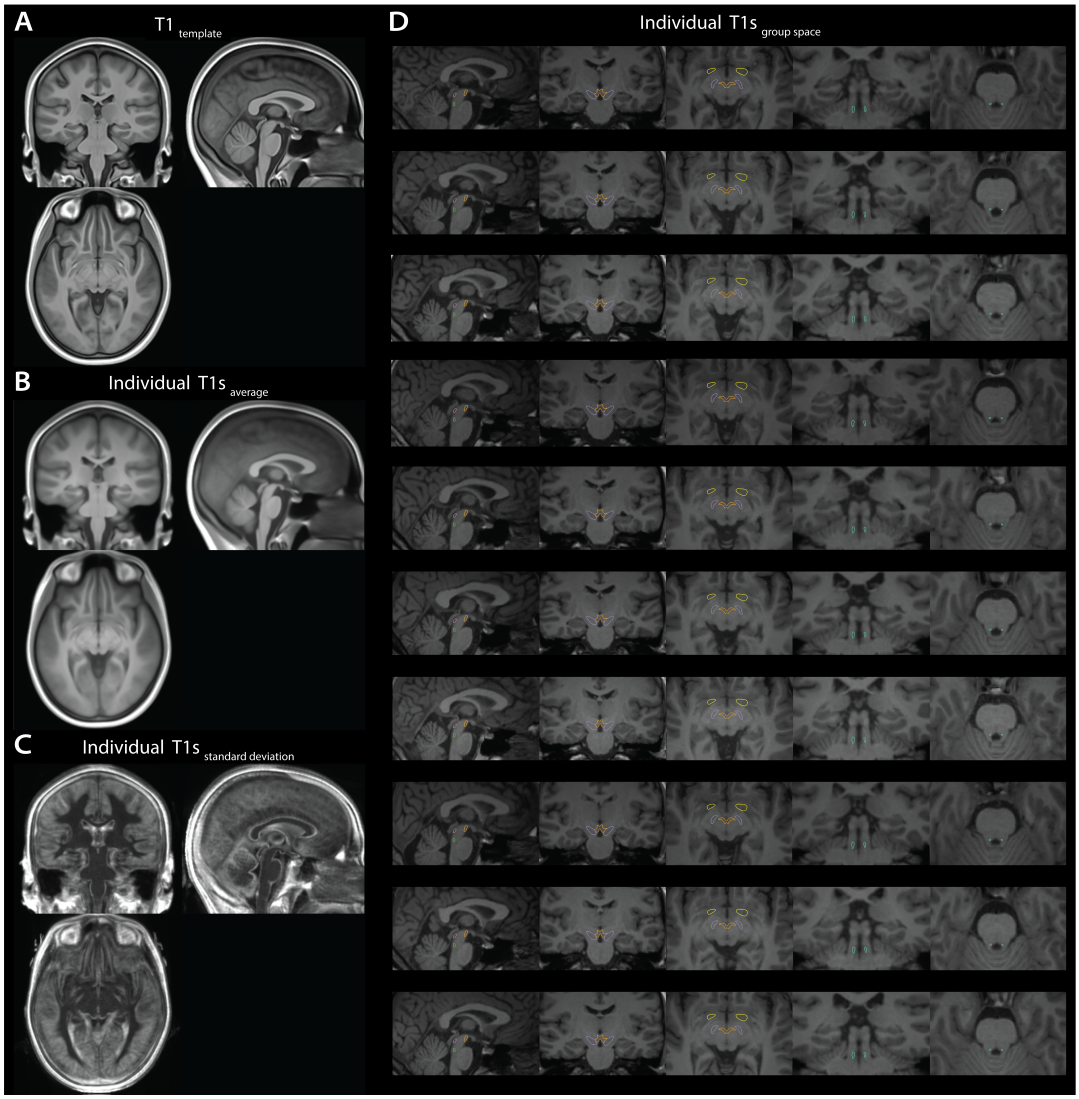


Figure A.2: Anatomical verification of accurate registration. (a) The sample-specific template T1. (b) The average of all individual warped T1 images. (c) The standard deviation of all individual warped T1 images. (d) Individual examples displaying the AAS ROI masks on top of the individual warped T1.

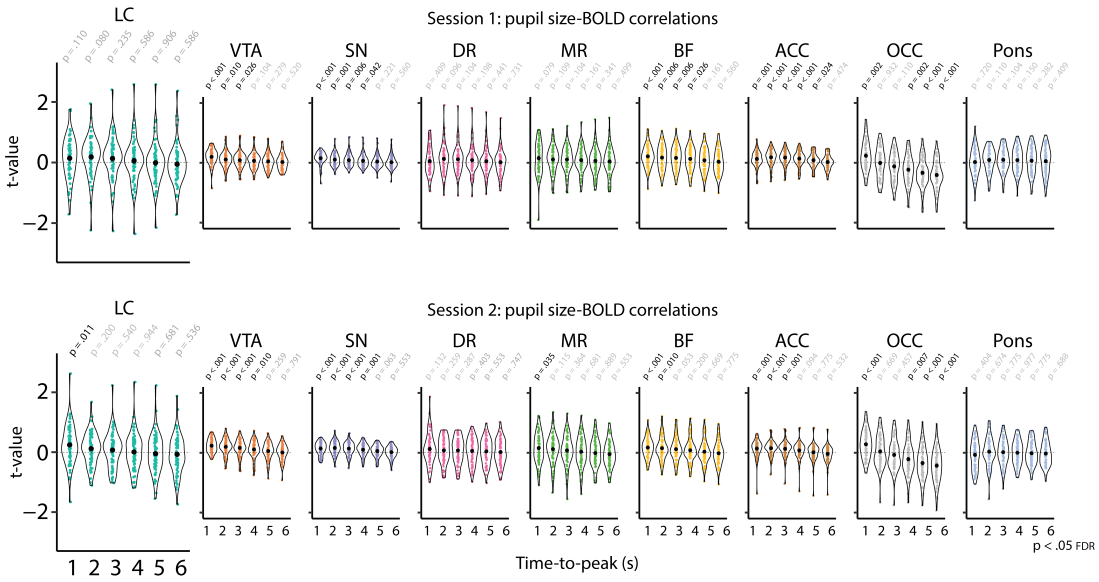


Figure A.3: Pupil size-BOLD correlations based on systematic adjustment of the time-to-peak of the HRF for both sessions separately. Graphs show the individual t-statistics (black point indicates the mean) of the pupil size-BOLD signal correlation as a function of the systematically adjusted TTP for all ROIs, p-values refer to one-sample t-tests (difference from zero; FDR-corrected). These results show that smaller ROIs, in particular the LC, DR, and MR, are more prone to a drop in statistical power when the data is halved. Abbreviations: LC – locus coeruleus, VTA – ventral tegmental area, SN – substantia nigra, DR – dorsal raphe, MR – medial raphe, ACC – anterior cingulate cortex, OCC – calcarine sulcus.

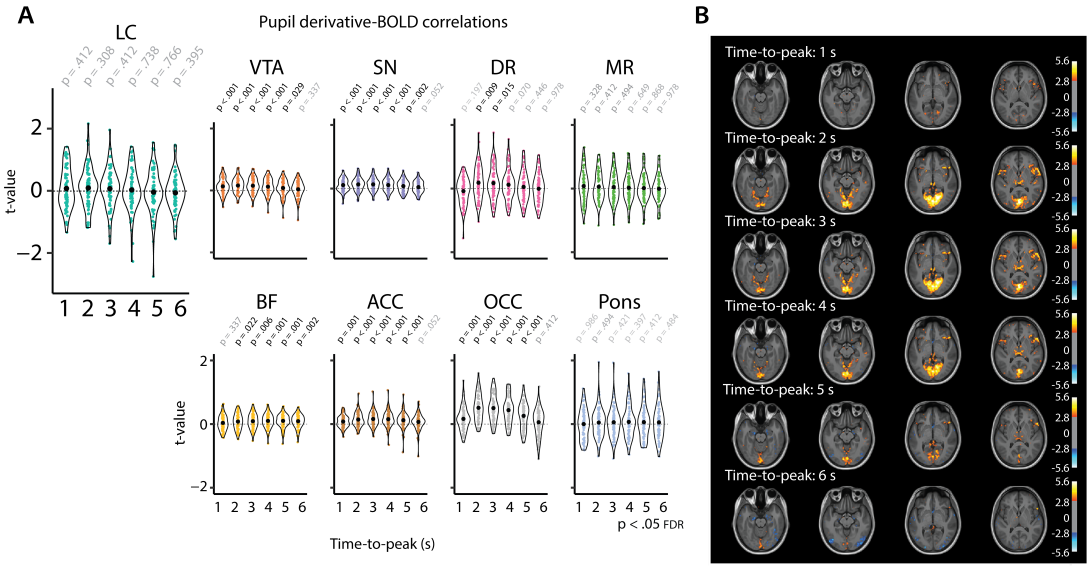


Figure A.4: Pupil derivative-BOLD correlations based on systematic adjustment of the time-to-peak of the HRF. (a) Graphs show the individual t-statistics (black point indicates the mean) of the pupil derivative-BOLD signal correlation as a function of the systematically adjusted TTP for all ROIs, p-values refer to one-sample t-tests (difference from zero; FDR-corrected). (b) The corresponding whole-brain associations between BOLD signal and the pupil derivative as a function of the time-to-peak (TTP) of the HRF (1-s TTP: top panel to 6-s TTP: bottom panel). The warm colours reflect areas in which BOLD activity is positively correlated with pupil derivative. The cold colours reflect areas where BOLD activity is negatively correlated with the pupil derivative. Both positive and negative contrast maps were sampled at $p < .005$ (uncorrected) for visualization only. Abbreviations: LC – locus coeruleus, VTA – ventral tegmental area, SN – substantia nigra, DR – dorsal raphe, MR – medial raphe, ACC – anterior cingulate cortex, OCC – calcarine sulcus.

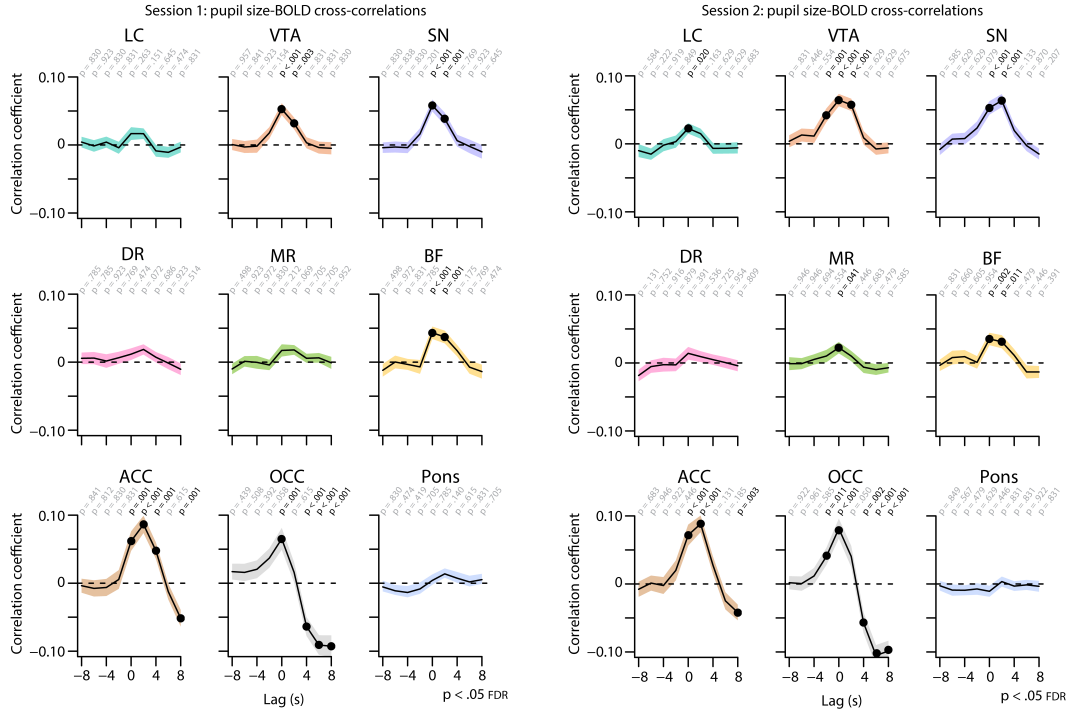


Figure A.5: Cross-correlations between the unconvolved pupil size time series and the BOLD time series at various time lags for each resting-state session. The BOLD time series was shifted forwards and backwards by 8 s in steps of 2 s. Positive (negative) time lags indicate that the pupil signal precedes (follows) the BOLD signal. Black lines indicate the grand mean and shaded regions indicate the standard error of the mean. Black dots indicate significant one-sample t-tests ($p < .05$, FDR-corrected). Abbreviations: LC – locus coeruleus, VTA – ventral tegmental area, SN – substantia nigra, DR – dorsal raphe, MR – medial raphe, ACC – anterior cingulate cortex, OCC – calcarine sulcus.

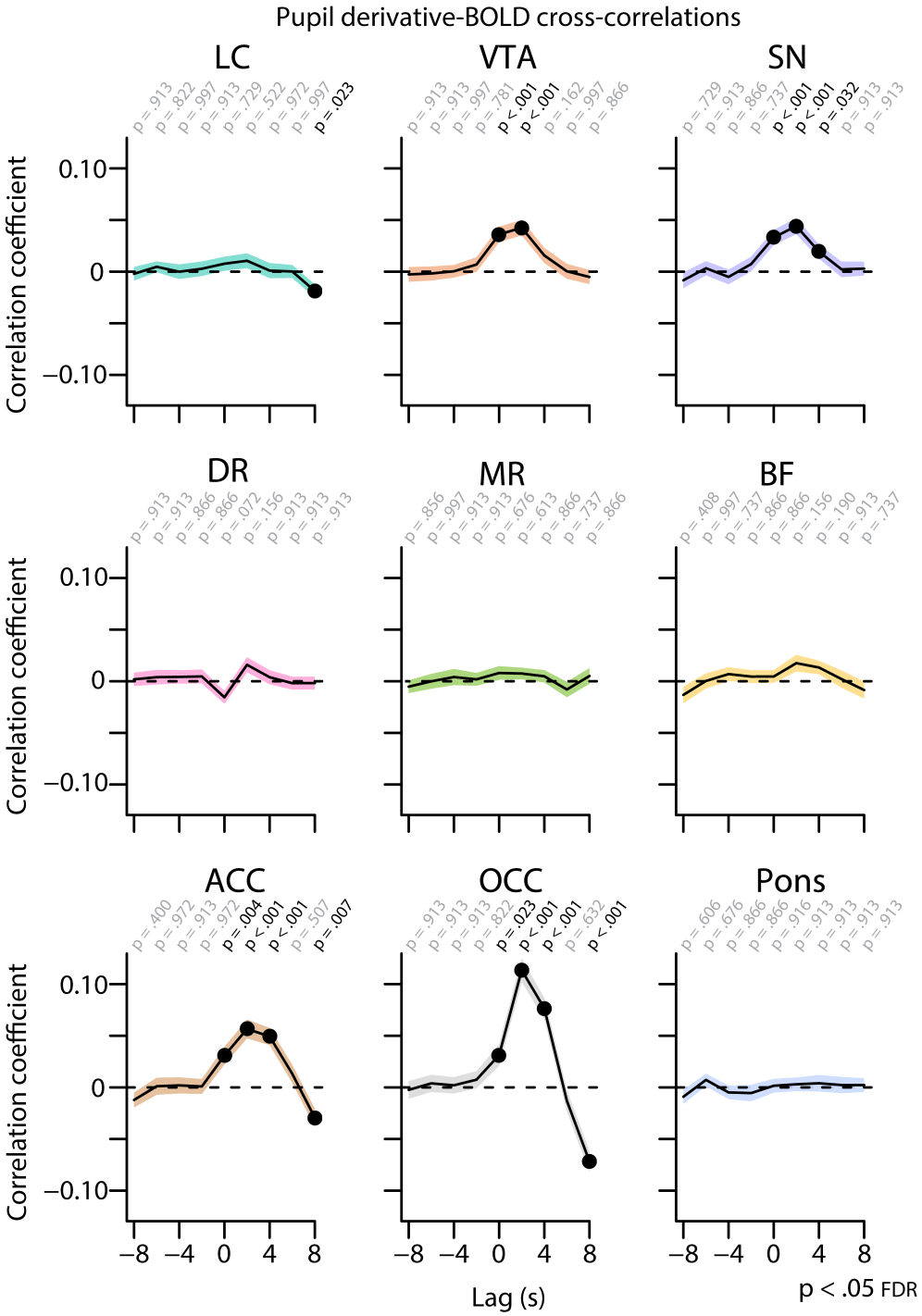


Figure A.6: Cross-correlations between the unconvolved pupil derivative time series and the BOLD time series at various time lags for each resting-state session. The BOLD time series was shifted forwards and backwards by 8 s in steps of 2 s. Positive (negative) time lags indicate that the pupil signal precedes (follows) the BOLD signal. Shaded regions indicate the standard error of the mean. Black dots indicate significant one-sample t-tests ($p < .05$, FDR-corrected). Abbreviations: LC – locus coeruleus, VTA – ventral tegmental area, SN – substantia nigra, DR – dorsal raphe, MR – medial raphe, ACC – anterior cingulate cortex, OCC – calcarine sulcus.

Appendix B

Supplementary Figures for Chapter 3

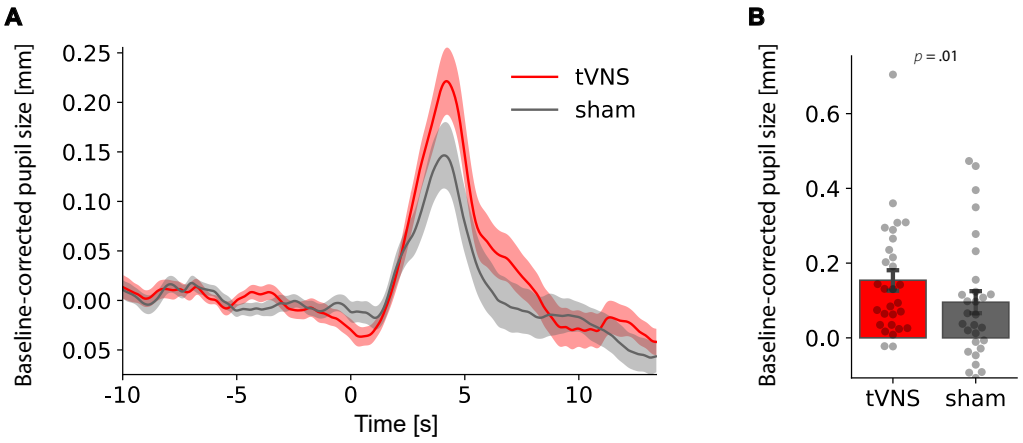


Figure B.1: Pupil dilation following taVNS stimulation compared to sham using subtractive baseline correction. A) Grand-average pupil dilation waveforms (% change) relative to the 10 s before stimulation onset. Shaded red and grey areas indicate ± SEM. B) Average pupil dilation during the period with a significant taVNS effect in (Sharon et al., 2021). Bars indicate the mean, grey points depict individual participants, error bars indicate ± SEM. Statistic refers to Wilcoxon signed-rank test.

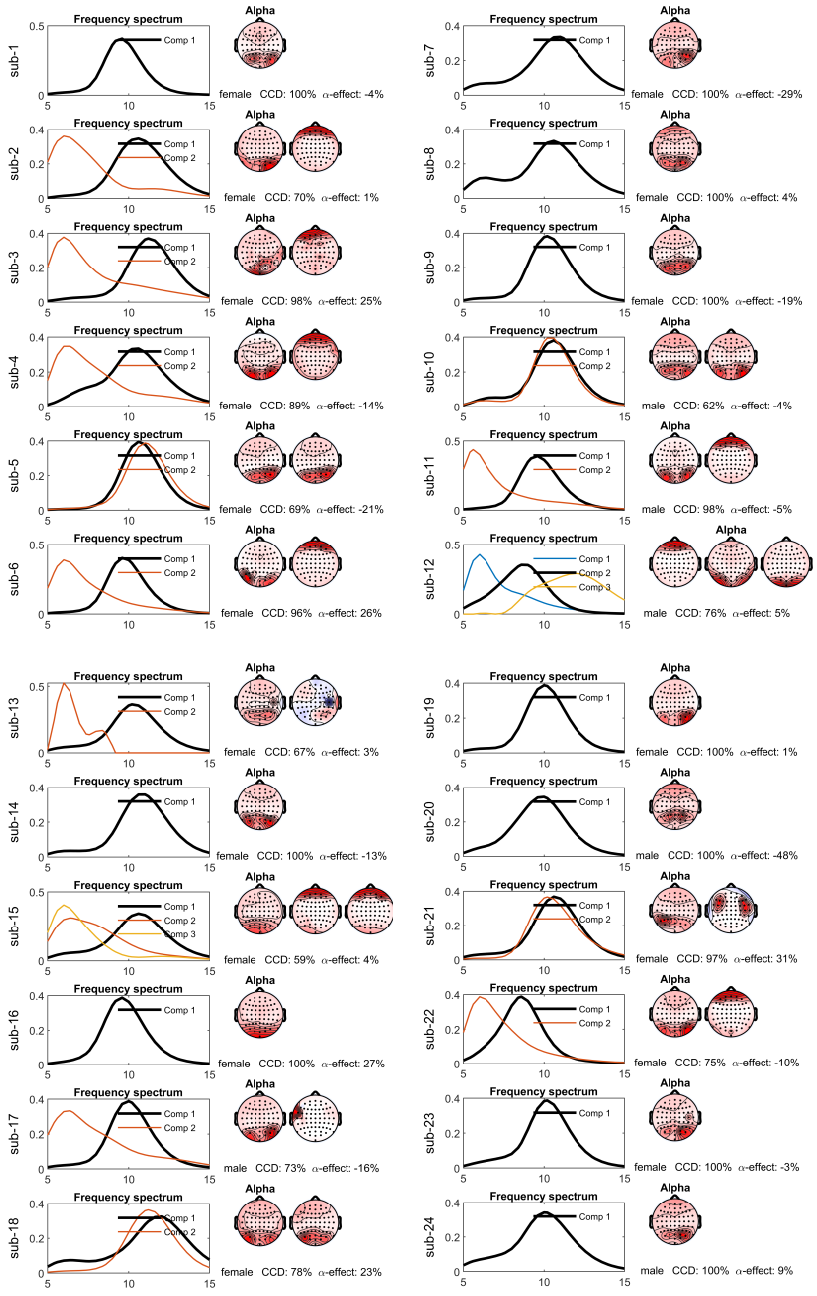


Figure B.2: Individual decomposition results of the PARAFAC method. The panels on the left show the frequency spectrum for each identified component. The topographies on the right show the spatial profile of the components in ascending order from left to right. Additional information about subjects' sex, core consistency diagnostic (CCD, used for model selection), and alpha effect is given below the topographies. The alpha effect is calculated as the power difference (taVNS minus sham) in a time window between 0 and 4 s.

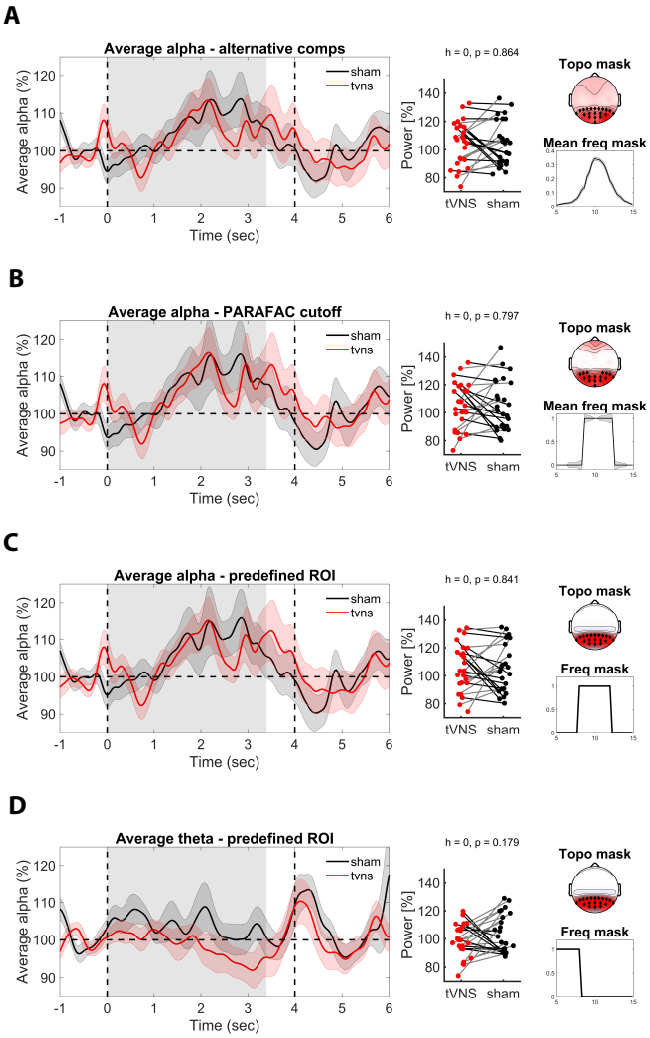


Figure B.3: Control analyses with different spatial and spectral profiles. Panels on the left show the grand-average power waveforms, using a weighted average of spectral and spatial profiles, as depicted in the right panels. Panels in the middle show the individual data points for the weighted average alpha power in the time window between 0 and 4 s. Grey lines indicate participants with lower alpha for taVNS compared to sham, black lines indicate the reversed pattern. Panels on the right depict the spatial and spectral profiles of the median alpha component. A) Weighted averages were derived using alternative component selection. For the five participants with ambiguous alpha components (5,10,12,18,21), we selected the alpha components that were not selected in the main analysis. B) Instead of using continuous values from the PARAFAC method, we derived dichotomized channel and frequency weights. The cutoff values for each participant were set to their respective mean. Only channels and frequencies above the mean were included in the analysis. C) Grand-average power waveforms were derived using manually chosen spectral and spatial profiles. For the spatial profile, we selected an occipital/posterior cluster comprised of channels Oz,PO7,PO3,O1,O2,PO4,PO8,P9,P7,P5,P3,P1,Pz,P2,P4,P6,P8,P10,POz. For the spectral profile, we included all frequencies in the alpha range between 8 and 12 Hz. D) Identical to D. Instead of the alpha range, the theta range between 5 and 8 Hz was selected for the spectral profile.

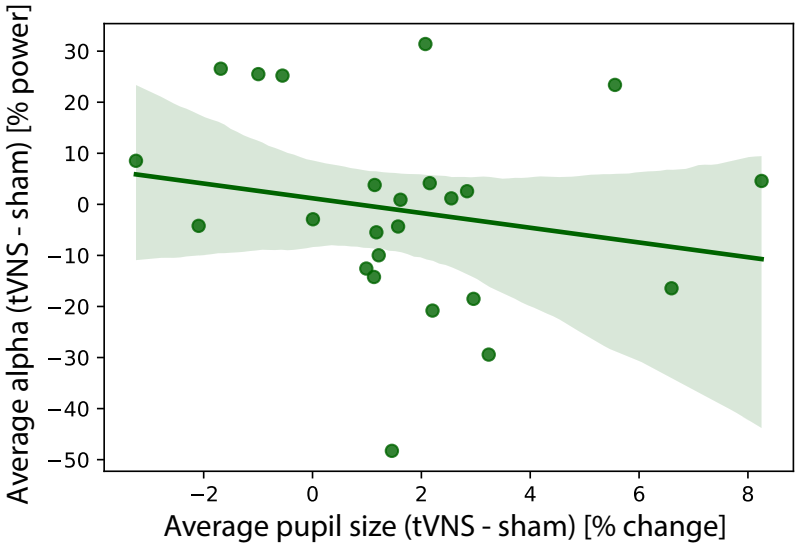


Figure B.4: Correlation between the stimulation effects (taVNS minus sham) on pupil size and EEG alpha power. Green points refer to average alpha power (0 to 4 s) and average pupil size (2.88 to 5.96 s) for each participant (n = 24). Spearman's rank correlation revealed no relationship between the two difference scores, $r(20) = -0.26$, $p = .21$.

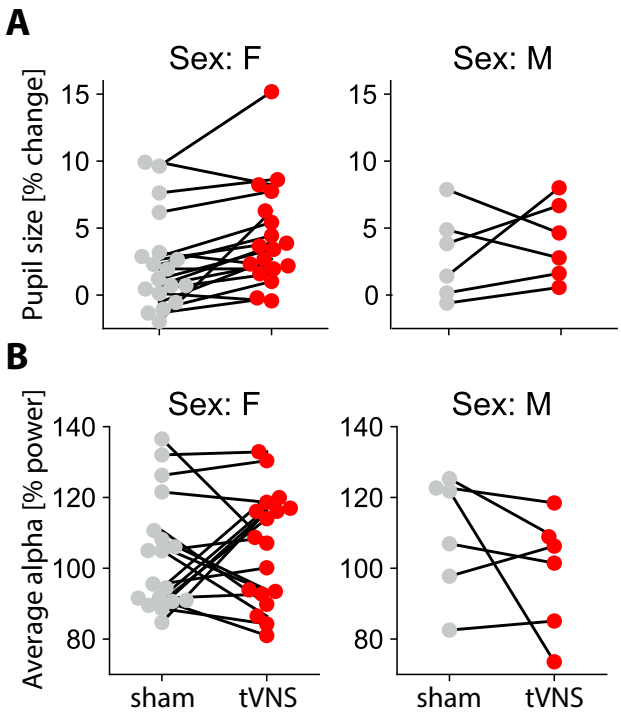


Figure B.5: The effect of taVNS vs. sham on pupil size or EEG alpha power does not differ between males and females. A) Average pupil size per condition during the period with a significant taVNS effect in Sharon et al. [31] for females (left) and males (right). B) Average alpha power (0 s – 4 s) split by condition for females (left) and males (right). A multiple linear regression with sex (M, F) and condition (tVNS, sham) predicting either pupil size or EEG alpha power revealed no interaction between sex and condition (pupil size: $p = .76$; average alpha: $p = .26$). Red points depict the participant means for the taVNS condition; grey points depict the participant means for the sham condition.

Appendix C

Supplementary Results for Chapter 4

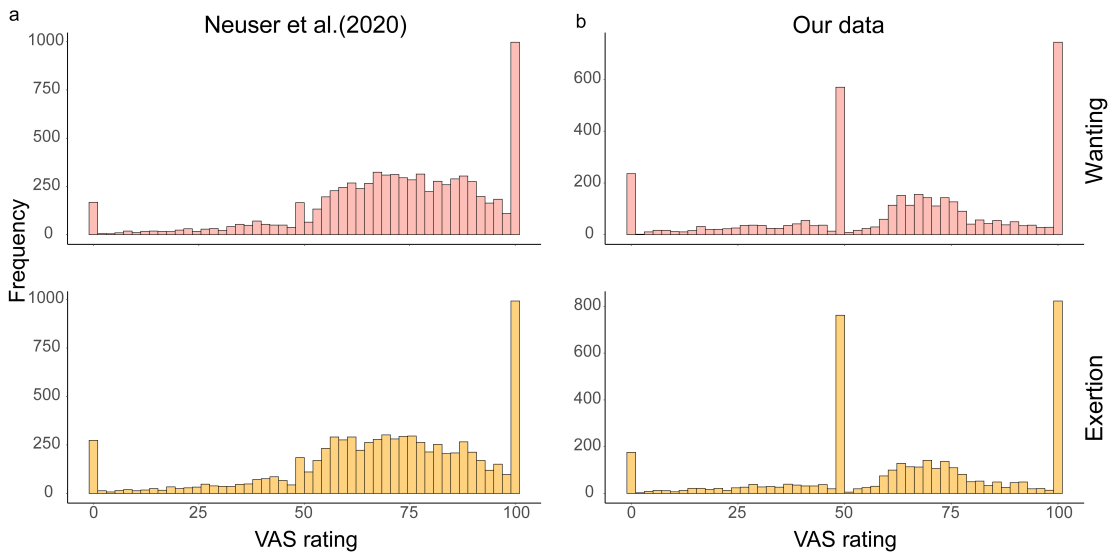


Figure C.1: Distribution of VAS ratings from a) Neuser et al. (2020) and b) the current study

Sex differences in the effects of taVNS on measures of motivation.

We examined whether men and women differed in the effect of taVNS on effort invigoration and effort maintenance. In Figure S1a below we show the effect of taVNS, separately for the female and male participants in Neuser et al. (2020). The plots suggest that the effects of taVNS on invigoration and effort maintenance were similar for females and males. To formally assess this, we ran the hierarchical linear models predicting invigoration and effort maintenance on Neuser's data, this time including sex (female, male) as an additional model predictor alongside order of stimulation and side of stimulation. Indeed, sex did not modulate the effects of tVNS on invigoration [$b = -0.94$, $t(78) = -0.43$, $p = .67$] and effort maintenance [$b = 0.06$, $t(78) = 0.04$, $p = .97$]. In Figure S2b, we show the same plots for our own data. These plots also do not show marked differences between female and male participants. For these data we did not compute inferential statistics, since there were too few male participants in our sample to expect reliable results.

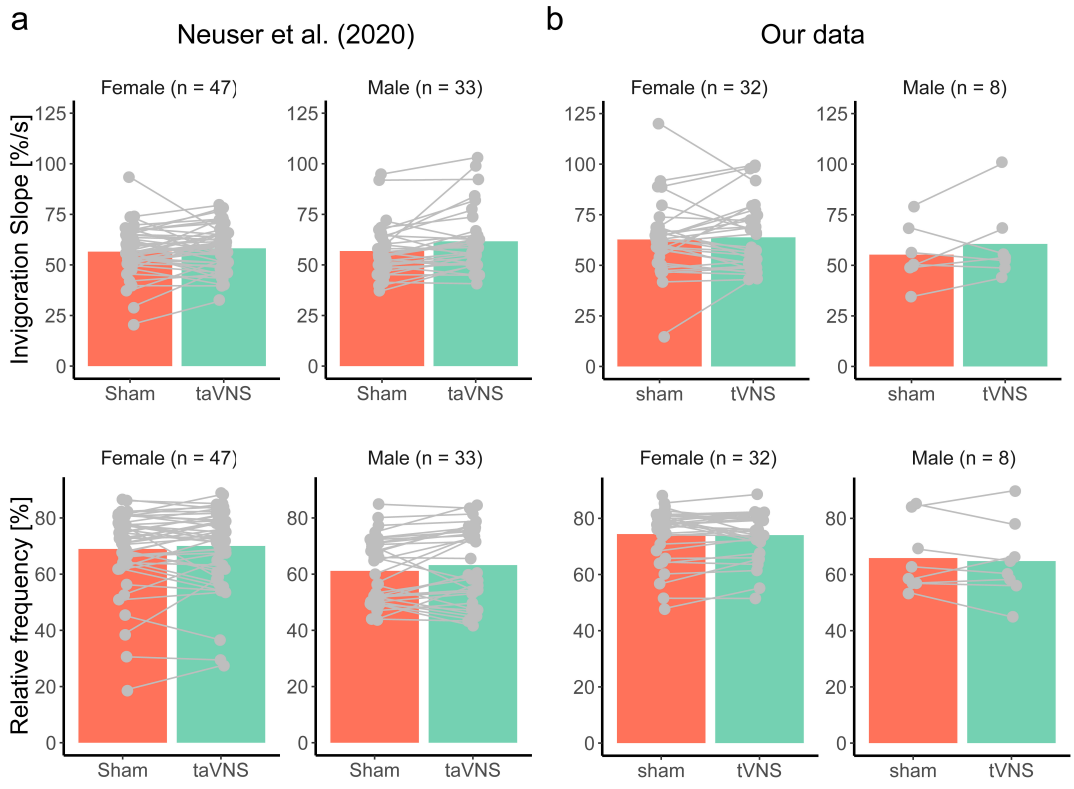


Figure C.2: Effort invigoration (top) and effort maintenance (bottom) as a function of stimulation (taVNS vs. sham) and sex. a) Results based on the data from Neuser et al. (2020). b) Results based on the current data. Colored bars indicate the mean. Grey lines indicate the results from individual participants.

Differences in motivation between the participants in Neuser et al. (2020) and the current study.

To examine if participants in the two studies may have differed in their motivation to perform well on the task, we first considered the overall winnings, which were considerably higher in our study (averages of 562.52 kcal and €6.07 per session) than in Neuser's study (362.8 kcal and €3.78). Unfortunately, when we examined these winnings more closely, we discovered a mistake in the task presentation script that was provided to us by Neuser and colleagues. In the original study the earned reward points were converted by the task presentation script into money and food at a rate of 1 kcal or 1 cent per 5 reward points and then displayed on the screen at the end of each session. In contrast, in the task presentation script shared with us, the parameter controlling the conversion rate between reward points and kcal/cents was different, resulting in a rate of 1 kcal or 1 cent per 3.125 reward

points. This explained the much higher winnings in our study. To examine if this difference could account for the discrepancy in results between the two studies, we repeated the key analyses of effort invigoration for sessions 1 and 2 separately. As shown in Figure S3ab, the discrepancy between the two studies was already present in session 1, before the participants were first informed about their winnings in terms of calories and cents. This excludes the higher winnings in our study as an explanation for our null result.

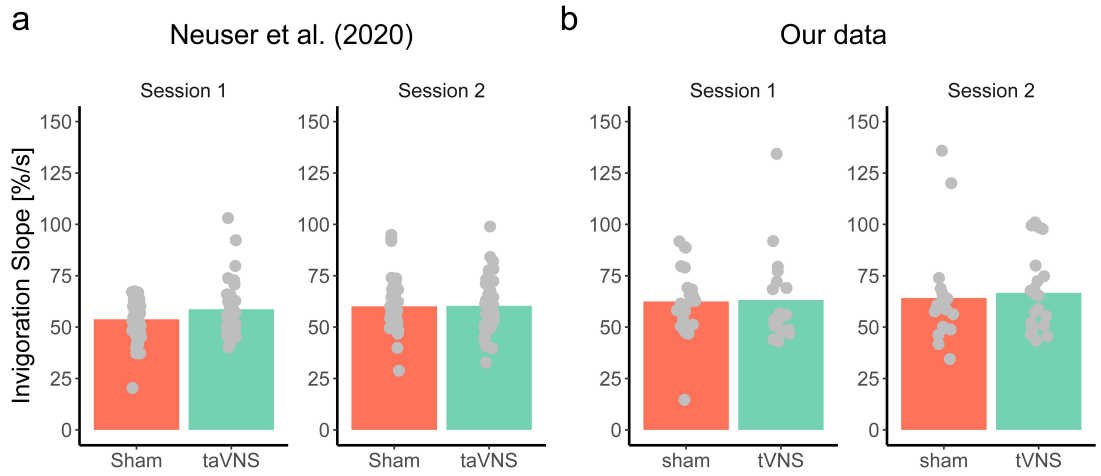


Figure C.3: Effect of taVNS on invigoration, separately for session 1 and 2. a) Results based on the data from Neuser et al. (2020). b) Results based on the current data.

For a fairer comparison of overall task performance in the two studies, we compared the average (SD) reward points won per session:

	Neuser et al. (2020)	**Our study**	**Independent-sample t-test**
Money points	1974 (944)	1795 (1129)	$t = -1.23$, $p = .22$
Food points	1897 (908)	1744 (1027)	$t = -1.13$, $p = .26$

Table C.1: Comparison of points between Neuser et al. (2020) and our study.

The results indicate that participants in our study received less reward points, but the differences with the Neuser study were not significant. The number of reward points reflects task performance in the experimental phase relative to a criterion, the maximum frequency of button presses, that was established for each participant during the practice phase. This means that differences between individuals in total reward points can be due to individual differences in motivation during the practice phase rather than, or in addition to, differences in motivation during the experimental phase. This principle is illustrated in Figure S4ab, which

shows strong negative relationships between the maximum frequency criterion determined during the practice phase and the overall winnings determined during the experimental phase.

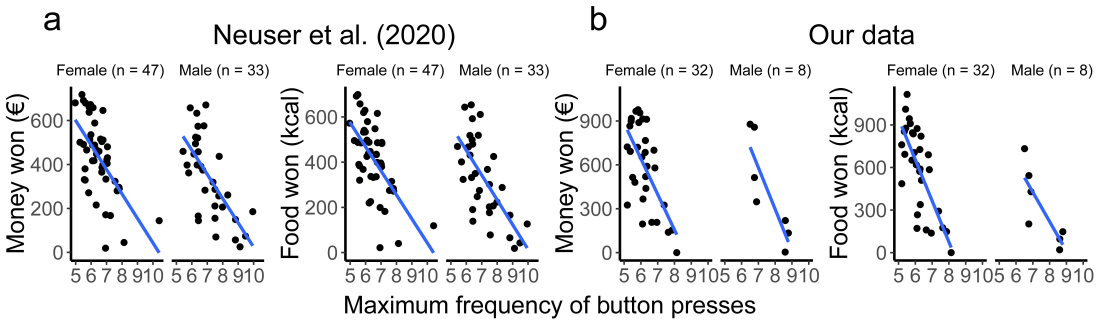


Figure C.4: Total money and calories won as a function of the maximum frequency of button presses recorded during the practice phase, separately for female and male participants for a) Neuser et al. (2020) and b) the current study.

The lower number of reward points of our participants could not be explained by a higher criterion (Neuser: women 7.1, men 6.5; our study: women 7.1, men 6.2 [see Figure S5]). In line with these results, we found that the average subjective wanting ratings, $t = -2.2$, $p = .03$, and exertion ratings, $t = -0.48$, $p = .63$, were somewhat lower in our study than in Neuser et al. (2020). Thus, the data suggest that, if anything, our participants were somewhat less motivated than the participants in the original study.

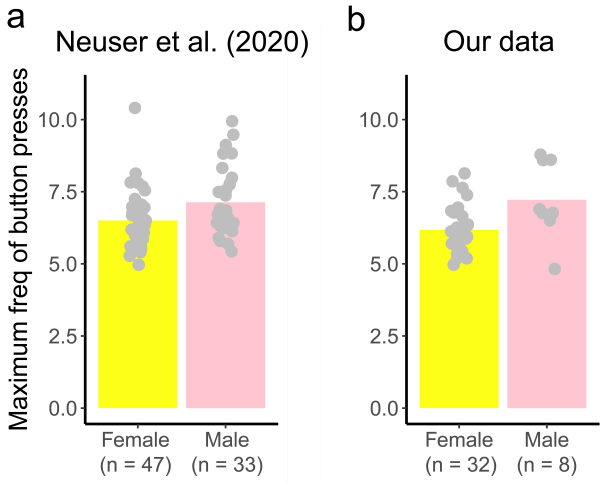


Figure C.5: The criterion value determined by the maximum frequency of button presses during the practice phase, separately for female and male participants for a) Neuser et al. (2020) and b) the current study.

Appendix D

Supplementary Figures for Chapter 6

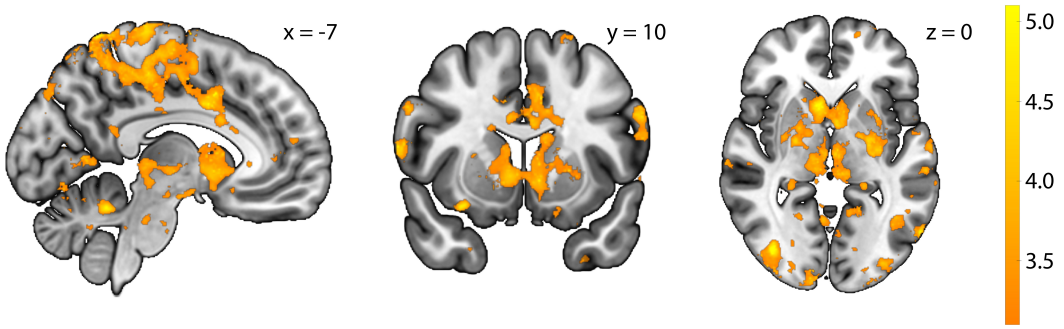


Figure D.1: Group-level statistical parametric map for the reward anticipation contrast across the whole brain in MNI-space. Activation maps are thresholded using false discovery rate (FDR) correction ($q < 0.05$, z-value = 3.1).

Region	Preferred Model	BF10	Evidence for Alternative
CA1	Reward + Memory	18.42	Strong evidence
CA3	Memory	2.08	Anecdotal evidence
DG	Reward	4.03	Moderate evidence
LC	Reward	3.59	Moderate evidence
BF	Reward	2.55	Anecdotal evidence
MRN	Reward	159.98	Very strong evidence
DRN	Intercept	0.92	Anecdotal evidence against
SN	Reward	478.31	Very strong evidence
VTA	Reward	373.1	Very strong evidence
Str	Reward	5.8×10^6	Very strong evidence

Table D.1: Bayes Factors (BF10) and evidence interpretation for different models.

Note. Results of Bayesian model comparisons for each ROI. The preferred model refers to the model with the highest Bayes factor. The null model includes only the intercept, while the alternative models include a condition-only predictor, a memory-only predictor, or condition and memory as joint predictors. Bayes factors are presented as BF10, where values greater than 1 indicate evidence in favor of the alternative model (preferred model), and values lower than 1 indicate evidence in favor of the null model (intercept-only). DG, dentate gyrus; LC, locus coeruleus; BF, basal forebrain; MRN, medial raphe nucleus; DRN, dorsal raphe nucleus; SN, substantia nigra; VTA, ventral tegmental area; Str, Striatum. BF: Bayes Factor.

Region	z	p	$p_{\mathbf{corr}}$	**Significance**
CA1	1.6	0.110	0.122	
CA3	1.04	0.299	0.299	
DG	1.93	0.054	0.067	
LC	2.73	0.006	0.012	*
BF	2.33	0.020	0.033	*
MRN	3.62	0.000	0.000	***
DRN	2.16	0.031	0.044	*
SN	3.42	0.001	0.002	**
VTA	3.48	0.001	0.002	**
Str	4.8	0.000	0.000	***

Table D.2: Statistics for the reward anticipation contrast after controlling for RT.

Note. Statistics for the reward anticipation contrast after controlling for RT ($p < .05$: *; $p < .01$: **; $p < .001$: ***). p_{corr} refers to the p-values after correcting for FDR. DG, dentate gyrus; LC, locus coeruleus; BF, basal forebrain; MRN, medial raphe nucleus; DRN, dorsal raphe nucleus; SN, substantia nigra; VTA, ventral tegmental area; Str, Striatum.

Region	Mean tSNR	Mean N Voxels	Source
CA1	40.81	292.96	freesurfer
CA3	43.34	103.62	freesurfer
DG	44.57	164.46	freesurfer
LC	41.54	59.69	custom scripts
BF	26.26	79.53	MASSP
MRN	40.39	37.5	MASSP
DRN	37.09	49.56	MASSP
SN	30.52	285.94	MASSP
VTA	36.84	164.07	MASSP
Str	49.7	3975.37	MASSP

Table D.3: Mean tSNR and Mean N Voxels across different regions.

Note. Mean tSNR refers to the transient signal-to-noise ratio, averaged across participant-level masks. Mean N voxels refers to the number of voxels in functional space (1.5 mm isotropic), averaged across all participant-level masks. Source: freesurfer (van Leemput et al., 2009); MASSP (Bazin et al., 2020); MT-TFL (magnetization transfer-weighted turbo flash; Priovoulos et al., 2018). DG, dentate gyrus; LC, locus coeruleus; BF, basal forebrain; MRN, medial raphe nucleus; DRN, dorsal raphe nucleus; SN, substantia nigra; VTA, ventral tegmental area; Str, Striatum.

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Data and code availability

Chapter 2

The raw data are publicly available here: https://doi.org/10.5061/dryad.7m0cfxpzn.
All numerical data and brain maps underlying all figures, tables, and figure supplements as well as the code to generate these figures and analyses are available here: https://osf.io/5rjcf/ (with a back-up on https://github.com/bethlloyd/Lloyd_etal_rsBOLD_pupil).
Code to preprocess the fMRI and pupil data can be found here: https://github.com/bethlloyd/Lloyd_etal_rsBOLD_pupil

Chapter 3

Preprocessing and analyses code can be found here: https://github.com/bethlloyd/sharon_replication.
Raw pupil and EEG data is available here: https://figshare.com/projects/Short-term_transcutaneous_vagus_nerve_stimulation_increases_pupil_size_but_does_not_affect_EEG_alpha_power_a_replication/169890

Chapter 4

Analysis code can be found here: https://github.com/bethlloyd/neuser_replication.
Raw and processed behavioral data can be found here: https://doi.org/10.6084/m9.figshare.24427312.v1.

Chapter 5

The raw and processed data as well as code to reproduce the results are publicly available without restriction: https://github.com/bethlloyd/Reward-related_mem_LloydNieuwenhuis.

Chapter 6

This chapter is still in preparation, and no public repository is available yet.

Chapter 7

The processed data as well as code to reproduce the results are publicly available without restriction: `https://github.com/bethlloyd/Lloyd_Nieuwenhuis_MemPrecision`.

Author contributions

Below is a list of the contributions made by each chapter (organised according to the Contributor Roles Taxonomy (CRediT) system).

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Beth Lloyd: Conceptualization, Data curation, Formal analysis, Validation, Investigation, Visualization, Methodology, Writing - original draft, Writing – review and editing; **Lycia D de Voogd**: Conceptualization, Resources, Data curation, Software, Supervision, Funding acquisition, Investigation, Project administration, Writing – review and editing; **Verónica Mäki-Marttunen**: Conceptualization, Supervision, Methodology, Writing – review and editing; **Sander Nieuwenhuis**: Conceptualization, Resources, Supervision, Funding acquisition, Methodology, Writing – review and editing

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Beth Lloyd: Conceptualization, Data curation, Visualization, Formal analysis, Writing – original draft; **Franz Wurm**: Conceptualization, Data curation, Visualization, Formal analysis, Writing – review & editing; **Roy de Kleijn**: Software, Writing – review & editing; **Sander Nieuwenhuis**: Conceptualization, Supervision, Funding acquisition, Writing – review & editing.

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