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The effect of cognitive load on preference and intensity processing of sweet taste in the brain

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ABSTRACT

Distracted eating can cause overconsumption. Whereas previous work has shown that cognitive load suppresses perceived taste intensity and increases subsequent consumption, the mechanism behind distraction-induced overconsumption remains unclear.

To elucidate this, we performed two event-related fMRI experiments that examined how cognitive load affects neural responses and perceived intensity and preferred intensity, respectively, to solutions varying in sweetness. In Experiment 1 ($N = 24$), participants tasted weak sweet and strong sweet glucose solutions and rated their intensity while we concurrently varied cognitive load using a digit-span task. In Experiment 2 ($N = 22$), participants tasted five different glucose concentrations under varying cognitive load and then indicated whether they wanted to keep, decrease or increase its sweetness.

Participants in Experiment 1 rated strong sweet solutions as less sweet under high compared to low cognitive load, which was accompanied by attenuated activation the right middle insula and bilateral DLPFC. Psychophysiological interaction analyses showed that cognitive load moreover altered connectivity between the middle insula and nucleus accumbens and DLPFC and middle insula while tasting strong sweet solutions.

In Experiment 2, cognitive load did not affect participants' preferred sweetness intensity. fMRI results revealed that cognitive load attenuated DLPFC activation for the strongest sweet solutions in the study.

In conclusion, our behavioral and neuroimaging results suggest that cognitive load dampens the sensory processing of strong sweet solutions in particular, which may indicate higher competition for attentional resources for strong sweet than weak sweet solutions under high cognitive load. Implications for future research are discussed.

1. Introduction

Due to ongoing technological and societal developments, people can now engage in eating and drinking while being distracted by a wide array of competing activities. Such distracted consumption is highly prevalent, with at least 80% of meals consumed during concurrent activities (van Meer et al., 2022). Several studies have linked distracted consumption to immediate and subsequent overconsumption (e.g. Cui et al., 2021; Higgs & Woodward, 2009; Oldham-Cooper et al., 2010; Robinson et al., 2013). One potential explanation for this overconsumption is that concurrent mental activities increase cognitive load, which limits the availability of working memory resources for somatosensory processing during consumption. The resulting suboptimal consumption experience, in turn, might trigger compensatory consumption such as increasing intake or of higher taste intensities (Van der Wal & van Dillen, 2013). However, it is yet unclear what neural mechanisms mediate this effect.

In support of this idea, previous studies have shown that cognitive load can disrupt the sensory processing of food and drinks. In one behavioral experiment, people perceived the taste of sweet, sour, and salty substances as less intense when their working memory was concurrently taxed by a high-load compared to a low-load digit span

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task (Van der Wal & van Dillen, 2013). The effect of cognitive load was most pronounced for strongest-tasting substances, possibly because stronger tastes draw more attention, leading to stronger competition over working memory resources between cognitive load and sensory perception. Another behavioral experiment, using a similar working-memory manipulation, found that high cognitive load reduced taste sensitivity for varying concentrations of sweet and bitter substances (Liang et al., 2018). Lastly, a neuroimaging experiment that combined the digit-span task with the presentation of low- and high-caloric odors found that under high compared to low cognitive load, participants perceived low- but not high-caloric odors as less intense. The fMRI results showed that under high cognitive load activation in the bilateral orbitofrontal and piriform cortex was reduced (Hoffmann-Hensel et al., 2017).

In addition to altered perceived taste intensity, cognitive load may also affect people's preferences for tastes of specific intensities. For example, under high cognitive load participants preferred sweeter lemonade than under low cognitive load in one experiment, and consumed more of salty, but not saltless crackers in another (Van der Wal & van Dillen, 2013). Furthermore, a recent neuroimaging study showed that cognitive load down-regulates neural reward processing in response to high-calorie compared to low-calorie food pictures in the nucleus accumbens (van der Laan, De Ridder, Viergever, & Smeets, 2011), suggesting that it selectively interferes with the valuation of hedonic stimuli - such as high-calorie foods.

Recent neuroimaging research conducted by Duif et al. (2020) presented preliminary evidence for a potential neural mechanism that contributes to the modified perception and preference for food in the presence of distractions. In the experiment, which consisted of two sessions, participants tasted a milkshake under high and low cognitive load in the scanner, after which they were provided with a buffet lunch. Whereas the authors failed to observe direct effects of cognitive load on taste intensity processing, the experiment revealed a decrease in connectivity between the insula, responsible for primary taste processing, and the orbitofrontal cortex, involved in higher-order processing, under high compared to low cognitive load. No significant difference in subsequent food intake at a buffet lunch was observed when individuals tasted the milkshake under high versus low cognitive load. However, intriguingly, participants with reduced insula activation due to high cognitive load compared to low cognitive load exhibited an increase in food consumption during the buffet lunch.

These results suggest that cognitive load during food intake may alter the neural communication between primary sensory and higher order evaluative processing, or preference coding, which may contribute to subsequent overconsumption. However, since this study observed no direct effect of cognitive load on the neural activation of the taste-processing areas and it did not examine effects on perceived intensity or sweetness preference, it remains unclear how these changes relate to the changes in perceived taste intensity and preferred taste intensity observed in earlier behavioral studies.

Building on and extending this earlier work, here we aimed to investigate the effect of cognitive load on perceived taste intensity, preferred taste intensity and the neural responses to taste in a more comprehensive manner. To specify, we examined whether the effect of cognitive load on the perceived intensity versus the preferred intensity of sweet solutions might be coded in different brain areas. Previous neuroimaging work has shown a dissociation between intensity and preference coding in the brain. For example, one neuroimaging experiment observed that when participants attended to the intensity when tasting umami there was stronger activation in the right insula than when participants paid attention to the pleasantness; conversely, there was stronger activation in the medial orbitofrontal and pregenual cingulate cortex when participants paid attention to the pleasantness rather than taste intensity (Grabenhorst & Rolls, 2008). Another neuroimaging experiment found stronger activation in the right putamen and bilateral middle insula when participants paid selective attention to pleasantness than when participants paid attention to intensity while tasting fruit juice and water. Intensity but not pleasantness ratings correlated with activation in the right insula (van Rijn et al., 2018). Although paying attention to the pleasantness of a taste stimulus is different from tasting a stimulus and indicating preferred intensity, both situations involve evaluating the hedonic aspects of tastes, which may be reflected in similar neural processes.

Based on these studies we expected that when participants consider the taste intensity of varying sweetness solutions, cognitive load may interfere more with intensity processing in primary taste areas such as the right insula. Whereas when participants consider their preference for the intensity of these solutions, cognitive load may have a greater impact on processing in areas involved in the evaluation of taste stimuli such as the striatum, bilateral middle insula, and orbitofrontal cortex.

To investigate this, we conducted two fMRI experiments where we systematically manipulated two factors. First, we manipulated the cognitive load of a secondary task, which was expected to engage the working-memory network, including the dorsolateral prefrontal cortex (DLPFC; D'Esposito & Postle, 2015; Palva, Monto, Kulashekhar, & Palva, 2010; van Dillen & van Steenbergen, 2018). Second, we manipulated the concentration of the sweet solutions offered to participants, which was expected to engage taste processing and valuation areas such as insula, striatum and orbitofrontal cortex. Participants rated the intensity of the taste stimuli in Experiment 1 and expressed their preferred intensity in Experiment 2.

In **Experiment 1**, using an event-related repeated measures design, we examined the effect of cognitive load on subjective intensity ratings and neural responses to strong and weak sweet solutions. In line with earlier behavioral work (Van der Wal & van Dillen, 2013), we hypothesized that high compared to low cognitive load would attenuate the perceived intensity of sweet drinks, in particular for strong sweet solutions. Furthermore, we expected that high compared to low cognitive load would attenuate responses to strong (relative to the weak) sweet solutions in the primary taste cortex, in particular the right insula. Although our predictions focused on the modulation of primary taste intensity processing areas, we also examined the effects of cognitive load and sweetness concentrations on higher-order taste processing areas such as the secondary taste cortex (OFC), the prefrontal cortex (PFC), and the striatum (van Rijn et al., 2018; Chen & Zeffiro, 2020; Duif et al., 2020; Yeung et al., 2018; Spetter, Smeets, de Graaf, & Viergever, 2010).

In **Experiment 2**, in a similar vein, we examined neural responses to five sweet solutions of varying concentration under low versus high cognitive load while this time, assessing participants' *preferred* intensity. In line with behavioral work (Van der Wal & van Dillen, 2013), we hypothesized that high compared to low cognitive load would lead to a preference for sweeter solutions. Furthermore, we hypothesized that this shift in preferred intensity under high cognitive load would be accompanied by attenuated reward activation under high compared to low cognitive load, so that under high cognitive load a sweeter solution would obtain the same neural reward response as a less sweet solution under low cognitive load, in line with the modulation of the nucleus accumbens our group reported earlier (van der Laan et al. (2011)). Furthermore, we hypothesized that task context (preferred intensity ratings) in this study would lead to the most pronounced differences between high and low cognitive load in evaluative (taste) processing areas such as the striatum, bilateral middle insula, and orbitofrontal cortex, as implied in earlier work (Grabenhorst & Rolls, 2008; Van Rijn et al., 2018).

2. Methods

2.1. Participants and design

2.1.1. Experiment 1: taste intensity

The data of 24 volunteers (4 males and 20 females, $M_{Age} = 22.29$, $SD = 3.30$ years) were analyzed. The data of an additional 24 participants had to be discarded, due to excessive movement (defined as having moved more than 3 mm; N = 11), problems with the experimental set-up such as occlusion of the taste delivery pumps (N = 9), and premature termination of the experiment (N = 4). All 24 participants were right-handed non-smokers who did not report any history of neurological or psychiatric problems. In addition, we verified that they were not currently on a diet and had a body mass index (BMI) between 20 and 25 kg/m^2. Participants provided written informed consent (according to the Declaration of Helsinki) after the study procedure had been explained to them and were paid €25 for participation at the end of the study. The study was approved by the Medical Ethics Committee of Leiden University (see https://osf.io/h9rwu/).

The experimental design was a 2 (cognitive load: high vs. low) x 2 (sweetness concentration: strong sweet solutions vs. weak sweet solutions) factorial design, both factors within participants. Dependent measures were participants' performance on the digit-span task and perceived intensity ratings, and brain activity (see below) time-locked to the digit-span task and the delivery of the solutions during the taste task.

2.1.2. *Experiment 2: taste preference*

The data of 22 volunteers (7 males and 15 females, $M_{Age} = 22.86$, $SD = 3.93$ years) were analyzed. The data of an additional 18 participants had to be discarded, due to excessive movement (defined as having moved more than 3 mm; N = 11), problems with the experimental set-up such as occlusion of the pumps (N = 2), and premature termination of the experiment (N = 5). Inclusion criteria and participant compensation were identical to Experiment 1.

The experimental design was a 2 (cognitive load: high vs. low) x 5 (sweetness concentration: ranging from weak sweetness to strong sweetness) parametric design, both factors within participants. Dependent measures were participants' performance on the digit-span task and preferred intensity ratings, as well as brain activity (see below) time-locked to the digit-span task and the solution administration during the taste task.

2.2. *Procedures and equipment*

2.2.1. *Experiment 1: taste intensity*

Participants were invited to the lab to participate in a brain-imaging experiment. Prior to starting the actual task, the experimenters verified that participants; had refrained from eating or drinking in the past 2 h, were non-smokers and were not suffering from cold symptoms (Van der Wal & van Dillen, 2013). Participants were instructed about the experimental set-up, MRI procedure and safety protocols. Next, participants were placed in supine position in the scanner and the ends of three rubber tubes were placed in their mouths and fixated onto the head coil. The ends of the three tubes were tied together to form a small bundle which participants held in place in between their upper and lower teeth. All stimuli were back-projected onto a screen which participants viewed via an angled mirror. During the task, participants tasted two different glucose water solutions and rated the taste intensity (see Fig. 1). The taste stimuli were presented to the participants via three computer-controlled pumps (Braun Infusomat) connected to three infusion bags, that were placed outside the scanner room and that were linked to a one-way syringe-activated check valve through 7 m tubes that covered the distance to the actual scanner.

The three infusion bags contained water, a low glucose-water solution (15% or 15 g glucose/100 ml water = 0.83 M) and a high glucose-water solution (25% or 25 g glucose/100 ml water = 1.39 M). The 0.83 M and 1.39 M concentrations were chosen based on pilot data to be well

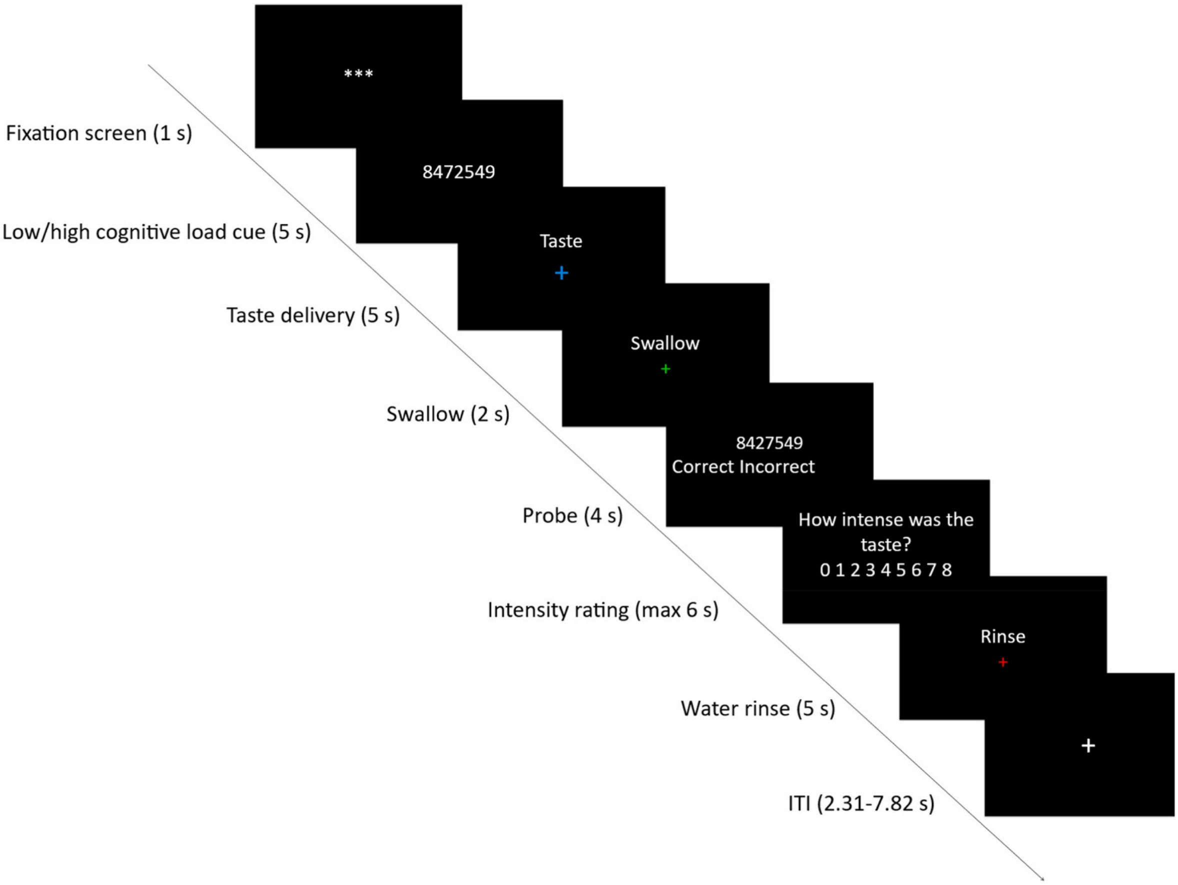

Fig. 1. Example of a trial in Experiment 1. Analyses focused on brain activity during cognitive load cue onset and during taste delivery (effect of cognitive load on processing strong sweet vs. weak sweet solutions). ITI = intertrial interval.

distinguishable and align with previous study set ups examining taste intensity ratings (Moskowitz et al., 1974; Van der Wal & van Dillen, 2013). The presentation of the taste stimuli by the Braun Infusomat pumps was controlled via an E-Prime task (Version 2.0, http://www.pstnet.com/eprime.cfm) on a trial-by-trial basis. Each solution delivery, both weak and strong glucose solutions as well as the rinse, had a volume of 0.5 ml.

The task consisted of 88 trials split over two runs of approximately 25 min (depending on intensity rating reaction times). The task started with 4 practice trials. Participants received the weak strong and strong glucose solutions a total of 40 times each, each 20 times per run. 8 catch trials of 0.5 ml water were added to prevent habituation, 4 per run. In the second run, different numbers were used for the cognitive load manipulation to account for habituation and learning effects.

Cognitive load was manipulated using the well-validated digit-span task (Sternberg, 1966), as described in the introduction, and following the procedure from an earlier study by our team (van der Laan et al., 2011). Before each taste delivery, participants were instructed to rehearse either a 1-digit (low cognitive load) or a 7-digit (high cognitive load) number. Each trial started with a row of asterisks. After the digit series was displayed for 5 s, the taste stimuli were presented to participants for 5 s, indicated by a blue fixation cross. Then, participants were instructed by a green fixation cross to swallow the solutions (2 s). After that, a second digit series was presented for 4 s that was either the same or a different number then the one first displayed. When a different number was presented, one of the digits varied, but at changing positions (except the first and last digit), so that participants could not use any strategies to offload their working memory. Participants then had to indicate whether this number was the same (correct) number, or a different number (incorrect). Finally, they were asked to rate the intensity (0 - not intense, 8 - intense) of the taste stimuli. They had a maximum of 6 s to give an answer, but the task would go on as soon as they pressed a button. Therefore, the task length varied between participants. To avoid overlapping BOLD responses within and between trials, the intertrial interval (ITI) was randomly varied with 88 varying ITI's ranging from 2.31 to 7.82 s. Participants indicated all their responses via fiber-optic buttons and response options were counterbalanced between participants between the right index and middle finger. For the intensity ratings, participants used their index finger (1) to select the intensity and their middle finger (2) to confirm it. After each trial, water stimuli were administered to the participants to rinse out the previous taste stimuli (5 s). At the end of the study, participants were debriefed, paid, and thanked for their efforts.

2.2.2. Experiment 2: taste preference

The procedure and task were very similar to Experiment 1, but in this experiment five different glucose water solutions were presented instead of two, and participants provided preferred intensity ratings by indicating whether they would like the solution to be less sweet, stay the same or sweeter. To this aim, three infusion bags containing water, a high glucose-water solution (35% = 1.94 M), and a low glucose-water solution (5% = 0.28 M) were used to mix five increasingly intense glucose concentrations: very weak sweet (0.28 M), weak sweet (0.69 M), intermediate sweet (1.11 M), strong sweet (1.3 M), very strong sweet (1.94 M). The different concentrations were informed by the work of Moskowitz et al. (1974) and fine-tuned based on pilot data to include both concentrations above and below people's average optimal preference, which was 1 M glucose in water solution (roughly equaling the third, middle concentration)). The mixing of concentration was triggered by an E-Prime task computer on a trial-by-trial basis. The task was split in two runs. The five glucose solutions were each presented 8 times in random order, resulting in 40 trials per run. To assess preferred intensity participants indicated via fiber-optic buttons whether they would want a less sweet solution (−1), the same solution (0) or a sweeter solution (1) than the solution they had just tasted. Participants used their index finger to select their preference and their middle finger to confirm it (again counterbalanced to prevent lateralization effects).

The answer the participants provided had no influence on which solution was presented next. This was determined in random order to maintain a balanced design.

2.3. MRI data acquisition

2.3.1. Experiment 1: taste intensity

Scanning was performed with a 32-channel head coil on a 3-T Philips Achieva MRI system (Best, The Netherlands) at Leiden University Medical Center. A high-resolution EPI scan (TR = 2.2 s; TE = 30ms, flip angle = 80°, 84 transverse slices, 1.964 × 1.964 × 2 mm) and a B0 field map for the static magnetic field were acquired. Subsequently, a 3D T1-weighted scan (TR = 9.8 ms; TE = 4.6 ms, flip angle = 8°, 140 slices, 1.166 × 1.166 × 1.2 mm, FOV = 224.000 × 177.333 × 168.000) and 2 runs of a minimum of 666 T2*-weighted whole brain EPIs were acquired. Each EPI scan sequence was preceded by 2 dummy scans to allow for equilibration of T1 saturation effects (TR = 2.2 s; TE = 30 ms, flip angle = 80°, 38 transverse slices, 2.75 × 2.75 × 2.75 mm + 10% interslice gap).

2.3.2. Experiment 2: taste preference

Data acquisition parameters were identical to Experiment 1. The EPI scans acquired during the taste task consisted of 645 vol

2.4. Behavioral analyses

2.4.1. Experiment 1: taste intensity

The behavioral analyses were conducted in R version 4.1.3 (R Core Team, 2021). To validate our cognitive load manipulation, a logistic regression model was fitted on the digit span task accuracy scores () as a dependent variable and regressors for cognitive load (high/low), run (first or second) and the cognitive load*run interaction. A regressor was added for sweetness concentration to account for effects of intensity on accuracy.

To test our primary hypotheses, a linear mixed model using lme4 was estimated with perceived intensity as dependent variable and regressors for cognitive load (high/low), sweetness concentration (weak/strong) and the cognitive load*sweetness concentration interaction. A regressor was added for run (first or second) to correct for any effect of time or fatigue as well as a random intercept for the participant variable.

2.4.2. Experiment 2: taste preference

The behavioral analysis used a similar approach as for Experiment 1. A logistic linear mixed model was estimated with digit span task accuracy as a dependent variable and regressors for cognitive load (high/low), run (first or second) and the cognitive load*run interaction. A regressor was added for sweetness concentration to account for effects of valence on accuracy as well as a random intercept for the subject variable.

Since the preferred intensity choice options were categorical ("less sweet", "keep the same" and "sweeter"), we performed a multinomial logistic linear mixed model analysis using the MCMCglmm package (Hadfield, 2010) in R. The MCMCglmm package is a powerful tool for fitting generalized linear mixed models with a range of response distributions and linking functions. It employs Markov Chain Monte Carlo (MCMC) methods to estimate the model parameters and offers flexible options for modeling complex hierarchical structures and accounting for within-group correlations. In our analysis, MCMCglmm allowed us to incorporate random effects, estimate fixed effects coefficients, and assess the uncertainty associated with parameter estimates using posterior distributions obtained through MCMC sampling. Preferred intensity choices were used as the dependent variable and regressors for cognitive load (high/low), sweetness concentration (5 levels; numerical predictor) and the cognitive load*sweetness concentration interaction were included. A regressor was added for run (first or second) to correct for any effect of time or fatigue as well as a random intercept for the subject variable. 40,000 iterations were done. Priors were set up as suggested in Hadfield (2010), see osf.io/h9rwu/for the analysis code.

2.5. fMRI preprocessing

2.5.1. Experiment 1: taste intensity

Functional MRI data was analyzed with FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac. uk/fsl; Jenkinson et al., 2012). Since task length varied between participants, the scans for the task runs were cut individually according to offset times of each run. Motion correction, slice-timing correction, brain extraction, spatial smoothing using a Gaussian kernel of FWHM 6.0 mm, grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100.0 s) were performed to preprocess the brain images. After spatial smoothing and before temporal filtering, ICA-AROMA (Pruim et al., 2015) was performed. This technique is a data-driven method to identify and remove motion-related ICA components from fMRI data. EPI scans were first registered to high-resolution EPI images, before being registered to the standard space of the MNI (Montreal Neurological Institute) with 2 mm resolution using FLIRT.

2.5.2. Experiment 2: taste preference

The preprocessing steps taken were identical to Experiment 1.

2.6. MRI statistical analyses and thresholding

2.6.1. Experiment 1: taste intensity

An event-related model was estimated at the participant level, which included two regressors to predict hemodynamic responses to cognitive load (high load, low load) and four regressors for the taste stimuli presentations (strong sweet solutions, weak sweet solutions crossed with low and high load). The moment of swallowing, probe stimulus, and a combined regressor for taste intensity rating and rinsing were modeled as nuisance regressors. We focus on the following contrasts: high vs. low cognitive load cue presentation to examine the main effect of the digit span manipulation, strong vs. weak sweet solutions to examine the main effect of sweetness concentration, and the effect of cognitive load on the processing of strong vs. weak solutions $[\text{strong sweet} > \text{weak sweet}]_{\text{Low load}} > [\text{strong sweet} > \text{weak sweet}]_{\text{High load}}$ to examine the interaction between cognitive load during tasting and sweetness concentration.

To explore differences in neural connectivity between high and low cognitive load, several psychophysiological interaction (PPI) analyses were performed to identify regions exhibiting altered correlation for the strong sweet versus weak sweet solutions under high versus low cognitive load. The seed regions were identified by the analysis of cognitive load on taste processing using the earlier described interaction contrast. The physiological regressor for this PPI model used extracted time-course information based on spheres centered around the peak of activation (radius 6 mm) from this contrast. The convolved psychological regressor represented the following contrast: $[\text{strong sweet} > \text{weak sweet}]_{\text{Low load}} > [\text{strong sweet} > \text{weak sweet}]_{\text{High load}}$. The PPI regressor was computed as the product of the demeaned physiological time course and the centered psychological regressor (O'Reilly et al., 2012). A separate main effect regressor of the psychological variable was added in order to partition out shared variance. Nuisance regressors for the remaining events were also modeled.

For all models, the trial-type regressors used square-wave functions time-locked to the onset and offset of the respective stimulus which were convolved with a canonical HRF and its temporal derivative. After a quality check of the registration and excluding participants with excessive head movement, contrasts were combined across runs on a subject-by-subject basis using fixed effect analyses. Second-level contrast images in standard space were merged into a single 4-D file for nonparametric voxel-wise permutation-based statistical testing using FSL Randomise (see below).

To enhance the statistical power for effect detection, we employed multiple predefined regions of interest based on prior research findings. Specifically, for the analysis of cognitive load, we utilized an anatomical mask corresponding to the dorsolateral prefrontal cortex (DLPFC), i.e. the "middle frontal gyrus" region defined in the Automated Anatomical Labeling Atlas. To investigate the impact of cognitive load on taste processing, we applied the DLPFC mask, as well as anatomical masks for the bilateral middle insula (e.g. Berridge, 2009; Duif et al., 2020; Nitschke et al., 2006; Rolls, 2015) and the nucleus accumbens (e.g. Duif et al., 2020; van der Laan et al., 2011).

To account for multiple comparisons within these ROI masks, we used a small-volume (SV) ROI analysis approach and employed FSL Randomise (Winkler et al., 2014), a nonparametric method that derives statistical significance from the observed null distribution of the maximum cluster size. We conducted 5000 permutations to estimate the null distribution per ROI mask. Statistical maps were generated using a height threshold of $t > 2.3$ or $F > 4.6$, accompanied by cluster-level correction with a significance threshold of $p < 0.05$, unless stated otherwise. It is important to note that our analysis focused on identifying clusters of activation within the ROI masks, rather than averaging the data across the masks.

Whole-brain analyses were reported for reasons of completeness and to aid meta-analyses. Because these clusters could span multiple anatomical regions, we used a more conservative cluster-forming threshold at $T > 4.1$, with a cluster-corrected probability of $P < 0.05$. For illustrative purposes, bar graphs with brain activity show mean values based on the extracted parameter estimates for each subject and run of the respective cluster. Brain images were created with Mango software (Research Imaging Institute, UTHSCSA).

2.6.2. Experiment 2: taste preference

An event-related model was estimated at the participant level, which included two regressors to predict hemodynamic responses to cognitive load (high load, low load) and ten regressors for the taste stimuli presentations (five different concentrations of sweet solutions crossed with the two levels of cognitive load). The moment of swallowing, probe stimulus, and a combined regressor for rating of sweetness preference and rinsing were modeled as nuisance regressors. The following contrasts were estimated: high vs. low cognitive load cue presentation, a contrast measuring the linear effect of sweetness concentration, the effect of cognitive load on the linear effect of sweetness concentration, and an *F*-contrast testing for any interaction between cognitive load and sweetness concentrations.

To explore differences in neural connectivity between high and low cognitive load, a psychophysiological interaction (PPI) analysis was performed to identify regions exhibiting altered correlation for the different concentration strengths under high versus low cognitive load. The seed region was identified by the analysis of cognitive load on taste processing using the earlier described *F*-contrast The physiological regressor for this PPI model used extracted time-course information based on a sphere (radius 6 mm) centered around the peak from this contrast. The convolved psychological regressor represented the following contrast: $[\text{solution 5} > \text{solution 3}]_{\text{Low-load}} > [\text{solution 5} > \text{solution 3}]_{\text{High-load}}$. The rest of the PPI analysis was identical to Experiment 1.

The statistical thresholding was identical to Experiment 1 and the same ROI masks were used.

3. Results

3.1. Behavior

3.1.1. Experiment 1: taste intensity

In order to maximize the power of the behavioral analyses, the data of all participants who had valid behavioral data were analyzed (N = 36, this includes the 12 participants who were excluded from the fMRI analyses due to excessive head motion). To check if task-engagement was affected by time, we first examined the effect of cognitive load and imaging run on accuracy on the digit-span task. To that aim, a logistic mixed effects model was estimated using the lme4 package, with accuracy (whether the answer was correct or incorrect) as dependent variable and regressors for cognitive load (low cognitive load and high cognitive load), sweetness concentration (strong glucose concentration and weak glucose concentration), run (1 and 2), and an interaction term for cognitive load and run. There was no main effect of imaging run on accuracy ($b = 0.07$, $SE = 0.06$, $t = 1.16$, $p = 0.25$) or sweetness concentration on accuracy ($b = 0.08$, $SE = 0.11$, $t = 0.70$, $p = 0.49$). There was a main effect of cognitive load: for the low cognitive load trials ($b = 2.06$, $SE = 0.15$, $t = 13.83$, $p < 0.001$), accuracy was 95.9% and for the high cognitive load trials accuracy was 77.1%, confirming the effectiveness of our cognitive load manipulation. There was no interaction of cognitive load and imaging run ($b = 0.18$, $SE = 0.15$, $t = -1.23$, $p = 0.22$). When the interaction term was excluded from the model the main effects remained similar and when we repeated this analysis including only the participants included for the fMRI analyses, we found the same pattern of results (see osf.io/h9rwu/).

To assess the effects of cognitive load and sweetness concentration on perceived intensity a linear mixed effects model was estimated. In this model, intensity rating was the dependent variable and the predictors were cognitive load (low cognitive load and high cognitive load), sweetness concentration (strong glucose concentration and weak glucose concentration), run (1 and 2), and the interaction between cognitive load and sweetness concentration.

There was no main effect of cognitive load ($b = 0.10$, $SE = 0.07$, $t = 1.41$ $p = 0.16$). There were main effects for sweetness concentration ($b = -1.41$, $SE = 0.07$, $t = -20.0$, $p < 0.001$) and run ($b = 0.15$, $SE = 0.03$, $t = 5.85$, $p < 0.001$). This indicates that overall participants rated the strong glucose solutions as sweeter than the weak glucose solutions and participants rated all solutions as sweeter during the second compared to the first run of the task.

Finally, there was a significant interaction between cognitive load and sweetness concentration ($b = -0.26$, $SE = 0.10$, $t = -2.58$, $p = 0.010$). As can be seen in Fig. 2, under high compared to low cognitive load, participants rated the weak glucose solutions as more intense and the strong glucose solutions as less intense (weak solutions – low cognitive load M = 4.20, SD = 1.67; weak solutions – high cognitive load M = 4.35, SD = 1.61; strong solutions – low cognitive load M = 5.90, SD = 1.54; strong solutions – high cognitive load M = 5.76, SD = 1.49).

When we repeated this analysis including only the participants who were included for the fMRI analyses, we again observed a similar pattern of results. However, the overall interaction between sweetness concentration and cognitive load was no longer significant ($b = -0.16$, $SE = 0.13$, $t = -1.28$, $p = 0.20$). The main effects of sweetness concentration ($b = -1.37$, $SE = 0.09$, $t = -15.33$, $p < 0.001$) and run ($b = 0.16$, $SE = 0.03$, $t = 4.97$, $p < 0.001$) remained significant.

3.1.2. Experiment 2: taste preference

In order to maximize the power of the behavioral analyses, the data of all participants who had valid behavioral data were analyzed (N = 33, this includes the 11 participants who were excluded from the fMRI analyses due to excessive head motion). To check if task-engagement was affected by time, we first examined the effect of cognitive load and imaging run on accuracy on the digit-span task. To that aim, a logistic mixed effects model was estimated using the lme4 package, with accuracy (whether the answer was correct or incorrect) as dependent variable and regressors for cognitive load (low cognitive load and high cognitive load), run (1 and 2), and an interaction term. We also added sweetness concentration (5 levels) as a regressor to check for effects of sweet taste intensity on performance. This showed a main effect of cognitive load on accuracy ($b = -1.55$, $SE = 0.18$, $z = -8.82$, $p < 0.001$) that validated our cognitive load manipulation, with accuracy being lower for the high cognitive load compared to low cognitive load trials. There were no main effects of run ($b = -0.11$, $SE = 0.08$, $z = -1.27$, $p = 0.20$) or sweetness concentration ($b = -0.002$, $SE = 0.07$, $z = -0.039$, $p = 0.97$). Furthermore, there was an interaction of cognitive load and run ($b = -0.41$, $SE = 0.17$, $z = -2.33$, $p = 0.02$). For the low cognitive load trials, accuracy went up in the second run (95.5% accuracy in the first, 97.4% in the second run), while for the high cognitive load trials accuracy went down (87.7% accuracy in the first run, 85.4% accuracy in the second run). This may indicate an effect of fatigue. The increased accuracy on the low cognitive load trials in the second run seems to contradict decreased task engagement. The accuracy for the high cognitive load trials overall was considerably higher in Experiment 2 (86.5%) than in Experiment 1 (77.3%).

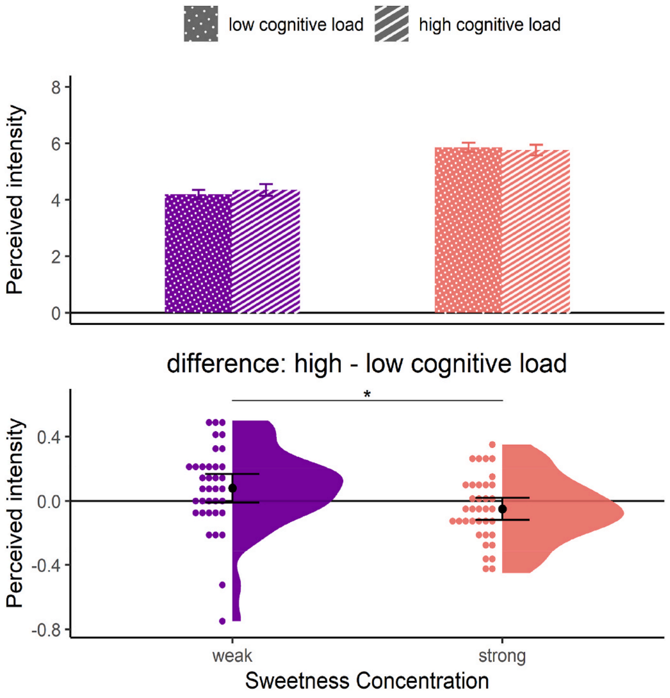

Fig. 2. Top panel: Bar plot of the intensity ratings of the weak (purple) and strong (red) glucose solutions on a scale from 0 (not intense) to 8 (intense), under high and low cognitive load (Experiment 1). Bottom panel: Half-violin, half-dot plot depicting the difference in intensity ratings between high and low cognitive load for the weak (purple) and strong (red) solution in Experiment 1. Error bars reflect within-subject 95% confidence intervals around the mean based on the Morey method (Morey, 2008).

In order to examine the effect of cognitive load on preferred intensity a multinomial mixed effects model was estimated with preferred intensity choice (“less sweet”, “keep the same” or “sweeter”) as dependent variable. This model showed main effects of sweetness concentration (posterior mean = −0.64, 95% credible interval (CI) −0.79 to −0.50, $p < 0.001$) and run (posterior mean = −0.25, 95% CI -0.36 to −0.15, $p < 0.001$). There was no main effect of cognitive load (posterior mean = −0.10, 95% CI -0.32 to 0.08, $p = 0.36$). In contrast to our hypothesis, this model showed that there was no interaction between cognitive load and sweetness concentration (posterior mean = 0.02, 95% CI -0.17 to 0.22, $p = 0.86$) on preferred intensity.

Repeating the analyses including only participants that had been included in the fMRI analyses did not change the results. See Supplemental Table S1 for the frequencies of each choice per solution and cognitive load condition.[2]

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[2] When preferred intensity is modeled as linear instead, with less sweet = −1, keep the same = 0 and sweeter = 1, the same pattern of results was found. See osf.io/h9rwu/.

As Fig. 3 shows, the sweeter the solutions, the more often participants preferred to have a less sweet concentration. Conversely, participants expressed a lower frequency of preference for solutions to stay the same as the sweetness levels increased. There was also a clear effect of run, e.g. in the second run participants preferred to have a less sweet solution more often (average frequency 9.10) than in the first run (average frequency 7.45). This may reflect sensory specific satiety with the sweet taste over time. Sensory specific satiety describes the decline in pleasantness associated with a food the more it is consumed (Rolls et al., 1981).

3.2. *fMRI results*

3.2.1. *Effect cognitive load*

3.2.1.1. Experiment 1: taste intensity. We first examined whether our cognitive load manipulation involved the DLPFC as a major hub of the working memory network of the brain (Curtis & D'Esposito, 2003). As hypothesized and replicating earlier findings using the same digit span task (van Dillen & van Steenbergen, 2018), our SV ROI analysis showed that during the presentation of the high cognitive load cue there was stronger activation in the bilateral DLPFC (see Table 1) than during the low cognitive load cue. In addition, and in line with the WM literature (e.g. Linden, 2007), there was stronger activation in the right opercular part of the inferior frontal gyrus during the presentation of the high working memory cue. Whole brain analysis furthermore showed load-related activation in the bilateral occipital gyrus, insula, precentral gyrus and cingulate cortex (see Table S2).

3.2.1.2. Experiment 2: taste preference. In Experiment 2 we again found bilateral activation of the DLPFC, replicating the findings from Experiment 1 and our earlier study (van Dillen & van Steenbergen, 2018) (Table 2). Again, whole-brain analyses revealed additional clusters in the occipital gyrus, bilateral precentral gyrus and insula, among other areas (see Table S3 in the supplementary information).

Table 1
SV ROI analysis on high > low cognitive load in the DLPFC in Experiment 1.

Areas	Cluster size (voxels)	*p* value of max	Peak MNI coordinates		
			x	*y*	*z*
Left inferior frontal gyrus, triangular part (DLPFC)	2388	<0.001	−36	26	16
Right inferior frontal gyrus, opercular part	1206	0.001	42	12	18
Right inferior frontal gyrus, triangular part (DLPFC)	642	0.014	36	32	10

Table shows clusters with height threshold of T > 2.3 and a cluster-corrected probability of $p < 0.05$.

Table 2
SV ROI analysis on high > low cognitive load in the DLPFC in Experiment 2.

Areas	Cluster size (voxels)	*p* value of max	Peak MNI coordinates		
			x	*y*	*z*
Left inferior frontal gyrus, triangular part (DLPFC)	3257	<0.001	34	36	10
Right inferior frontal gyrus, triangular part (DLPFC)	2488	<0.001	−36	36	6

Table shows clusters with height threshold of T > 2.3 and a cluster-corrected probability of $p < 0.05$.

3.2.2. *Main effect sweetness concentration*

3.2.2.1. Experiment 1: taste intensity. We did not find areas with significant activation for strong sweet > weak sweet independent of cognitive load in our ROIs. Whole-brain analyses showed stronger activation in the bilateral precentral gyrus for weak than strong sweet solutions (see Table S4).

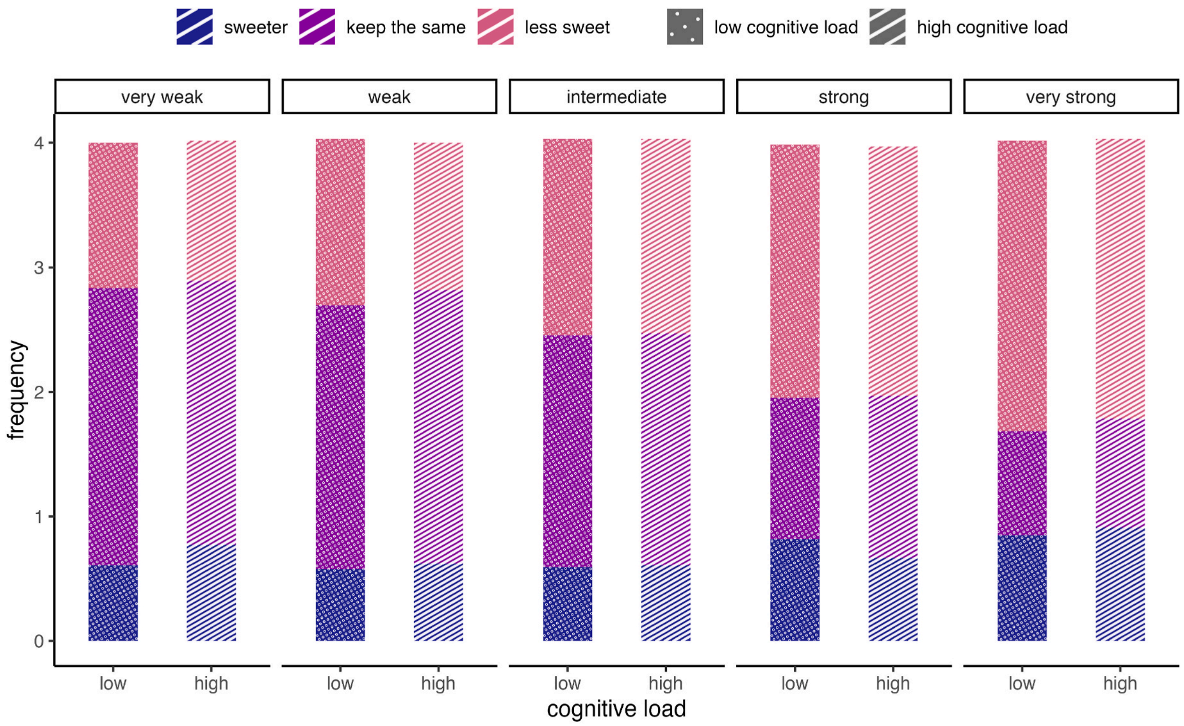

Fig. 3. Proportion of different preference options selected for the five glucose solutions under high versus low cognitive load (Experiment 2). Preferred intensity answer options were *sweeter* (dark purple), *keep the same* (purple), and *less sweet* (pink). Y-axis indicates the average frequency that a certain answer was chosen per solution under low and high cognitive load.

3.2.2.2. Experiment 2: taste preference. To investigate in which areas activation covaried with sweetness concentration independent of cognitive load, we calculated a contrast for the linear effect of glucose solution intensity. We only found significant activation that scaled negatively with sweetness concentration (stronger glucose concentration linked with weaker activation) in the bilateral insula and left opercular part of the inferior frontal gyrus (Table 3, Fig. S1 in the supplement). Whole-brain analysis revealed activation that scaled negatively with sweetness concentration in the bilateral pre/postcentral gyrus, like in Experiment 1, and the left occipital gyrus (see Table S5 in the supplemental information).

3.2.3. Interaction of cognitive load and sweetness concentration

3.2.3.1. Experiment 1: taste intensity. Next, we examined whether there was an interaction between cognitive load and sweetness concentration. As hypothesized, we found that in the right insula the effect of cognitive load differed across concentrations (Table 4; Fig. 4a). Comparing the effects of cognitive load between the sweetness concentrations showed that for the strong sweet solutions there was a more pronounced difference between high and low cognitive load than for the weak sweet solutions; there was no significant difference in activation between the load conditions for the weak sweet solutions but activation under high-load was weaker compared to under low-load for the strong sweet solutions. Additionally, we found that in the bilateral triangular part of the inferior frontal gyrus (DLPFC) the effect of cognitive load differed between sweetness concentrations as well (Fig. 3b). Again, for the weak sweet solution there was no significant effect of cognitive load, but for the strong sweet solution there was weaker activation in these areas under high compared to low cognitive load. There were no clusters that survived the threshold in the whole brain analysis.

3.2.3.2. Experiment 2: taste preference. We then examined whether brain areas displayed a difference in activation between low and high cognitive load that scaled linearly with sweetness concentration. We did not find such an effect in our SV ROI or whole-brain analyses. Since we administered five different glucose solutions and cognitive load could affect the response to certain solutions differently than others, as we saw in Experiment 1, as a next step, we performed an omnibus F-test to probe for any interaction between cognitive load and sweetness concentration. As Fig. 5 shows, this yielded a cluster in the left DLPFC (−34, 34, 40), within our DLPFC ROI (Table 5). The cluster was in close proximity to the cluster observed in Experiment 1 (see Fig. 4b).

Examining the parameter estimates of the responses to the different glucose concentrations within the cognitive load conditions showed that, in this left DLPFC area, the high working memory load reduced left DLPFC activity to the very strong sweet solutions (as in Experiment 1), but that the opposite effect of working memory load was observed for the intermediate and strong sweet solutions. The difference between the very strong sweet solution on the one hand and the strong and intermediate sweet solutions on the other hand was also significant. For the other solutions there was no significant difference in activation between high and low cognitive load in this area.

Table 3
ROIs showing a linear negative effect of sweetness concentration in Experiment 2.

Areas	Cluster size (voxels)	*p* value of max	Peak MNI coordinates		
			x	y	z
Insula ROI					
Right middle insula	3257	0.013	36	−6	6
Left middle insula	2488	0.045	−32	−8	6
Middle frontal gyrus ROI					
Left inferior frontal gyrus, opercular part	678	0.031	−38	10	20

Table shows clusters with height threshold of $T > 2.3$ and a cluster-corrected probability of $p < 0.05$.

Table 4
SV ROI analysis of the interaction of cognitive load and sweetness concentration in the insula and DLPFC (Experiment 1).

Areas	Cluster size (voxels)	*p* value of max	Peak MNI coordinates		
			x	*y*	*z*
Right middle insula/putamen	89	0.042	32	−4	−6
Right inferior frontal gyrus, triangular part (DLPFC)	680	0.033	50	32	8
Left inferior frontal gyrus, triangular part/Middle frontal gyrus (DLPFC)	508	0.048	−56	22	30

Table shows clusters with height threshold of $T > 2.3$ and a cluster-corrected probability of $p < 0.05$.

3.2.4. PPI

3.2.4.1. Experiment 1: taste intensity. PPI analyses were performed on all peaks of the brain clusters where an interaction was found of cognitive load and sweetness concentration (Table 6), to examine if cognitive load affected the functional connectivity of these areas differently for strong sweet versus weak sweet solutions. The behavior of interest was the interaction between sweetness concentration and cognitive load (strong sweet solutions high cognitive load-weak sweet solutions high cognitive load) - (strong sweet solutions low cognitive load-weak sweet solutions low cognitive load). For the right insula/putamen seed (32, −4, −6), there was a greater difference in right insula – right nucleus accumbens connectivity between high cognitive load and low cognitive load when tasting the strong sweet solutions, than when tasting the weak sweet solutions (Table 6 and Fig. 6a). Whole brain analysis did not reveal any additional clusters.

For the right DLPFC seed (50, 32, 8), no significant clusters were found in the ROIs or whole brain.

For the left DLPFC seed (−56, 22, 30), there was a greater difference in left DLPFC-right insula connectivity between high cognitive load and low cognitive load when tasting the strong sweet solutions, than when tasting the weak sweet solutions (Table 6 and Fig. 6b).

3.2.4.2. Experiment 2: taste preference. A PPI analysis was performed to examine the effect of cognitive load on differences in connectivity of the left DLPFC between the intermediate sweet solutions and the strongest sweet solutions. No significant clusters were found in the SV ROI or whole brain analyses.

4. General discussion

The present study investigated the effect of cognitive load on the sensory processing of and preference for sweet taste in the brain. We hypothesized that cognitive load would decrease perceived intensity and increase preferred intensity at a behavioral level, much in line with previous findings pointing to compensatory tendencies following suboptimal tasting (Van der Wal & van Dillen, 2013). We moreover predicted that this would be accompanied by attenuated activation in the primary and secondary taste cortex. Additionally, we expected that in Experiment 2, where the task context emphasized sweetness preference instead of sweetness intensity, there would be more pronounced cognitive load-related attenuation in brain areas involved in reward processing and valuation of taste.

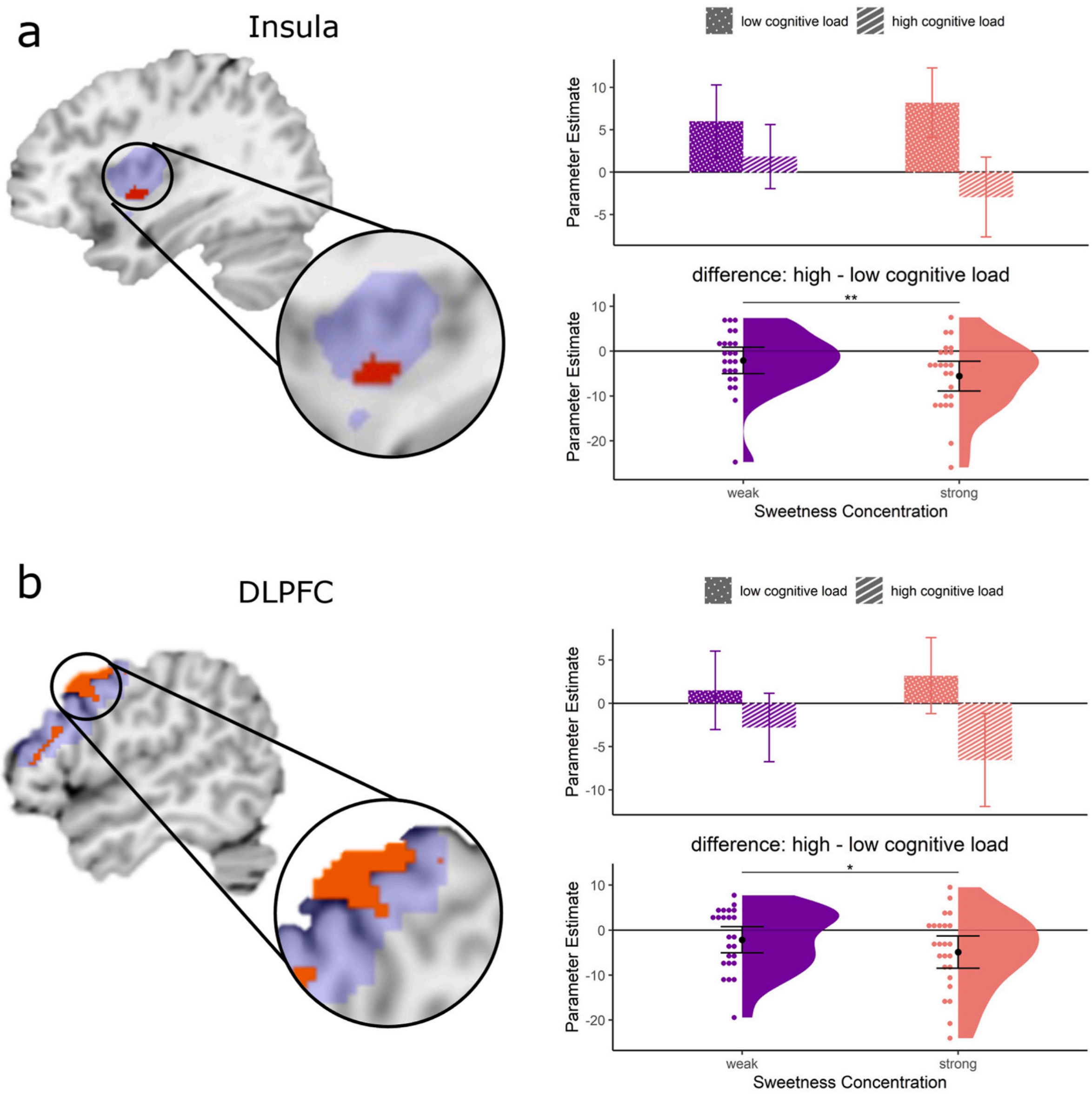

Fig. 4. Interaction between cognitive load and sweetness concentration in the right insula (a) and bilateral DLPFC (b) (Experiment 1). Left panel (a) cluster in the right insula (peak 32–4 -6); Left panel (b) cluster in the right DLPFC (peak 50 32 8), cluster in left DLPFC not visible. The middle insula and DLPFC masks are shown in purple. Top right panel (a & b): bar plot of the parameter estimates (arbitrary units) of the clusters during the presentation of the weak (purple) and strong (red) glucose solutions under high and low cognitive load, average of left and right DLPFC cluster for 3 b; Bottom right panel (a & b): half-violin, half-dot plot depicting the difference in parameter estimates (arbitrary units) between high and low cognitive load for the weak (purple) and strong (red) glucose solutions. Error bars reflect within-subject 95% confidence intervals around the mean based on the Morey method (Morey, 2008). Peaks listed are significant at $p < 0.05$, cluster-corrected within middle insula and DLPFC mask with FSL Randomise.

4.1. The effect of cognitive load on perceived intensity and sensory processing

In Experiment 1, we examined the effect of cognitive load on taste intensity ratings and neural responses to strong versus weak sweet solutions. In the behavioral analyses we found that cognitive load interacted with sweetness concentration, so that participants perceived weak glucose solutions as more intensely sweet and strong glucose solutions as less intensely sweet. This is in line with our hypothesis and with earlier findings (Hoffmann-Hensel et al., 2017; Van der Wal & van Dillen, 2013) and suggests that because stronger tastes draw more attention, there may be greater competition over working memory resources between task-related cognition and stimulus-driven sensory perception. In the fMRI analyses, we found an interaction between sweetness concentration and cognitive load in the right insula and bilateral DLPFC, so that for the weak sweet solutions there was no significant effect of cognitive load, while for the strong sweet solutions there was weaker activation under high compared to low cognitive load. This same interaction between cognitive load and sweetness concentration was visible in the brain responses in the right middle insula and bilateral DLPFC. The area in the right middle insula is the site of the primary taste cortex and has been found to be involved primarily in taste intensity processing (Duif et al., 2020; Dalenberg et al., 2015; Grabenhorst & Rolls, 2008; Spetter et al., 2010). DLPFC activation in response to different flavors has been reported by Kringelbach et al. (2004) and later by Van Rijn et al. (2018) and has been attributed to higher-level cognitive processes such as response integration, attention, and action selection (Kringelbach et al., 2004).

The PPI analysis to examine the effect of cognitive load and sweetness concentration on neural connectivity in Experiment 1 revealed

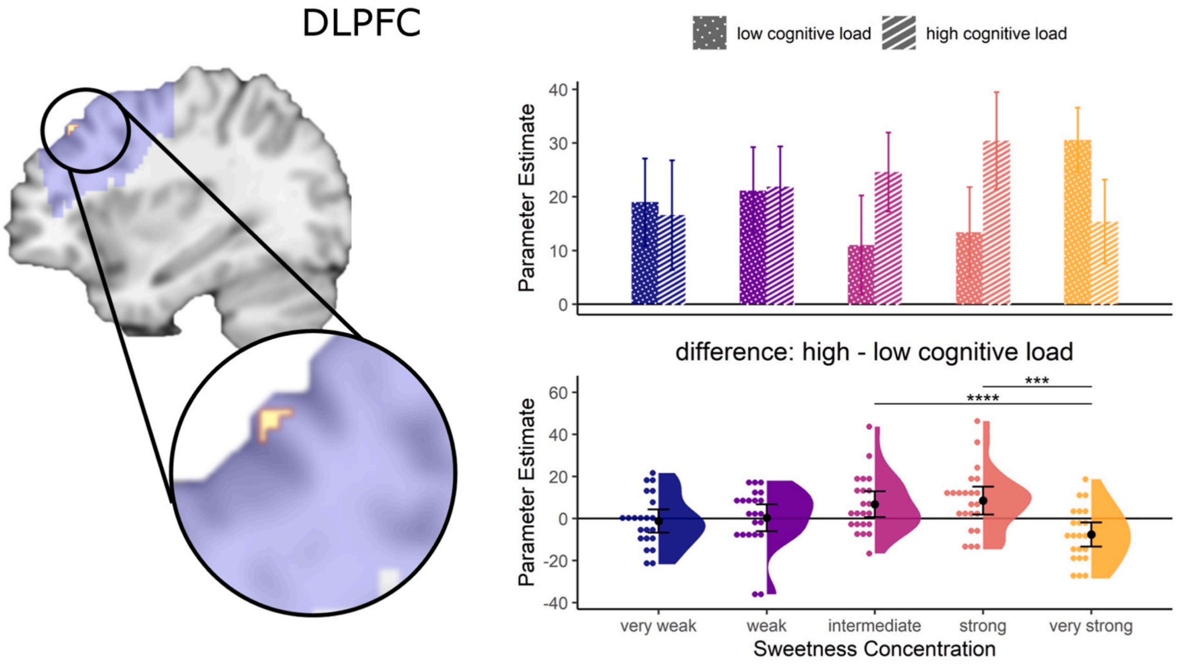

Fig. 5. Interaction between cognitive load and sweetness concentration in the left DLPFC (Experiment 2). Left panel: cluster in the left DLPFC (peak −34 34 40); Top right panel: bar plot of the parameter estimates (arbitrary units) of the cluster during the presentation of the glucose solutions under high and low cognitive load. The MFG masks is shown in purple. Bottom right panel: half-violin, half-dot plot depicting the difference in parameter estimates (arbitrary units) between high and low cognitive load for the glucose solutions. Error bars reflect within-subject 95% confidence intervals around the mean based on the Morey method (Morey, 2008). Peak significant at $p < 0.05$, cluster-corrected within DLPFC mask with FSL Randomise.

Table 5
SV ROI analysis of the interaction between cognitive load and sweetness concentration in the PFC (Experiment 2).

Areas	Cluster size (voxels)	*p* value of max	Peak MNI coordinates		
			x	*y*	*z*
Left middle frontal gyrus (DLPFC)	41	0.028	−34	34	40

Table shows clusters with height threshold of F > 4.6 and a cluster-corrected probability of $p < 0.05$.

Table 6
SV ROI PPI analysis on the interaction between cognitive load and sweetness concentration (Experiment 1).

Areas	Cluster size (voxels)	*p* value of max	Peak MNI coordinates		
			x	*y*	*z*
Right insula seed					
Right nucleus accumbens/ olfactory bulb	59	0.034	−10	14	−12
Left DLPC seed					
Right insula	108	0.038	36	−8	2

Table shows clusters with height threshold of T > 2.3 and a cluster-corrected probability of $p < 0.05$.

altered connectivity between the right middle insula and the nucleus accumbens under high compared to low cognitive load. These regions were found to be anticorrelated, possibly reflecting mutual inhibition due to competition between the different representations in these two areas. This is in line with the findings of van der Laan et al. (2011) who found that under high compared to low cognitive load there was a lower anticorrelation between the nucleus accumbens and the DLPFC while viewing high-calorie pictures, but not low-calorie food pictures. Previous studies have suggested that the ventral striatum (nucleus accumbens) supports selective working memory maintenance by reduced gating of task-irrelevant activity through attenuating functional connectivity (Haeger et al., 2015). This would suggest that our results reflect a negative coupling between right middle insula and right nucleus accumbens while tasting solutions during the digit-span task, since the sensory taste information is irrelevant to the task of memorizing digits. However, this may change when tasting the strong sweet solutions under high cognitive load, where the anticorrelation decreases. This could be because strong sweet solutions are more biologically relevant, which may then lead to increased gating, something that would be in line with the idea of stronger competition over working memory resources between task-related cognition and sensory perception of stronger sweet solutions when concurrent task demands are high. Our finding that task performance was not affected by solution strength suggests that most participants prioritized attention to the digit span task at the expense of the sensory processing of the strong sweet flavor.

The second PPI finding in Experiment 1 revealed altered connectivity between the left DLPFC and right middle insula under high compared to low cognitive load for the strong sweet but not weak sweet solutions. Similar to the right middle insula-nucleus accumbens results, there was a lower anticorrelation while tasting the strong sweet solutions under high cognitive load. Taken together with the overall modulation of DLPFC activity by cognitive load, this finding suggests that increasing cognitive load not only dampens the processing of strong sweet tastes in the DLPFC, but also changes the connectivity between the DLPFC and the middle insula. This may again reflect competition between attentional and perceptual processes and increased gating due to increased competition between sensory processing and task-related processing. In contrast to other studies (Duif et al., 2020; Veldhuizen et al., 2011), we found no areas in which there was stronger activation for strong sweet than weak sweet solutions independent of condition. This may be due to the observed interaction effect between cognitive load and sweetness concentration possibly flattening intensity-related connectivity in neural taste processing.

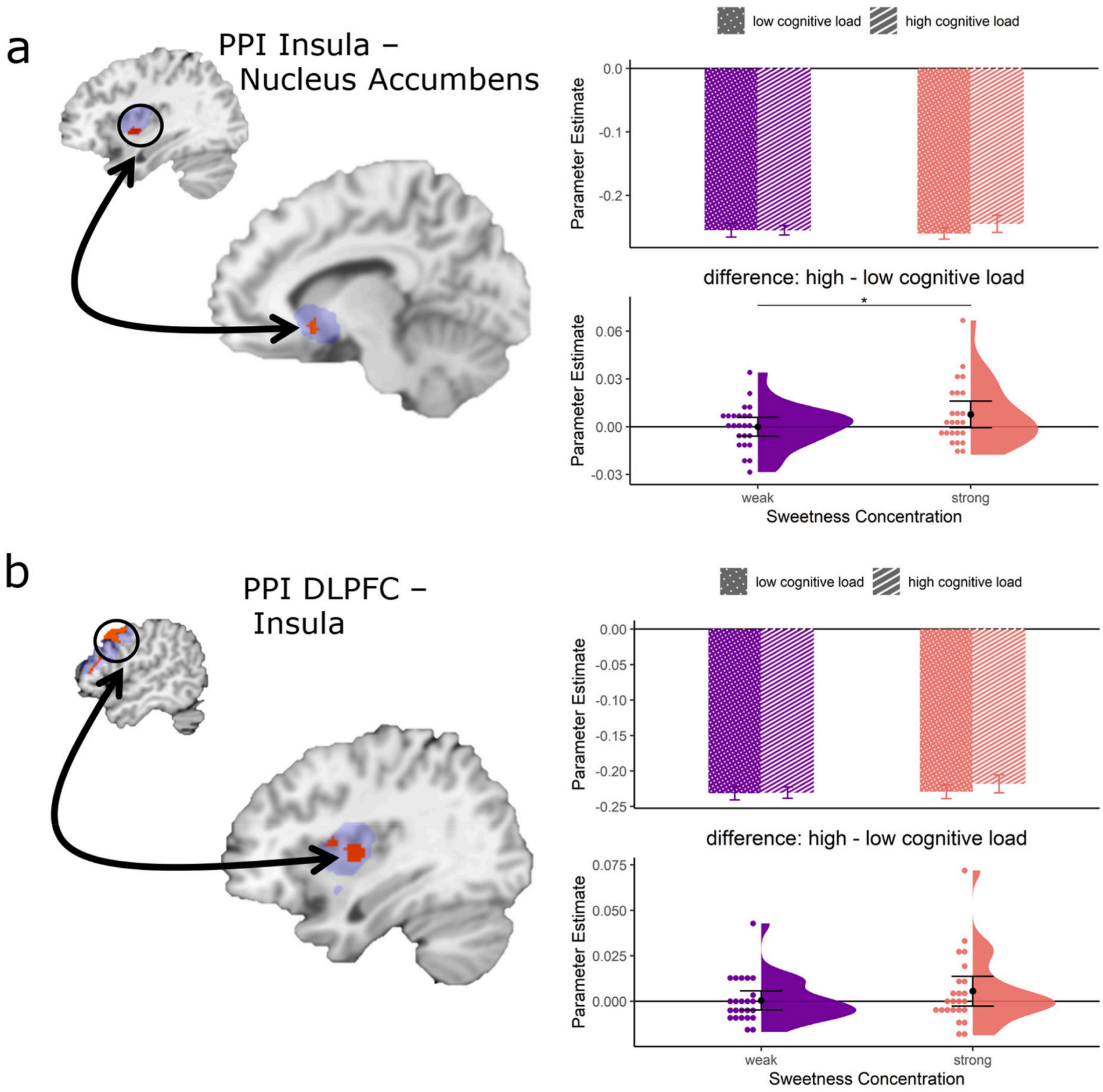

Fig. 6. Functional connectivity between right middle insula and nucleus accumbens (a) and between left DLPFC and right middle insula (b) as a function of cognitive load and concentration strength (Experiment 1). Left panel (a) seed in the insula (32–4 -6); and cluster in the nucleus accumbens (peak −10 14–12); Left panel (b) seed in the DLPFC (−56 22 30); and cluster in the middle insula (peak 36–8 2). The nucleus accumbens and middle insula masks are shown in purple. Top right panel (a & b): bar plot of the parameter estimates (arbitrary units) of the connectivity between the areas during the presentation of the weak (purple) and strong (red) glucose solutions under high and low cognitive load; Bottom right panel (a & b): half-violin, half-dot plot depicting the difference in parameter estimates (arbitrary units) between high and low cognitive load for the weak (purple) and strong (red) glucose solutions. Error bars reflect within-subject 95% confidence intervals around the mean based on the Morey method (Morey, 2008). Peaks listed are significant at $p < 0.05$, cluster-corrected within nucleus accumbens & middle insula mask with FSL Randomise.

4.2. The effect of cognitive load on preferred intensity

In addition to the effects on the sensory processing of taste, we hypothesized that cognitive load would alter preferred taste intensity as well. Previous work has shown that in addition to decreased tasting, cognitive load may yield preferences for higher concentrations, as well as increased consumption of especially high-concentration hedonic (e.g., sweet and salt) substances (Van der Wal & van Dillen, 2013). In Experiment 2 participants therefore indicated for five different sweetness concentrations, to what extent they wished these to be sweeter, the same or less sweet. Contrary to our predictions, we observed no effects of load on people's self-reported preferred intensity.

Based on previous literature we would have expected that the intermediate sweet solution, which with 1.11 M glucose came closest to the 1 M concentration that is generally most preferred (Moskovitz et al., 1974), would receive the highest number of 'keep the same' responses, with more frequent choices for sweeter (less sweet) concentrations for lower (higher) concentrations. However, our pattern of results did not replicate this earlier work. On average, participants expressed a lesser preference for stronger intensities (i.e., they opted the most for less sweet solutions compared to keeping them the same or sweeter), even for the weakest sweetness solutions. Moreover, over time, i.e., from the first to the second run of the task, participants increasingly indicated that they wanted all solutions to be less sweet, even the 'optimal' sweet solutions. This could possibly be explained by the satiation caused by repeated exposure to a similar (sweet) taste (Thomas et al., 2015). Finally, contrary to our hypothesis, we failed to observe any modulatory effects of cognitive load on participants' taste preferences.

Likewise, in the imaging analyses we did not find an interaction between cognitive load and sweetness concentration in brain regions involved in taste valuation or preference. Whereas some studies have reported cognitive load to yield compensatory consumption effects, such as overconsumption after distracted eating (Cui et al., 2021; Higgs & Woodward, 2009; Oldham-Cooper et al., 2010; Robinson et al., 2013; van Meer, Murphy, Hofmann, van Steenbergen, & Van Dillen, 2023) and consumption of sweeter and saltier foods under high cognitive load (Van der Wal & van Dillen, 2013), other studies have found no effects of cognitive load on food preferences, e.g. there was no effect of distracted eating on pleasantness ratings (Morris et al., 2020) or hedonic ratings (van Meer, Murphy, Hofmann, van Steenbergen, & Van Dillen, 2023). Preferences involve a more uniquely individual and highly context-dependent experience that has not been consistently linked with actual consumption (DiFeliceantonio et al., 2018; Tang et al., 2014). Therefore, preference processing may be affected by cognitive load in a more subtle manner than more basic, sensory perception such as taste intensity processing that is more tightly linked to specific stimulus features, something that our current experimental design may not have been able to capture.

Whereas we thus observed no effects of cognitive load on behavioral or neural indices of sweetness preferences, we did find that participants were more likely to opt for less sweet solutions with increasing sweetness concentration. Additionally, we saw that over the two runs, participants increasingly preferred all solutions to be less sweet. This pattern of findings resonates with the much-observed pattern of satiation, the decrease in liking which occurs when people repeatedly consume the same taste stimuli (Thomas et al., 2015). In support of this interpretation, we observed a similar inversed effect of sweetness concentration on bilateral middle insula activation. In previous studies, the bilateral middle insula has been found to activate when participants focus on the pleasantness of the taste, and even stronger than when they focused on the intensity of the taste (Van Rijn et al., 2018). Furthermore, a study that examined the functional specialization of the insula found that the left middle insula especially encoded pleasantness, while the right middle insula was additionally involved in the encoding of concentration strength (Dalenberg et al., 2015). Thus, the inverse pattern of a decrease in activation with increasing glucose solutions in Experiment 2 may reflect the decrease in perceived pleasantness that was visible in the behavioral data as well.

4.3. *DLPFC modulation in experiment 1 and 2*

In a similar location as where we observed DLPFC modulation in Experiment 1, we found that DLPFC activation to the strongest sweet solutions was suppressed under high relative to low load. When we compare the results between Experiment 1 and Experiment 2 directly, there are differences and commonalities. The most striking difference is that DLPFC activity in response to the strong sweet solution in Experiment 1 was inhibited by cognitive load, whereas a similar concentration level in Experiment 2 tended to increase brain activity under cognitive load. One possibility that this pattern of findings suggests, is that the modulation of neural activity in this area is context-dependent and reflects aspects of neural taste processing that are relatively rather than absolutely coded in the brain (Seymour & McClure, 2008). This interpretation also aligns well with our observation that people's responses to the exact same sweetness stimuli changed over time, in line with the well-documented process of satiation. However, the differences between Experiment 1 and 2 in the effect of cognitive load on DLPFC activity in response to the sweet solutions are difficult to explain fully without making additional assumptions about the differences in task context that are hard to validate with the data at hand.

The commonalities, on the other hand, are clear: both experiments show that working memory load inhibits DLPFC activation to the solutions with the highest sweetness concentration. Given the evolutionary value of sweet stimuli, stimuli with the strongest sweetness concentration in a particular environment might be the most salient and relevant ones and might involve enhanced attention and optimization of action control. For example, activation in the left DLPFC in response to food stimuli has been shown to increase after satiation, and it has been suggested that this reflects the enhancement of inhibitory control as a mechanism to decrease further food intake (Thomas et al., 2015). The fact that cognitive load selectively reduces DLPFC activity for these stimuli only is consistent with the idea of competition over attentional resources between task-induced cognitive load and stimulus-induced sensory perception, which is most prominent when stimuli require more attentional resources (i.e., when they are more potent). Another commonality between both experiments is that cognitive load itself activated a more anterior part of the prefrontal cortex that did not overlap with the modulation of brain activity during taste processing. This is additional evidence that the modulation we observed cannot simply be attributed to the cognitive effects of working memory load per se, but rather involves the interaction between cognitive and taste processes.

Note that we did not find any other brain areas in which activation was affected by the interaction of sweetness concentration and cognitive load when preferred intensity was indicated. Furthermore, we did not find any additional areas where cognitive load altered connectivity with the DLPFC for the different sweetness concentrations in our PPI analysis in Experiment 2. All in all, our findings suggest that the DLPFC modulation we observed might play a key role in the interaction between cognitive load and taste processing. We hope that future studies can further elucidate the exact role of this brain region.

4.4. *Limitations*

Our experiments come with several limitations. To keep the timing of our working memory load manipulation constant, we did not include a jitter between the digit span cue and the taste delivery. Due to lack of a jitter between the digit span cue and the taste delivery, however, main effects of cognitive load on the neural processing of the different solutions would be confounded by temporal autocorrelation between the cue and taste events. This limited the scope of our analysis as we could not reliably estimate the difference in brain activity under high and low cognitive load independent of sweetness concentration. Future studies that include a jitter between the cognitive load manipulation and the taste administration, may disentangle the main effects of the two manipulations on taste activation.

A further limitation of the two experiments was that a high number of participants had to be excluded because of excess head movement and technical issues. Accordingly, the sample size per study was lower than intended, which affected the power of our statistical analyses, in particular for Experiment 2 which had a more complex experimental design. This may have affected the sensitivity of our analysis, and explain some of the null findings for the hypothesized higher-order interaction effects of Experiment 2. Our results therefore require independent replication using larger sample sizes.

Another limitation is that, because the perceived intensity and preferred intensity ratings were assessed in different samples, these rating cannot be directly compared. To illustrate, the accuracy scores of the high cognitive load trials of the digit-span task were substantially higher for participants in Experiment 2 than in Experiment 1. This could be attributed to the participant sample, but it may also indicate that due to the somewhat different experimental set up, the cognitive load induced was lower in Experiment 2, or that its more dynamic task design (with five instead of two different taste stimuli) kept participants more engaged. To reduce the influence of such contextual variations, and to allow for a direct comparison, future studies could assess the effects of cognitive load on perceived intensity and preferred intensity within the same sample and/or within the same experiment. Future research could moreover examine if our results can be extended to different tastes to further disentangle the neural mechanism behind the effect of cognitive load on consumption.

4.5. Conclusion

The current study demonstrated that cognitive load affects the sensory processing of sweet solutions in the brain. Our results show that high compared to low cognitive load decreased perceived taste intensity, accompanied with decreased activation in areas involved with sensory and attentional processing, such as the middle insula and DLPFC. This was especially the case for strong sweet solutions, which may indicate a higher competition for attentional resources between task demands and more potent stimuli. In line with this, cognitive load affected functional connectivity during the presentation of strong but not weak sweet solutions between the middle insula and nucleus accumbens and middle insula and DLPFC. When we examined the effect of cognitive load on preferred intensity, we again found that cognitive load affected attention-related brain activation particularly for the relatively strongest sweet concentrations. Taken together, the results of this study suggest that cognitive load or distraction may dampen the sensory perception of strong tasting, biologically relevant foods and drinks, due to increased competition for attentional resources. This in turn may lead to compensatory overconsumption of these often high-calorie, unhealthy foods and drinks in our modern society (Bray & Popkin, 2014).

Author contributions

LvD designed the experiments with the assistance of HvS. LvD collected the data. FvM and HvS performed the analysis of the neuroimaging data, LvD, HvS and FvM performed the analysis of the behavioral data. FvM took the lead in writing the manuscript. All authors provided critical feedback and helped shape the analysis and manuscript.

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Ethical statement

Participants provided written informed consent (according to the Declaration of Helsinki).

The study was approved by the Medical Ethics Committee of Leiden University (see https://osf.io/h9rwu/).

Declaration of competing interest

None.

Data availability

The behavioral data and R analysis script: https://osf.io/h9rwu. The T-maps of the higher-level analyses are available at https://neurovault.org/collections/WOFLHJNT/.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.appet.2023.106630.

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