Individual differences in late positive potential amplitude and theta power predict cue-induced eating

Kyla D. Gibney[a,b,*], George Kypriotakis[b], Francesco Versace[a,b,*]

[a] *Neuroscience Graduate Program MD Anderson UTHealth Graduate School of Biomedical Sciences, Houston, TX, United States*

[b] *Department of Behavioral Science, The University of Texas MD Anderson Cancer Center, Houston, TX, United States*

* Corresponding author at: Department of Behavioral Science, Unit 1330, The University of Texas MD Anderson Cancer Center, 1515 Holcombe Boulevard, Houston, TX 77030, United States.

E-mail address: KDGibney@mdanderson.org (K.D. Gibney) or fversace@mdanderson.org (F. Versace).

Abbreviations

ANOVA: analysis of variance

BIS: Barratt Impulsiveness Scale

C>P: LPP responses that are larger to food cues than to pleasant images

EEG: electroencephalogram

ERP: event-related potential

LPP: late positive potential

P>C: LPP responses that are larger to pleasant images than to food cues

PANAS: Positive and Negative Affect Scale

ROI: region of interest

SLIM: Satiety Labeled Intensity Magnitude

θBE>θCA: theta power that is higher under the bead condition than under the candy condition

θCA>θBE: theta power that is higher under the candy condition than under the bead condition

WREQ: weight-related eating questionnaire

HIGHLIGHTS

- LPP responses to motivationally salient stimuli predict cue-induced eating.
- Theta power in the presence of food rewards predicts cue-induced eating.
- The LPP & theta may inform the development of personalized weight-loss interventions.

ABSTRACT

Both the brain's affective and cognitive systems are known to regulate cue-induced behaviors. Although it is established that individual differences in affective processing of food-related cues predict cue-induced eating, we have yet to investigate how both affective and cognitive mechanisms act in tandem to regulate cue-induced eating. We recorded electroencephalogram (EEG) from 59 adults while they viewed emotional & food-related images that preceded the delivery of food rewards (candies) or nonfood objects (beads). We measured the amplitude of the late positive potential (LPP) in response to images and power in the theta (4-8 Hz) frequency band after the candy or bead was dispensed to the participant. We found that individuals with larger LPP responses to food cues than to pleasant images (C>P group) ate significantly more during the experiment than did those with the opposite response pattern (P>C group, $p < 0.001$). Furthermore, we found that individuals with higher theta power after dispensation of the candy than of the bead (θCA>θBE) ate significantly more than did those with the opposite response pattern (θBE>θCA, $p < 0.001$). Finally, we found that the crossed P>C and θBE>θCA group ate less ($p < 0.001$) than did the other three groups formed by crossing the LPP and theta group assignments, who exhibited similar eating behavior on average ($p = 0.662$). These findings demonstrate that motivational salience and cognitive control converge to independently confer vulnerability or resilience to cue-induced behaviors, underscoring the need for individualized treatments to mitigate maladaptive behaviors.

Keywords: Motivational salience, Cognitive control, Late positive potential, Theta band, Event-related potentials, Time-frequency analysis

1. Introduction

Overweight and obesity, characterized by a body mass index of at least 25 kg/m^2 and at least 30 kg/m^2, respectively, increase the risk of cardiovascular disease, diabetes, and several types of cancer [1]. Losing even a modest amount of weight can have substantial health benefits, but most weight-loss interventions yield short-lived, suboptimal results [2,3]. Identifying the neurobiological mechanisms underlying excessive eating, the ultimate cause of weight gain [4,5], can help clinicians target the root causes of overeating, personalize interventions for weight loss, and improve weight loss treatment outcomes.

Neurobiological models of obesity have demonstrated that the brain's reward and cognitive control systems both play a major role in regulating food intake [6,7]. The reward system guides eating behavior with "bottom-up" signals that dynamically assign motivational salience to food rewards and the cues associated with them [8,9]. In contrast, cognitive control systems exert "top-down" control over eating behavior by enabling the implementation of intentional, goal-directed behavior [10]. Failure of either mechanism can lead to maladaptive eating patterns, overeating of hyper-palatable foods, and weight gain [11].

Preclinical findings demonstrated that animals differ in their tendency to engage bottom-up versus top-down driven behaviors in the presence of cues signaling the impending delivery of food rewards (i.e., food-related cues) [12]. Individuals who attribute high motivational salience to food-related cues are prone to cue-induced compulsive reward-seeking behaviors [13]. On the other hand, those who do not attribute high levels of motivational salience to reward-related cues are less prone to cue-induced compulsive behaviors and are likely to implement goal-directed behaviors when faced with these cues [14].

We have demonstrated that humans are also characterized by individual differences in the tendency to attribute motivational salience to food-related cues [15] and that these differences underlie vulnerability to cue-induced eating [16]. In our experiments, we recorded event-related potentials (ERPs)—a direct measure of brain activity [17]—during a cued food delivery task. In this task, participants viewed emotional, neutral, and food-related images while we recorded electroencephalogram (EEG) from the scalp. After the presentation of some food-related images, we dispensed chocolate candies to the participants, which they could eat or discard [18]. To estimate the motivational salience of these images, we measured the amplitude of the late positive potential (LPP) in response to each image. The LPP is an ERP component that is reliably modulated by

motivational salience: highly salient images such as erotica and mutilations prompt larger LPP responses than do images with lower salience, such as romantic or sad images [19–21]. We found that individuals with larger LPP responses to food-related cues than to pleasant images (C>P group) ate significantly more during the experiment than did those with larger LPP responses to pleasant images than to food-related cues (P>C group) [16].

These findings support the hypothesis that attributing higher motivational salience to food-related cues than to pleasant non-food-related stimuli increases vulnerability to cue-induced eating, but they are silent about the role of individual differences in the engagement of cognitive control systems in regulating cue-induced eating. Because results from animal models suggest that individuals who attribute high levels of motivational salience to food-related cues might also have poor top-down control over cue-induced behaviors [12,14,22,23], the present study aimed to elucidate how both cognitive and affective mechanisms act in tandem to regulate cue-induced eating.

Activity in the theta frequency band has been proposed as a reliable correlate of the engagement of higher cognitive functions [24,25]. Theta power over midfrontal scalp sites increases when participants engage cognitive control mechanisms to inhibit prepotent responses [26,27] or perform difficult tasks [28]. In light of these findings, we used theta power in an exploratory fashion to approximate the engagement of cognitive control systems in food-related decision-making during a cued food delivery task.

The present study aimed at investigating the role that individual differences in both the attribution of motivational salience to food-related cues and the engagement of cognitive control systems have in regulating cue-induced eating during the cued food delivery task. We expected to replicate our previous findings: namely, that individual differences in affective processing of cues predict cue-induced eating. We also aimed to elucidate whether the engagement of cognitive control systems—as indexed by theta power—differs between P>C and C>P individuals, or if cognitive control mechanisms contribute to cue-induced eating behavior irrespective of C>P and P>C status. Results demonstrating that midfrontal theta power differs between the C>P and P>C groups would suggest that individuals attributing higher motivational salience to food-related cues might also have difficulty engaging cognitive control mechanisms when making food-related decisions, in a manner similar to what has been observed in animal models. Meanwhile, results demonstrating that

individual differences in midfrontal theta power predict eating behavior regardless of C>P vs and P>C status would suggest that the engagement of cognitive control systems regulates cue-induced eating independently from the tendency to attribute motivational salience to food-related cues. By elucidating whether motivational salience and cognitive control mechanisms converge to regulate cue-induced eating or do so independently, we may inform clinical researchers of effective mechanistic targets for weight loss and other clinical interventions aimed at reducing maladaptive, reward-seeking behaviors.

2. Materials and methods

2.1. Participants

We recruited sixty research participants from the Houston, TX, metro area using flyers and magazine and newspaper advertisements. Participants were eligible if they were 18 to 65 years of age, were neither pregnant nor breastfeeding, and did not have a history of psychiatric disorders, seizures, head injuries with loss of consciousness, uncorrected visual impairments, eating disorders, or allergies, or any other illnesses that would prevent them from eating chocolate candy. Participants received monetary compensation for their time and travel totaling up to $60 each. One participant was excluded from the final analysis due to incomplete data. Tables 1 and 2 show the demographic information for the participant sample.

2.2. Study procedures

The study consisted of an eligibility screening of potential participants via telephone followed by an in-person laboratory visit. A research assistant met with the participant at each laboratory visit to explain the study and obtain informed consent. The research assistant then collected the participant's biometric information, including height and weight, and then administered a series of computerized questionnaires. After completing the questionnaires, the research assistant placed an EEG net on the participant's head and instructed the participant on how to complete the cued food delivery task. The research assistant then left the room and began both the EEG recording and the cued food delivery task. After completion of the EEG session and task, the participant was debriefed and given financial compensation. All study procedures were approved by The University of Texas MD Anderson Cancer Center Institutional Review Board.

135 *2.3. Questionnaires*

136 Our computerized questionnaires consisted of those assessing hunger and satiety, eating habits,
137 impulsivity, mood, affect, and hedonic tone. To assess hunger and satiety, we administered the Satiety
138 Labeled Intensity Magnitude (SLIM) scale [29] to each participant before and after completion of the cued food
139 delivery task. To ascertain eating habits, we used the weight-related eating questionnaire (WREQ) [30], the
140 Power of Food Scale [31], and the Food Cravings Questionnaire [32], which measure variables such as
141 susceptibility to external cues, the influence of a food-abundant environment on eating, and food cravings,
142 respectively. To measure impulsivity, we administered the Barratt Impulsiveness Scale (BIS) [33]. Finally, to
143 identify variables relating to affect, mood, and hedonic tone, we administered the Positive and Negative Affect
144 Schedule (PANAS) [34], the Center for Epidemiologic Studies Depression Scale [35], and the Snaith-Hamilton
145 Pleasure Scale [36], respectively.

146

147 *2.4. Cued food delivery task*

148 Participants completed the cued food delivery task depicted in Fig. 1 [18] with the addition of a control
149 condition in which they were also dispensed plastic beads. During the task, participants viewed emotional,
150 neutral, and food-related images presented on a 17-inch computer screen using E-Prime software (version
151 2.0.8.74; Psychology Software Tools, Inc., Pittsburgh, PA) while EEG was recorded from the scalp. After
152 viewing a food-related image, each participant was dispensed a chocolate candy, which they had the option to
153 eat or discard, or a bead. Food-related images consisted salty or sweet contents (for example: pizza [salty],
154 cake [sweet]). One of these two categories of food images (counterbalanced across participants) preceded the
155 delivery of the candy, whereas the other preceded the delivery of the bead. Each participant was told at the
156 beginning of the EEG session which category of food image would precede the candies and which would
157 precede the beads. The pictures used in this task were selected from the International Affective Picture System
158 (IAPS) [37] and a set of pictures used in our previous studies [15,16]. See Supplementary Table 1 for a list of
159 the IAPS pictures used in the experiment.

160 The cued food delivery task consisted of six experimental blocks that lasted about 5 min each. In each
161 block, 55 images were presented pseudorandomly (no more than two images belonging to the same picture

category were presented consecutively): 10 neutral (people and objects), 10 pleasant (erotica and romance), 15 unpleasant (mutilations, violence, and pollution), and 20 food-related (savory or sweet) images.

No images were repeated during the task. For the food images, the candy or bead was dispensed 1000 ms after the food cue appeared on the screen through a tube into a receptacle. The participant then could either pick up and eat the candy or discard it in a box. Each food image remained visible until the participant either deposited the candy or bead into the box or pressed a button indicating that they had finished eating the candy. All non-food images were presented for 2.2 s, and a random intertrial interval (ITI) of 3-5 s separated each trial. To familiarize the participants with the task, we ran 11 practice trials, two of which were followed by a candy or bead.

2.5. EEG acquisition

We continuously recorded EEG during the task using a 129-channel Geodesic Sensor Net that was amplified with an AC-coupled high-input-impedance (200 MΩ) amplifier (Geodesic EEG System 200; EGI, Eugene, OR) and referenced to electrode Cz. EEG data were collected at a sampling rate of 250 Hz and filtered online using a 0.1-Hz high-pass and 100-Hz low-pass filter. The scalp impedance was kept under 50 KΩ as per the manufacturer's instructions.

2.6. Data reduction

After collecting the EEG, the EEG data were filtered using a 30-Hz low-pass filter and visually inspected to identify broken channels, which were defined as any channels contaminated by artifacts in more than 50% of the recording. Any broken channels were interpolated using spherical splines. Next, the EEG recordings were corrected for blinks and horizontal eye movements using a spatial filtering method implemented in the BESA software program (version 5.1.8.10; MEGIS Software GmbH, Gräfelfing, Germany). Next, the data were transformed to the average reference and segmented as follows. For the analysis of ERPs, each segment of EEG was time-locked to the onset of each picture in segments that started 1500 ms before the onset of the picture and lasted until 1500 ms afterward. For the time-frequency analyses, each segment of EEG was time-locked to the delivery of a candy or bead in segments that started 1500 ms before the dispensation of the

candy or bead and lasted until 1500 ms afterward. The data were baseline-corrected using a 100-ms time bin before the onset of the pictures (ERPs) or the onset of the candy or bead dispensation (time-frequency) as the baseline. Artifacts in the -1000- to +1000-ms time window for each segment were then detected based on the following criteria: EEG amplitude above 100 or below -100 μV, an absolute voltage difference between any two points in a segment no greater than 100 μV, maximum voltage step between two contiguous data points of 20 μV, and less than 0.5 μV of variation in activity for more than 100 ms. Channels that were marked bad in more than 40% of the segments were interpolated, and any segment that included more than 12 bad channels after interpolation was discarded.

2.7. LPP

We used the amplitude of the LPP as a measure of cues' motivational salience. To calculate the LPP for each subject and picture category, the EEG responses that were time-locked to the onset of each picture during the 400- to 800-ms time window using a pooled set of centroparietal sensors (EGI HydroCel Geodesic Sensor Net sensors 7, 31, 37, 54, 55, 79, 80, 87, 106, 129; see also Fig. 2 inset) were averaged together. This is the same temporospatial region of interest (ROI) used in our previous studies investigating the LPP [15,38,39].

2.8. Theta power

To calculate theta power, the EEG data time-locked to the delivery of the candy or bead were transformed into the time-frequency domain using a continuous wavelet transform. The wavelet transform was based on a complex Morlet wavelet function with a Morlet parameter of 5 using 40 linear frequency steps from 1 to 40 Hz. The data were normalized using Gabor normalization and were baseline-corrected using a reference interval from -875 to -625 ms. To calculate theta power, the 4- to 8-Hz frequency bands were averaged.

2.9. Classification of participants

To classify the participants based on their LPP responses to cues, we followed a procedure used in our previous studies [15,16]. Specifically, we *z*-transformed each participant's LPP data for each picture category, then we applied a *k*-means (k = 2) clustering algorithm to these *z*-transformed LPP values for each participant. The number of clusters (k = 2) was decided a priori based on previous findings [16,38].

To classify the participants based on their theta power amplitudes, we followed a similar strategy Specifically, each participant's theta power values were *z*-transformed for the candy, bead, and neutral conditions during a 0- to 200-ms time bin using a pooled set of mid-frontal sensors. We then applied a *k*-means (k = 2) clustering algorithm to these z-transformed theta power values, with the a priori hypothesis that two distinct patterns of theta activity would be observed, much like our previous findings using the LPP.

2.10. Eating behavior

Because the number of candies the participants ate during the experiment is a count variable, we tested differences in eating behavior between participant groups using Poisson regression analysis. First, we compared the number of candies eaten during the experiment between the two LPP-derived groups. Second, we conducted another Poisson analysis to compare the number of candies eaten between the two theta power-derived groups. Third, we compared the number of candies eaten by the four groups formed by crossing the LPP and theta power-based groups using Poisson regression.

2.11. Demographics and questionnaires

To identify whether any demographic or psychological factors had confounding effects on the trends in eating behavior we observed in the participant groups, we conducted Poisson regression modeling the effect of group assignment (LPP and theta power) on eating behavior. The demographic, biometric, and self-reported data outlined in Table 1 were included in the model as covariates.

3. Results

3.1. ERPs

Fig. 2 shows the grand averaged ERPs for each picture category. As expected, the amplitude of the LPP increased as a function of motivational salience irrespective of hedonic content. We formally tested this effect using LPP amplitude as a dependent variable in a repeated-measures analysis of variance (ANOVA) with the picture category as an eight-level factor (candy cues, bead cues, erotica, romance, neutral, pollution, violence, and mutilations; $F[7, 399] = 22.1$, $p < 0.001$). We also tested the quadratic trend of increasing LPP as a function of motivational salience under both pleasant and unpleasant conditions ($F[5, 290] = 46.3$, $p < 0.001$). Furthermore, we found that on average, food images preceding dispensation of the candy elicited larger LPPs than did food images preceding dispensation of the bead ($F[1, 58] = 5.02$, $p = 0.029$).

3.2. Classification of participants: LPP

Cluster analysis of the LPP responses identified the two hypothesized reactivity profiles: one group (C>P) had larger LPP responses to food cues than to pleasant images, and the other group (P>C) had larger LPP responses to pleasant images than to food cues. Both groups exhibited the canonical pattern of progressively larger LPP responses for both pleasant and unpleasant images as a function of their motivational salience (C>P group: $F = 87.5$, $p < 0.001$; P>C group: $F = 77$, $p < 0.001$) (Fig. 3A). However, the P>C group had significantly larger LPP responses to pleasant images than to food cues ($F = 6.51$, $p = 0.013$), whereas the C>P group had significantly larger LPP responses to food cues than to pleasant images ($F = 59$, $p < 0.001$). See Supplementary Fig. S1 for the averaged LPP amplitudes across all pleasant picture contents by group assignment.

After determining the group assignment for each participant, we then compared the number of candies eaten by the C>P and P>C groups (Fig. 3B). Poisson regression analysis demonstrated that individuals in the C>P group ate significantly more during the experiment than did individuals in the P>C group (Wald $X^2[1] = 43.1$, $p<0.001$). Demographic, biometric, and self-reported questionnaire data for the C>P and P>C groups are reported in Table 1.

3.3. Time-frequency power

To identify a set of EEG sensors to pool together in our analysis of theta power, we used the following procedure. Using theta power as a dependent variable, we performed a repeated-measures ANOVA with condition (candy, bead, and neutral) as a factor for each time point and each EEG sensor. To identify the sensors and time points at which theta power exhibited statistically significant differences across conditions, we determined thresholds for the *F*-values resulting from these ANOVAs using Bonferroni correction. We then selected the sensors that showed statistically significant differences between conditions (candy, bead & neutral) during the 0- to 200-ms time bin (see inset in Fig. 4 for this set of sensors), during which cognitive control-related effects in theta power are typically greatest [25]. See Supplementary Fig. S2 for the topography of these *F*-values during this time bin. We then averaged theta power in the 0- to 200-ms time bin from this pooled set of sensors to obtain a single theta power value for each participant under the candy, bead, and neutral conditions. Figure 4 shows the time course of theta power in the Candy, Bead & Neutral conditions. We found that, on average, power increased when either candies or beads were dispensed to the participant, but not when they passively viewed neutral pictures.

Next, to determine whether theta power differed between the C>P and P>C groups, we averaged the pooled and binned theta power values for these two groups. We found that the groups had similar dynamics in theta power under the candy, bead, and neutral conditions. A repeated-measures ANOVA demonstrated no significant interaction effect of group assignment (C>P and P>C) and condition (candy, bead, and neutral) ($F[2, 114] = 0.667$, $p = 0.515$) on theta power. These data are shown in Supplementary Fig. S3.

3.4. Classification of participants: theta power

Cluster analysis of theta power identified two participant groups (Fig. 5A): one with higher theta power for the candy condition than for the bead condition (θCA>θBE group) and the other with higher theta power for the bead condition than for the candy condition (θBE>θCA group). We then compared the number of candies eaten by these two groups during the experiment (Fig. 5B). Poisson regression analysis demonstrated that the θCA>θBE group ate significantly more candies than did the θBE>θCA group (Wald $X^2[1] = 41.5$, $p < 0.001$). Demographic, biometric, and self-reported questionnaire data for the θCA>θBE and θBE>θCA groups are reported in Table 1.

294

295 *3.5. Classification of participants: LPP and theta power*

296 Next, to determine how both individual differences in the attribution of motivational salience to food
297 cues and the engagement of cognitive control confer vulnerability to cue-induced eating, we created four
298 participant groups by crossing the results of the LPP and theta power classification procedures. We labeled
299 these four groups 00 (the P>C and θBE>θCA groups), 01 (the P>C and θCA>θBE groups), 10 (the C>P and
300 θBE>θCA groups), and 11 (the C>P and θCA>θBE groups). Demographic, biometric, and self-reported
301 questionnaire data for these four crossed groups are reported in Table 2.

302 After crossing the group assignments for both the LPP and theta power cluster analyses, Poisson
303 regression analysis demonstrated a significant effect of group assignment on the number of candies eaten
304 during the experiment (Wald $X^2[3] = 106.2$, $p < 0.001$). Notably, although the individuals in group 00 ate the
305 least, those in the three remaining groups had similar levels of eating behavior on average (Wald $X^2[2] = 0.825$,
306 $p = 0.662$) (Fig. 6).

307

308 *3.6. Demographics and covariates*

309 We conducted Poisson regression analysis modeling the effect of crossed group assignment on eating
310 behavior which included the demographic, biometric, and questionnaire data outlined in Table 2 as covariates.
311 We found a significant main effect of group assignment on eating behavior for all groups except for those with
312 both LPP and theta risk factors (group 01 AKA the P>C and θCA>θBE group) after controlling for factors such
313 as hunger and satiety [29], eating behavior [31,32], sensitivity to reward and punishment [40], mood [34], and
314 impulsivity [33].

315

316 **4. Discussion**

317 This study aimed at determining the role that individual differences in affective and cognitive brain
318 systems have in regulating cue-induced eating. This work is informed by results from animal models
319 demonstrating that individual differences in top-down attentional control and bottom-up attribution of
320 motivational salience to food-related cues influence reward-seeking behaviors. By investigating both food-

321 related decision-making and the motivational salience of cues, we aimed to elucidate how these mechanisms
322 contribute to cue-induced eating behavior in humans. Because we found that both LPP and theta power-based
323 groups showed statistically significant differences in eating behavior, we may conclude that these mechanisms
324 likely act independently to regulate eating behavior during the cued food delivery task

325 By applying cluster analysis to the LPP responses evoked by food-related and non-food-related
326 motivationally salient images, we identified two reactivity profiles associated with vulnerability to cue-induced
327 eating: individuals with larger LPP responses to food-related cues than to pleasant images (C>P group) ate
328 significantly more than did individuals with larger LPP responses to pleasant stimuli than to food-related cues
329 (P>C group). These results replicate those from previous studies [15,16] and support the hypothesis that
330 individual differences in the tendency to attribute motivational salience to food-related cues than to other
331 pleasant stimuli underlie vulnerability to cue-induced eating [12,13,39,41].

332 Furthermore, we found that midfrontal theta power increased after the delivery of candies & beads and
333 that individual differences in midfrontal theta power were associated with vulnerability to cue-induced eating.
334 Specifically, individuals with higher phasic theta power following the delivery of candies than of beads
335 (θCA>θBE) ate more during the cued food delivery task than did individuals with the opposite theta response
336 pattern (θBE>θCA). Authors have proposed that changes in theta power over midfrontal scalp sites represent
337 an index of the engagement of cognitive control mechanisms [25] because midfrontal theta tends to increase
338 when an individual is executing a task that requires increased attentional demands, such as inhibiting
339 prepotent responses [26,27] and performing otherwise cognitively demanding tasks [28]. In light of these
340 findings, the results of the present study suggest that some individuals struggle with food-related decision-
341 making and that these individuals are more likely to engage in cue-induced eating when a palatable food
342 option is available [10,42].

343 In addition, we found that the LPP-based and θ-based reactivity profiles reflect affective and cognitive
344 mechanisms that independently contribute to cue-induced eating. This is evidenced by the finding that the C>P
345 and P>C groups had similar theta power dynamics during food-related decision-making. Furthermore, after
346 crossing the group assignments for the LPP and theta-based cluster analyses, we found that the group with
347 neither the LPP nor the theta risk factor (P>C and θBE>θCA group) ate the least of all four groups and that the

three remaining groups exhibited similar levels of eating behavior on average. These results imply that individuals at risk for cue-induced behaviors due to the presence of both LPP and theta-based risk factors are no more vulnerable to cue-induced behaviors than are those who have only one of these two risk factors. Further studies are needed to determine if this finding is consistent across populations and paradigms.

Whereas the validity of the LPP in predicting cue-induced behavior has been well replicated [16,38,43] and is consistent with theoretical models concerning the motivational salience of cues [12,14], the predictive validity of a theta-based correlate described in the present study is novel and should be considered preliminary until it is replicated. Although in previous studies researchers have used theta power to index the engagement of higher cognitive functions during the execution of cognitively demanding tasks [25], in the present study, we did not explicitly manipulate cognitive load during food-related decision-making. Because we did not explicitly manipulate cognitive control via a cognitively demanding task, inferring from our results that the observed dynamics in theta power are in fact due to the engagement of higher cognitive functions remains speculative.

Also, although our results suggest that individual differences in the ability to exert cognitive control are independent from the tendency to attribute motivational salience to cues, studies using preclinical models suggested that these two cognitive-motivational styles are coupled: animals with high motivational salience attributed to food-related cues are also more impulsive and less able to implement top-down attentional control in the presence of cues than are those who do not attribute high motivational silence to food-related cues [12,44–46]. In light of these incongruous findings, theta power analysis as implemented in the present study may not capture the same aspects of cognitive control that are captured using animal models, which may be more related to impulsivity than to top-down attentional control. Our self-reported data did not demonstrate significant differences in impulsivity scores between groups, which may explain the divergent findings of the present study and those in the animal literature. Meanwhile, results from human and animal studies of cue-induced behavior may be inconsistent because of the inherent differences between humans and animal models [41]: complex human behaviors result from a more evolved cognitive control system [10] than that of animal models and thus might not be probed as effectively using animal behavioral approaches. Further studies leveraging the paradigm that we used here will facilitate the bidirectional translation and improvement of both animal models and human subjects research investigating cue-induced behavior.

375 Our findings are consistent with those for neurobiological models suggesting that both high reactivity to
376 food-related cues and deficits in cognitive control can lead to excessive eating [11]. Furthermore, because our
377 results suggest that cognitive control and reward networks independently contribute to cue-induced eating,
378 these findings further emphasize the need for individualized treatments of maladaptive reward-seeking
379 behaviors. This has worthwhile clinical implications: by separating the roles of both affective and cognitive
380 psychophysiological correlates in predicting cue-included eating, we may identify potential biomarkers of
381 vulnerability to overeating and obesity that could guide treatment decisions. For example, using repetitive
382 transcranial magnetic stimulation (rTMS), a non-invasive neuromodulation technique [47], we can upregulate
383 brain activity in cognitive control networks [48] or downregulate brain activity in reward networks [49]. Thus, a
384 patient identified to have high affective vulnerability may be selected for inhibitory rTMS of the ventromedial
385 prefrontal cortex, which is commonly implicated in reward processing [50]. Also, a patient with cognitive
386 vulnerability may be more effectively treated with excitatory rTMS of the dorsolateral prefrontal cortex, which is
387 commonly implicated in executive control [51].
388 In conclusion, our results demonstrated that both the amplitude of the LPP and theta power are
389 predictive of cue-induced eating behavior, suggesting that both affective and cognitive mechanisms are
390 implicated in the regulation of cue-induced eating. By simultaneously measuring both the amplitude of the LPP
391 and theta power while participants were in the presence of food-related cues and actual food rewards, we
392 clarified the mechanisms underlying cue-induced eating behaviors. Continuing this line of investigation may
393 inform clinicians of mechanisms underlying maladaptive eating and may foster the development of
394 personalized clinical interventions for excessive eating.
395
396 **Declaration of Competing Interest**
397 The authors declare no conflicts.
398
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556 **Figure Captions**

557 **Fig. 1.** A schematized representation of the timing of events in the cued food delivery task. In this task,
558 participants viewed emotional, neutral, and food-related images and made food-related decisions. After a food-
559 related image was presented on the screen, the participant received either a candy (reward condition), which
560 they could eat or discard, or a bead (control condition). ITI: intertrial interval.

561

562 **Fig. 2.** ERPs for centroparietal scalp sites (see inset for EEG electrode locations) showing that, on average,
563 the LPP amplitude was higher for motivationally relevant pictures, such as mutilations or erotic images, than for
564 other types of pictures. The box outlines the temporal ROI used to calculate the LPP for each picture category.
565 Each picture was presented on the screen at time 0.

566

567 **Fig. 3.** We replicated the finding that individual differences in LPP responses to food cues & non-food-related
568 pleasant images are predictive of cue-induced eating. (**A**) *K*-means clustering of the LPP responses identified
569 two groups: one with higher LPP amplitudes for food cues than for pleasant images (C>P group) and one with
570 higher LPP amplitudes for pleasant images than for food cues (P>C group). Both groups exhibited the
571 canonical pattern of progressively larger LPP responses for both pleasant and unpleasant images as a function
572 of their motivational salience. Error bars: 95% CI. (**B**) The C>P group ate significantly more candies during the
573 cued food delivery task than did the P>C group. SE: standard error. Error bars: 95% CIs.

574

575 **Fig. 4.** Time series data showing changes in average theta power over mid-frontal scalp sites during the
576 candy, bead & neutral experimental conditions. Theta power over midfrontal scalp sites (see inset for EEG
577 electrode locations) increases during the candy and bead conditions but not when the participant is passively
578 viewing neutral pictures. The box indicates the temporal ROI used to calculate theta power. The candies and
579 beads were delivered at time 0.

580

581 **Fig. 5.** We found that individual differences in theta power during food-related decision-making were predictive
582 of cue-induced eating. (**A**) *K*-means clustering of theta power data identified two groups: one with higher theta

power for the candy condition than for the bead condition (θCA>θBE group) and one with higher theta power for the bead condition than for the candy condition (θBE>θCA group). Error bars: 95% CIs. (**B**) The θCA>θBE group ate significantly more candies during the cued food delivery task than did the θBE>θCA group. SE: standard error. Error bars: 95% CI.

Fig. 6. Number of candies eaten per group, by crossed LPP and theta power groups. After crossing the participant groups according to the LPP and theta-based cluster analyses, we found that individuals with neither LPP nor theta-based "risk factors" (P>C and θBE>θCA [group 00]) ate the least of all four groups. The three remaining groups exhibited similar levels of eating behavior on average. SE: standard error. Error bars: 95% CIs.

Figure 1

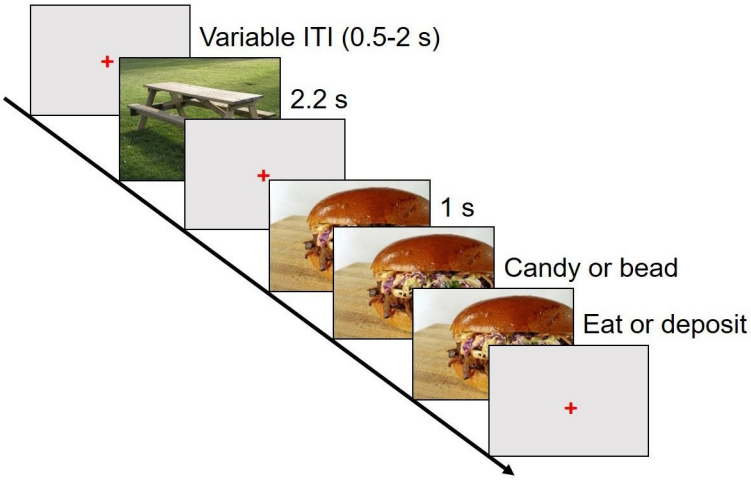
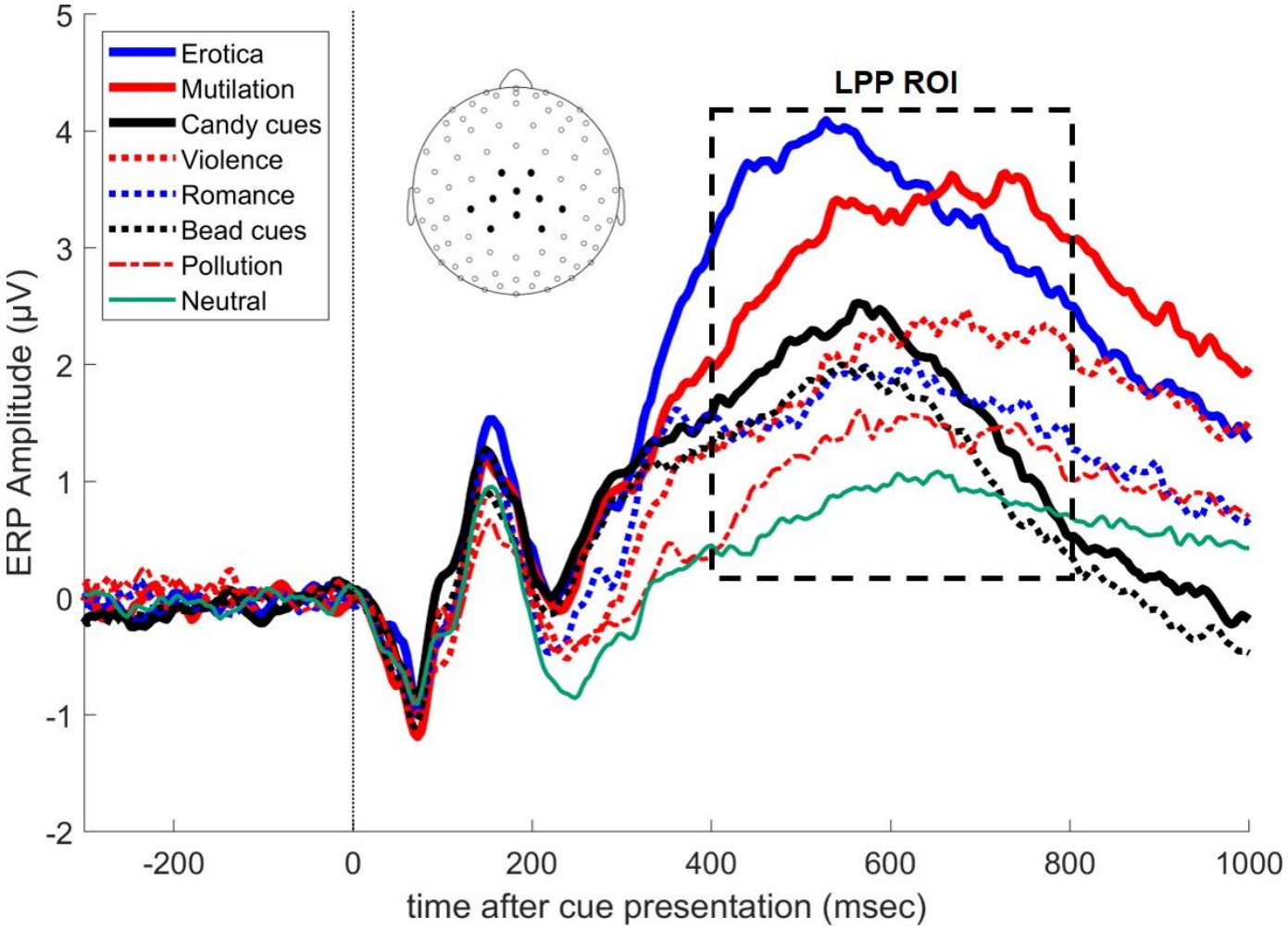
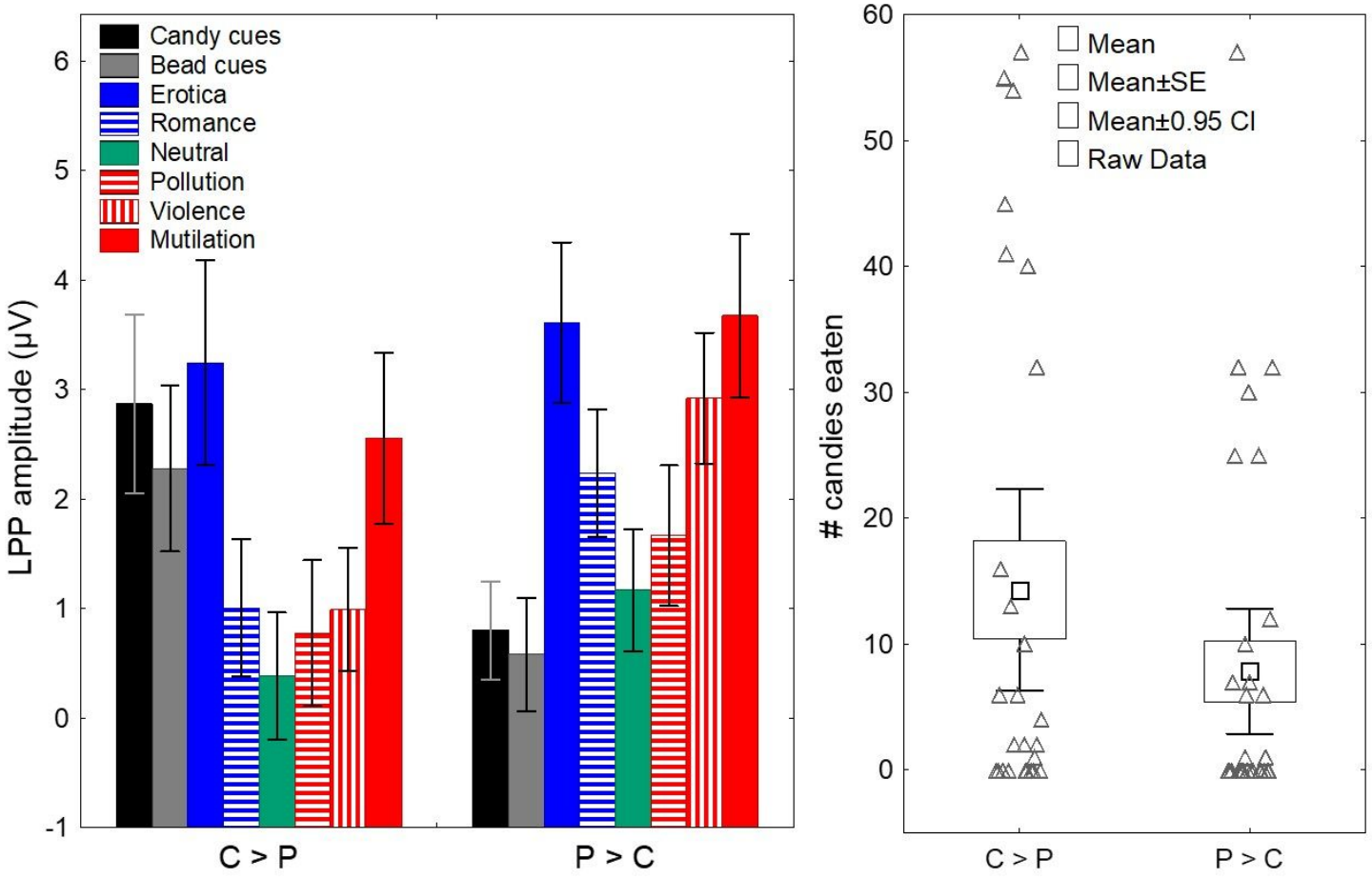


Figure 2


Erotica
Mutilation
Candy cues
Violence
Romance
Bead cues
Pollution
Neutral
LPP ROI
ERP Amplitude (μV)
time after cue presentation (msec)
5
4
3
2
1
0
-1
-2
-200
0
200
400
600
800
1000

601 Figure 3A (left)-3B (right)



603 Figure 4

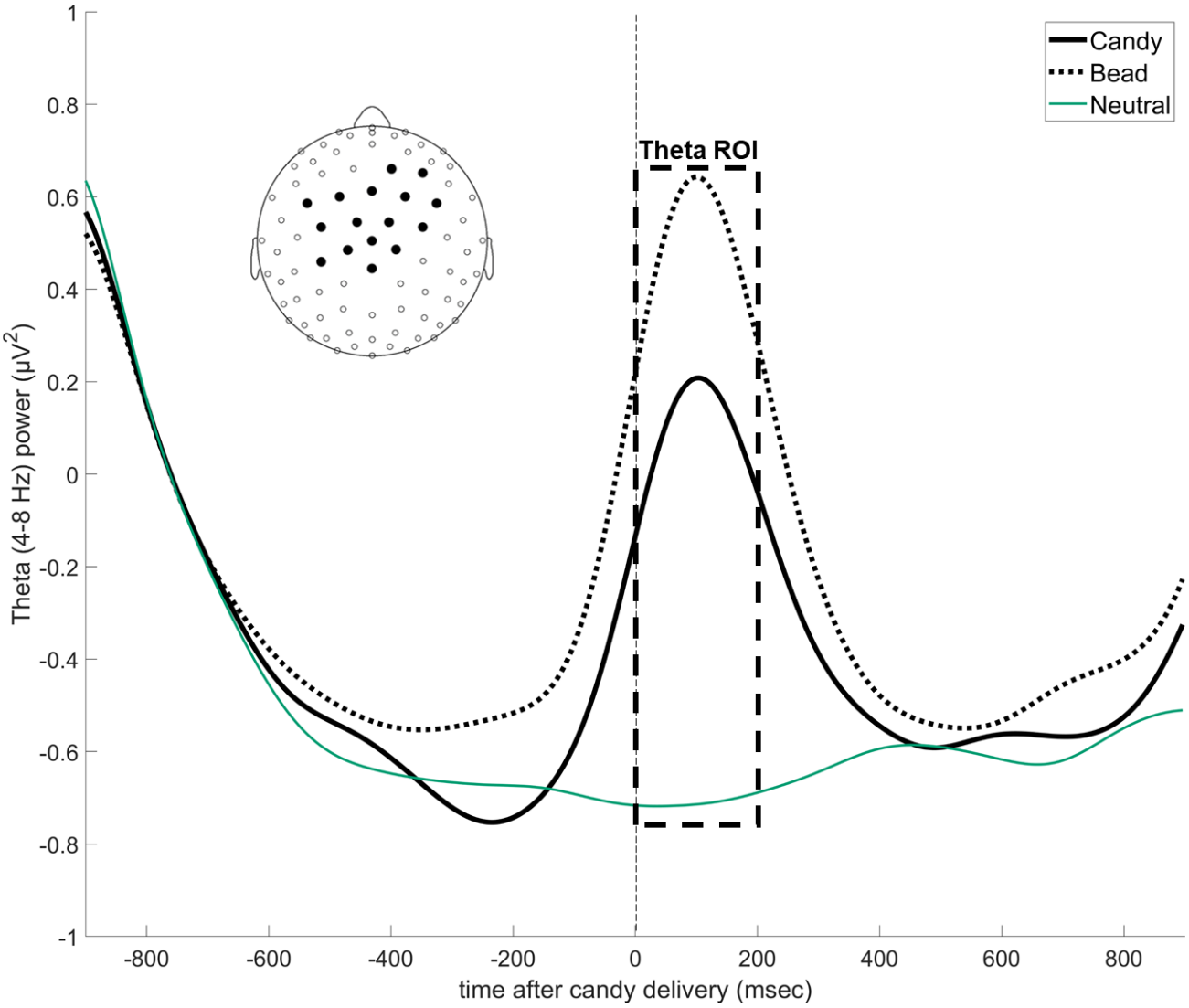

Candy
Bead
Neutral
Theta ROI
Theta (4-8 Hz) power (μV²)
time after candy delivery (msec)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-800
-600
-400
-200
0
200
400
600
800

Figure 5A (left)-5B (right)

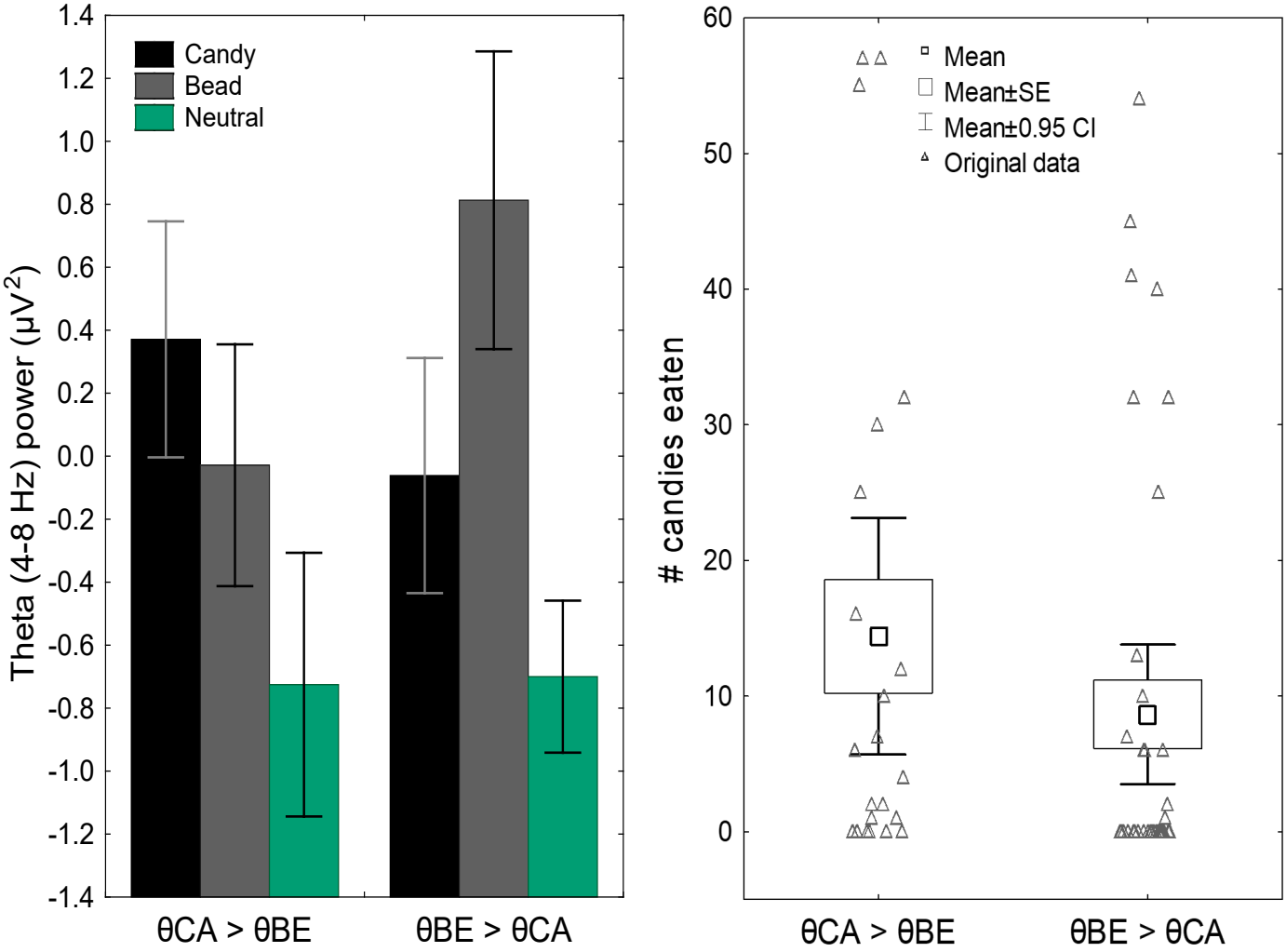
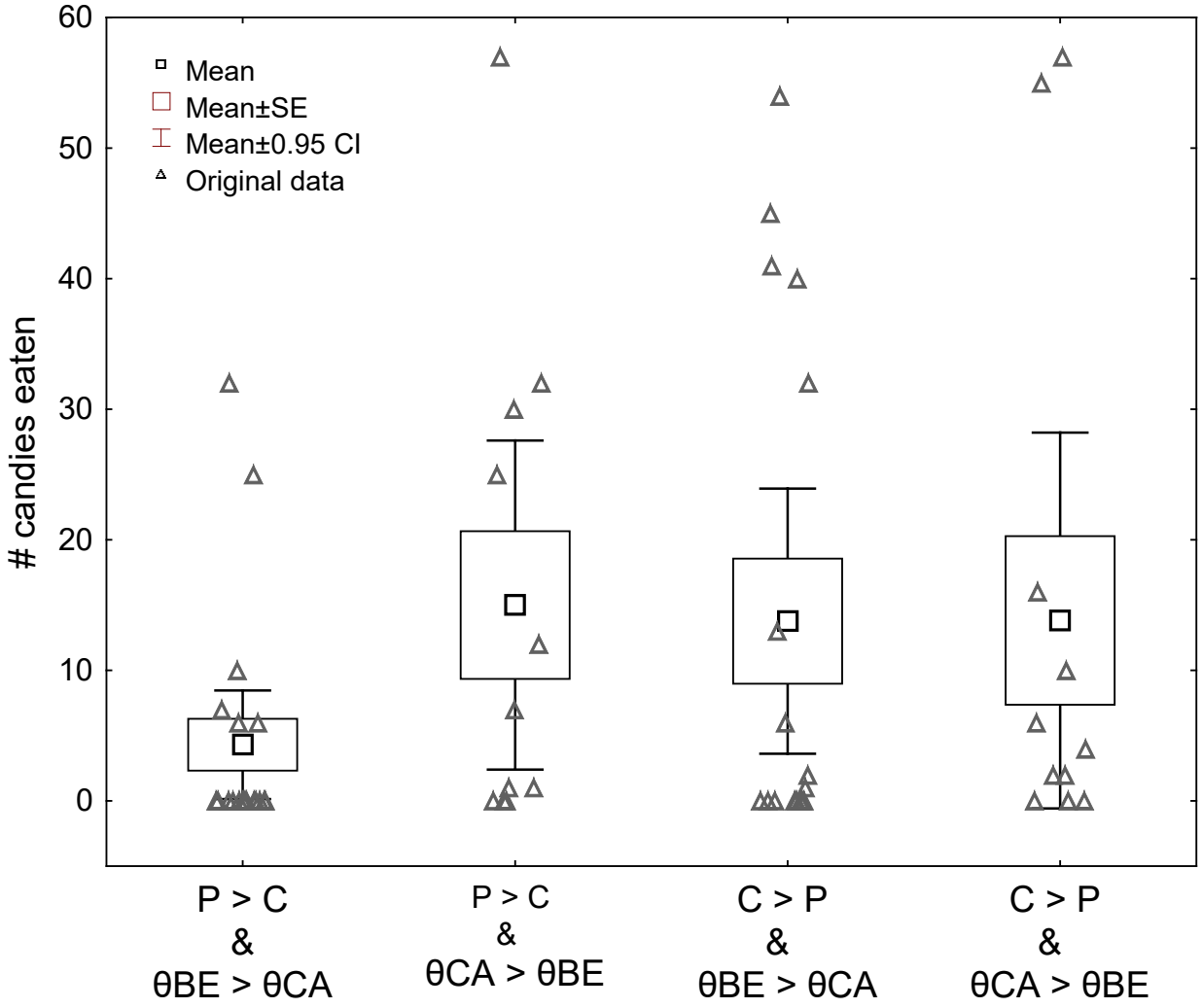


Figure 6


Mean
Mean±SE
Mean±0.95 CI
Original data
candies eaten
60
50
40
30
20
10
0
P > C & θBE > θCA
P > C & θCA > θBE
C > P & θBE > θCA
C > P & θCA > θBE

613 **Table 1**

614 Demographic, biometric, and self-reported data for all subjects and the LPP and theta-based participant

615 groups.

	Mean (SD)				Mean (SD)		
Characteristic	All subjects (*n* = 59)	C>P (*n* = 28)	P>C (*n* = 31)	*p* (C>P vs. P>C)	θCA>θBE (*n* = 22)	θBE>θCA (*n* = 37)	*p* (θCA>θBE vs. θBE>θCA)
Age, years	45 (11.67)	43 (14.09)	48 (8.52)	0.10	43 (11.61)	47 (11.62)	0.21
Women, %	46	39	52	0.34	82	24	0.56
Race, %							
Black/African American	64	75	55		73	59	
White/Caucasian	24	14	32		18	27	
Asian	7	11	3		5	14	
More than one race	3	0	6		5	3	
I prefer not to say	2	0	3		0	3	
BMI, kg/m^2	31 (7.75)	30 (8.19)	31 (7.43)	0.69	31 (0.92)	31 (7.42)	0.85
Hispanic or Latino ethnicity, %	12	18	6		14	11	

BIS attention	15.57 (3.63)	15.52 (4.10)	15.61 (3.23)	0.92	15.62 (2.40)	15.54 (4.20)	0.94
BIS motor	21.26 (3.96)	21.33 (4.27)	21.19 (3.74)	0.89	21.62 (4.20)	21.05 (3.86)	0.61
BIS Non-planning	13.22 (2.63)	13.04 (2.68)	13.39 (2.62)	0.62	12.57 (2.20)	13.59 (2.80)	0.16
Center for Epidemiologic Studies Depression Scale	8.53 (4.76)	8.85 (5.44)	8.26 (4.15)	0.64	7.81 (3.76)	8.95 (5.24)	0.39
Snaith-Hamilton Pleasure Scale	1.14 (2.54)	1.33 (2.99)	0.97 (2.12)	0.59	1.05 (3.04)	1.19 (2.26)	0.84
PANAS (+)	33.28 (9.59)	31.15 (10.08)	35.13 (8.89)	0.12	33.90 (8.74)	32.92 (10.14)	0.71
PANAS (-)	17.62 (7.64)	18.19 (7.24)	17.13 (8.05)	0.60	16.95 (8.37)	18.00 (7.28)	0.62
Power of Food Scale	51.88 (19.22)	48.70 (19.88)	54.65 (18.50)	0.24	50.00 (21.7)	52.95 (17.87)	0.58
Food Cravings Questionnaire	101.69 (36.56)	99.07 (37.65)	103.97 (36.05)	0.62	96.62 (37.19)	104.57 (36.40)	0.43
WREQ routine restraint	1.64 (0.87)	1.43 (0.58)	1.83 (1.04)	0.08	1.46 (0.69)	1.75 (0.95)	0.23

WREQ compensatory restraint	2.17 (0.84)	2.05 (0.81)	2.27 (0.85)	0.32	2.17 (0.92)	2.16 (0.80)	0.96	616
WREQ susceptibility to external cues	2.30 (1.00)	2.21 (1.06)	2.37 (0.96)	0.57	2.41 (1.15)	2.23 (0.92)	0.52	
WREQ emotional eating	2.09 (1.02)	1.95 (1.18)	2.21 (0.86)	0.34	2.13 (1.15)	2.06 (0.95)	0.79	
SLIM	0.72 (39.15)	-3.24 (33.45)	4.30 (43.92)	0.46	-11.70 (36.43)	8.11 (39.31)	0.06	
Number of candies eaten	11 (17.19)	14 (20.02)	8 (13.94)	0.21	14 (19.66)	9 (15.42)	0.22	

617 **Table 2**

618 Demographic, biometric, and self-reported data for crossed participant groups

	Mean (SD)			Mean (SD)		Mean (SD)	
Characteristic	Group 00 (*n* = 20)	Group 01 (*n* = 11)	*p* (00 vs. 01)	Group 10 (*n* = 17)	*p* (00 vs. 10)	Group 11 (*n* = 11)	*p* (00 vs. 11)
Age, years	47 (9.15)	48 (7.62)	0.77	46 (14.26)	0.76	37 (12.63)	0.02
Women, %	50	55	0.81	47	0.86	27	0.22
Race, %							
Black/African American	50	64		71		82	
White/Caucasian	35	27		18		9	
Asian	5	0		12		9	
More than one race	5	9		0		0	
I prefer not to say	5	0		0		0%	
BMI, kg/m^2	30 (5.73)	33 (9.83)	0.28	32 (9.11)	0.46	28 (6.15)	0.34
Hispanic or Latino ethnicity, %	10	27		12		0	
BIS attention	15.20 (3.38)	16.36 (2.94)	0.35	15.94 (5.08)	0.60	14.80 (1.32)	0.72
BIS motor	21.20 (3.07)	21.18 (4.90)	0.99	20.88 (4.72)	0.81	22.10 (3.48)	0.47
BIS Non-planning	13.65 (2.85)	12.91 (2.17)	0.46	13.53 (2.83)	0.90	12.20 (2.30)	0.17

Center for Epidemiologic Studies Depression Scale	8.05 (4.02)	8.64 (4.54)	0.71	10.00 (6.36)	0.27	6.90 (2.60)	0.42
Snaith-Hamilton Pleasure Scale	1.45 (2.52)	0.09 (0.30)	0.09	0.88 (1.93)	0.45	2.10 (4.25)	0.60
PANAS (+)	34.95 (9.60)	35.45 (7.85)	0.88	30.53 (10.52)	0.19	32.20 (9.75)	0.47
PANAS (-)	16.25 (6.26)	18.73 (10.75)	0.42	20.06 (8.02)	0.11	15.00 (4.37)	0.58
Power of Food Scale	54.45 (17.61)	55.00 (20.90)	0.94	51.18 (18.56)	0.59	44.50 (22.32)	0.19
Food Cravings Questionnaire	105.05 (37.51)	102.00 (34.93)	0.83	104.00 (36.19)	0.93	90.70 (40.54)	0.34
WREQ routine restraint	1.98 (1.13)	1.55 (0.82)	0.27	1.47 (0.61)	0.10	1.37 (0.53)	0.12
WREQ compensatory restraint	2.28 (0.81)	2.24 (0.97)	0.90	2.02 (0.79)	0.32	2.10 (0.90)	0.58
WREQ susceptibility to external cues	2.25 (0.83)	2.58 (1.18)	0.37	2.21 (1.05)	0.90	2.22 (1.14)	0.94
WREQ emotional eating	2.12 (0.73)	2.36 (1.07)	0.46	1.99 (1.18)	0.68	1.88 (1.24)	0.51
SLIM	17.95 (39.16)	-20.50 (42.70)	0.02	-3.45 (37.31)	0.10	-2.91 (28.17)	0.13

Number of candies eaten	4 (8.89)	15 (18.76)	0.04	14 (19.74)	0.06	14 (21.42)	0.09

621 **Supplementary Materials**

622

623 **Supplementary Figure Captions**

624

625 **Supplementary Table 1**. A list of the IAPS images used in the experiment by picture category and content.

626

627 **Supplementary Fig. S1.** Average LPP responses for each parent picture category (Pleasant, Unpleasant,
628 etc) by LPP group. After averaging LPP amplitudes for the emotional image subcategories (pleasant: erotica
629 and romance; unpleasant: mutilations, violence, and pollution) together, we found that the C>P group had
630 higher LPP amplitudes for food cues than for pleasant images, whereas the P>C group had higher LPP
631 amplitudes for pleasant images than for food cues. Error bars: 95% CIs.

632

633 **Supplementary Fig. S2.** After conducting a repeated-measures ANOVA comparing the theta power under the
634 candy, bead, and neutral conditions for each time point and EEG sensor, we identified the *F*-values that were
635 statistically significant during the 0- to 200-ms time window, during which theta effects are usually the highest.
636 Shown are the EEG sensors that were statistically significant during the 0- to 200-ms time bin based on a
637 Bonferroni correction. The color bar in red indicates the *F*-value magnitude. Critical $F \approx 10$.

638

639 **Supplementary Fig. S3.** Average theta power from the pooled midfrontal sensors in the 0-200 ms time bin
640 under the candy, bead, and neutral conditions by C>P and P>C groups. We compared the theta power for the
641 candy, bead, and neutral conditions in the participant groups formed using *k*-means clustering with LPP data.
642 We did not find significant differences in theta power in the C>P and P>C groups.

643

644

645 **Supplementary Table 1**

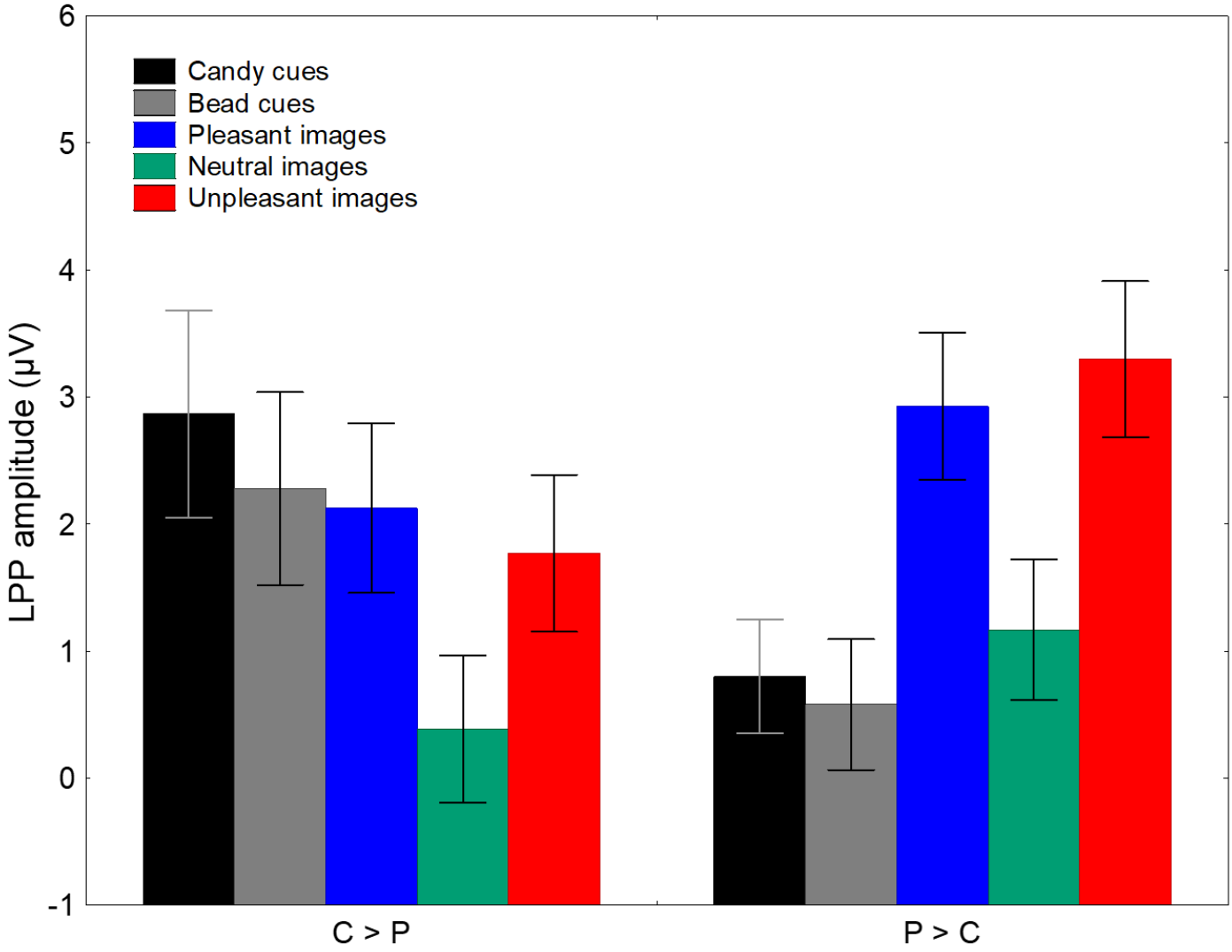
Picture Category	Picture Content	IAPS codes
Pleasant, high arousing	Erotica	4604, 4611, 4647, 4650, 4653, 4658, 4659, 4660, 4666, 4668, 4669, 4677, 4680, 4687, 4690, 4691, 4693, 4694, 4695, 4696, 4698, 4800
Pleasant, low arousing	Romance	2501, 2550, 4597, 4600, 4612, 4616, 4619, 2208, 4599, 4610, 4624, 4625, 4640, 4641, 4643, 4700
Neutral people	People	2037, 2039, 2102, 2107, 2190, 2191, 2210, 2273, 2305, 2359, 2374, 2377, 2383, 2393, 2396, 2397, 2411, 2435, 2441, 2500, 2511, 2512, 2575, 2594, 2595, 2620, 2630, 2635, 7550, 9070
Neutral objects	Household objects	5390, 7000, 7001, 7002, 7006, 7009, 7010, 7011, 7012, 7018, 7020, 7021, 7026, 7030, 7034, 7040, 7041, 7050, 7052, 7053, 7054, 7055, 7056, 7059, 7061, 7062, 7081, 7090, 7150, 7233
Unpleasant objects	Pollution	9322, 9902, 9941, 6020, 7079, 7521, 9010, 9090, 9110, 9290, 9291, 9295, 9300, 9301, 9320, 9373, 9560, 9600, 9621, 9911, 9912
Unpleasant, low arousing	Violence	2703, 6211, 6312, 9429, 9520, 9530, 2811, 3500, 3530, 6210, 6230, 6231, 6242, 6260, 6313, 6315, 6350, 6360, 6510, 6540, 6550, 6560, 6571, 6832, 9414
Unpleasant, high arousing	Mutilation	3000, 3030, 3051, 3053, 3060, 3064, 3068, 3069, 3071, 3080, 3100, 3103, 3110, 3120, 3130, 3140, 3150, 3170, 3180, 3181, 3211, 3213, 3225, 3261, 3400, 6021, 9253, 9265

646

647

648

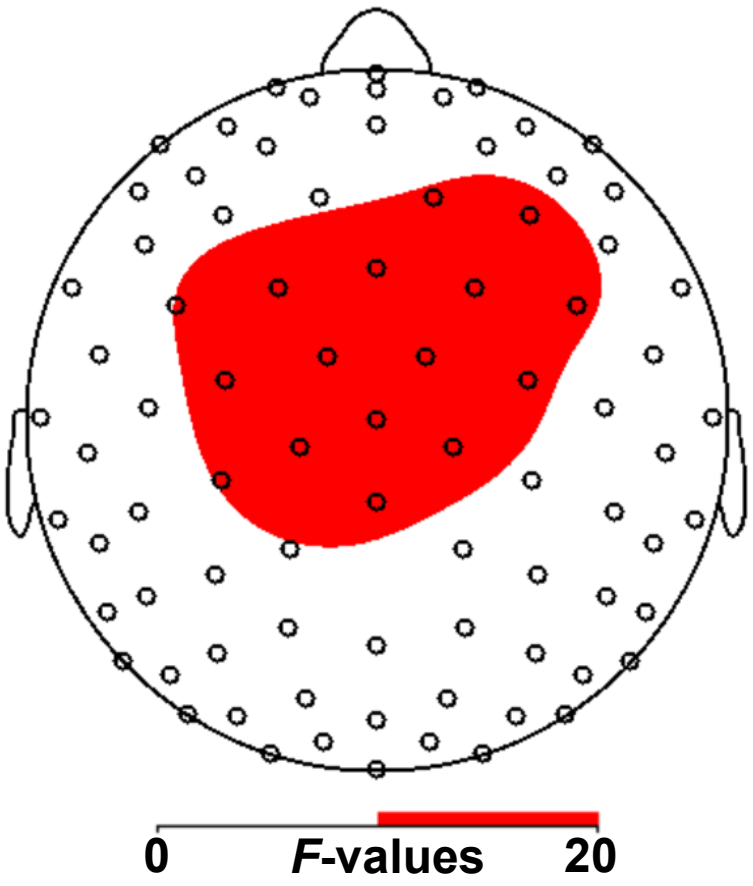
649 **Supplementary Figure S1**

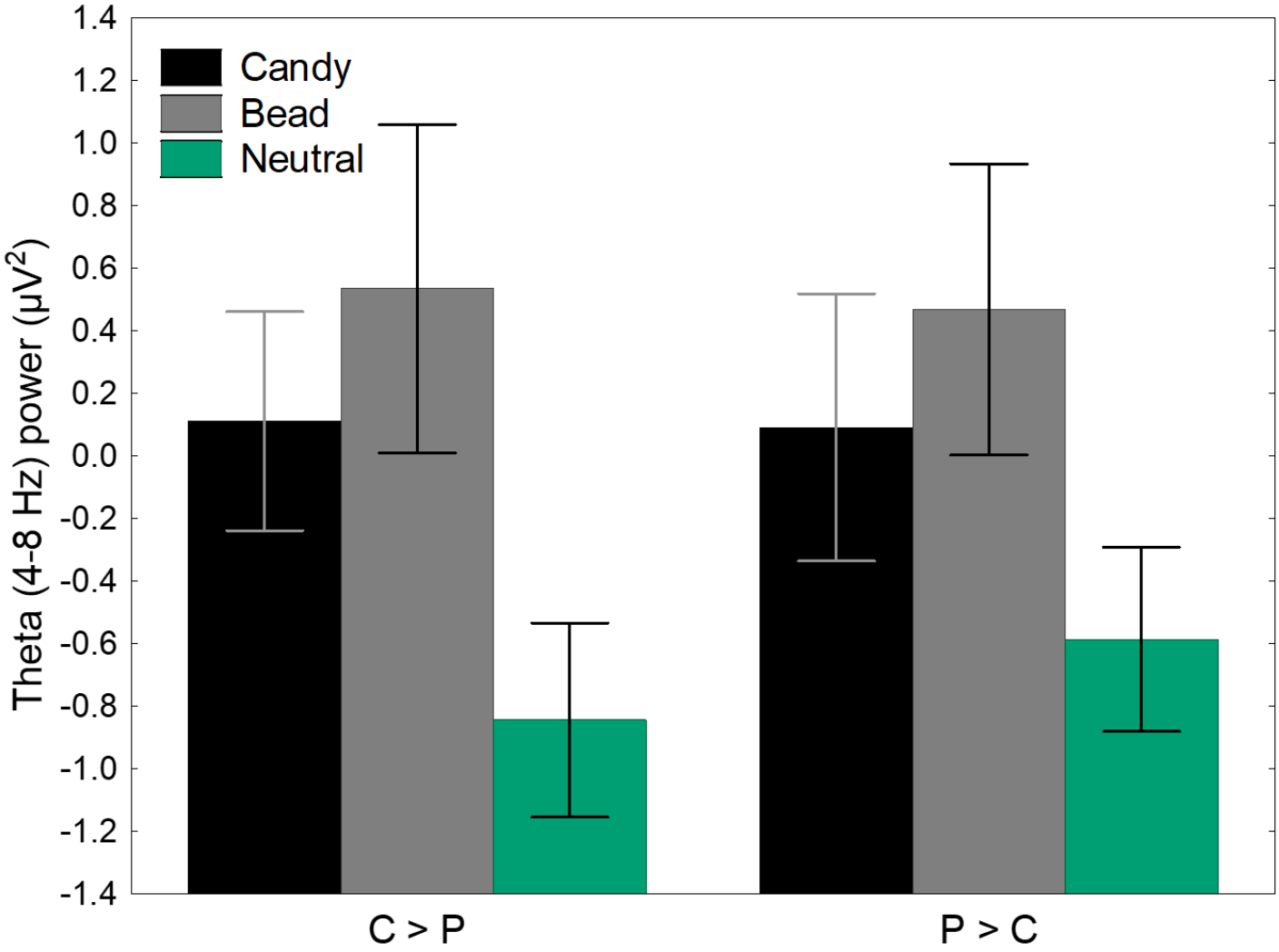


651

652 **Supplementary Figure S2**

653




Candy
Bead
Neutral
Theta (4-8 Hz) power (μV²)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
C > P
P > C

656

657