Go/no-go training affects frontal midline theta and mu oscillations to passively observed food stimuli

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A B S T R A C T
The mere perception of high-calorie food items can trigger strong action tendencies towards these foods. Go/no-go training has successfully been applied to reduce such action tendencies. This study investigated the electrophysiological mechanisms that may underlie the beneficial effects of go/no-go training on food consumption. EEG was measured while 19 participants passively observed pictures of food and non-food items, both before and after the go/no-go training. During training, 50% of the food and non-food items were consistently paired with a go/no-go response. After training, food items that had been associated with a response induced larger mu desynchronization at electrodes over sensorimotor regions, whereas food items that had been associated with withholding from responding induced larger increases in theta power at frontal midline electrodes. These findings suggest that the exerted cognitive control during go/no-go training with attractive food stimuli may become associated with these stimuli and signal the required level of control during subsequent encounters.

1. Introduction
Rising numbers of overweight people are a global health problem (Swinburn et al., 2011). Many people struggle with regulating their behavior towards attractive food items that are omnipresent in their environment (Stroebe, 2008). Indeed, the mere perception of high-calorie food items, but also of related stimuli such as their pictures, triggers a strong Pavlovian approach bias, resulting in an action tendency towards these foods even without a metabolic need (Foroni et al., 2016; Johnson, 2013; Watson et al., 2014). There is no established psychological intervention that prevents weight gain or results in lasting weight loss. Recent studies have investigated interventions that change the immediate response to food items through cognitive training (Becker et al., 2015; Hollands et al., 2011; Kemps et al., 2014; for a review see Stice, Lawrence et al., 2016). One cognitive training designed to change response tendencies to food is go/no-go training, in which pictures of target food items are repeatedly presented on no-go trials of a go/no-go training. This way, the automatic, Pavlovian go response associated with appetitive food pictures is replaced with an instrumentally learned no-go response. These associations have been demonstrated to transfer to other contexts and result in reduced target food valuation, choice and consumption in healthy-weighted and overweight individuals (for recent meta-analyses see Allom et al., 2016; Jones et al., 2016; Turton et al., 2016). However, little is known about the functional mechanisms that underlie these effects. The aim of the current study is to gain further insight into the neural mechanisms that contribute to the effectiveness of go/no-go training in reducing food consumption.

Food consumption is controlled by multiple interactive brain systems: in particular the hypothalamus (Saper and Lowell, 2014), the reward system (Kenny, 2011), and cognitive control areas (Volkow et al., 2011). The hypothalamus monitors and controls the metabolism of nutrients and drives feeding behavior (Berthoud and Morrison, 2008). Yet, palatable foods also present potent rewards that may promote eating even in the absence of a homeostatic need: High-calorie food activates mesolimbic dopaminergic pathways (Kenny, 2011; Volkow et al., 2008) and may blunt satiety signals (Erlanson-Albertsson, 2005). This has led to an addiction model of obesity in which overeating results from an imbalance between overly active hedonic responses to food, and impairments in impulse control regulation (Volkow et al., 2008; Volkow and Wise, 2005).

The perception of palatable food is also accompanied by activations of sensorimotor structures involved in grasping, tasting, and eating. The sight and anticipation of palatable food and food-related stimuli lead to enhanced activity in sensorimotor and premotor brain areas representing parts of the mouth, possibly inducing simulation of eating...
and tasting (de Araujo and Rolls, 2004; Gearhardt et al., 2014; Geliebter et al., 2006; Rapuano et al., 2016; Stic et al., 2013, 2008, 2011). Relatedly, increased activation is found in prefrontal, premotor and parietal cortex during the observation of food being grasped (Cheng et al., 2007; Iacoboni et al., 2005), being moved to the mouth (Fogassi et al., 2005), and being ingested and manipulated in the mouth (Ferrari et al., 2003). More generally, mere perception of manipulable objects such as tools and foods can automatically activate motor representations of their use (reviews in van Elk et al., 2008; Martin, 2007; see Girardi et al., 2010, for behavioral studies). Especially objects associated with an inherent or trained approach bias, such as attractive food items, can activate the motor system up to the primary motor cortex (Chiu et al., 2014; Freeman et al., 2015, 2014).

Whereas a reasonable amount of knowledge has been gathered about the neural systems that regulate food consumption, less is known about the functional mechanisms underlying the behavioral effects of go/no-go training with food stimuli. There is some work on food presented in non-training go/no-go tasks. Watson and Garvey (2013) found that food stimuli generated stronger P3 and N2 (only in females) event-related potentials than non-food stimuli when presented as infrequent no-go cues in a go/no-go task. These findings suggest that food stimuli more easily capture attention (reflected in the P3) and demand enhanced cognitive control (reflected in the N2) than non-food stimuli. A few fMRI studies also used go/no-go tasks in the context of eating disorders. Lock et al. (2011) found that patients with binge eating behaviors more strongly activated precentral motor regions, dIPFC, and ACC on no-go trials of a classical go/no-go task than anorexic patients and healthy controls (Lock et al., 2011). This finding suggests that binge eaters required more extensive cognitive control to suppress their motor impulses during no-go trials. Batterink et al. (2010) furthermore found that participants with high BMIs demonstrated more impulsive behavior on a go/no-go task with healthy food as go and palatable food as no-go stimuli (Batterink et al., 2010). Their BMIs correlated negatively with frontal lobe activation and positively with activations in reward areas.

In the present study, we focused on two functional mechanisms that may underlie the behavioral effects of go/no-go training with food stimuli (for a review see Veling et al., 2017). First, as suggested by Watson and Garvey (2013), reduced food consumption after go/no-go training could reflect enhanced recruitment of cognitive control in association with these foods. During the training, on food go trials, the Pavlovian automatic motor activation is congruent with the instrumental instruction to respond, resulting in faster responses and increased go-response learning (Chiu et al., 2014; Guitart-Masip et al., 2014; van Wouwe et al., 2015). On food no-go trials, however, the instruction not to respond may conflict with the automatic response tendency triggered by the food items, resulting in Pavlovian-instrumental conflict (Guitart-Masip et al., 2014).

Frontal cognitive control processes likely play a role in resolving this type of conflict and suppressing the response impulse (Cavanagh et al., 2013; Guitart-Masip et al., 2012; Hall, 2016; Ly et al., 2016). Specifically, larger increases in frontal midline (FM) theta-band oscillations (4-8 Hz, measured at medial frontal electrode sites) coincide with a better ability to overcome valence-action conflicts (Cavanagh et al., 2013). FM theta oscillations have generally been associated with the online regulation of behavior (Cavanagh and Frank, 2014; Cohen et al., 2011; Mitchell et al., 2008). They are consistently observed in situations requiring conflict detection and resolution (see, e.g., Cohen and Cavanagh, 2011; Cohen and Donner, 2013; Nibgur et al., 2012), including no-go trials in go/no-go tasks (Brier et al., 2010; Harmony et al., 2009; Harper et al., 2016; Kirmizi-Alsan et al., 2006; Yamanaka and Yamamoto, 2010). FM theta has been localized to the medial frontal cortex (MFC), in particular the ACC and pre-supplementary motor area (pre-SMA; Ishii et al., 1999; Pizzagalli et al., 2003; Tsujimoto et al., 2006; see review in Cavanagh and Frank, 2014). Thus, consistently pairing food items with withholding a response may result in increased cognitive control, reflected as increased FM theta power.

A second mechanism that could underlie the effects of go/no-go training with food stimuli is an attenuation of the automatic sensorimotor activations associated with palatable foods. Indeed, consistently pairing objects with an inherent or trained approach bias with a no-go cue diminishes motor cortex activation (Chiu et al., 2014; Freeman et al., 2015, 2014). Motor cortex activation coincides with a decrease in local mu power (9–14 Hz, measured over motor cortex). Mu oscillations over sensorimotor cortex desynchronize during action execution and action observation (Braadbaart et al., 2013; Muthukumaraswamy et al., 2006; Pulvermüller, 2005), and also in response to the mere visual perception of objects with a motor function (Proverbo, 2012). Thus, consistently pairing food items with a no-go response may also result in decreased automatic activation of sensorimotor cortex (Verbruggen and Logan, 2008), reflected as increased mu power.

As a first step towards understanding the mechanisms underlying the effect of go/no-go training on behavior towards food, in the current study we focused on the effects of training on how food items are subsequently processed in the brain. Therefore, we explored how training of consistent associations between food stimuli and go versus no-go responses affected oscillatory brain activity during processing of the same food items after training. First, we measured EEG while participants passively observed food and non-food pictures. Next, participants performed a go/no-go training. Half of the food and the non-food pictures were consistently paired with a go response, while the other half of the pictures were consistently paired with a no-go response. Finally, passive observation of the stimuli was repeated to investigate training-induced changes in EEG power dynamics. Based on the hypothesis that go/no-go training may affect cognitive control, we expected an increase in theta oscillations at FM electrodes for food stimuli that were paired with no-go responses during training. Based on the hypothesis that the training may affect automatic sensorimotor activation, we expected a reduction in mu desynchronization at electrodes over sensorimotor cortex for food stimuli that were paired with no-go responses during training.

Since weight increases and a desire to lose weight are not restricted to obese individuals, but prominent in a large part of our society (Santos et al., 2017; Stroebe et al., 2013), and since no-go training with food stimuli is found to be effective in overweight as well as non-obese individuals (Allom et al., 2016; Chen et al., in press; Jones et al., 2016; Turton et al., 2016), this first study started by examining the underlying brain processes in healthy-weighted adults.

2. Methods

2.1. Participants

19 Radboud University undergraduate students participated in this experiment for course credits or a financial compensation of € 15. At the time of conducting this study (in 2014), this sample size was based on previous behavioral work (Veling et al., 2013) and EEG studies investigating effects of motor experience on passive observation (Marshall et al., 2009; Paulus et al., 2012). Because EEG data quality of one participant was insufficient, the data of 18 participants were included in all analyses (age M 22.0, SD 2.03; 4 male; all right-handed). Their BMIs ranged from 17.63 to 24.54 (M 21.45, SD 2.05) and most participants did not adhere to a diet on a regular basis (M 2.06, SD 1.00 on a 5-point Likert scale with 0 being “never”).

Participants were asked to refrain from eating for at least 2 h before the experiment, to prevent them from being fully satiated (e.g., Veling et al., 2013). The onset time of the testing sessions varied between 8.30 and 15.30 h. Two participants reported that they did not have breakfast before participation, so their last meal took place on the day before. The remaining participants indicated that their last meal was on average 198 min prior to participation (SD 75, range 90–360). Participants rated how hungry they were on a 7-point Likert scale (with 0 being “not at
all” and 7 being “very much”) on average as 4.74 (SD 1.52), with 15/18 ratings being a 4 or higher. Participants provided written informed consent, and all procedures were executed in line with institutional guidelines and international laws.

2.2. Stimulus materials

Pictures of high-calorie food items and non-food items were adapted from the Full4Health-Collection (Charbonnier et al., 2016). Pictures displayed either non-food items (office supplies, e.g., pencils, calculators) or food items (e.g., chocolate sticks, cakes). Food items were presented on a white plate, non-food items were presented on a flat, white disk of the same size. All items were concrete objects that could be picked up and held with one hand. All food items could be handled manually, and for the majority this would be the preferred method of interaction (as compared to interaction using cutlery, see Supplementary Material Section S1 for pictures of all the stimuli that were included in our final sample). All food items were high in caloric value. Prior to the current experiment, 24 separate undergraduate students (age M 20.63, SD 2.31; 6 male) rated 60 food and non-food pictures on six characteristics, mainly reflecting visual attractiveness and properties related to their use, on a continuous scale ranging from 0 to 100: eagerness to grasp the object, visual likability, weight, requirement to handle the object with force or with precision, size, and comfort of the grasping movement in case the object would have to be picked up. Questions related to object use were included to control for differences in motor activation between conditions reflecting previous experience with these objects. We did not ask this group to restrict their food consumption before participation. Comparable food and non-food pictures were selected based on the correlations between these independent ratings. We included the 20 food and 20 non-food pictures that correlated over participants on the most dimensions (at least 3 out of 6). The average ratings of the included pictures on all characteristics are reported in Table 1. We tested per characteristic whether the ratings of the selected pictures differed significantly between food and non-food pictures with t-tests (see Table 1). This was only the case for the eagerness to grasp the object, and marginally for how comfortable grasping the object would be.

2.3. Tasks

2.3.1. Passive observation task

Participants observed pictures of food and non-food items. Pictures were presented for 1000 ms, separated by the presentation of a fixation cross for 1000–1500 ms (Fig. 1a). 20 food and 20 non-food pictures were each shown 6 times. Presentation order was randomized per set of 40 trials (one presentation of each stimulus). These 240 passive observation trials were interspersed with 24 filler trials (at least one every 10 trials), which were included to ensure task engagement. On these trials, (non-task) food or non-food pictures were presented upside down, and participants were required to press the space bar with their right hand. Before the real task started, participants performed 6 practice trials (including 1 filler), featuring non-task pictures. The passive observation task was administered twice, once before and once after performance of the go/no-go training (referred to as POT1 and POT2, respectively). Stimulus order was independently randomized on both occasions. The duration of the passive observation task was 12 min on average.

2.3.2. Go/no-go training

During the go/no-go training, the same 40 stimuli were presented as in the passive observation tasks. Half of the food and half of the non-food stimuli were now consistently coupled with the instruction to respond versus to withhold from responding. Every condition (food go; food no-go; non-food go; non-food no-go) comprised 10 stimuli that were each presented 6 times, resulting in 60 trials per condition. The total set of 240 trials was presented as one block without breaks.

On each trial, participants were presented with a fixation cross (Fig. 1b). After the participant pressed the left mouse button with their right index finger and a delay of 1000–1500 ms, the stimulus was presented (max. 2000 ms). 100 ms after the stimulus appeared, a low or a high pitch sound cue indicated whether the participant was required to release the mouse button and press the space bar (go) with the same hand, or maintain pressure on the mouse button (no-go). The reason for instructing participants to keep pressing the mouse button during no-go trials was that for the analysis of mu power it is beneficial to have an accurate trigger of movement onset. Release of the mouse button during go-trials provided this trigger (and an accurate measure of reaction times). The relation between sound pitches and the requirement to

<table>
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<tr>
<th>Aspect</th>
<th>Food</th>
<th>Non-food</th>
<th>t-test</th>
<th>p</th>
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</thead>
<tbody>
<tr>
<td>Wanting to grasp</td>
<td>62.30</td>
<td>5.98</td>
<td>33.49</td>
<td>4.35</td>
</tr>
<tr>
<td>Looking nice</td>
<td>48.11</td>
<td>6.83</td>
<td>50.61</td>
<td>4.90</td>
</tr>
<tr>
<td>Weight</td>
<td>46.54</td>
<td>14.79</td>
<td>51.33</td>
<td>13.36</td>
</tr>
<tr>
<td>Grasp with force or precision</td>
<td>47.22</td>
<td>13.53</td>
<td>52.31</td>
<td>12.38</td>
</tr>
<tr>
<td>Size</td>
<td>46.66</td>
<td>9.63</td>
<td>48.15</td>
<td>9.40</td>
</tr>
<tr>
<td>Comfortable to grasp</td>
<td>47.68</td>
<td>6.24</td>
<td>51.34</td>
<td>5.19</td>
</tr>
</tbody>
</table>

Note: t-tests were conducted to compare food and non-food pictures.
respond or not was counterbalanced over participants. The distance between the mouse and the space bar was 30 cm. Responses (release of the mouse button) were detected in an interval of 1600 ms following stimulus presentation. The correctness of the participant’s behavior was determined on-line and feedback was provided in the form of a red (incorrect) or green (correct) square surrounding the stimulus object for a duration varying between 500 and 800 ms. If no response was detected within the response window of 1600 ms, feedback presentation followed this window immediately. If a response was initiated within the response window, feedback presentation was postponed to maximally 2000 ms after stimulus onset. Consecutively, the fixation cross reappeared and participants could start the next trial by pressing the mouse button.

At the start of the go/no-go training participants completed 6 practice trials (50% go, 50% no-go), featuring non-task stimuli. The duration of the training was on average 17 min.

2.3.3. Ratings of desire to grasp and demographics

Immediately following POT2, participants indicated for each picture that was included in the experiment “how eagerly they wanted to grasp the object” on a continuous scale ranging from 0 to 100, with 0 being “not at all” and 100 being “very eagerly”. The session ended with a demographics questionnaire, including questions on hunger status, dieting behavior, weight, and height.

2.4. EEG recordings and preprocessing

EEG data were recorded at 500 Hz using Ag/AgCl scalp electrodes (Brain Products GmbH, Germany), using a SYNAMPS amplifier (Neuroscan, Herndon, VA). Electrodes were placed at 26 scalp locations (FP2, AFz, F3/4, F7/8, FCz, FC1/2, FC5/6, Cz, C3/4, T7/8, CP1/2, CP5/6, Pz, P3/4, P7/8; placement according to the international 10–20 system), the left collarbone (ground), the right (online reference) and left mastoid (used as additional reference), below the left eye (VEOG), and at the outer canthi of both eyes (HEOG). EEG data were preprocessed in Matlab (The Mathworks, Natick, MA) using EEGLAB functions (Delorme and Makeig, 2004) and custom-written scripts. The data from the three tasks (POT1, go/no-go, and POT2) were preprocessed separately. Preprocessing consisted of the application of a band-pass filter at 0.5–30 Hz, extraction of stimulus-locked epochs (POTs: −1.5 to 2.0 s; go/no-go: −3.0 to 4.0 s), and re-referencing to the linked mastoids. Trials containing artifacts (sudden, irregular changes in the EEG signal at one or multiple electrodes, including large fluctuations in amplitude, bursts of activation, and baseline shifts) were manually selected and removed (POT1: M 6.62%, SD 4.77% of the trials removed; go/no-go: M 10.56%, SD 8.49%; POT2: M 8.24%, SD 6.56%). Blinks, horizontal eye-movements, and other consistent artifacts were removed using independent component analysis (POT1: M 3.56, SD 1.46 components removed; go/no-go: M 3.28, SD 1.23; POT2: M 2.67, SD 1.08). Finally, EEG data were converted to the scalp Laplacian transformation (Kayser and Tenke, 2006) to decrease volume conduction and increase spatial specificity.

2.5. Time-frequency decomposition

Error and filler trials were excluded from further analyses (POT1: M 0.61, SD 0.70 errors on non-filler trials; go/no-go M 3.44, SD 3.50; POT2: M 1.11, SD 1.88). The included number of trials per condition was on average 56.00 (SD 3.25) for the POT1, 52.78 (SD 5.94) for the go/no-go training, and 54.85 (SD 4.51) for the POT2. The lowest number of trials in any participant in any condition was 47 for the POT1, 23 for the go/no-go training, and 40 for the POT2. Time-frequency decomposition was conducted via complex Morlet wavelet convolution. Specifically, to decrease processing time, we multiplied the FFT-derived complex power spectra of the EEG time series per trial with a family of Morlet wavelets, and then took the inverse Fourier transform of this signal. The wavelets were defined as complex sine waves $\psi_{2f}(t) = e^{2\pi if \cdot t}$, where $i$ is the complex operator, $f$ the frequency, and $t$ the time point, tapered by a Gaussian distribution $e^{-\pi t^2/2}$, where $S = c/2\pi f$ defines the width of the Gaussian at each frequency, and $c$ is the number of oscillatory cycles. Frequencies ranged from 1 to 30 Hz in 40 logarithmically spaced steps, $c$ increased from 3 to 7 cycles over frequencies. Oscillatory power was defined as the modulus of the resulting complex signal $Z(t): p(t) = \text{real}(Z(t))^2 + \text{imag}(Z(t))^2$. Power was normalized with a decibel (dB) conversion using $10 \log_{10}$ (power baseline).

2.6. Statistical analyses of behavior

Ratings of the desire to grasp the objects depicted in the four conditions after training were entered into a $2 \times 2$ ANOVA with factors Response (Go, No-go) and Object category (Food, Non-Food). Additionally, ratings per condition were correlated with hunger status.

Behavioral accuracy during the go/no-go training was quantified as the percentage correctly given or withheld responses, depending on whether a response was expected. Accuracy scores were entered into a $2 \times 2$ ANOVA with factors Response (Go, No-go) and Object category (Food, Non-Food). Reaction times during the go/no-go training were quantified as the time difference between the sound cue and the moment the mouse button was released. Reaction times on go trials were compared between food and non-food stimuli with a t-test. Because behavior was perfect in many participants and conditions, the computation of $d'$ scores (requiring a transformation to z-scores) was impossible.

2.7. Statistical analyses of the EEG data

Control-related differences in FM theta power commonly peak at electrode FCz (e.g., Cohen and Cavanagh, 2011; Cohen and Donner, 2013; Nijburg et al., 2012) and mu power changes related to hand movements at electrodes C3/4 (e.g., Pfurtscheller et al., 2006, 1997; Sauseng et al., 2009). Because topographical plots of condition-average post-stimulus power in the go/no-go training confirmed the relevance of these electrodes in the current experiment (Fig. 2a), we focused our statistical analyses on FCz for theta power (4–8 Hz) and C3 (electrode over sensorimotor cortex contralateral to the right hand, which was used for responding during the go/no-go training) for mu power (9–14 Hz).

Visual inspection of condition-average fluctuations in theta and mu power at these respective electrodes indicated that during the go/no-go training theta power peaked between 300 and 700 ms post-stimulus, whereas mu power decreased most between 500 and 900 ms post-stimulus (Fig. 2b). Additionally, mu showed a more sustained decrease between 900 and 1300 ms post-stimulus. For the passive observation task, we inspected condition-average power fluctuations in the version administered after the go/no-go training (POT2) to determine the relevant time windows, as control- and motor-related activations were expected to be strongest after the training. Here, both theta and mu power peaked ~100 ms earlier than during the go/no-go training, possibly because there was no sound cue to be awaited (Fig. 2c). We selected a window of 200–600 ms post-stimulus for theta power and windows of 400–800 ms and 800–1200 ms post-stimulus for mu power in the POT analyses.

Per electrode, frequency band, and time window, we extracted trial-average power for each condition separately. For the go/no-go training, power values were entered into a $2 \times 2$ ANOVA with factors Response (Go, No-go) and Object category (Food, Non-Food). For the passive observation tasks, the variable Session (Before, After training) was added to this design. Greenhouse-Geisser corrections were applied when necessary, but uncorrected degrees of freedom are reported.
3. Results

3.1. Ratings of the desire to grasp the depicted stimuli after training

Ratings of the desire to grasp were significantly higher for food than for non-food pictures ($F(1,17) = 26.304$, $p = 0.001$, $\eta^2_p = 0.607$; Fig. 3a): ratings were on average 62.7 for food pictures ($SD = 15.9$, range 22.0–87.1 averaged over stimuli per participant) and 33.6 for non-food pictures ($SD = 14.0$, range 6.3–49.6). Ratings did not differ between go and no-go conditions ($F(1,17) = 1.101$, $p = 0.309$, $\eta^2_p = 0.061$), nor was there an interaction effect of Response and Object category ($F(1,17) = 0.254$, $p = 0.621$, $\eta^2_p = 0.015$). Because previous studies have reported a difference in liking of food stimuli associated with a go versus a no-go response (e.g., Veling et al., 2013), we performed an additional $t$-test to specifically investigate this effect in the current measure of the desire to grasp. Even though 72% of the participants (13/18) had higher mean ratings for food items associated with a go compared to a no-go response, this difference was not significant ($t(17) = 0.929$, $p = 0.366$, $d = 0.218$). Hunger status predicted the desire to grasp food pictures (go: $r = 0.668$, $p = 0.002$; no-go: $r = 0.639$, $p = 0.004$; Fig. 3b), but not non-food pictures (go: $r = -0.159$, $p = 0.529$; no-go: $r = -0.324$, $p = 0.190$), in both response conditions.

3.2. Behavioral accuracy during go/no-go training

Behavioral accuracy during the go/no-go training was higher for no-go compared to go responses ($F(1,17) = 15.648$, $p = 0.001$, $\eta^2_p = 0.479$; Fig. 3c), even though participants behaved very accurately in both conditions. Accuracy did not differ between food and non-food stimuli ($F(1,17) = 1.755$, $p = 0.203$, $\eta^2_p = 0.094$), and there was no interaction of Response and Object category ($F(1,17) = 0.456$, $p = 0.508$, $\eta^2_p = 0.026$). Reaction times (time of mouse button release) were incorrectly registered for 4 participants. Reaction times in the remaining 14 participants did not differ between food go and non-food go stimuli ($t(13) = 0.471$, $p = 0.645$, $d = 0.111$; Fig. 3d); note that the data of 18 participants were included in all other analyses of behavior and EEG.

3.3. Theta and mu power during go/no-go training

During training, theta power at electrode FCz between 300 and 700 ms did not differentiate between food and non-food pictures ($F(1,17) = 1.216$, $p = 0.286$, $\eta^2_p = 0.067$), or between go and no-go trials ($F(1,17) = 0.188$, $p = 0.670$, $\eta^2_p = 0.011$; Fig. 4a). Object category also did not interact with Response ($F(1,17) = 0.267$, $p = 0.612$, $\eta^2_p = 0.015$).

Similarly, mu power at electrode C3 between 500 and 900 ms showed no effect of Object category ($F(1,17) = 1.475$, $p = 0.241$, $\eta^2_p = 0.080$), no effect of Response ($F(1,17) = 2.681$, $p = 0.120$, $\eta^2_p = 0.136$), and no interaction effect ($F(1,17) = 0.472$, $p = 0.501$, $\eta^2_p = 0.027$). Between 900 and 1300 ms after stimulus onset, mu power decreased significantly more in go than no-go trials ($F(1,17) = 12.560$, $p = 0.002$, $\eta^2_p = 0.425$). There was again no effect of Object category ($F(1,17) = 1.637$, $p = 0.218$, $\eta^2_p = 0.088$), nor an interaction between Response and Object category ($F(1,17) = 1.703$, $p = 0.209$, $\eta^2_p = 0.091$).

Visual inspection of the post-stimulus increase in theta power suggested a difference in peak latency between go and no-go trials. We therefore additionally extracted the individual theta power peak latencies between 300 and 700 ms, and compared them with an ANOVA with factors Response and Object category. Indeed, theta power peaked significantly faster for go compared to no-go trials (go: $M = 499.31$ ms, $SD = 95.24$; no-go: $M = 554.17$, $SD = 96.63$; $F(1,17) = 6.591$, $p = 0.020$, $\eta^2_p = 0.279$). Theta power latencies did not differ between food and non-food pictures ($F(1,17) = 0.106$, $p = 0.749$, $\eta^2_p = 0.006$), and there was no interaction effect of Response and Object category ($F(1,17) = 1.756$.

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Fig. 2. Condition-average power distributions. (a) During go/no-go training, theta power (4–8 Hz) was largest at electrode FCz, and mu power (9–14 Hz) showed the largest decrease at contralateral motor electrode C3. White dots indicate electrodes of interest (top row: FCz, bottom row: C3/4) (b) During go/no-go training, the increase in theta power was largest between 300 and 700 ms, and the decrease in mu power between 500 and 900 ms after stimulus onset, followed by a more sustained decrease. (c) During passive observation after the training, the increase in theta power was largest between 200 and 600 ms and the decrease in mu power between 400 and 800 ms after stimulus onset, followed by a second decrease (black dotted boxes indicate windows of interest; stim = stimulus).
Changes in theta and mu power during passive observation

Theta power during passive observation demonstrated a 3-way interaction of Object category, Response, and Session (F(1,17) = 4.803, p = 0.043, η₂ = 0.220; Fig. 4b and c). There were no main effects and no other interaction effects (Object category × Response F(1,17) = 2.055, p = 0.170, η₂ = 0.108; all other p-values > 0.2, η₂ < 0.08). Separate ANOVAs for the sessions before and after training revealed a significant interaction of Object category × Response after training (POT2: F(1,17) = 5.088, p = 0.038, η₂ = 0.230), whereas there was no interaction before training (POT1: F(1,17) = 0.503, p = 0.488, η₂ = 0.029). Follow-up t-tests demonstrated that after training, theta power for food pictures was larger when pictures had been associated with a no-go compared to a go response (t(17) = -2.505, p = 0.023, d = 0.590), whereas there was no difference for non-food pictures (t(17) = 0.584, p = 0.567, d = 0.138).

Mu power between 400 and 800 ms showed a significantly larger decrease for pictures that had been associated with a go than with a no-go response (F(1,17) = 4.566, p = 0.047, η₂ = 0.212; Fig. 4b). Additionally, there was a 3-way interaction of Object category, Response, and Session (F(1,17) = 7.050, p = 0.017, η₂ = 0.293; Fig. 4d). There were no other significant main or interaction effects (Session F(1,17) = 2.453, p = 0.136, η₂ = 0.126; all other p-values > 0.2, η₂ < 0.09). Separate ANOVAs for the two sessions indicated that after training there was a marginally significant effect of response: the decrease in mu power was larger for objects paired with go than with no-go responses (F(1,17) = 4.299, p = 0.054, η₂ = 0.202). Additionally, only after training there was a significant interaction of Object category and Response (POT1: F(1,17) = 3.487, p = 0.079, η₂ = 0.170; POT2: F(1,17) = 4.584, p = 0.047, η₂ = 0.212). Follow-up t-tests demonstrated that mu power decreased more after training for food stimuli that had been associated with a go response, as compared to food stimuli paired with a no-go response (t(17) = -2.511, p = 0.022, d = 0.592). No such difference was found for non-food stimuli (t(17) = -0.828, p = 0.419, d = 0.195). Although the interaction of Object category and Response was also marginally significant before training, none of the follow-up t-tests showed a significant difference.

In the later time window (800–1200 ms), mu power was still significantly lower for stimuli associated with a go than with a no-go response (F(1,17) = 9.329, p = 0.007, η₂ = 0.354). The three-way interaction of Session, Response, and Object category was no longer significant (F(1,17) = 3.205, p = 0.091, η₂ = 0.159). There were no other significant main or interaction effects in this window (Session: F(1,17) = 3.171, p = 0.093, η₂ = 0.157, all other p-values > 0.3, η₂ < 0.06).

For both theta and mu power, Object category and Response demonstrated significant interactions after, but not before, go/no-go training. Additional post-hoc comparisons of pre- and post-training power levels for each object type separately are reported in the Supplementary Material Section S2.

To sum up, go/no-go training affected the processing of stimuli in a subsequent passive observation task. In particular, food stimuli associated with a go response were associated with a stronger suppression of motor-related mu power as compared to stimuli associated with a no-go response. Furthermore, food stimuli that had been associated with a no-go response were accompanied by stronger theta power after training than food stimuli paired with a go response.

Relation between task-related theta and mu power dynamics

After testing our a-priori hypotheses about the separate effects of go/no-go training on frontal theta and sensorimotor mu oscillations, we continued with a post-hoc exploration of the relation between the two processes. Inspection of post-stimulus, condition-average theta power at electrode FCz and mu power at electrode C3 suggested that the theta power increase peaked earlier than the mu power decrease (see Section 2.7). Additionally, the post-training power results showed a larger increase in theta power for food no-go than food go pictures, and a smaller decrease in mu power for food no-go than food go pictures. This
could suggest a relation between the two processes: more control may have resulted in less motor activation. To further investigate this idea, we first statistically compared the latencies of the two responses. We searched for individual peak latencies in both bands between 200 and 1000 ms after stimulus presentation. FCz theta power indeed peaked significantly earlier than C3 mu power, both during the go/no-go training ($t(17) = -5.276$, $p < 0.001$, $d = 1.243$) and during passive viewing after the training (POT2, $t(17) = -3.411$, $p = 0.003$, $d = 0.804$).

Next, we computed the correlations between theta-power increases and mu-power decreases over participants in the food no-go condition, where the largest increase in control would have resulted in the largest decrease in motor activation (values as used in the previous ANOVAs). However, correlations were not significant for either the training or the passive viewing task (go/no-go: $r = 0.285$, $p = 0.251$; POT2: $r = 0.143$, $p = 0.570$), so participants with higher theta power did not have higher power values during food no-go trials. We also explored trial-to-trial correlations between theta and mu power in the same condition for each participant individually. These correlations were not significant in any participant ($p$-values > 0.3 in 16 out of 18 participants). Finally, we entered these single-subject correlations for all four conditions into ANOVA's with the factors Object category, Response, and Session. The correlations in the food no-go condition did not differ significantly from the correlations in the other conditions, nor were there any other significant differences (GNG: all $p$-values > 0.2, $\eta_p^2 < 0.08$; POT: Session * Response $F(1,17) = 3.044$, $p = 0.099$, $\eta_p^2 = 0.152$, all $p$-values > 0.1, $\eta_p^2 < 0.130$). Thus, whereas post-stimulus theta-power increases consistently preceded mu-power decreases, our results did not provide support for a direct relation between the two processes.

To explore the relation between brain dynamics and subjective ratings of the stimuli, post-hoc we also correlated theta and mu power...
during go/no-go training and passive observation with the ratings of the desire to grasp the stimuli, as well as with hunger status. These analyses are reported in the Supplementary Material Section S3.

4. Discussion

With the current study, we provide one of the first attempts to investigate the neural dynamics underlying the effects of go/no-go training on subsequent food picture processing and, ultimately, food consumption. We aimed to complement previous studies investigating the effect of go/no-go training using behavioral and self-report measures (e.g., Chen et al., 2016; Houben and Jansen, 2011; Lawrence et al., 2015b; Veling et al., 2013). We examined how go/no-go training with food and non-food items affected processing of these items during subsequent passive viewing, compared to passive viewing before training (similar to, for example, Rüther et al., 2014; Weisberg et al., 2007). In line with current theories on the brain systems underlying food consumption (Volkow et al., 2011), we hypothesized that go/no-go training with palatable food items would (1) stimulate the recruitment of cognitive control in association with these foods, and (2) attenuate the automatic sensorimotor activations associated with these foods. Theta power at FM electrodes was used as a measure of cognitive control, mu power over lateral sensorimotor regions as a measure of sensorimotor activation.

We demonstrated that go/no-go training affected both cognitive control (theta) and sensorimotor processes (mu) associated with specific food items. That is, training to execute (go) or withhold motor actions (no-go) towards specific food stimuli influenced the processing of these stimuli during a subsequent passive viewing task. Importantly, these findings suggest that sensorimotor and cognitive control processes remain associated with specific stimuli after training, and may become activated again during subsequent perception of these stimuli, influencing behavioral decision making.

4.1. Specificity of effects of go/no-go training

The effects of go/no-go training on both theta and mu power were specific to food as compared to non-food stimuli, and were only found after training. These results are in line with the results of Veling et al. (2008), who showed that go/no-go training reduced the perceived value of attractive but not of neutral or unattractive stimuli (also see Chen et al., 2016). According to the Behavior Stimulus Interaction theory (BSI; Veling et al., 2008), repeated suppression of response tendencies towards an attractive stimulus will result in devaluation of the stimulus to avoid a continuing cycle of automatic approach tendencies and response inhibition. In addition to the previously reported influence of go/no-go training on the stimulus value (Chen et al., 2016, 2018; Lawrence et al., 2015a; Veling et al., 2013, 2008), the current findings suggest that the training also affects the cognitive control and sensorimotor activations associated with food stimuli (Verbruggen et al., 2014). The training effect on behavioral measures such as food evaluation and selection likely involves interactions between stimulus valuation and cognitive control and sensorimotor activations (Wessel et al., 2015). However, as stimulus value is processed in brain areas that are hard or impossible to measure with EEG (e.g., the basal ganglia and/or vmPFC), the current results do not allow us to speculate on the details of these interactions.

4.2. Theta power over frontal midline areas

Theta at FM electrodes consistently increased in response to stimulus presentation, peaking between 200 and 600 ms during passive observation, and between 300 and 700 ms during the go/no-go training. Previous studies have implicated FM theta and the MFC in general in learning and behavioral adaptation (reviews in Cavanagh and Frank, 2014; Ullsperger et al., 2014). Similar increases in FM theta have been reported in response to, for example, novel stimuli, stimulus-response conflict, response errors and negative feedback stimuli (see, e.g., Cavanagh et al., 2012, 2010, 2009, Cohen, 2016, 2011a; Cohen and van Gaal, 2013; Mas-Herrero and Marco-Pallarés, 2014; Nigbur et al., 2012; van de Vijver et al., 2011). FM theta oscillations can signal the need for increased cognitive control to other brain areas such as IPFC, which will in turn exert the required control (Gehring and Knight, 2000; Kouneiher et al., 2009; Ridderinkhof et al., 2004; Shenhav et al., 2013), and theta oscillations can also themselves be part of the physiological mechanism that instantiates cognitive control through, for instance, long-distance coherence and cross-frequency coupling (see, e.g., Cohen, 2011b; Narayan et al., 2013; Womelsdorf et al., 2010a, 2010b).

The presumed sources of theta oscillations measured at FM electrodes reside in the MFC, including dorsal ACC (dACC) and pre-SMA (see review in: Cavanagh and Frank, 2014). Neurons in the macaque ACC support the animal to adjust its behavior to changing reward contingencies in the environment (Shima and Tanji, 1998). Accordingly, the Predicted Response Outcome model (PRO) (Alexander and Brown, 2011) proposes that MFC predicts action outcomes and uses the predictions to select behavior. Interestingly, other studies in macaques (Kennerley et al., 2011, 2009) and rats (Cowen et al., 2012; Hillman and Bilkey, 2010) found that neurons in the MFC also code the costs and effort associated with particular behaviors. In line with these findings, the recent Expected Value of Control theory (EVC) of dACC function proposes that dACC determines the optimal level of control that is needed for the processing of a specific stimulus (Shenhav et al., 2013). In this perspective, the current training effects in theta power might reflect changes in the expected cost and benefit values associated with specific stimuli that were included in the go/no-go training (Shenhav et al., 2014). Note, however, that we cannot distinguish whether the current post-training differences in theta power reflect increased conflict associated with food no-stimuli, or increased expected costs reflecting the learned effort to withhold responses to specific food objects.

4.3. Mu power over sensorimotor areas and interactions between theta and mu

In line with previous studies showing that objects become associated with specific actions when they are consistently trained together (Proverbio, 2012; Rüther et al., 2014; Weisberg et al., 2007; review in: van Elk et al., 2014), we found that go/no-go training increased mu desynchronization in response to food stimuli associated with a go compared to a no-go response. No such effect was found for non-food stimuli. This difference in results between food and non-food stimuli may be caused by the difference in attractiveness of the two stimulus categories. Food stimuli are palatable and characteristically associated with action and consumption (Berridge, 2009). The current non-food stimuli were also manipulable, but participants’ desire to grasp these objects was rated much lower than for the food items. Thus, the stronger training effect for food compared to non-food stimuli may have resulted from the alignment between go training and the strong Pavlovian tendency to approach food items, in particular when participants have not eaten for a while (Berridge, 2009), as was the case in the present study. In support of this idea we found that the desire to grasp food items was strongly influenced by the participant’s hunger status.

Whereas the perception of manipulable objects such as the items presented in our task can activate motor-related brain areas (reviews in van Elk et al., 2008; Martin, 2007) no mu desynchronization was found during the passive observation task before the training in any of the conditions. This suggests that participants may have used a shallow processing strategy to detect the filler trials, on which the image was flipped across the horizontal axis. Attending to superficial features of an image significantly decreases brain-wide cortical activations as well as memory performance (e.g., Mandzio et al., 2004; Marzi and Viggiano, 2008).
The current filler stimuli could be detected using such a strategy, as the distance between the upper edge of the plate and the edge of the image was larger for flipped compared to non-flipped pictures. Repeated practice with the stimuli in the go/no-go training may have contributed to deeper encoding in the second passive observation task, enabling effects of object category and motor instruction on mu desynchronization.

We also explored the relation between effects in theta and mu power, considering the possibility that cognitive control as signaled by FM theta may influence subsequent sensorimotor activation as indicated by mu. In line with this idea, theta peaked significantly earlier than mu. Although the opposite patterns of effects in theta and mu in the food go and food no-go conditions appear to be consistent with the idea that more cognitive control is associated with less sensorimotor activation to food objects, additional correlational analyses of theta and mu power at subject level and at trial level did not indicate significant cross-frequency coupling between theta and mu power. Note, however, that the absence of a correlational effect does not rule out a relationship between cognitive control processes and sensorimotor activation. Such a relationship may be indirect, or it may be found in, for example, phase–amplitude coupling between theta phase and mu amplitude (Axmacher et al., 2010; Canolty and Knight, 2010). The current sample size and trial count did not permit such sophisticated analyses. More detailed investigation of the relationship between cognitive control and sensorimotor activation is left for future research.

4.4. Limitations and future directions

In accordance with previous research, we expected differences between go and no-go trials during the go/no-go training especially in the size of the increase in theta power (Harmony et al., 2009; Harper et al., 2016; Kirmizi-Alsan et al., 2006; Yamanaka and Yamamoto, 2010). Whereas we found that theta power peaked earlier in go trials than in no-go trials, no difference in the amount of theta power was observed between go and no-go trials. Rather, theta power increased in all conditions, suggesting an increase in control on go as well as no-go trials. A possible explanation for the absence of condition differences is that the go/no-go training included auditory cues to signal go and no-go responses. Considering that auditory evoked potentials (including responses in the theta frequency band) from Heschl’s gyrus typically project to midline frontocentral electrodes (Bruneau et al., 1993; Fuenteamilla et al., 2008; Picton et al., 1974) theta activations associated with auditory processes may have overshadowed the effects of response inhibition.

Another possible explanation for the absence of theta power differences between go and no-go trials could be that the training did not elicit strong response conflict in the no-go trials. Behavior during training seems to support this idea: the number of errors on no-go trials is close to zero, and RTs are longer than in standard go/no-go tasks (Wessel, 2017). However, the mu power decrease in all conditions for food stimuli as reflected in mu desynchronization, no effect of training was found on the desire to grasp food objects. However, our procedure differed from previous studies in multiple ways. Firstly, our procedure did not include a pre-measurement of the desire to grasp the stimuli. Hence, we cannot assess the change in ratings caused by the training. Despite our attempt to match the food and non-food stimuli, any effect of training may still have been masked by initial differences between go and no-go stimulus conditions in the extent to which items evoked a desire to grasp. Secondly, we did not assess the willingness to grasp the stimuli immediately after the go/no-go training, but only after the second passive observation task. Consciously rating the stimuli might change the automaticity of the acquired associations and, thus, their processing during passive observation. Yet, not responding to any pictures during passive observation might also interfere with the trained associations between stimuli and go versus no-go responses. Because our main focus in the current study was on the changes in functional brain mechanisms, we first included the second passive observation task, at the risk of decreasing differences in picture evaluations, which we have robustly demonstrated elsewhere (Chen et al., in press, 2016, 2018; Veling et al., 2008). Finally, the assessment of the willingness to grasp the objects may not completely align with their perceived attractiveness, as the evaluation of the willingness to grasp may more strongly reflect physical aspects of the objects such as their texture and weight. Future research may examine multiple, separate aspects of picture evaluation in addition to the desire to grasp, such as the perceived attractiveness (Lawrence et al., 2015a; Veling et al., 2013, 2008), but also, for example, the desire to consume and the imagined tastiness of food items (de Araujo and Rolls, 2004; Stice et al., 2013, 2011).

Relatedly, we now assessed changes in brain processing of stimuli due to the go/no-go training by comparing activation during passive viewing before and after training with ANOVAs. When subjective picture evaluation would be assessed in more detail, future research might utilize mediation analyses to examine whether changes in brain processing after training are related to evaluation effects (or other changes) in the subjective evaluation scores. Such an analysis would allow a better understanding of the functional relationship between changes in brain processing and changes in subjective evaluation of the pictures due to the go/no-go training.

Finally, it is important to note that the current study featured only a limited number of food and non-food stimuli, and that all food stimuli were high in calories. Although we tried to match the food and the non-food items on as many of the selected characteristics as possible, differences may still remain, both within and between stimulus categories (such as their texture and the complexity of the action required to use to object). Note though that variations in caloric value and functional use of objects cannot explain the effects of the go/no-go training, as counterbalancing ensured that each stimulus was paired with go and no-go responses across participants. Still, more research is needed to examine the robustness of the current findings and the generalizability of the current results to other stimulus categories, including different types of foods as well as different control stimuli.

4.5. Conclusion

In sum, our study investigated the functional brain mechanisms that may underlie the effects of go/no-go training on food stimulus
processing and consumption. Go/no-go training influenced food stimulus processing during subsequent passive observation at multiple cognitive levels: theta power was larger for food stimuli that were paired with no-go as compared to go responses, whereas mu desynchronization was stronger for food stimuli that were paired with go as compared to no-go responses. Our theta findings suggest that the training-induced increase in cognitive control for particular stimuli may remain associated with these stimuli. This interpretation is consistent with recent neurocognitive models of behavioral adaptation suggesting that MFC determines the appropriate level of cognitive control that is required for particular stimuli. Additionally, our findings suggest that go/no-go training may be most effective for highly rewarding and attractive stimuli. This may extrapolate to stimulus domains other than food, such as cigarettes or alcohol, and also suggests this training to be especially effective in obese individuals. Within the domain of food consumption, further research is needed to determine the robustness and the generalizability of the current findings over food items, the transfer of these effects to subsequent behavior, and the persistence of training effects over time. It is our hope that the current research will contribute to effective interventions within the domain of eating disorders and impaired behavioral regulation in general.

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Data accessibility

The datasets generated during and/or analyzed during the current study are stored in the Radboud University repository, and are available from the corresponding author upon request.

Appendix A. Supplementary material

Supplementary data related to this article can be found in the online version at doi:10.1016/j.neuropsychologia.2018.08.023

References


