Benefits of a hungry mind: When hungry, exposure to food facilitates proactive interference resolution

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ABSTRACT

Hunger is an everyday motivational state, which biases cognition to detect food. Although evidence exists on how hunger affects basic attentional and mnemonic processes, less is known about how motivational drive for food modulates higher cognition. We aimed to investigate the effects of food deprivation on proactive interference resolution, in the presence and absence of food. Normal-weight participants performed a recency probes paradigm providing an experimental block with food and object stimuli as well as a control block with object stimuli only, in a fasted and a sated state. Results showed that the interaction of shifts in nutritional state with the perception of food cues evoked an altered resolution of proactive interference. Satiety led to impaired performance, whereas a hungry state resulted in strengthened resistance to proactive interference and lying in between, the control block presenting neutral objects remained unaffected by nutritional state manipulation. Additionally, a further increase in proactive interference resolution occurred when the conflicting probe depicted food compared to non-food objects. We conclude that when exposed to food, hunger initiates biased competition of active memory representations in favor of prioritized source information at cost of familiar, but irrelevant information. The implications of these findings are discussed in terms of an arousal-biased competition in working memory.

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Food intake plays an essential part in all living organisms (Allen, 2012). Hunger is a motivational state, which prioritizes the goal to reach nutritional homeostasis (Berthoud, 2007; Zheng & Berthoud, 2007). In fact, food deprivation recalibrates cognitive systems to a heightened sensitivity for food, leading to a more vivid imagination of meals (Schmid et al., 2005), an attentional bias to food (Higgs, Rutters, Thomas, Naish, & Humphreys, 2012; Piech, Pastorino, & Zald, 2010) and selective alteration of brain responses during sensory (Frank et al., 2010; Goldstone et al., 2014; LaBar et al., 2001; Stockburger, Schmälzle, Flaisch, Bublatzky, & Schupp, 2009) as well as mnemonic processing of food stimuli (Kanoski et al., 2011; Rutters, Kumar, Higgs, & Humpreys, 2015; Morris & Dolan, 2001; Talmi et al., 2013). Moreover, apart from hedonic quality of food reward (Epstein, Leddy, Temple, & Faith, 2007), already the visual

detection of food cues when hungry (Chen, Lin, Kuo, & Knight, 2015) might act as reinforcement by reducing hunger-induced aversive signals (Sternson, Betley, & Cao, 2013; Betley et al., 2015) and leads to an enhanced wanting for food (Berridge, 2009; Ziauddeen et al., 2012). The dynamic motivational salience of food (Berridge, 2009) results from an interplay between stimulus-driven appetence of the cue and fluctuations of the nutritional state (Jiang et al., 2008; Medic et al., 2014; Ziauddeen et al., 2012). Therefore, in a state of nutritional deficiency, the presence of food cues creates a powerful motivational context, strong enough (Lissek, Pine, & Grillon, 2006) to hijack active cognition by motivational arousal (LaBar et al., 2001; Marien, Custers, Hassin, & Aarts, 2012; Morris & Dolan, 2001). Although recent research addressed the question of how food deprivation affects low-level cognitive processes (e.g. psychomotor speed, visual attention), there is a lack of knowledge about effects of hunger on higher cognition in terms of executive control processes. The poor existing evidence suggests that fasting might have a deleterious effect on executive functioning (Benau, Orloff, Janke, Serpell, & Timko, 2014), leading to decreased inhibitory control (e.g. Doniger, Simon, & Zivotofsky,

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2006) and reduced cognitive flexibility (e.g. Piech, Hampshire, Owen, & Parkinson, 2009). However, previous work examined performance in "cold" conflict resolution paradigms, i.e. experimental tasks without motivational content, and thereby left unanswered whether hunger shapes cognition in different ways, depending on the presence or absence of food.

Conflict resolution is a key challenge for higher cognition and susceptible to motivation (Botvinick & Braver, 2015; Goschke & Bolte, 2014). Since both conflict signals (Botvinick, 2007; Dreisbach & Fischer, 2015; Fritz & Dreisbach, 2013) and cognitive effort to resolve conflicting situations (Schouppe, De Houwer, Ridderinkhof, & Notebaert, 2012; Shackman et al., 2011; Shenhav, Botvinick, & Cohen, 2013) are being perceived as inherently costly and aversive, motivation is needed to invigorate cognitive control processes for conflict resolution (Botvinick & Braver, 2015). Since motivation determines the degree of mobilized control efforts, speed of conflict resolution reflects the vigor of motivation. In fact, a multitude of evidence shows that cognitive control is susceptible to monetary reward (e.g. Chiew & Braver, 2015). Reinforcing efforts to resolve cognitive conflicts by performance-contingent monetary incentives leads to sustainedly enhanced task focus (Chiew & Braver, 2013, 2014) by increased proactive effort to prepare for an upcoming task (Chiew & Braver, 2015; Fröber & Dreisbach, 2012; Zedelius, Veling, Bijleveld, & Aarts, 2012). However, most research on motivational modulations of cognitive control focused on the effects of motivation in terms of reward gain, but less is known about how more basic and ecologically valid drives in everyday life, like hunger (Kenrick, Griskevicius, Neuberg, & Schaller, 2010), modulate conflict resolution.

The purpose of the current study was to explore how hunger as a fundamental need affects conflict resolution in the presence and absence of food cues. We measured control over conflict based on resolution of proactive interference, a main source of forgetting in memory and crucial determinant of ongoing use of working memory in a variety of tasks (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Nee & Jonides, 2013; Shipstead & Engle, 2013). Proactive interference describes the conflict between previous, yet no longer relevant information (familiarity) and the processing of currently relevant information (source recognition; Jonides & Nee, 2006; Lewandowsky, Oberauer & Brown, 2009). Proactive interference can lead to forgetting because old information competes for access to working memory with new, currently relevant information. Based on the view that working memory is capacity limited, proactive interference can cause forgetting because retrieval of relevant information is disrupted by the presence of highly interfering, older memory (Unsworth & Engle, 2007). For instance, when you change a password, you may encounter problems when trying to remember the new one. Resolution of competition between multiple active memory representations requires enhancement of relevant source memory and rejection of familiarity information as the origin of conflict (Dulas & Duarte, 2016; Jonides & Nee, 2006; Yi & Friedman, 2011). The recency-probes task (Monsell, 1978) constitutes an elegant paradigm which is well suited for a robust induction of proactive interference by generating a conflict between source recognition and familiarity within working memory (Jonides & Nee, 2006). Using the recency-probes paradigm with emotional material, Levens and Phelps (2008) observed a transient facilitation of proactive interference resolution, specifically when presenting arousing content at the behavioral relevant point in time when the conflict arises. Since arousal as one inherent aspect of emotion indicates motivational intensity of affective states (Gable & Harmon-Jones, 2010) and thereby the vigor of the underlying motivational system (Lang, 2010), these findings provide a first strong indication that motivation affects

control over proactive interference and that the recency-probes paradigm is sensitive for such motivation-driven effects. In fact, existing evidence suggests that motivational arousal biases competition of active representations in memory to amplify currently relevant information (Mather, Clewett, Sakaki, & Harley, 2016; Sakaki, Fryer, & Mather, 2014; Sutherland & Mather, 2012). In addition, amplification of relevant representations constitutes a crucial mechanism of control processes to enhance performance in response to conflict (Egner & Hirsch, 2005). Since in the presence of food cues, hunger triggers a state of heightened arousal (LaBar et al., 2001; Privitera, Antonelli, & Creary, 2013), we predict that hunger-driven arousal amplifies the weights of ongoing selection processes in favor of prioritized source memory and at the cost of irrelevant familiarity information (Mather & Sutherland, 2011) leading to a facilitated proactive interference resolution (see Fig. 1, for an illustration). Moreover, in a hungry state, repeated presentation to food cues should induce persistent arousal and thereby promote faster conflict resolution over a larger timescale, i.e. throughout the entire exposure to food. Thus, in our major hypothesis, we predict that when food deprived, repeated exposure to task-relevant, valuable food stimuli should exert a *sustained* enhancement of proactive interference resolution in the recency-probes paradigm (hypothesis one). On the same note, this hunger-induced benefit in control efforts should disappear when participants are sated and therefore food stimuli are devaluated. With regard to the arousing effect of food cues, changes in nutritional state allow to go beyond testing for merely transient, short-lived alterations of interference resolution in the recency-probes paradigm (Levens & Phelps, 2008; Mizrak & Öztekin, 2016), enabling the experimental examination of sustained, longer lasting effects. Apart from the expected sustained alterations, previous research by contrast described a transient facilitation of conflict resolution due to presentation of an arousing content at the timepoint when the conflict arises (Levens & Phelps, 2008; Mizrak & Öztekin, 2016). Consistent with these findings, in our second hypothesis we expect that presentation of approach-valenced, palatable food precisely at the time of response exerts a *transient* boost of interference resolution (hypothesis two). Since the latter effect acts at a short timescale and regardless of shifts in nutritional state, it should occur when hungry and sated and additionally to the sustained effect outlined in hypothesis one.

To test these predictions, we manipulated the features of food cues to elicit motivational arousal (Lang, 2010) by cue valorization through experimental feeding restriction and devaluation through satiation, respectively (Cabanac, 1971; Jiang et al., 2008; Talmi et al., 2013). We designed two blocks of a recency-probes paradigm (Monsell, 1978), an experimental block with food items as well as matched object items and a control block with objects only. More specifically, since the experimental block comprises food and object items, it can be distinguished between trials showing food at the critical timepoint of conflict and trials showing objects. In a within-subject design, we tested whether exposure to food cues affects resistance against proactive interference in a hungry compared to a sated state. To rule out general effects of experimental fasting, we expected no alteration in performance in the control block. By contrast, our first hypothesis would be supported by facilitation of interference resolution in the experimental block when hungry, as compared to a sated state. Since this alteration relies on the presence of food cues, the effect should appear whenever exposed to food, i.e. in the experimental block and regardless of the content (object, food) presented at the timepoint of interference. Evidence for the second hypothesis would be an additional, short-lived facilitation of interference resolution for trials showing food compared to an object stimulus when the conflict occurs. This latter effect is expected to occur in both nutritional states, but when hungry, it should facilitate conflict resolution superimposed to the
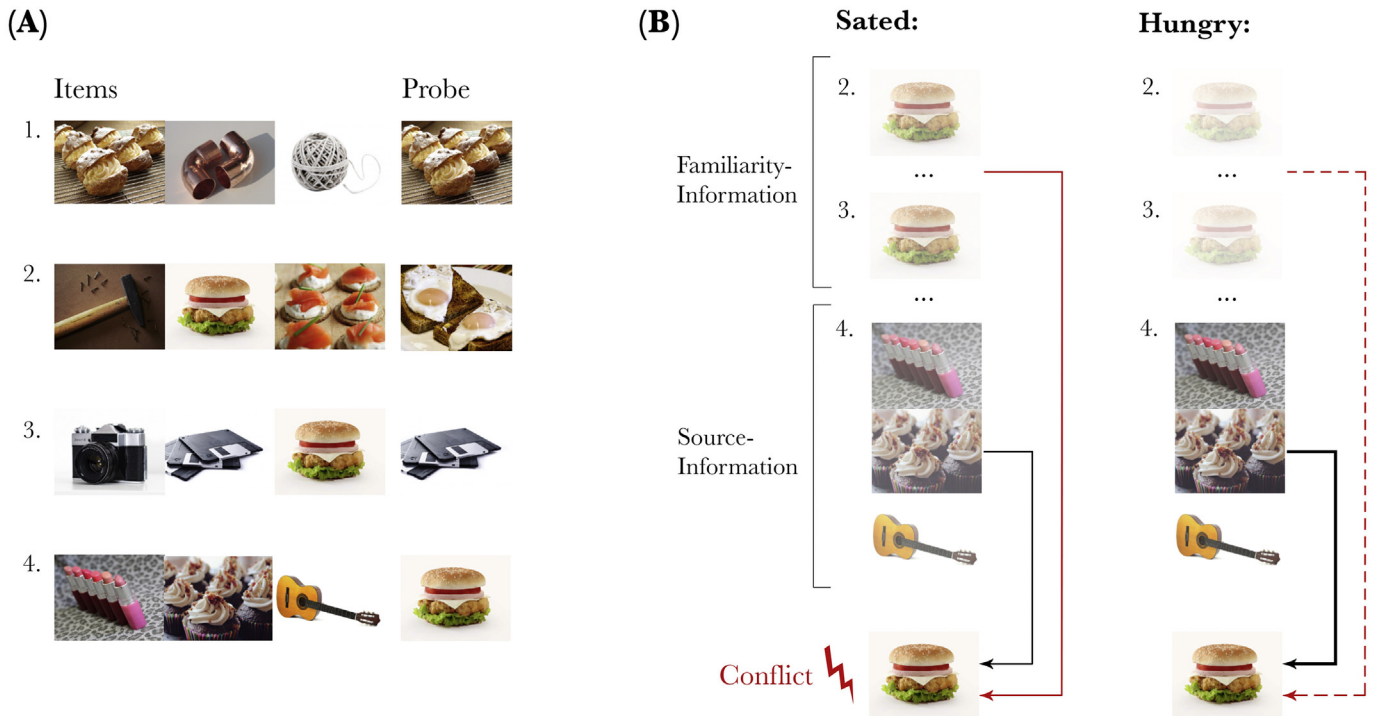
(A)

(B)

Fig. 1. (A) Sample trials and trial types are shown from the experimental block, consisting of object and food pictures, with the following trial types: 1 non-recent positive, food probe trial; 2 non-recent negative, food probe trial; 3 non-recent positive, food distractor trial; 4 recent negative, food probe trial. The control block consists of the identical trial types, but with object pictures only (object probe trials). (B) When hungry, repeated exposure to food should lead to an enhanced prioritization of task-relevant source information (bold black line) at the cost of familiarity information deriving from recently presented cues (dashed red/gray line). This hunger-induced biased resource allocation is hypothesized to result in a facilitation of proactive interference resolution, selectively in the presence of food and regardless of the probe content (i.e. food probe trials and food distractor trials). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sustained acceleration of conflict resolution described in hypothesis one. Both hypotheses differ with regard to the timescale of the expected effect: whereas hypothesis one supposes a sustained, block-related alteration of proactive interference resolution, hypothesis two refers to a transient, stimulus-related effect. In addition, whereas the former effect is sensitive to shifts in nutritional states, the latter is not state-dependent (Levens & Phelps, 2008; Mizrak & Öztekin, 2016).

1. Materials and methods

1.1. Participants

All participants were undergraduate students and received research credits for participation in the experiments. All had normal or corrected-to-normal visual acuity. None of the participants indicated suffering from a diagnosed psychiatric disease or having first-degree relatives who did, being under the influence of psychoactive substances or psychopharmacologic treatment, or having suffered severe head injuries in the course of their lives (self-report). Thirty-five participants (23 females, 12 males; $M_{age} = 23.11$ years, $SD = 2.94$; age range: 20—34 years) were tested. It was ensured that participants exhibited a body mass index (BMI; weight [kg]/height [m]^2) not considered as underweight (BMI < 18.5, i.e. less than the 5th percentile of the CDC growth charts) or obese (BMI ≥ 30.0, i.e. equal to or greater than the 95th percentile of the CDC growth charts; Centers for Disease Control and Prevention; Kuczmarski et al., 2002), $M = 22.67$ kg/m^2, $SD = 3.05$ (range: 17.97 kg/m^2 to 29.76 kg/m^2). Informed consent was obtained according to the guidelines of the Ethics Committee of the Department of Psychology, University of Innsbruck.

1.2. Experimental manipulation of the nutritional state

Participants were informed that the goal of the experimental feeding restriction was an examination of glucose levels and their effects on memory, therefore it was necessary to take part in the experiments once hungry, once sated. In order to achieve a food deprived state, participants were instructed to fast overnight and to attend the experiment after waking up with an empty stomach, not having eaten for at least six hours as minimal requirement and only having drunk a glass of water when thirsty. To ensure a sated state, participants were asked to eat breakfast consistent with their habits, or have at least one beverage and a serving of solid food before the experiment. After both experimental sessions, participants were asked if they had seen through the intent of the study to examine the effect of food cues in different states. Both experimental sessions were conducted between 9:00 a.m. and 10:30 a.m. to facilitate participants to meet this requirement. Following experimental testing participants neither reported having noticed differences between the stimuli presented in the control block compared to the experimental block, nor having seen through the pretended aim of the experimental design. Afterwards, participants were truthfully informed about this pretense and the actual purpose of the study and provided informed consent again regarding the usage of their data.

In the food deprived condition, all participants confirmed not having had breakfast and indicated not having eaten a meal within $M = 13.12$ h, $SD = 2.66$. In the sated condition, all participants specified having had breakfast within $M = 0.92$ h, $SD = 0.42$, before the experiment. All participants reported eating breakfast on a daily basis and having had at least one piece of bread or pastry and a beverage on the day of being tested in the sated condition. In order

to verify the manipulation of nutritional state, three items of a scale regarding subjective sense of hunger (Friedman, Ulrich, & Mattes, 1999; nine-point Likert scale) were chosen ("How hungry do you feel right now?"; "How strong is your desire to eat right now?"; "How much food do you think you could eat right now?"). To check the effects of food deprivation on positive and negative affectivity, we registered participants' affect at the beginning of the experimental task by using the "Positive and Negative Affect Schedule" (PANAS; Watson, Clark, & Tellegen, 1988; German translation by Krohne, Egloff, Kohlmann, & Tausch, 1996, five-point Likert scale). Both scales allow capturing hunger or current mood by an evaluation of a series of words which describe various feelings and were presented before the start of the experimental task.

1.3. Visual stimuli

As stimuli for the modified recency-probes paradigm, thirty-two food stimuli (e.g., turkey, ice cream, cake) and ninety-six non-food stimuli (objects, e.g., tools, cup, book) from the IAPS (Lang, Bradley, & Cuthbert, 2005) were chosen and presented in full-screen size. A *t*-test on ratings of valence and arousal provided by the IAPS (Lang et al., 2005) revealed significant differences in perceived valence of the two stimuli groups, $t(38.96) = -14.41$, $p < 0.001$, food stimuli ($M = 6.69$, $SD = 0.58$) being experienced as more pleasant than the neutral control stimuli ($M = 5.12$, $SD = 0.35$). Likewise, food pictures ($M = 4.97$, $SD = 0.42$) and neutral objects ($M = 3.28$, $SD = 0.68$) differed regarding evoked arousal $t(87.08) = -16.60$, $p < 0.001$. Hence, photographs of food were rated appearing more pleasant and more arousing than the neutral control stimuli and therefore might arouse appetitive motivation (Lang, 2010), even without systematic manipulation of nutritional state.

1.4. Modified recency-probes paradigm

Participants performed two blocks of a modified recency-probes paradigm (Levens & Phelps, 2008; Monsell, 1978). Each trial started with a fixation cross (1500ms), then participants were instructed to encode a series of three items one after another (1300ms) each and to hold them for a retention interval of 3000ms. To conclude, participants were presented with a single probe item for 1500ms and had to decide as quickly as possible by clicking two keys on a keyboard ("C" yes, "M" no) whether this probe matched one of the previously viewed items (positive trials) or not (negative trials). This was followed by an interstimulus interval, mean value 2000ms (randomized between 1500ms and 2500ms). The IAPS stimuli were presented in full-screen size with equal frequency within each block. In every block, one half of the trials of the probe was part of the source items (positive trials), whereas the other half was not (negative trials). In order to induce proactive interference, during one half of the trials the current probe item was presented directly among the preceding two trials as one of the three source items (recent trials), whereas during the other half, the current probe was not part of the presented stimuli in the preceding trials (non-recent). Stimulus category was manipulated by the presentation of neutral objects (object probe) exclusively in the control block and a combination of food stimuli and neutral objects in the experimental block. In the latter, the trials were divided into two trial types: trials showing a neutral stimulus (food distractor) and such featuring a food stimulus as probe item (food probe). Prior to testing, participants performed a practice block of twelve trials.

1.5. Procedure and design

In a 2 (nutritional state) × 3 (trial type) × 2 (recency) within-subject factorial design, each participant was tested in each

nutritional state (sated, food deprived) and performed two blocks of the experimental task, one control block (object probe) and one experimental block (food probe, food distractor), consisting of both interference trial types (recent, non-recent). The order of the nutritional states as well as the blocks was counterbalanced across the participants.

The experimental task was developed using E-Prime software (Version 2.0; Psychology Software Tools, Pittsburgh, PA; Schneider, Eschman, & Zuccolotto, 2012) and presented on a Samsung 943BM monitor (32-bit true colour; resolution 1280pixels × 1024pixels, refresh rate = 60 Hz).

2. Results

Response times for correct responses in negative trials were used for data analysis. For both state conditions, 7.71% of cases were eliminated due to incorrect responses. To deal with outliers, we applied the median absolute deviation method (Leys, Ley, Klein, Bernard, & Licata, 2013) to response times separately for each condition of each factor. In doing so, overall 7.10% of the trials were identified as outliers and therefore eliminated. Degrees of freedom were corrected in case of deviance from sphericity (Greenhouse-Geisser). Effect sizes are reported by partial eta squared η_{P2} [0.01 = small; 0.06 = medium; 0.14 = large] for analyses of variance and by Cohen's *d* [0.3 = small; 0.5 = medium; 0.8 = large] as well as *r*-values [0.2 = small; 0.3 = medium; 0.5 = large] for *t*-tests (Elis, 2010).

2.1. Effects of the experimental manipulation of the nutritional state

T-tests for dependent measures were applied to analyze the self-report data in terms of assessing the effects of food deprivation on subjective sense of hunger and mood. Compared to the sated condition [$M = 2.30$, $SD = 2.09$], results in the food deprived condition [$M = 5.61$, $SD = 1.21$] indicated a higher level of subjective sense of hunger $t(34) = -8.94$, $p < 0.001$, Cohen's $d = 1.94$ ($r = 0.84$), on the hunger scale. On the other hand, food deprivation exerted no effects on current mood states as indicated by PANAS scores. Results showed no significant differences between both measurements for positive, $t(34) = 1.85$, $p = 0.075$ [t_{Sated}: $M = 2.90$, $SD = 0.59$; $t_{Deprived}$: $M = 2.64$, $SD = 0.62$], and negative affectivity, $t(34) = 0.76$, $p = 0.46$ [t_{Sated}: $M = 1.33$, $SD = 0.34$; $t_{Deprived}$: $M = 1.26$, $SD = 0.36$]. Altogether, results of the self-report data confirm successful induction of subjective hunger, while confounding effects by a change in mood state can be excluded (see Fig. 2). This hungry state, induced by food deprivation, should have alliestetic effects on appetence and therefore add motivational value to food stimuli (Jiang et al., 2008), which we expect to invigorate control effort exertion.

2.2. Interaction of states, trial types and recency

Considering the hypothesized interplay between state-dependent and stimulus-driven effects on interference resolution as formulated by prediction one, we first performed a 2 × 3 × 2 ANOVA for repeated measures on rectified response times with the within-subject variables nutritional state (sated, food deprived), trial type (object probe, food probe, food distractor) and interference (non-recent, recent). Results showed a strong interaction effect between all three within-subject factors, $F(2, 68) = 10.47$, $MSE = 765.48$, $p < 0.001$, $\eta_{P2} = 0.24$. This result confirms the hypothesis stating that nutritional state and stimulus category interact in order to influence conflict resolution. To further explore interactions, contrasts were performed comparing interference resolution for both states, as well as food probe trials and food
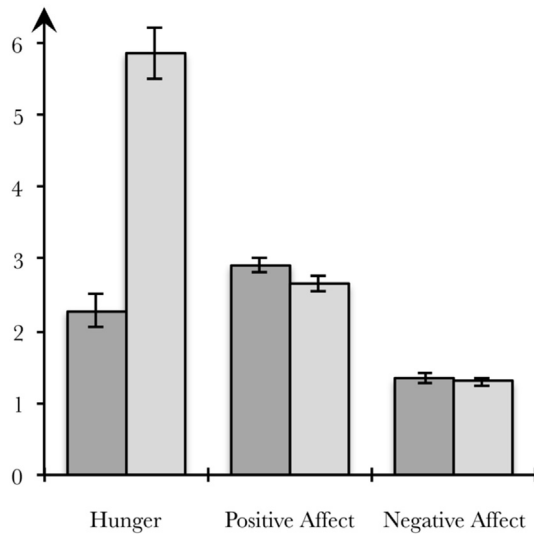
Fig. 2. Assessment of the experimental nutritional state manipulation. Hunger, positive and negative affectivity were assessed via self-report scales for the sated (dark gray bars) and the food deprived session (bright gray bars). Standard errors are represented in the figure by the error bars attached to each column.
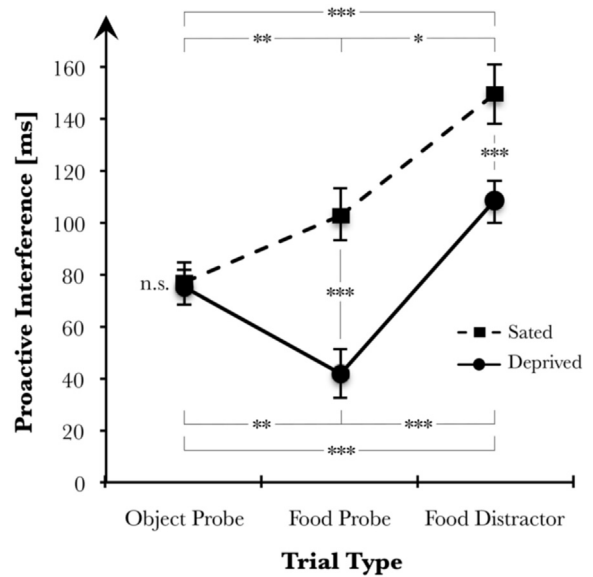

Fig. 3. Interference measures [ms] calculated as differences between recent and non-recent no-response trial reaction times for each trial type and condition. The difference between non-recent and recent no-response times for food probe trials and food distractor trials is significantly less in a food deprived state as compared to a sated state, yet object probe trials remain unaffected by nutritional state. Standard errors are represented in the figure by the error bars attached to each data point ($^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$).

distractor trials with object probe trials. Contrasts revealed different control performance (recent versus non-recent) comparing both states and food probe trials [$M_{Sated} = 103ms$, $SE_{Sated} = 10ms$; $M_{Deprived} = 42ms$, $SE_{Deprived} = 9ms$] with object probe trials [$M_{Sated} = 77ms$, $SE_{Sated} = 8ms$; $M_{Deprived} = 75ms$, $SE_{Deprived} = 7ms$], $F(1, 34) = 33.58$, $MSE = 3677.43$, $p < 0.001$, $\eta_{P2} = 0.50$, as well when comparing food distractor trials [$M_{Sated} = 149ms$, $SE_{Sated} = 12ms$; $M_{Deprived} = 108ms$, $SE_{Deprived} = 8ms$] with object probe trials, $F(1, 34) = 9.19$, $MSE = 6037.19$, $p = 0.005$, $\eta_{P2} = 0.21$. The means reveal contrast effects reflecting an altered hunger-induced conflict resolution for trials of the experimental block (food probe, food distractor) as compared to control block trials (object probe). Further contrasts between states, recency and food probe trials compared to food distractor trials showed no interaction effect, $F(1, 34) = 1.55$, $MSE = 8656.89$, $p = 0.221$. The absence of any difference between trial types of the experimental block indicates that hunger affects conflict resolution irrespective of the stimulus category (objects or food) presented within the probe context, i.e. when interference arises. Thus, state-driven, enhanced resolution of proactive interference is attributable to a characteristic which both trial types have in common: repeated exposure to motivating, valuable food cues. The described results provide evidence in favor of our first prediction (hypothesis one), reflecting a state-dependent alteration of conflict resolution when repeatedly confronted with motivationally relevant material.

It is fundamental that in accordance with previous studies, another main effect was detected for the factor recency, $F(1, 34) = 291.76$, $MSE = 3062.00$, $p < 0.001$, $\eta_{P2} = 0.90$, reflecting the strong proactive interference induced by the recency-probes design. Since we were able to clearly replicate proactive interference by the recency-probes design (Jonides & Nee, 2006), the difference between recent and non-recent trials was used as behavioral measure for induced conflict (see Fig. 3 and Table 1, for interference scores for each state and trial type).

2.3. Effects of nutritional state within trial types

Second, to further expatiate sustained effects of food

deprivation on control efforts, we directly examined alterations in conflict resolution as reflected by response time differences between recent and non-recent trials among both nutritional states for each trial type in a separate manner. In line with our first prediction (hypothesis one), results of paired t-tests revealed faster interference resolution for both food probe trials, $t(34) = 5.42$, $p < 0.001$, Cohen's $d = 1.07$ ($r = 0.68$), and food distractor trials, $t(34) = 3.48$, $p = 0.001$, Cohen's $d = 0.69$ ($r = 0.51$), when food deprived. By contrast, performance for object stimuli which were not relevant for the current nutritional state did not change between states, $t(34) = 0.22$, $p = 0.828$.

2.4. Effects of trial type within nutritional states

Next, to explore stimulus-driven effects on interference resolution for both states in more detail, differences for each nutritional state were examined for interference measures using ANOVAs with the within-subject factor trial type. Results demonstrated a main effect of the variable trial type in the sated condition $F(2, 68) = 17.93$, $MSE = 2657.66$, $p < 0.001$, $\eta_{P2} = 0.35$. Bonferroni corrected comparisons revealed slower interference resolution for food distractor trials compared to object probe trials ($MD = 72.85$, $p < 0.001$), and food probe trials ($MD = 26.26$, $p = 0.034$), as well as slower interference resolution for food probe trials compared to object probe trials ($MD = 46,59$, $p = 0.005$). Considering the food deprived state, Mauchly's test indicated that the assumption of sphericity had been violated for the within-subject variable $\chi^2(2) = 19.14$, $p < 0.001$. The degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.69$). Again, ANOVA for repeated measures also revealed a strong main effect for the within-subject variable trial type, $F(1.39, 47.22) = 20.85$, $MSE = 2647.68$, $p < 0.001$, $\eta_{P2} = 0.380$, reflecting faster interference resolution for food probe trials as compared to object probe ($MD = -33.14$, $p = 0.003$) and food distractor trials ($MD = -66.18$, $p < 0.001$), as well as faster conflict resolution performance in

Table 1
Interference measures [ms] calculated as differences between recent and non-recent no-response trial reaction times for each trial type and condition. Standard errors in parentheses.

Trial Type	Sated		Food deprived	
	Mean	(SE)	Mean	(SE)
Object Probe	84.57	(9.39)	82.27	(6.84)
Food Probe	111.97	(11.64)	50.69	(10.49)
Food Distractor	151.44	(14.62)	108.54	(8.67)

object probe trials compared to food distractor trials ($MD = -33.04$, $p < 0.001$). These results support hypothesis two, showing a specific facilitation of interference resolution for probes depicting a food cue compared to an object stimulus, irrespective of whether participants were food deprived or not.

3. Discussion

The principle objective of the current study was to explore how hunger as a fundamental need affects resistance against memory intrusions of no longer relevant information. Results showed that the interaction between changes in nutritional state and the perception of food cues (Castro & Berridge, 2014; Medic et al., 2014; Ziauddeen et al., 2012) evoked an altered resolution of proactive interference. Satiety-induced devaluation of food cues led to impaired performance in conflict resolution, whereas a hungry state resulted in strengthened resistance to proactive interference and lying in between, the control block presenting neutral objects remained unaffected by nutritional state manipulation. This latter finding is intriguing, since equal performance in the control block for both states allows for ruling out general effects of experimental fasting on proactive interference resolution. More precisely, only performance in the experimental block was sensitive to shifts in nutritional state. The crucial distinction between trials in the experimental block versus the control block is the presence of visual food stimuli within the source items encoded in the former block and their absence in the latter. In addition, since results exclude an interaction of hunger and trial type in the experimental block, the extent of state-driven improvement in conflict resolution did not differ between food probe trials and food distractor trials. Thus, we can draw three conclusions: first, shifts in nutritional state alter resolution of proactive interference, second, these state-driven alterations in performance rely on the presence of food cues and third, these alterations were not probe-related (transient; e.g. Kanske, 2012; Levens & Phelps, 2008) but rather block-related (sustained; Pessoa & Engelmann, 2010). This result pattern provides strong evidence in favor of hypothesis one, indicating that in a deficient nutritional state, presentation of visual food cues acts as an overall enhancer of proactive interference resolution leading to a sustained boost of behavioral performance. Furthermore, results showed facilitated conflict resolution in food probe trials compared to food distractor trials. Both trial types differed with regard to the content presented at the timepoint of conflict, showing food in the former and objects in the latter, but both comprised source items presenting foods and objects with the same frequency. In addition, the absence of any interaction between nutritional state and trial type in the experimental block indicates that effects of trial type on performance were not affected by satiation. Hence, alterations of conflict resolution by trial type were probe-related (Levens & Phelps, 2008; Mizrak & Öztekin, 2016) and occurred in both nutritional states in the same direction. These findings support hypothesis two, suggesting a transient facilitation of proactive interference resolution by presentation of approach-valenced food

at the time of response, i.e. in food probe trials, regardless of the actual nutritional state. In fact, food is perceived as more appetitive and pleasant than objects, even when satiation is reached (e.g. Plailly et al., 2011). But surprisingly, although we suggested that food deprivation alters the value of food and thereby its ability to trigger arousal (Balleine, 2005; LaBar et al., 2001), the probe-related effect is not more pronounced in a hungry state compared to a sated state. This result is consistent with previous findings using an emotional recency probes paradigm. Levens and Phelps (2008) showed transiently improved interference resolution when a probe depicted either a low arousing, pleasant content or high arousal content, regardless of valence. Finally, apart from the predictions of our hypotheses, it is noteworthy that although food distractor trials in the experimental block comprised food cues, when hungry, resolution of proactive interference was impaired compared to object probe trials in the control block. Whilst at first sight, this result seems contradictory, the competition of active memory representations for limited resources probably accounts for this finding (Nee & Jonides, 2013). In fact, since food stimuli are appetitive cues (Plailly et al., 2011), they bias competition for memory resources (Mather & Sutherland, 2011), leading to enhanced representations in working memory (Rutters et al., 2015), most likely at the cost of neutral object representations, e.g. object probes in food distractor trials. Taken together, our major finding (hypothesis one) highlights that an optimal fit (Kruglanski, Chernikova, Rosenzweig, & Kopetz, 2014; Veltkamp, Aarts, & Custers, 2008) between current nutritional state (hunger) and contextual stimulation (food) is a necessary condition to channel deprivation-induced drive into enhanced conflict resolution. With regard to this finding, two pivotal questions need further clarification: *why* occurred this hunger-driven boost of proactive interference resolution exclusively when exposed to food and *how* enhanced visual food detection conflict resolution?

First, we address the question *why* a motivational context like exposure to food during a hungry state results in sustainedly boosted proactive interference resolution. In conflicting situations, prioritization of information according to current behavioral goals relies on cognitive control processes (Botvinick & Braver, 2015). Focusing on the aversive nature of cognitive control mobilization, recent accounts proposed that willingness to exert cognitive efforts depends on the expected value of control, resulting from a cost-benefit analysis which offsets inherent effort costs against the value of prospective benefits (Cools, 2015; Kool & Botvinick, 2013, 2014; Rangel & Hare, 2010; Shenhav et al, 2013; Westbrook & Braver, 2015). The capability of food cues to initiate motivational readiness depends on their relevance for the nutritional state of an individual (Robinson & Berridge, 2013). Thus, when deprived, visual food detection might enhance the expected value of cognitive effort exertion to an extent which outweighs the inherent cost of effort to resolve interference, thereby strengthening the cognitive operations required to successfully perform the ongoing task in a sustained fashion (Chiew & Braver, 2015). This is an intriguing finding: although the highly valuable food stimuli were task-relevant, they were not presented as reinforcement in a performance contingent manner (e.g., Braem et al., 2013), therefore food cues exerted their effects implicitly. The mere facts that successful task performance does not require explicit focus on the content of an item and participants were not aware of the purposeful experimental exposure to food cues support the assumption of an enhancing effect of food content being unconscious by nature (Custers & Aarts, 2010; Hart & Gable, 2013; Marien et al., 2012). In fact, subliminal priming of motivational relevant cues turns deprivation into motivational readiness (Veltkamp et al., 2008), boosts effort and facilitates performance (Bijleveld, Custers, & Aarts, 2012) as well as executive control (Capa, Bustin,

Cleeremans, & Hansenne, 2011). Moreover, since processing of food reward is suggested to act at an unconscious level (Anselme & Robinson, 2016; Tibboel, De Houwer, & Van Bockstaele, 2015), participants could have implicitly associated task engagement with the value of food cues by the repeated presentation of food throughout the experimental block. Surprisingly, food cues failed to motivate additional effort to resolve proactive interference when participants were sated (Mohanty, Gitelman, Small, & Mesulam, 2008), as reflected by a deceleration of conflict resolution. Although even in a sated state, food cues can act as reward due to the expected pleasantness of its consumption, after satiation those cues are no longer relevant to the individual's current physiological state (Balleine, 2005; Pool, Sennwald, Delplanque, Brosch, & Sander, 2016). Moreover, the perceived pleasantness of food cues and the willingness to consume presented food is adversely affected by increased repletion (Jiang et al., 2008; Medic et al., 2014). Consequently, once satiation is reached, the ability of food cues to enhance the value of effort exertions forfeits. Quite on the contrary, devaluing food cues by experimental satiety led to impaired conflict resolution, suggesting a deleterious effect of devaluated cue exposure on performance. Presumably, this finding reflects an adjustment of control efforts on the decreased value signaled by task-relevant food cues. To summarize, although sensory properties of food cues stay the same, states of hunger or fullness change their motivational value and thereby affect the vigor of control efforts to resolve proactive interference, as reflected by the speed of conflict resolution. Despite value-based decision-making explains why enhanced control over conflict is energized by hunger, it remains to be clarified *how* conflict resolution is accelerated by hunger as motivational drive.

Second, we focus on the question *how* food exposure leads to an accelerated conflict resolution in hungry subjects. In the recency-probes paradigm, a successful strategy (Dreisbach, 2012) requires strengthened focus on source memory and its shielding against intrusions by recently presented, familiar information (Jonides & Nee, 2006; Lewandowsky et al., 2009). Applying this task rule should enhance the accessibility of the three source items and weaken representation strength of currently irrelevant items from activated memory. In his seminal work, Easterbrook (1959) noted that when the direction of behavior is constant, increase in arousal leads to reduction in the range of cue use by narrowing attention to prioritized cues at cost of irrelevant information (see also Gable & Harmon-Jones, 2010). Visual food detection signals access to food, thus exposure to food results in a heightened arousal state under restricted food availability (Balleine, 2005; LaBar et al., 2001; Privitera et al., 2013; Ribeiro et al., 2007). This should initiate biased competition of active representations in memory (Talmi et al., 2013), leading to "winner-take-more" and "loser-take-less" effects (see Fig. 1; Easterbrook, 1959; Mather & Sutherland, 2011; Mather et al., 2016; Sakaki et al., 2014; Sutherland & Mather, 2012). Hence, when implicitly exposed to food, hunger-triggered arousal might strengthen rule-based prioritization of currently relevant source items and thereby enhance their accessibility at the cost of previously encoded, but no longer relevant memory representations. The assumptions of the described arousal-biased competition account fit in well with our results and involve two crucial aspects of cognitive control: first, the application of task rules (Dreisbach, 2012; Meiran, Pereg, Kessler, Cole, & Braver, 2015), second the attentional amplification of task-relevant information in the face of conflict (Chechko, Kellermann, Schneider, & Habel, 2014; Egner & Hirsch, 2005). This is in line with previous findings, showing that arousing states in response to motivational content automatically sustain task engagement (Hart & Gable, 2013), strengthen the active task set (Liu & Wang, 2014; Plessow, Fischer, Kirschbaum, & Goschke, 2011), improve the discriminability of

currently relevant information (Etzel, Cole, Zacks, Kay, & Braver, 2015; Mohanty et al., 2008), and even shield task-relevant memory representations against task-irrelevant stimulus properties (Maran, Sachse, & Furtner, 2015). Altogether, the *why* and *how* of hunger-driven biased conflict resolution describe two sides of the same coin. Due to increased value of food, deprivation-induced hunger raises cognitive efforts in terms of an enhanced rule-based prioritization of representations. In turn, this biased competition in favor of task-relevant information is a result of motivational arousal (Lang, 2010), evoked by detection of food (Ziauddeen et al., 2012).

More recently, the emotion-driven acceleration of proactive interference resolution (Levens & Phelps, 2008) was interpreted as a result of slower buildup of proactive interference (Mizrak & Öztekin, 2016). This approach by Mizrak and Öztekin (2016) offers an alternative, but not contradictory explanation for our results, arguing that arousing probe content might delay the accrual of familiarity information as the source of conflict and thereby defuse proactive interference. But, in contrast to our study, their work found facilitated interference resolution solely when confronted with an arousing content at the behavioral relevant point in time, e.g. within the conflicting probe interval (Levens & Phelps, 2008; Mizrak & Öztekin, 2016). In addition to these findings, our results indicate that when hungry, repeated exposure to food, i.e. the presence of visual food cues within the source items, is the crucial factor for acceleration of interference resolution, regardless of probe content. In fact, when hungry, simply the visual detection of food leads to an enhanced appetitive drive for food (Ziauddeen et al., 2012) and promotes a state of heightened arousal through emotional brain networks (LaBar et al., 2001; Privitera et al., 2013). Motivational arousal inhibits memory for contextual information (Bisby & Burgess, 2014; Kensinger, 2009), probably by a deleterious impact of arousal on the use of episodic memory systems (Packard & Goodman, 2012; Schwabe, 2013). Therefore, proactive interference resolution is facilitated not only by confrontation with an arousing probe when the conflict appears (e.g. food probe trials; see Kanske & Kotz, 2011; Zinchenko, Kanske, Obermeier, Schröger, & Kotz, 2015), but also by state effects through repeated exposure to arousing contents just before response (food distractor trials). This finding expands the explanation by Mizrak and Öztekin, suggesting that arousal hampers the accrual of familiarity information in a sustained manner, in addition to a merely transient, probe related alteration of proactive interference (Levens & Phelps, 2008; Mizrak & Öztekin, 2016).

Our findings provide strong evidence that hunger alters resistance to proactive interference depending on the presence of food cues. Nevertheless, there are a few limitations of the present study that should be considered. We experimentally manipulated nutritional state using a proven procedure, i.e. instruction for food consumption with predetermined minimal requirements considering the time intervals of meals (e.g. Xu, Schwarz, & Wyer, 2015). We encourage future research to provide standardized meals, which would allow to examine the impact of timing and size of meal consumption as well as different types of meals (i.e. sensory specific satiety) on ongoing cognition. Second, our finding of an altered resolution of proactive interference by shifts in nutritional state and exposure to food suggests that food-related content in active memory might prevent the intrusion of other information, which is not currently activated. Probably, this mechanism also promotes reduced accessibility of more general food-related information (e.g. dietary goals). Replicating our findings based on more elaborate food-related memory content (e.g. putting in conflict a prescribed dietary plan with food consumption, when hungry or sated) would be a promising approach to elucidate cognitive processes involved in the impulsive failure to follow dietary goals

or to resist cue-driven temptations (e.g. Stroebe, van Koningsbruggen, Papies, & Aarts, 2013). Third, in our study, the ability of nutritional states to enhance or impair resolution of proactive interference depends on the presence or absence of food cues, respectively. Perception of food cues can stimulate appetitive behavior by both expected pleasantness of food consumption (Balleine, 2005), i.e. cognitive desires based on past episodic memories of hedonic liking experiences, and wanting for food, i.e. the motivational drive for food (Berridge & Robinson, 1998; Berridge, 2009; Pool et al., 2016). Although the measurement of this component of food reward in humans is subject to controversies and needs further clarification (Finlayson & Dalton, 2012; Havermans, 2011, 2012; Pool et al., 2016), future research should examine the relative impact of both components of food reward on higher cognition and whether these alterations act at an unconscious level (Anselme & Robinson, 2016; Berridge & Robinson, 2003; Tibboel et al., 2015; Veltkamp et al., 2008).

To conclude, in line with our main hypothesis our results provide first evidence for hunger-driven modulation of proactive interference resolution occurring selectively when implicitly exposed to food cues. In the presence of food, hunger biases resource competition of active memory representations in favor of prioritized source memory and at cost of activation strength of irrelevant familiarity information (Mather & Sutherland, 2011). Modern food-rich environments seduce to overconsuming easily available, palatable food (Martin & Davidson, 2014). The ubiquitous presence of food cues promotes the readiness to eat (Ziauddeen et al., 2012) and biases active cognition in favor of these cues (Higgs et al., 2012; Rutters et al., 2015). Our findings complement this existing picture, suggesting that in a hungry state, food-related contents in working memory disrupt the access of contextual food-related information to active memory. This biased competition of representations in memory could have a strong impact on eating behavior by suppressing episodic memories of recent meals or dietary information, e.g. appropriateness of eating, healthiness of food or dietary goals (Higgs, 2016; Stroebe et al., 2013; Ziauddeen, Alonso-Alonso, Hill, Kelley, & Khan, 2015). Future research is needed to address the question whether the revealed effect impacts the retrieval of this latter type of information. In addition, our findings emphasize the importance of an optimal fit between motivational states (sated, hungry) and environmental stimulation (object, food) to reinforce task engagement (Hart & Gable, 2013). Our results go beyond our initial finding that when deprived, cues for wanted objects act as a potent reward, showing a detrimental effect of the exposure to the same cues when satiation is reached. The study advances our understanding of motivation-cognition interactions in everyday life by unveiling the beneficial effects of unconscious, need-tailored stimulation on higher cognition.

Disclosure statement

Acknowledgements

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