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ORIGINAL ARTICLE

Does hunger sharpen senses? A psychophysics investigation on the effects of appetite in the timing of reinforcement-oriented actions

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Abstract Evidence exists about the influence of interoception on time-keeping functions. In the current study we further addressed this topic by testing the effect of fasting and snack on the ability to estimate the duration of reinforcement-oriented grasping actions. We found that, after fasting, the time estimation for the grasping of a primary reinforcement (i.e., a muffin) was positively influenced by moderate hunger. By contrast, high hunger after fasting interfered with the timing estimation for the grasping of a neutral object (i.e., a notepad). We also reported that, after snack, individuals with high residual levels of hunger showed higher variability of responses for the timing of primary-reinforcement-oriented actions; conversely, those with low level of hunger (after snack) showed higher response variability in the timing of secondary-reinforcement-oriented actions. Finally, timing variability in the fasting condition negatively correlated with the Body Mass Index of our participants. Overall, our results indicate that both the modification of the physiological state and individual traits related to appetite might affect the subjective experience of time. This is in line with the accumulating evidence documenting the influence of interoception in temporal processing and, more in general, with the *New Look in Perception* theoretical view, stating that the perception of external events might be influenced by motivational states.

Introduction

In one of his fables (The Hungry Bear), the ancient Latin fabulist Fedro recognized a prodigious quality to hunger "*etiam stultis acuit ingenium fames*" (Hunger increases intelligence even to fools). From an evolutionarily perspective this statement, which can be resumed with the more general Latin proverb "*Mater artium necessitas*" (Necessity is the mother of invention), makes sense, as an empowerment of sensory-perceptual skills in response to food depletion might be functional to successful food search in a risky environment.

Research investigating the effect of fasting on cognitive functions has provided inconsistent results. There is evidence that fasting interferes with the execution of several behavioral tasks such as finger tapping (e.g., Green, Elliman, & Rogers, 1997), reaction times (e.g., Owen, Scholey, Finnegan, Hu, & Sünram-Lea, 2012; Roky, Iraki, HajKhlifa, Lakhdar, & Hakkou, 2000), word list recall (e.g., Benton & Parker, 1998), stroop (e.g., Owen et al., 2012) and problem solving (e.g., Doniger, Simon, & Zivotofsky, 2006). However, other studies did not confirm such food deprivation effects on behavioral performance (e.g., Doniger et al., 2006; Green et al., 1997; See Benau et al., 2014, for a complete review). Finally, there is at least one study showing that fasting can even improve performance in the execution of tasks involving visual attention skills

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such as identification and detection tasks (Tian, Aziz, Png, Wahid, & Yeo, 2011).

The aim of the present study is providing a contribution to this fragmented literature by exploring the effect of appetite manipulation on the ability to keep track of the elapsing time. Surprisingly, no research has tested the effects of food deprivation on such cognitive skill in healthy humans, although extensive literature suggests that hunger can affect the experience of time. One source of evidence is provided by the effect of fasting on ghrelin production, a hormone that is released by the stomach and accumulates during fasting (Palmiter, 2007). There is evidence that this hormone provokes a pro-cognitive effect on spatial memory in animal models (e.g., Atcha et al., 2009), which is likely to reflect effects on spine synapses in the hippocampus (Diano et al., 2006). Since hippocampal cells have been shown to code for either spatial or temporal properties of an experience (Eichenbaum, 2014), one might expect that acute fasting may improve timing skills by means of the action of ghrelin on temporal processing cells in the hippocampus. Moreover, this hormone is considered to directly promote the activation of dopamine neuron firing (Palmiter, 2007). Thus, the dopaminergic system may be involved in the cognitive effects of fasting, which also keeps with the known role of dopamine in the regulation of time-keeping functions (see Meck 1996; Lewis & Miall, 2006; Vicario et al., 2010; Baldwin et al., 2004; Ben-Pazi, Shalev, Gross-Tsur, & Bergman, 2006; Koch et al., 2008; O'Boyle, Freeman, & Cody, 1996; Rubia, Halari, Christakou, & Taylor, 2009; Vicario, Gulisano, Martino, & Rizzo, 2016; Allman, Teki, Griffiths, & Meck, 2014 for review).

Insights in support of a possible effect of fasting on temporal processing are also provided at the neuroanatomical level. The insular cortex, a region implicated in the encoding and decoding of interoceptive signaling (Craig, 2009a), including the visceral emotion of disgust (see Vicario et al., 2017 for review), is known to be implicated in the processing of both sub-second and supra-second durations (e.g., Ferrandez et al., 2003; Maquet et al., 1996; Tregellas, Davalos, & Rojas, 2006; see also Wiener, Turkeltaub, & Coslett, 2010 and Craig, 2009b, for review). It is also involved in the detection and regulation of hunger signals in healthy humans (i.e., hunger increases insula activity. see Tataranni et al., 1999; Del Parigi et al., 2002). Neuroimaging evidence has shown that the degree of the anterior insular/opercular cortex activation predicted subjects' accuracy in judging the timing of their own heartbeats (Critchley, Wiens, Rotshtein, Ohman, & Dolan 2004). Moreover, the study by Pollatos, Yeldesbay, Pikovsky, & Rosenblum (2014a) has provided evidence about the role of the interoceptive awareness of the cardiac cycle for the encoding and reproduction of time in the range of 2–25 s (see also Meissner & Wittmann, 2011; Pollatos, Laubrock, & Wittmann, 2014b, for further evidence in this field). Interestingly, altered interoceptive functions have been reported in several disorders characterized by abnormal time processing. This is true for Parkinson's disease (Ricciardi et al., 2016), Schizophrenia (Ardizzi et al., 2016), Borderline Personality Disorders (Müller et al., 2015), and Depression (Simmons et al., 2016). For references concerning time processing deficits in the clinical disorders mentioned above please refer (respectively) to: Koch et al. (2008), Thoenes and Oberfeld (2017), Berlin and Rolls (2004), Thöne and Oberfeld (2015). This corroborates the relevance of the interoception-related brain activity in the experience of time. Finally, an altered insula activity has been documented in clinical populations suffering from eating disorders such as AN (e.g., Kaye & Bailer, 2011) and Obesity associated with binge eating (Watkins et al., 2016). Interestingly, a recent study by Mata et al. (2015) has found a co-occurrence between hypoactive insula activity, reduced timing ability and interoceptive sensitivity, as measured via heartbeat perception task, in a group of obese participants.

Overall, the literature discussed above provides a rationale for testing the hypothesis that acute food deprivation might affect the subjective experience of time, compared to the intake condition. We addressed this hypothesis by comparing the ability of a group of participants in estimating the residual duration of ongoing body actions, which were interrupted a few seconds ahead of their completion. In particular, participants were presented with three types of videos showing the movements of a hand grasping: (1) a muffin (*primary reinforcement action*); (2) a banknote (*secondary reinforcement action*); or (3) a notepad (*neutral action*). This design allowed testing the specific influence of food deprivation on the perception of grasping movements directed to reinforcement and no-reinforcement outcomes (i.e., the control condition). Moreover, it allowed comparing the impact of primary vs. secondary reinforcement, to investigate whether any potential bias toward the primary reinforcement can be generalized to the secondary reinforcement. For the primary reinforcement category, we chose a muffin, as it is a popular sweet among different cultures. This is important given the international student population at Bangor University. A 20 lb banknote was chosen in line with the local currency where the study was performed. The notepad was chosen because it is a familiar object not linked to any reinforcement.

To investigate whether food deprivation affects timing performance, our participants were tested, on two separate days, under two different physiological conditions: (1) while being in food deprivation (i.e., after at least 12 h of fasting) and (2) after having consumed a snack (i.e., after at least 12 h of fasting). Importantly, for each physiological condition, participants were asked to rate their subjective hunger rating. This way, it was possible to distinguish the effect of food deprivation/intake from the effect due to changes in the hunger sensation associated with the two physiological conditions.

According to the evidence of (1) positive effects of fasting on attention-related skills (Tian et al., 2011), which are known to be critical for time processing (e.g., Casini & Ivry, 1999; Enns, Brehaut, & Shore 1999; Tse, 2004; Brown, 2006; Vicario, Rappo, Pepi, & Oliveri, 2009; Vicario, Rappo, Pepi, Pavan, & Martino, 2012; Vicario & Martino, 2010; Vicario, Bonni & Koch, 2011); and (2) enhanced insular activity with hunger signaling (Tataranni et al., 1999; Del Parigi et al., 2002) and better timing prediction abilities (Critchley et al., 2004), we expected that short-term fasting improves timing performance (i.e., higher accuracy and/or lower variability), compared to the snack condition. In the context of our research, we also expected to detect specific effects of hunger on the timing of *primary-reinforcement*-oriented actions (i.e., muffin grasping actions), as compared to *secondary-reinforcement*-oriented and neutral actions, given the relevance of food stimuli for the physiological status (higher appetite) of participants. Finally, we predicted significant correlation between timing performance and two variables linked to the digestive system: (1) the self-reported hunger rating, which provides a direct measure of the subjective appetite (i.e., the status) during task execution; (2) the Body Mass Index (BMI), which has been here taken as a measure of individual trait of feeding habits, although several other variables such as genetic and environmental factors can play a role on it (Ortega-Alonso, Pietiläinen, Silventoinen, Saarni, & Kaprio, 2012).

Materials and methods

Participants

Participants were a convenience sample of 20 students (4 males, 3 left-handed. Age: M = 21.0, SD = 2.92) of Bangor University, who completed this study in return for £ 6 or for course credits. Our sample size was decided in relation to a previous work of our group in this field (Vicario, Makris, & Urgesi, 2016). A post hoc power analysis performed with the G Power 3 software (Faul, Erdfelder, Lang, & Buchner, 2007) showed that, with an *alfa* level of 0.05 and an estimated medium effect size in the population of $f = 0.25$ (Cohen, 1992), testing 20 participants with our repeated-measure design (assuming a correlation of 0.5 among repeated measures) allows a power of 0.97. The mean BMI was 20.77 kg/m^2 (SD = 2.42). Information to calculate the BMI was collected during the first meeting, before starting the experimental session. All participants had normal or corrected-to-normal visual acuity and gave their written informed consent prior to their inclusion in the study and were naïve as to its purpose. Specific information concerning the motivation of the study and its predictions was provided only after the subjects completed all the experimental sessions. The exclusion criteria were being older than 30 years and/or a fasting time lower than 12 h. The study was approved by the ethics board of the School of Psychology at Bangor University and was conducted in agreement with the principles of the 1964 Helsinki.

Materials and procedure

To test our hypothesis, we used a temporal prediction task similar to the one used in two recent works (Avanzino et al., 2013; Martino et al., 2015). Each experimental session included three different visually perceived grasping movements: (1) a muffin grasping movement; (2) a banknote grasping movement; (3) a notepad grasping movement. The notepad grasping movement was chosen as control condition as our intent was testing the effects of appetite manipulation on the temporal prediction of reinforcement-oriented vs. no-reinforcement-oriented actions. The three videos displayed movements under the same visual angle. Each movement was completed in 5000 ms. The presentation of one of these three videos in the experimental block was randomly selected by a computer program (i.e., E-prime 2 professional). Before starting the task, participants were shown the three videos for the full length (one presentation for each video type) without receiving any instructions. Participants had the opportunity to see the full presentation of the three videos only in the first session. During the experimental block, the same videos were presented and were interrupted after a variable interval from their onset by presentation of a dark screen. In particular, videos were interrupted after 2000 or 3000 ms from onset. Each video was preceded by a 2 s fixation cross that represented the ready signal. During the dark screen interval, which was presented until response, participants were asked to indicate the instant at which the interrupted movement reached its end (i.e., when the hand in the video grasped and lifted from the shelf the muffin, the banknote, or the notepad). This temporal prediction task was executed by keeping pressed the spacebar of a computer keyboard for a temporal amount corresponding to the time participants judged was required to complete the interrupted ongoing actions. Thus, participants were asked to press the spacebar soon after video interruption and to keep it pressed until the time when they estimated the action was completed (according to their internal representation of action deployment as learned in the initial

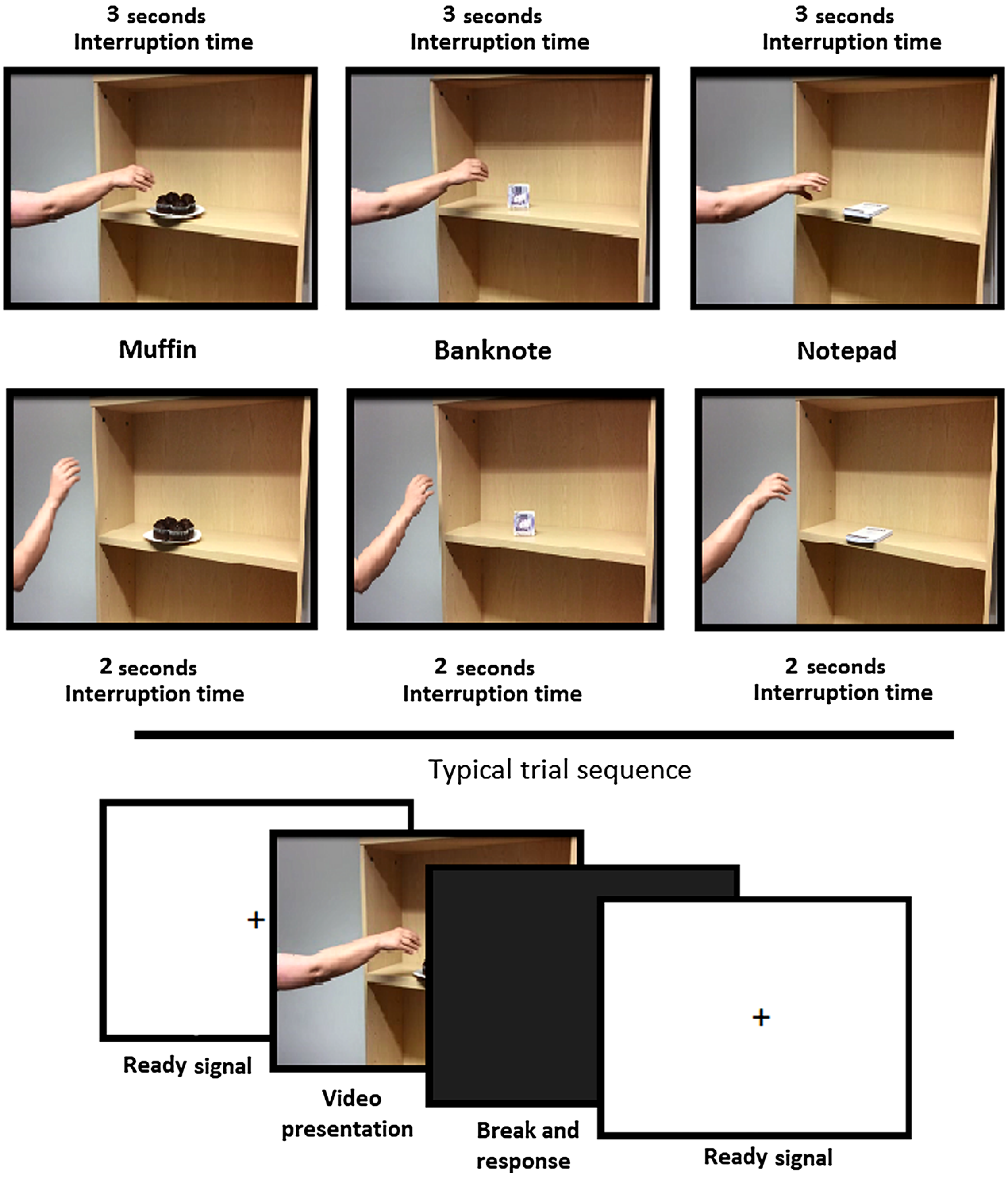

Fig. 1 The figure shows the 2 and 3 s interruption time snapshots associated with a hand grasping a muffin, a banknote and a notepad. The lower part depicts a typical trial sequence

familiarization phase). Figure 1 shows a schematic depiction of the grasping action for the three types of stimuli and the two interruption times and a typical trial sequence.

Thus, participants used their knowledge of the hand movement speed and its distance from the goal at the interruption time in order to extrapolate the duration of the movement presented in the videos. Two randomly presented interruption times (i.e., 2000 and 3000 ms) were used for the three different videos to investigate any performance difference in relation to the temporal distance from the goal. Each video was administered 20 times (i.e., 2 interruption times × 10 trials). Therefore, each experimental session consisted of 60 trials (i.e., 3 videos × 2 interruption times × 10 trials). Each participant was individually tested in two sessions (i.e., fasting and snack), which were administered in two consecutive days and in a counterbalanced order. All participants were tested in the morning time (i.e., between 08:00 am and 11:30 am). Each participant was asked to attend the two sessions at the same hour of the day. They were always asked to eat their last meal at least 12 h before the scheduled sessions. In one session (i.e., fasting session), participants performed the task after at least 12 h of overnight fasting; in the other session (i.e., snack session) the task was performed immediately after having eaten a snack (i.e., bananas) following at least 12 h of overnight fasting. Participants were randomly assigned to one or the other order of physiological status manipulation. Participants were invited to eat the snack until satiation. They also provided hunger ratings both before and after breaking their fast using a 10-cm VAS, with anchor points labeled “Not at all hungry” to “Extremely hungry”.

Data analysis

A two-tailed *t* test was performed to compare appetite ratings in the fasting and the snack conditions. Participants’ task performance was evaluated by considering the: (1) mean time estimation (TE) of temporal intervals provided for the presented actions, which indicates how accurate participants were in estimating the time required to complete the presented actions. Since actions lasted 5000 ms in total, TE closer to 2000 or 3000 ms, respectively for the interruption times of 3000 or 2000 ms, indicated better performance; (2) coefficient of variation (CV) of estimations provided for the presented actions. The CV was calculated as the ratio between the SD and mean values of TE (SD/M) for each condition, and provides an index of performance variability in temporal judgment.

TE and CV were entered into separate 2 (fasting, snack – physiological status) × 3 (muffin, banknote, notepad – grasping object) × 2 (3000, 2000 ms – interruption time) repeated measures analyses of covariance (ANCOVAs), entering the appetite ratings in the fasting and the snack conditions as continuous predictors. This way, we could test not only the effects of food depletion and intake (i.e., in association to fasting vs. snack condition), but also those of the individual perceived level of hunger in each condition. If the covariate showed significant interactions with the other variables, we assessed the effects of these within-subjects variables (or their interaction) on the dependent variable at particular levels of the covariate using a mixed-model ANOVA design (Green & Salkind, 2011) with hunger rating group (High vs. Low) as between-subjects factor. In particular, we entered into the follow-up ANOVA design the scores of those individuals with a hunger rating above the 60° percentile (High; $N = 7$) vs. those with a hunger rating below the 40° percentile (Low; $N = 7$), thus dropping out the data of the individuals with intermediate hunger ratings ($N = 6$). All post hoc comparisons were performed by using the Duncan test, which has been developed to reduce the risk of false negative (Type II) error (Ijsmi, 2016). In particular, the Duncan test is a sequential post hoc test that reduces the size of the critical difference depending on the number of steps separating the ordered means; this procedure is optimal for testing in the same design effects that may have different sizes (Duncan, 1955; Dunnett, 1970; McHugh, 2011), as it is expected from the manipulation of different levels of motivational values (i.e., primary and secondary reinforcement) of the target object in our design.

For all statistical analyses, a *p* value of < 0.05 was considered to be significant. Partial-eta squared were used to calculate the effect size index. This measure has been recommended by Keppel (1991) to improve the comparability of effect sizes between studies. Data analysis was performed using Statistica software, version 8.0, Stat Soft Inc., Tulsa, USA. Furthermore, correlation analyses were implemented to measure any relationship between the average timing measures (i.e., TE and CV) provided in the fasting and snack conditions and the BMI measure of each participant. The average timing scores for both the TE and CV measures were obtained by collapsing the performance scores provided for the three object-grasping videos and at the two interruption times.

Results

The two-tailed *t* test documented higher self-reported hunger ratings in the fasting condition ($M = 6.42 \pm 1.65$ SD), compared to the snack ($M = 3.32 \pm 2.21$ SD) condition [$t\ (19) = 5.01$, $p < 0.001$).

Time estimation

The ANCOVA on TE detected no significant main effects [all $F\ (1,\ 17) < 2.91$, $p > 0.1$, $\eta_p^2 < 0.15$]. Crucially, a marginally significant interaction between physiological status and object [$F\ (2,\ 34) = 2.96$, $p = 0.065$, $\eta_p^2 = 0.148$] was qualified by significant interaction between physiological status, object and the covariate of hunger ratings in the fasting condition [$F\ (2,\ 34) = 4.96$, $p = 0.013$, $\eta_p^2 = 0.226$]. This suggested that the experimental manipulation of the physiological status had different effects on the time estimation of the three object-grasping actions according to the actual level of perceived hunger reported by the participants in the fasting condition. The covariate of hunger ratings in the snack condition had no effects [all $F < 2.3$, $p > 0.14$, $\eta_p^2 < 0.12$]. All other interactions were far from significance [all $F < 2.4$, $p > 0.10$, $\eta_p^2 < 0.13$], with the exception of a marginally significant interaction between object and interruption time [$F\ (2,\ 34) = 3.26$, $p = 0.051$, $\eta_p^2 = 0.161$]. Post hoc analysis revealed that, unsurprisingly, TE values at the early interruption time (i.e., 2000 ms) were higher than those at the late interruption time (i.e., 3000 ms) for videos showing the muffin ($M = 1134.8$ ms. vs. $M = 622.15$ ms, $p < 0.001$), banknote ($M = 1.087$ ms vs. $M = 652.96$ ms, $p < 0.001$), and notepad ($M = 1{,}092.4$ ms vs. $M = 646.41$, $p < 0.001$) grasping actions. However, at the early interruption time, TE values were higher, and thus closer to the target duration, for muffin than for both banknote ($p = 0.034$) and notepad ($p = 0.048$) actions, which in turn did not differ ($p = 0.795$). This suggests an overall better performance in predicting, at the early interruption time, the duration of the primary-reinforcement grasping movement, compared to the secondary-reinforcement and neutral object-grasping movements. No significant between-object differences were instead observed at the late interruption time (all $p > 0.16$). The non-significant interaction between physiological status, object and interruption time suggests that the effects of physiological status on the time estimation of the three object-grasping movements, as moderated by the covariate hunger ratings in the fasting condition, was comparable at the two levels of interruption time. Thus, the amount of information gathered before video interruption or the duration of the required space-bar-pressing response did not affect the influence of hunger on time estimation.

To explore the source of the significant modulation of hunger ratings in the fasting condition on the interaction between physiological status and grasping object, we conducted a follow-up mixed-model ANOVA with the group factor of Low vs. High hunger ratings after fasting (see "Materials and methods") and grasping object and physiological status as within-subject variables. The ANOVA revealed a significant interaction between the two within-subject variables and the group factor [F (2, 24) = 3.89, $p = 0.034$, $\eta_p^2 = 0.245$]. Post hoc analysis showed that the individuals who reported low hunger levels after fasting condition had higher TE values in the fasting than snack condition for muffin grasping actions ($M = 988.29$, SEM = 250.11 ms vs. $M = 930.34$, SEM = 194.97 ms, $p = 0.041$), but not for banknote ($M = 948.63$, SEM = 255.16 ms vs. $M = 953.99$, SEM = 195.32 ms, $p = 0.825$) or notepad ($M = 970.58$, SEM = 248.05 ms vs. $M = 929.07$, SEM = 206.36 ms, $p = 0.138$) grasping videos. The Fig. 2 shows a graphical representation of the TE scores described above in the fasting condition.

This indicates that, during the fasting condition, a moderate level of hunger improves the timing performance but only for the grasping of the primary-reinforcement object, which is relevant for the physiological condition of the participant. Conversely, the individuals who reported high levels of hunger after fasting showed comparable TE values in the fasting and snack physiological status conditions for either the muffin grasping videos ($M = 905.7$, SEM = 250.11 ms vs. $M = 917.66$, SEM = 194.97 ms, $p = 0.622$) or for the banknote grasping videos ($M = 902.95$, SD = 255.16 ms vs. $M = 893.97$, SEM = 195.32 ms, $p = 0.711$). Interestingly, however, for the notepad grasping actions, they showed significantly lower, and thus further away from target duration, TE values in the fasting than in the snack condition ($M = 864.8$ ms, SEM = 248.05 vs. $M = 940.58$, EMD = 206.32 ms, $p = 0.001$). Please see Fig. 1b for details. This indicates that, during the fasting condition, high hunger levels worsen time estimation, but only for actions that involve an outcome that is non-relevant for the physiological status of participants (i.e., a notepad). No other between-object—physiological status, or—group pairwise comparisons resulted significant (all $p > 0.1$).

Coefficient of variation

The ANCOVA on the CV revealed only a marginally significant main effect of grasping object [F (2, 34) = 2.63, $p = 0.087$, $\eta_p^2 = 0.245$], which was significantly moderated by the covariate of hunger ratings after snack [F (2, 34) = 8.52, $p = 0.001$, $\eta_p^2 = 0.334$]. No other effects resulted significant [all $F < 2.2$, $p > 0.16$, $\eta_p^2 < 0.134$]. The mixed model ANOVA with grasping object as within-subjects variable and the group factor of Low vs. High after-snack Hunger raters showed a significant two-way interaction [F (2, 24) = 7.27, $p = 0.003$, $\eta_p^2 = 0.377$]. Post hoc analysis showed that for those individuals that reported high hunger levels after snack we detected an overall higher CV for the estimation of the timing of muffin grasping actions ($M = 0.284$) than of banknote ($M = 0.222$; $p = 0.004$) or notepad ($M = 0.239$; $p = 0.03$) grasping actions; the latter two conditions did not differ ($p = 0.363$). See also Fig. 3a for a graphical representation of this result. This suggests that the individuals with high residual levels of hunger after snack showed higher variability of responses for estimating the time of primary-reinforcement-oriented actions in both fasting and snack conditions.

Conversely, those individuals who reported low hunger levels after snack showed higher CV for the estimation of banknote ($M = 0.294$) than of notepad grasping actions ($M = 0.248$; $p = 0.031$); the difference between banknote and muffin grasping actions ($M = 0.259$) was only marginally significant ($p = 0.082$), while the difference between muffin and notepad grasping actions was far from the significance threshold ($p = 0.577$). See also Fig. 3b for a graphical representation of this result. This suggests that the individuals with low level of hunger after snack showed

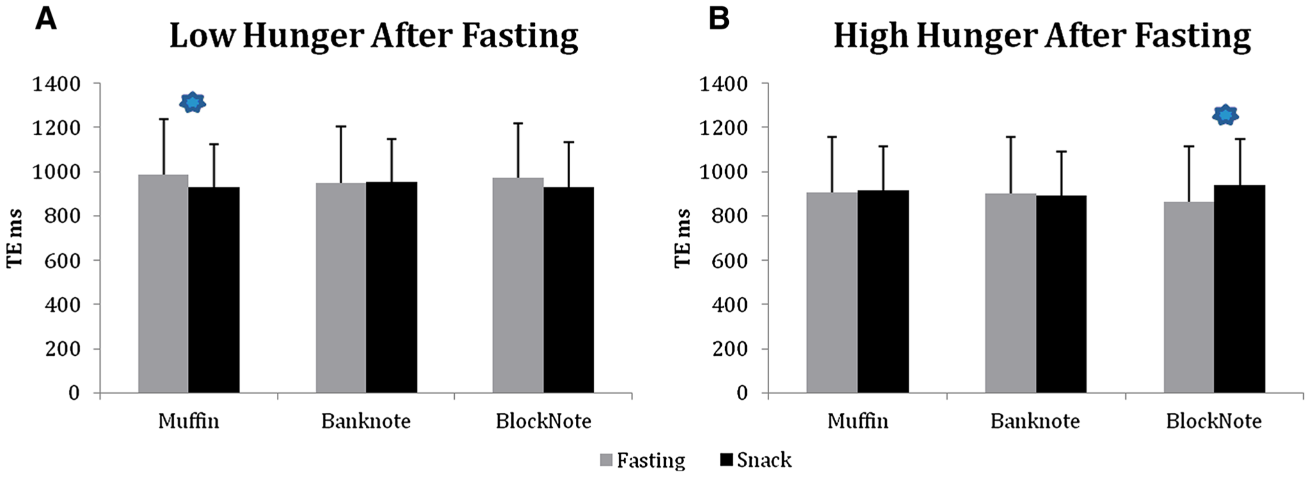

Fig. 2 The figure shows the temporal estimations (TE) scores for the three types of grasping movements in the two physiological conditions (i.e., fasting vs. snack) for participants with low (**a**) and high (**b**) hunger ratings after fasting. The asterisk symbol indicates a significant difference

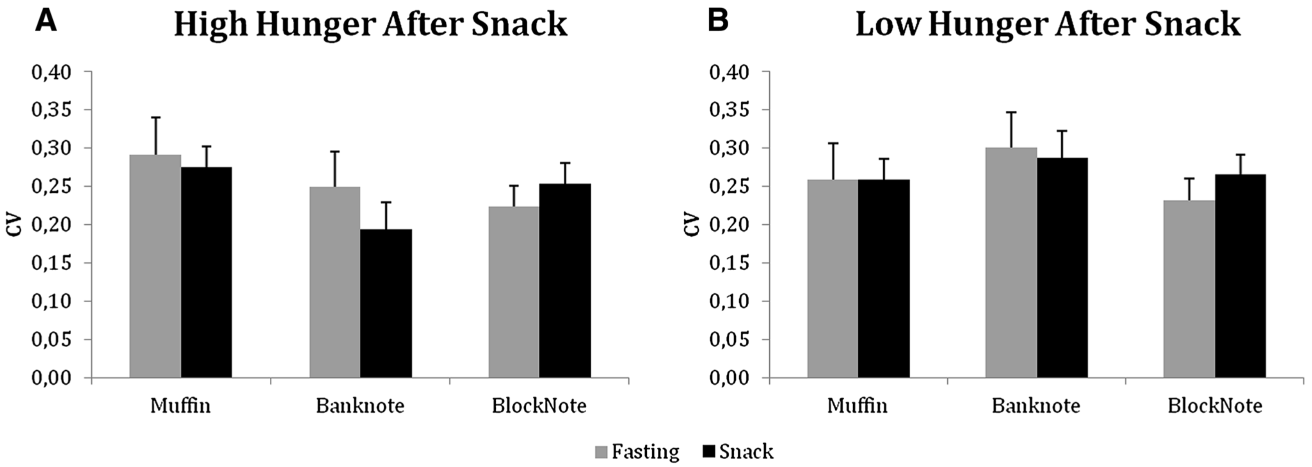

Fig. 3 **a** The figure shows the coefficient of variation (CV) scores for the three types of grasping movements in the two physiological conditions (i.e., fasting vs. snack) for participants with low (**a**) and high (**b**) hunger rating after snack

higher variability of responses in estimating the time of secondary-reinforcement-oriented actions.

Correlations

The correlation analysis documented a significant negative relationship between individual BMI and the CV scores provided by our participants in the fasting condition for the lower interruption time (i.e., 2000 ms interruption time: $r = -0.549$, $p = 0.012$), while the correlation was only marginally significant for the late interruption time (3000 IT: $r = -0.437$, $p = 0.054$). This result indicates that timing variability decreases with the increasing of BMI. On the other hand, no significant results were obtained for the snack condition at both interruptions times (all $p > 0.1$). Moreover, no significant results were obtained for the TE scores with regard to the all the above-mentioned conditions (all $p > 0.1$). We also detected a positive correlation between hunger ratings in the snack condition and TE for the 3000 ms interruption time ($r = 0.504$, $p = 0.023$). No other significant results were obtained (all $p > 0.1$).

Discussion

In the current research, we provided evidence that temporal estimation can be influenced by appetite. This is in agreement with research linking timing skills with the neural mechanism involved in appetite regulation at both neurochemical (see Lewis & Miall, 2006) and neurofunctional (Tomasi, Wang, Studentsova, & Volkow, 2015) levels, as well as with the literature documenting a relationship between interoceptive perception and the experience of time (e.g., Pollatos et al., 2014a, b).

Overall, our results showed that participants tended to underestimate the duration of the interrupted actions, independently of the object to be grasped. In fact, estimation times were much lower (on average less than 1300 ms) than the time interleaving from the interruption to the end of video, which was 3000 ms in the 2000 ms interruption time condition and 2000 ms in the 3000 ms interruption time condition. However, higher estimation times were provided in the early than late interruption time condition, albeit this effect was modulated according to the object to be grasped. This suggests that participants were appropriately performing the task, but tended to underestimate the duration of the interrupted actions. This pattern of results is in keeping with the well-known Vierordt's law (Lejeune & Wearden, 2009), which predicts that participants tend to overestimate "short" durations and underestimate "long" durations. It is also possible, however, that the strong underestimation bias obtained in the present study might reflect the reference to internal models of the spatiotemporal kinematics of the movements to grasp the objects during motor execution, rather than to visual memory of the previously observed action video (Makris & Urgesi, 2015; Urgesi, Savonitto, Fabbro, & Aglioti, 2012; Vicario et al., 2016). Moreover, at the early interruption time, TE scores were higher, and thus closer to the target duration, for muffin than for both the two other conditions. This indicates an overall better timing performance in response to the exposure to a primary reinforcement object, as compared to the other two conditions.

In agreement with our research hypothesis, our results indicate that time processing skills can be influenced by the modification of the physiological status (i.e., fasting), as well as by individual traits (i.e., BMI) linked to appetite at the cognitive and neural levels. However, the link between state modification and time estimation is strictly dependent from the subjectively perceived hunger and the nature of the action goal. Under fasting, participants with low hunger levels were more accurate in the time estimation of only those grasping actions that were oriented to a primary reinforcement (i.e., a muffin). This suggests that, under fasting, a moderate hunger might even improve time estimation, if this includes information (i.e., a primary reinforcement) relevant for the physiological status (i.e., fasting) of the participant. The positive effects of moderate levels of hunger on time estimation performance after fasting might indicate an interference of satiation status with cognitive performance, in line with the *postprandial dip* effect (Craig, 1986), which is known to negatively affect cognitive performance (see also the study by Fischer, Colombani, & Wenk, 2004, which has reported a positive relationship between self-reported hunger sensation associated with morning food ingestion and objective cognitive performance). Conversely, high hunger levels under fasting affected TE accuracy, but only for those grasping actions that were oriented to a no-reinforcement goal (i.e., notepad). While this result is in line with previous evidence of a negative influence of hunger on cognitive performance (Benau et al., 2014, for a review), it also suggests that exposure to reinforcements might reduce such negative influence. In fact, no difference was obtained for the timing of grasping actions toward a primary or a secondary reinforcement. Furthermore, it is interesting to note that no effects were found for the snack session. This suggests a specific role of the physiological status associated with fasting in explaining the results on TE.

Overall, our findings show that, beyond the possible effects of high levels of hunger on cognitive functions in general (Benau et al., 2014) and on action timing estimation in this study, the presentation of a reinforcement had positive effects on performance, by improving the estimation of reinforcement-oriented actions under moderate level of hunger and by reducing the negative effects of high levels of hunger on the timing of primary and secondary reinforcement-oriented actions.

A possible neural mechanism for the positive effect of moderate hunger on the temporal estimation of food-directed actions might be related to the activity of the dopaminergic system. Indeed, a study by Volkow et al. (2002) has showed a positive relationship between DA release in the dorsal striatum (i.e., a key circuit in time processing, Lewis & Miall, 2006) and self-reports of hunger rating after food exposure (via smell and taste). Moreover, there is evidence that the fasting related ghrelin hormone promotes the activation of dopamine neurons (Palmiter, 2007). An alternative, not mutually exclusive, explanation for the current research might refer to the contribution of the insula cortex, which represents a key region for processing appetite signaling (e.g., Tomasi et al., 2015) and the encoding of interoceptive states (see Craig, 2009b for a review). The manipulation of appetite might have influenced the activity of the insular cortex, with a direct modulation of the subjective experience of time, given the sensitivity of this region to unexpected cross-modal disparities in time synchronization (Craig, 2009b). For example, there is evidence of a graded response of the anterior insula cortex to a cross-modal timing mismatch between auditory and visual stimuli that are normally synchronous (e.g. a speaking mouth) (Bushara, Grafman, & Hallett, 2001). According to this suggestion, one might speculate that, since hunger is associated with activation of the insula, it may heighten general bodily awareness, thus leading to better time-keeping abilities, as suggested in some research (Meissner & Wittmann, 2011). However, this hypothesis remains speculative, as we did not assess body awareness in the current research.

Worthy of discussion are also our results on variability. We found that individuals with high residual levels of hunger after a snack showed higher variability of responses for estimating the grasping time of primary-reinforcement objects (i.e., the muffin). This result can be interpreted as a nonspecific effect of the exposure to a primary reinforcement stimulus, which might have reduced the attentional capacity toward the temporal features of this movement, because of its high salience in those individuals who reported high levels of hunger even after snack. On the other hand, participants with low level of hunger after snack showed higher response variability in estimating the time of secondary-reinforcement-oriented actions, which likely reflects higher relevance of the secondary than primary reinforcement goal in those individuals who reported low levels of hunger after snack. Crucially, similar effects were obtained in both the snack and fasting conditions, thus suggesting that the influence of residual hunger after snack on the variability of time estimation performance is more linked with persisting traits of the individuals rather than on state modifications. This is further corroborated by the negative correlation between BMI and CV measure reported in our study, which showed that individuals with higher BMI had lower variability in time estimation.

The dopaminergic system can be called into question to explain the negative relationship between BMI and the CV measure reported in our study. In fact, there is evidence that BMI negatively correlates with the availability of striatal DA transporter, which has been demonstrated to be implicated in time processing (e.g., Rao, Mayer, & Harrington, 2001). Moreover, a recent study (Cho, Yoon, & Kim, 2015) has found a positive relationship between BMI and DA D2/3 receptor availability in the dorsal putamen of healthy subjects. Thus, BMI might closely reflect the default striatal dopaminergic activity, which has been reported to be part of the internal clock system (e.g., Lewis & Miall, 2006) and to be involved in the execution of temporal prediction tasks (see Tomasi et al., 2015).

The negative relationship between BMI and timing variability reported in our study can be also explained in relation to the insula cortex. There is at least one study (i.e., Yokum, Ng, & Stice, 2011) reporting a positive relationship between BMI and insula activation. Thus, the negative relationship between BMI and timing variability might reflect a different degree of default insula activation, which is known to predict timing performance (Critchley et al., 2004).

Conclusion

Overall, our study provides a new contribution to the literature on the effects of appetite and food depletion/intake at cognitive level and, more in general, to the research line exploring the contribute of interoception in the subjective experience of time. Here we reported a positive effect of moderate hunger associated with fasting on time-keeping accuracy, although it was specific for actions directed to a primary reinforcement. This result is in line with the *Embodied Cognition* theoretical perspective (e.g., Gallese & Sinigaglia, 2011; Lakoff, 2012) proposing that body states might influence mental states, including the cognitive processes that mediate the experience of time (Vicario, Martino, Pavone, & Fuggetta, 2011). Moreover, it might be interpreted in agreement with an evolutionistic perspective, suggesting that the benefit of moderate hunger on timing skills could represent the residual effect of a crucial mechanism for the survival of the human species in the ancient world. Crucially, however, the positive effects of extreme levels of hunger extended to actions directed to secondary-reinforcement goals, since both types of actions were less affected by fasting, as compared to the estimation of the time of non-reinforcement actions. This suggests that such ancestral mechanism has evolved by including a type of reinforcement that has begun to be part of human history only later. Finally, the results of our work are in line with the *New Look in Perception* theoretical perspective (Bruner, 1957; Erdelyi, 1974), which recognizes the central role of motivational states (e.g., attitudes, values, expectancies, needs) in influencing the perception of external stimuli.

Compliance with the ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights statement All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

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