Gut-brain interaction: exploring the link between bodily states and decision making

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Abstract

Physiological need states adaptively shape decision-making, yet its effects on distinct behavioural components remain poorly characterised in humans. In particular, behavioural dimensions such as impulsivity and motivation are often treated as stable traits, overlooking how bodily signals dynamically regulate behaviour in response to energetic demands. Here, we aim to clarify the importance of metabolic signalling in adaptive behavioural control of food and non-food behaviour in humans. Following an overnight fast, healthy participants completed tasks probing food- and money-related impulsivity, effort-based motivation, and valuation, alongside assessments of fasting duration and body composition. Fasting selectively increased impulsive responding for food (compared to monetary) rewards, as indexed by longer stop-signal reaction times. This food-specific increase in impulsivity was robust across analyses and was not explained by higher subjective valuation of food; rather, greater willingness to pay for food was associated with improved impulse control. Body fat percentage moderated fasting effects, suggesting an interaction between short-term energy deficit and long-term energy reserves. In contrast, effort exertion in an incentive-motivation task was strongly up-regulated by energy deficit in a domain-general manner, independent of reward type. Effort decreased with higher body fat percentage, but this effect was partially normalised by fasting. A composite measure of relative energy deficit, integrating fasting duration and fat mass, provided a parsimonious account of individual differences in effort spending and outperformed models based on fasting or body composition alone. Valuation measures further revealed a higher willingness to pay for food with increasing body fat percentage, but did not account for behavioural effects observed in impulsivity or effort tasks. Finally, questionnaire-derived trait measures showed limited correspondence with state-dependent behavioural changes, highlighting the dynamic nature of energy-dependent decision processes. Together, these findings demonstrate dissociable and complementary effects of energy status on impulse control and motivated behaviour, showing how adaptive decision making emerges from the interaction between acute metabolic signals and long-term bodily energy reserves.

Introduction

In order to survive, all animals need to continuously adapt their behaviour to the constraints of their environement and the needs of their body (Flavell et al., 2022). Deciding how and when to act, or how much energy to invest, will have different consequences for fitness depending on the context and the energetic state. Yet, behavioural dimensions such as impulsivity and motivation are often conceptualized as static traits, dismissing how bodily signals dynamically shape their highly adaptive nature.

Hunger is a perfect example of how caloric needs can control our behaviour. From an ecological perspective, energy deprivation should bias decision-making systems toward strategies that favour the acquisition of food. While the benefit of hunger in motivating eating is evident (it thus satisfies the underlying caloric needs), the influence of hunger might extends, beyond food consumption, to other behavioural dimensions and reward domains. Consistent with this view, there is evidence that, beyond food reward processing (Siep et al., 2009), short term fasting could alter impulse control (Howard et al., 2020; Voigt et al., 2021), risk assessment (van Swieten et al., 2023), temporal discounting (Skrynka & Vincent, 2019), or action vigor (Hanssen et al., 2021; Pirc et al., 2019). Yet, the nature and domain (i.e. food vs. non-food oriented) specificity of hunger's effects are still not well delineated, and the role of energetic need on the flexible adjustment of behaviour beyond food intake remains largely unclear, especially in humans (Bamberg & Moreau, 2025; Benau et al., 2014). One possibility is that fasting induces a domain-general reduction in self-control and an increase in motivation across reward types. Alternatively, fasting may selectively prioritise biologically relevant rewards, such as food, while leaving decision-making for abstract rewards relatively unaffected. Empirical evidence has been limited by a focus on single reward domains, most commonly food, making it difficult to distinguish between these accounts. Clarifying whether hunger produces domain-general or domain-specific changes in behaviour is essential for understanding the adaptive logic of state-dependent decision making.

At the neural level, cumulative animal literature shows that metabolic and hormonal signals associated with hunger, such as insulin, ghrelin, or glucagon like peptide-1 (GLP-1), modulate various brain circuits and especially the dopaminergic system (Cassidy & Tong, 2017; Geisler & Hayes, 2023; Palmiter, 2007). Given the importance of midbrain dopamine signalling for reward processing, motivation, and impulsivity, these findings offer a mechanistic pathway to explain the importance metabolic signalling in the control of those behaviourial dimensions. Recent studies further support this theory by showing that dopaminergic circuits are also affected by metabolic state in humans (Hanssen et al., 2021; Kullmann et al., 2021). Importantly, the same dopaminergic neurocircuits are involved in both food and non-food reward processing (Oren et al., 2022), suggesting that the behavioural consequences of their state-dependent modulation could generalize to other domains than food reward. Despite those advances, evidence for state-dependent modulation of the neural circuits underling food and non-food behaviour in humans is still lacking, further prompting the need to clarify the importance of metabolic signalling in adaptive behavioural control.

In addition to transient energetic states, individuals differ in their long-term energy reserves. Body fat mass, long term storage of energetic resources in the body, also influences metabolic and hormonal signalling relevant for reward processing and decision making. Notably, leptin, a hormone produced by the adipose tissue, can directly alter dopaminergic function in the brain (Fulton et al., 2006; Opland et al., 2010). Accordingly, obesity have been robustly associated with dopaminergic dysregulations (Kroemer & Small, 2016), supporting the theory that reward processing is affected by metabolic changes. Yet most studies treat adiposity as a static individual characteristic emerging as a *consequence* of food preferences and eating habits: the same dopamine-dependent behavioural dimensions outlined above are classically conceptualised as fixed psychometric traits defining food behaviour, and thus body composition. More precisely, higher body fat is robustly associated with higher impulsivity (Bartholdy et al., 2016; Garcia-Garcia et al., 2022; Mobbs et al., 2010) and, although less conclusively, with lower motivation (Giesen et al., 2010; Hanssen et al., 2022; Mathar et al., 2016). Importantly, those conclusions are derived independently of acute physiological challenges, leaving open the question of possible interaction between acute regulation by hunger and (chronic) body composition on dopaminergic function and thus adaptive behavioural control. In addition, lean body mass is the main driver of resting energy expenditure of an individual (Dulloo et al., 2017). The ratio between fat and lean mass therefore reflects the relative energy reserve available, defining the urgency of the need to find food, and constraining potential effort expenditures. From an ecological perspective, behavioural responses to fasting should thus depend not only on immediate hunger signals but also on longer-term energy reserves and basal energy consumption, as the same degree of deprivation may carry different biological significance across individuals. The role of body-composition in the modulation of hunger-dependent behavioural adaptation is however, as of today, largely unexplored.

To adress this gap, we assess in a series of experiments in humans how an acute an energy deficit induced by fasting interacts with long term energy requirements, as reflected by body composition, to modulate impulsivity (inhibitory control) and incentive motivation (willingness to exert physical effort). Additionally, we test the relative influence of food and non-food incentives to explore the domain specificity of those adaptive behavioural modulations.

Results

Based on the hypothesis that metabolic needs adpatively regulates decision making, we aimed to determine the influence of the long- and short-term fluctuations in energy levels on the measured behavioural dimensions, contrasting food and monetary conditions to assess the generality or food specificity of those influences. We invited healthy participants (N=94) to come to the lab after an overnight fast. During the testing session, they had the opportunity to earn food and monetary outcomes in a set of behavioural experiments (see Fig. 1 and Methods) designed to assess their outcome-specific motivation (incentive force task) and impulsivity (stop signal task). After completing an auction task capturing the subjective valuation of the food vs. monetary rewards, they were allowed to consume their wins (eat the food and pocket the money) before filling in various questionnaires related to their drive, impulse control, and food behaviour. In addition to those behavioural and self-report markers, we recorded the body composition and fasting duration of each participant to assess their metabolic status.

Fasting selectively increases impulsivity for food

To quantify the variations in impulse control across our participants, we adapted the classic stop signal task (Verbruggen et al., 2008) as a first behavioural task (Fig. 1 top). Briefly participants were instructed to press a button or refrain from pressing it in response, respectively, to go and stop signals. Trials were organised in alternating blocs rewarding performances with either food or money, as clearly indicated by pictures of the outcomes at the beginning of each bloc and flanking the go/stop cues. For each participant and each bloc type, we computed the stop signal reaction time (SSRT) which captures the relative time needed to stop an ongoing response process, that is a longer SSRT indicates a weaker executive control and therefore a more "impulsive" responding.

A mixed effect model revealed a strong interaction between fasting duration and reward type ($p<0.001$, Fig. 2 a) which was further modulated by body composition (3 way interaction, $p=0.044$). This effect was driven by a fasting x fat% in the SSRT in the food condition ($p=0.040$) which could not be observed in the money condition ($p=0.362$). To unpack this complex interaction, we calculated the difference in our impulsivity measures between the two conditions, $\Delta SSRT = SSRT_{food} - SSRT_{money}$.

A first analysis suggested a fasting x fat% interaction ($p=0.022$) which could be understood by the fact that the relative impulsivity for food tend to increase with body fat % (short fast: $r=0.261$, $p=0.077$) but fasting mitigates this tendency (long fast: $r=-0.176$, $p=0.264$; Fig. 2 b). Strikingly, the impact of fasting on the $\Delta SSRT$ was stronger for participant with a lower body fat percentage (low body fat: $r=0.396$, $p=0.030$; high body fat: $r=0.308$, $p=0.098$, Fig. 2 c), suggesting that energy reserves modulate the influence of fasting induced energy deficit. The body composition modulatory effect, however, reduced to a simpler but highly significant effect of fasting ($p<0.001$, Fig. 2 d) when confounding factors were included in the linear model, confirming the strong influence of energy deficit on food-specific impulse control. This follow-up analysis also revealed that the relative impulsivity for food decreased with the willingness to pay for food ($p=0.005$,

Fig. 2 e). While slightly counterintuitive, as one could expect that a higher subjective valuation of food should yield a more impulsive behaviour, this falls in line with previous results demonstrating that impulse control improves for higher reward prospects (Giuffrida et al., 2023).

Together, these results demonstrate that changes in physiological state induced by fasting modulate impulse control for food rewards. Further, fat reserves moderated this dynamics, hinting at a more complex interplay between short and long term energy status on cognitive control. Critically, those effects could not be explained by an increase in the subjective value of food which, on the contrary, improved performances.

Relative energy deficit drives motivation to effort

In order to assess the role of metabolic state on effort regulation, we adapted also classic incentive motivation task (Pessiglione et al., 2007), Fig. 1 b as our second behavioural measure. Briefly, participants held a dynamometer in their hand which they could squeeze to raise the level of a thermometer-like scale on the screen and thus increase their chances of earning a reward. The color of the scale indicated the rate at which the thermometer would rise, allowing participant to gauge their behaviour as a function of the effort required to fill the scale up (difficulty level) and therefore the actual cost/benefit ratio at stake. As for the stop signal task, trials were organised in alternating blocs (indicated by food or money pictures displayed next to the scale) prescribing which type of reward performance will be translated to at the end of the session.

Performances were renormalised to each participant's strength before entering a linear model fitted for each cue typ and including an intercept, the difficulty level, and the trial number. A group level analysis showed that, unsurprisingly, participants exerted less force and were therefore ready to forego their chances of reward, as difficulty increased ($p<0.001$; Fig. 3 a). While the type of reward at stake also affected the performances (interaction with intercept $p<0.001$; difficulty: $p<0.001$; trial: $p=0.011$), this was mainly driven by the difference in subjective valuation of the outcomes (all $p<0.033$) and not by an interaction of metabolic factors (all $p>0.446$). Accordingly, we averaged the two conditions before exploring the influence of the energy status on behaviour. Interestingly, fluctuations in average performances were explained by an interaction between fasting duration and body composition ($p=0.006$, correcting for sex differences). Indeed, while overall performances drastically declined with body fat percentage ($r=-0.34, p=0.001$, Fig. 3 b), this effect was partially mitigated by fasting (short fast, $p<0.002$; long fast, $p=0.9$; Fig. 3 c) suggesting that fasting could partly normalise the negative influence of fat mass on motivation. Looking at the effect of fasting in subgroups of participants split by their body fat % (Fig. 3 d) provides a possible explanation for this complex pattern. Indeed, motivation appears to related to fasting when appraised not by its duration but in terms of the relative energy deficit in induces. To test this hypothesis, we estimated the amount of calories burned during the fasting period relative to the amount of calories stored in the body as fat (see methods). This measure of relative energy deficit (RED) was strikingly similar to our motivation measure (Fig. S1): participants with a high body fat percentage (ie. a slow metabolic rate and large reserves) had a low RED which slowly increased with fasting; in contrast, participants with a lower body fat percentage (ie. burning calories fast, with low energy stocks) had a higher RED which was less consitently affected by fasting as body composition dominated the variations between individuals. Accordingly, RED strongly predicted effort spending ($p<0.001$; Fig. 3 e) and provided a more parsimonious explanation than the fasting x body fat interaction (Δ BIC = 2.1).

In summary, our results demonstrate that effort spending is powerfully up-regulated by short term energy deficits. In contrast to impulse control measurements reported above, this metabolic effect appears very pervasive and do not depend on outcome quantity or identity which additionally influence motivated behaviour.

Changes in willingness to pay for food does not not explain impulsivity nor effort variations

During the first two tasks, capturing respectively impulsivity and motivation, participants were instructed that good performances will earn them food and money tokens, depending on blocs, to be exchanged for actual food items and money at the end of the experiment (Fig. 1 bottom). The subsequent auction task was framed as an opportunity to reallocate the tokens they won by betting on 30 pairs of fortune wheels. On a given trial, each of 10 tokens could be placed either on wheel associated with one of 30 of the available food items, or on another associated with a equivalent monetary value. As each token granted a 10% chance of the fortune wheel to stop on a win, participants could decide to either place all their bets on one wheel, and thus ensure to win the associated outcome, or split their bets and have a chance to win both rewards.

The total amount of tokens allocated to snacks, irrespective of the strategy, reflected the willingness to pay (WTP) for food. While a linear model including fasting duration and body composition did not yield any significant effect, WTP correlated with body fat percentage when tested separately ($p=0.040$, Fig. 4 a).

Importantly, prospects of reward are strong predictors of both motivation and impulsivity, higher incentives being associated with better performances in both of those measures. While WTP for food was not robustly modulated by metabolic state in our data, it could still partially explain the influence of bodily-state on performances. To control for this potential confound, WTP was systematically included as a covariate in the analysis of the stop signal and the incentive motivation tasks. However, adding this control did not affect the results. In conclusion, the influence of metabolic state on behaviour we identifed above can not be simply explained by a change in the subjective value of food rewards, and rather reflect a fundamental regulatory process of action by the physiological state.

Questionnaires capture static but not adaptive behavioural phenotypes

We performed an exploratory factor analysis to summarize the 15 questionnaires filled in by each participant, yielding five factors (Fig. 5 a). The first two ones related to food behaviour, and more precisely to sensitivity to external food triggers ("uncontrolled eating", similar to the previously reported factor (Vainik et al., 2015)), and the active tendency to restraint one's food behaviour ("cognitive restraint"). The next two factors related to more general behaviour, namely sensitivity to rewards vs. punishement ("drive"), and impulsive tendencies ("impulsiveness"). The last factor captured associations between depressive traits an compulsive tendencies along with food coping strategies (“compulsiveness”).

To understand the link between each participant’s traits, as captured by the self-report questionnaires, and their actual implementation in actions, we then correlated the factor scores with the task performances (Fig. 5 b).

Concerning the stop signal task, we found a single correlation between accuracy in the go condition (ie. correctly following the arrow direction) and the impulsiveness factor. While surprising at first, as SSRT is the metric expected to capture impulsivity in this task, this finding is in line with previous reports showing that innaccurate action responses were more predictive of trait impulsivity than action inhibition (Portugal et al., 2018). A more direct explanation for the lack of correlation between trait impulsivity and the SSRT performances is that the latter is a highly dynamic phenotype continuously adapating to physiological state and therefore unlikely to be captured by questions intended to aprehend static qualities. Overall, our results highlight the fundamental shortcomings of questionnaires when quantifying fast fluctuating behaviours such as (fasting-dependent, food-specific) impulsivity.

The force task evidenced a simpler, domain general, behavioural marker summarized by the average effort performance. This metric positively correlated with the “drive” factor, reflecting the well known importance of reward sensitivity in the regulation of effortful actions. Effort was further anti-correlated with the “uncontrolled eating” factor, which could be explained by the fact that this factor also captured a negative drive dimension (ie. sensitivity to punishment) which partially mirrored the “drive” factor. Finally, average effort was negatively associated with our last factor we labelled “compulsiveness”. This factor also loaded depression and stress questionnaires and could reflect a more general mood downregulation that would negatively affect motivation.

Finally, in the auction task, proportion of certain bets (the number of snacks secured by placing all tokens on the food wheel) positively correlated with cognitive restraint and negatively with impulsivity factors, suggesting that those traits can translate into risk aversion when implementing actual food choices and are therefore also pertinent to understand weight regulation.

Next, we explored the link between trait dimensions and body weight. Almost all factors correlated with body composition, indicating that higher fat percentage is related to a higher sensitivity to food cues along with stronger attempts to restraint such urges, and more compulsiveness. The factors we identified are in line with previous reports, in particular uncontrolled eating (Vainik et al., 2015). Body fat was also associated with a lower drive, hinting that the motivational deficit we measured in the effort task might not be due only to a dampened fasting effect in the more corpulent participants but also to a more general lack of reward sensitivity.

Interestingly, "impulsiveness" did not correlate with body composition. While various measures of impulsivity have been associated with body weight before, these associations originate from clinical populations suffering from food related disorders such as morbid obesity or binge eating disorder and might not hold for the general population (Bartholdy et al., 2016; Lavagnino et al., 2016).

All together, our observations show that while self-report questionnaires can capture some behavioural phenotypes and their importance for weight regulation, they also overlook the dynamical aspects of behaviour and therefore fail to fully capture the adaptive nature of metabolic regulation.

Discussion

In this study, we explored in healthy participants the modulatory role of metabolic state on various facets of behaviour. First, we revealed that fasting increases impulsivity selectively for food, an effect which was dampened by body fat percentage. Second, we identified that energy deficit drives a global motivation to exert effort, an effect also dependent on body composition. Together, our results demonstrate that behavior is higly adaptive and depends on a complex interaction between short-term and long-term energy state variations.

Concerning impulsivity, our results generalise recent findings that identified a difference in inhibitory control between fed and fasted states in a food-related task (Howard et al., 2020) by showing that impulsivity progressively increases with fasting duration. We also demonstrated that the effect of fasting was specific to food rewards, confirming the existence of a domain specific impulsive behaviour (Zhang et al., 2017). Notably, an other work, relying on a different measure of impulsivity (information sampling), reported non-food related changes in impulsivity with hunger (Voigt et al., 2021). This discrepency can be resolved by aknowleding that impulsivity is a multifaceted construct encompassing distinct neurobehavioural mechanisms (Mobbs et al., 2010). In light of this litterature, our results suggests that state-dependent modulation of impulsive behaviour might be domain specific, or not, contingent on the underlying process actually measured. Interestingly, the stop signal task we used in this study is recognized to yield highly volatile results within individuals (Thunberg et al., 2024), and to offer only mediocre correlation with obesity (Bartholdy et al., 2016). According to our data, these negative results could be explained by the fact that fasting duration has a strong impact on behaviour, a confounding factor systematically neglected in the litterature. Collectiveley, these results highlight that to understand the exact relation between body composition and impulsivity, future studies should carefully account for the fluctuations (or the lack thereof) induced by hunger state.

Concerning motivation, our data confirms previous reports showing an augmentation of effort to obtain food with increasing hunger (Arumäe et al., 2019; Pirc et al., 2019; Ziauddeen et al., 2012). Notably, those studies relied solely on food rewards, suggesting a food specific effect. In contrast, our study revealed that fasting increases vigor regardless of the type of outcome, suggesting a general motivational effect. We also found a negative correlation between body fat and motivation. While this result align with previous studies (Mansur et al., 2019; Mathar et al., 2016), we however suggest a different interpretation to this relation: instead of being a hallmark of adiposity that could arguably be attributed to dopaminergic dysregulation, the reduction in vigor in participants with higher body fat could be due to a reduced influence of fasting. More precisely, we propose that the caloric deficit induced by fasting needs to be put in perspective with the energy reserve of the body: with higher body fat, fasting is less dramatic for survival and thus has a lower impact on behaviour. Mechanistically, this could be explained by the observation that, in rodents, fasting induced increase in motivation depends on the switch to a ketosis metabolic regime, the timing of which depends on fat reserves (Koubi et al., 1991). Contrasting with this conclusion, other studies found an increase in motivation with BMI (Epstein et al., 2007; Giesen et al., 2010; Hanssen et al., 2021). Differences in the experiental design might explain these discrepencies. First, those studies compared lean to obsese populations, while we only tested healty weight participants. Morbid obesity is associated with numerous metabolic and neural changes that could dysrupt the normal regulation of motivation by bodily state. Second, they offered to win high-calorie snack foods, while our selection contained healthy options. As motivation seems to be dependent on the type of food at stake (Mathar et al., 2016), it is possible that a more granular approach would reveal distinct effects depending on the macronutrient composition of the food reward. More generally, our work underscore the need to account for variations in energy needs to correctly identify motivational phenotypes.

While we can only postulate about the neurobiological mechanisms implementing the adaptive behavioural regulation we identified, our findings are consistent with the metabolic regulation of dopaminergic circuits (T. M. Hsu et al., 2018), critical for the control of the willingness to exert effort (T. M. Hsu et al., 2018) and impulse control (Eagle & Baunez, 2010; Winstanley, 2011). Indeed, hunger related hormones, such as ghrelin, potentiate dopaminergic activity and thus motivation, while leptin, produced by the adipose tissue, tend to dampen it (see Geisler & Hayes (2023) for a review). Furthermore, obesity has been robustly associated with dopaminergic dysregulations, although the exact relation with body weight regulation is still unclear (Janssen & Horstmann, 2022). A better understanding how the various metabolic signals interact, at their respective timescales, to control dopaminergic function is needed to decipher state-dependent regulation of behaviour.

From an ecological perspective, our data are in line the hypothesis that energy requirements shift behaviour toward food acquisition by increasing effort expanditure and biasing decisions toward more immediate actions. While we also found that adiposity was associated with a lower motivation, we proposed that this only reflect a blunted or delayed effect of fasting in participant with higher energy reserves. Our interpretation is thus at odds with the classical view in the literature, associating obesity with a set of "traits" or cognitive phenotypes assessed by psychometric questionnaires (Gerlach et al., 2014; Robinson et al., 2020). The importance of fast metabolic influences, overlooked by this approach, could explains why the multifaceted relation between body composition and cognitive dimensions still remains poorly predictive (Vainik et al., 2019). Here, we challenge the idea that body weight management is caused by a static behavioural phenotype and suggest a reverse causality: higer body fat weakens the ability to adapt behaviour to rapid metabolic fluctuations. We further argue that behaviour needs to be approached as a dynamical process tightly regulated by physiological states such as energy levels. Follow-up studies could explore how environemental factors, such as food availibity, come in to play to affect decision making and the resulting metabolic trajectory.

Methods

Participants

A total of 116 volunteers were recruited from a local database. A first screening for exclusion criteria allowed us to identify volunteers either being underweight (BMI < 18.5, n = 2), obese (BMI > 30, n = 6), following a restrictive diet (n = 1), having a physiological condition that could affect their food behaviour (n = 7), suffering or having a history of psychiatric disorder(s) (n = 3), scoring high on depression scale (BDI>17, n = 3), or being pregnant (n = 1). One participant was further excluded for failing to come fasted the day of the experiment. In total, 94 healthy participants underwent the full experimental protocol.

Experimental design: behavioural

Before being invited, participants first had to fill in all questionnaires related to food or used for exclusion utilising a dedicated online platform (LimeSurvey) hosted in our institute. They were then requested to refrain from consuming any food or caloric beverages after 10 PM the day before coming to the lab for a single testing session starting at 8AM. Upon arrival, participants were familiarized with the general course of experiment. In particular, they were told they will need to perform two behavioural tasks (a stop signal task and incentive motivation task, order counterbalanced across participants) allowing them to earn, depending on the experimental block, “food tokens” or “money tokens”. Critically, we informed them that those tokens could respectively be traded afterwards for actual food items and cash from from a selection of snacks and a cashbox on display in the room. In addition, participants had to rate their liking of each of the 30 food items using a visual analog scale before starting the behavioural tasks. This setup ensured that the framing of the tasks in “food” and “money” blocs was clearly mapped onto real and concrete outcomes of different nature. Moreover, we explicted that as they filled in the remaining questionnaires afterwards they would be allowed to consume the food they won. In addition, they would have to stay in the lab until the end of the experiment, at 11 AM, with no access to any other food. This helped preventing strategies based on the exchangeability of the outcomes, eg. buying food with the money earned or stashing the snack for later use or trade. Unbeknonwst to the participant before the end of the effort and stop signal tasks, the conversion of the collected tokens into actual rewards was carried out using a “fortune wheel” auction task. This procedure allowed us to measure to willingness of the participants to pay for food, i.e. to quantify the subjective value of the two reward type one relative to the other.

Throughout the session, participants had to rate on a visual analog scale their level of hunger, thirst, and satiety for a total of seven rating blocs. Finally, the session ended with a series of anthropometric measurement to assess the body composition of the participants and estimate the muscle size of their forearm.

All procedures were approved by the ethics committee of the University of Cologne and we obtained written informed consent from all participants prior to the experiment.

Stop signal task

The stop signal task is adapted form the “STOP-IT” open-source software developed by Verbruggen et al. (2008). Participants were seated in front of a computer screen and were asked to keep their index finger in the center of the left and right arrow key of the keyboard until a white arrow appears (go-signal). In this case, they were instructed to quickly indicate the direction of the arrow with their index finger by pressing the appropriate arrow key (go-trials). In 25% of the trials, the white arrow turned blue (stop-signal) and participants were told to withhold their response (stop-trials). After a short practice block (32 trials), participants completed six experimental blocks with 96 trials each. Every new block was initiated by the presentation of a stimulus picture (Appendix A, Appendix B) announcing the incentive to play for in this block. The incentive type varied from block to block. The incentive type of the first block (food tokens or money tokens) was counterbalanced across subjects. In between blocks, the word “pause” was centered in white letters on a black screen for 15 seconds.

Every experimental trial started with the presentation of a small white dot (fixation sign) in the center of a black screen. On the left and right side of the fixation sign two small stimulus pictures of the incentive were displayed. After a jittered delay between 850 ms, the white dot was replaced by a white arrow after a random time of at least 500 ms (intertrial interval) and at most 1350 ms. The visual stimuli of the incentive were not displayed in the practice part. While there is no feedback presentation in the experimental part, participants were offered the information about the success of their responses in the practice part to increase their consciousness of performance and improve learning. In total the go stimulus and the possibly following stop-signal were displayed for a maximum time of 1500 ms (maximal reaction time) or until the response occurred.

The delay of a stop-signal (SSD) was adapted according to the participant’s performance by using the staircase tracking procedure (i.e., Jahfari et al, 2011, p. 6892). Each incentive type had its own staircase: For example, the second food-token block began with the SSD of the first food-token block. The practice and the first experimental block were initialized by a SSD of 250 ms, but the first SSD of the second experimental block was given by the last SSD of the first experimental block. In the first two experimental blocks of each incentive type, the initial SSD (i.e., 250 ms) was increased by 50 ms, when successfully withholding a response in a stop-trial, and decreased by 50 ms when responding to a go stimulus in a stop-trial. In the last block of each incentive type, the SSD increased or decreased by one thirtieth of a second. By using this staircase procedure, the probability of successful stop performance was about 50% and led to a maximal competition of go and stop processes. The idea of a competition between the terminations of the respective two processes is called horse race model (Logan & Cowan, 1984).

Effort task

The effort incentive motivation task is adapted from (Pessiglione et al., 2007). First, the participants are given a hand dynamometer (Vernier Software & Technology) in their dominant hand. During a initial calibration phase, they are given three attempts (4 seconds each) to squeeze the device as hard as he can. The maximal force is then used to define the difficulty of the effort task as describe below. Each trial started with the display of the type of outcome at stake (food or money) and a thermometer-like scale. By squeezing the handle (within 3s), the participant could then fill up the thermometer, the “mercury” height being proportional to the exerted force. Critically, we instructed the participants that the higher the mercury, the more tokens, and therefore the more food of money, depending on the cue, they would obtain at the end. In order to assess the subjective motivation to effort, the reward cue (picture of food items of cash) was kept constant but the amount of force required to fill the thermometer up the difficulty was systematically varied from trial to trial. More precisely, reaching the top of the scale required 90% (easy), 115% (medium), or 140% (hard) of the calibration force. This difficulty level was indicated by the color of the “mercury” (respecitvely green, orange, and dark red) to allow the participants to plan their effort before pressing. While this implementation contrasts with the original experiment, where the reward at stake rather than the force scaling was altered, both task variations effectively modulate the conversion rate between the exerted force and the amount of reward earned which is the main determinant of motivation to effort behaviour. This modified design prevented the use of explicit quantities of tokens as cues, making it more similar to the stop signal task and allowing us to give the same amount of tokens to all participants in the auction task without arousing too much suspicion in the participants.

Similarly to the stop signal task, the complete task consisted of one practice bloc (12 trials) followed by an alternation of 20 food and money blocs (12 trials each), each starting with a full screen picture of the outcome to come, for a total of 240 trials. The bloc order was counterbalanced across subjects.

Auction task

The auction task was run last and allowed the participants trade the tokens they earned for actual food snacks and cash.

We first informed all participants that they won 300 tokens during the force and stop-signal tasks and that they now had the opportunity to bid on food and monetary items in a sequence of 30 lotteries. Each lottery consisted of two independent fortune wheels, one associated with a fixed amount of money (0.70€), the other to a snack of equivalent value changing in each trial (so 30 different snacks in total). The position and order of the snacks were randomized across trials and participants. In a given trial, participants had to allocate 10 tokens between the wheels in order to increase the probability of winning the associated outcome using the rule one token = 10% chance. Tokens could be moved to and between the wheels using the arrows of the keybord, each bet being displayed as a slice (1/10th) of the wheel being colored. Therefore, the participants had the choice between securing one of the option (put all tokens on one wheel and none on the other, outcome probability = 100% / 0%) or try and win both outcomes with a risk of winning nothing (eg. put 7 tokens on the food wheel and get a 70% chance of getting the snack and 30% of earning the cash). After bidding on all the lotteries, 6 out of 30 were actually implemented by spinning the wheels on the screen. Although the outcome appeared random, the result was biased to ensure that the participant won its 3 most desired snacks in order to observe the following food consumption, during the questionnaires.

The rational for this task is two-fold. First, by letting participant bet their tokens concurently on food or money rewards, we could measure the relative preference of the participants for the two types of outcome (ie. their willingness to pay for food, or relinquish food for money). Second, the lottery implemented here allowed to indirectly assess the risk aversion or seeking profile of the participant. Critically, the two dimensions were relatively independent: the preference for one outcome could be expressed either by balancing the bets within trial (risky behaviour), or betting all tokens on one of the outcome at each trial (risk averse behaviour) but alternating across trials according to their inclinations.

Questionnaires

Participants filled in a total of 15 questionnaires relating to impulsivity, compulsivity, control, drive, and eating behaviour (see tbl. 1 for details). Questionnaires related to disorders or food behaviour were completed online to repectively allow for exclusion before coming to the lab and avoid making participants too self-conscious about their food behaviour as we observed their snack consomption. Other questionnaires were filled on paper on the testing day.

Hedonic ratings

A picture of each snack was displayed in the center of the screen above the question "How strongly do you like or dislike this item?" ("Wie stark ist Ihre Vorlieb bzw. Abneigung"). On the left side was a labeled hedonic scale (Lim et al., 2009) ranging from "greatet imaginable dislike" ("Stärkste Abneigung, die vorstellbar ist") at the bottom to "greatest imaginable like" ("Stärkste Vorliebe, die vorstellbar ist") at the top. Participants moved the cursor to indicate their preference on the scale and clicked to validate their response, and so on until all items were rated.

State ratings

Subjective state (hunger, satiety, and thirst) was measured using a visual analog scale. For each dimension, a question on the sreen ("How hungry/sated/thirty are you at the moment?"; "Wie hungrig/satt/durstig sind Sie momentan?") prompted the participant to rate their current state. To this end, they used the mouse to move a cursor to any point between the left ("not hungry/sated/thirsty at all"; "gar nicht hungrig/satt/durstig") and right ("very hungry/sated/thirsty"; "sehr hungrig/satt/durstig") anchors which best reflected their feeling, and validated their response using a left click.

Software

All experiments were run using the Psychtoolbox 3.0 (http://psychtoolbox.org) on Matlab (The Mathworks Inc.). The measurements from the hand dynamometer were captured using a homemade Matlab code (https://github.com/lionel-rigoux/vernier-toolbox).

Body composition

We first measured body composition using a SECA mBCA 515/514 impedance scale which provided, in addition to the total body weight, the absolute fat mass, fat percentage, fat-free mass, and skeletal muscle mass (full body and limb by limb) of the participant. We also measured the participant's height to compute their Body Mass Index (BMI) according to the formula $BMI = bodyweight/height^2$ (all measurements in SI units). To control for the natural difference in adiposity between males and females, we also computed a "normalized fat percentage" score by demeaning the fat percentage within each gender group.

Statistical analyses

Maximal Physiological Force

The maximal force a muscle can generate is directly proportional to the number of fibers it contains, which can be approximated by the muscle cross sectional area (CSA). In other words, we can predict the maximal physiological force (MPF) of a participant by approximating, using anthropometric measurements, the CSA of their muscles (Maughan et al., 1983) — in our case, the muscles of the forearm in charge of gripping. Practically, we first measured the length (L, between the ulna's head and the styloid process) and maximum circumference (C, 1/3rd from the ulna's head) of the forearm. Then, we used calipers to measure the skinfold (S, skin + fat layers) of the interior and exterior sides of the forearm. Approximating the forearm geometry with a cylinder, the CSA can then be computed as the total area of the limb section minus the fat + bone area (Heymsfield et al., 1982):

$$CSA = \frac{(C - \pi S)^2}{4\pi} - B$$

Where C and S are in cm, and B, the bone area, in cm^2 (set to 1.8 according to E. S. Hsu et al. (1993)). Finally, the MPF can be calculated by simply scaling the CSA:

$$MPF = CSA * F$$

where $F = 2.45 + 0.288 * L$ was previously measured in a large cohort of adults (Neu et al., 2002).

We validated our measure by regressing the MPF on the body composition measures. As expected, the MPF was highly predicted by the participants' fat-free mass, which is mainly composed by skeletal muscles (main effect: $p < 0.001$). Critically, this relation was not affected by the fat mass (interaction term: $p = 0.398$) nor, alternatively, by the fat mass percentage (interaction term: $p = 0.545$).

Relative energy deficit

In order to estimate the relative energy deficit induced by fasting in our participant, we first estimated the basal metabolic rate (*BMR*), which represent the number of calories burned by the body, at rest, during a day. Using the Mifflin-St Jeor equation, the BMR can be derived from the lean mass (*LM*) measured with the impedance scale:

$$BMR = 370 + (21.6 * LM)$$

From this, we computed the caloric deficit (*E_deficit*) induced by a fast of T hours:

$$E\_deficit = BMR * T/24$$

Assuming that a gram of body fat stores around 9 kcal, an using the absolute fat mass (*FM*) measured with the impedance scale, the total energy stored in the body fat (*E_available*) is given by:

$$E\_available = 9 * 1000 * FM$$

Finally, the relative energy deficit (*RED*) can expressed as the log ratio between the caloric deficit induced by fasting and the calories available in the fat storage:

$$RED = log(E\_deficit \, / \, E\_available)$$

Stop signal reaction time

We first computed the average reaction time (RT) in the GO condition (RT_{GO}) as an indicator of the response process efficiency. We used a geometric mean to counterweight the heavy tail of the RT distribution and therefore avoid an overestimation. To obtain a signature of the relative efficiency of the inhibition process, we estimated the Stop Signal Reaction Time (SSRT; see Matzke et al. (2018) for a review) from the STOP trial behaviours as follow: We started by performing a logistic regression to predict correct STOP responses as a function of the SSD. To this end, we located the inflection point of the fitted logistic function to obtain the SSD for which the participant had a 50% chance of stopping, known as the critical SSD (SSD_{crit}). Finally, SSRT was computed as the difference between the inhibitory and response latencies: $SSRT = SSD_{crit} - RT_{GO}$. Note that a shorter SSRT correspond to a relatively faster supression of the action and therefore a more efficient inhibitory process.

We checked the performances of all subjects for signs of failures of the experimental procedure. First, performances in this task are usually close to nominal and an error rate higher than a few percents indicates that the participant did not fulfilled the task properly. Accordingly, we excluded participants who, in the GO condition, responded incorrectly in more than 10% of the trials, or failed to respond at all in more than 25% of the trials. We also excluded participants who achieved a proportion of correct inhibition outside of the [40% - 60%] range, as it indicated that the staircase did not converge. In total, 7 participants were excluded from any further analyses relying on the SSRT measurements.

Effort task

The maximum of the force profile was extracted for each trial. For each subject and cue, this peak force was fitted with a linear model to capture the average force (intercept) and the incentive effect. The respective beta estimates where then entered in follow-up linear models to infer group-level statistics related to between subject effects. When appropriate, the subject-level statistics were averaged across cues to derive domain general influences.

One subject was excluded from the analyses relying on the effort task due to a calibration error.

Auction task

For each of the 30 pictures, the response was measured as the relative number of tokens (between 0 and 1) bet on the food item. We then computed the mean and variance of the responses across all trials reflecting respectively the general preference for food and the strategy used for betting. Indeed, on the one hand, the most risky strategy is to always split the bet proportionally to one's mean preference on each trial, e.g. to bet 5 tokens on food and 5 tokens on money if the participant has no bias toward one type of reward. In that case, the variance across trials will be 0 (in our example, the response is always 0.5). On the other hand, the safe strategy is to bet all the tokens either on the food item or on the money wheel in a given trial and to alternate the type of reward thus 'secured' across trials. In our example above, a risk averse participant would bet all tokens on the food wheel in 15 trials and on the food item in also 15 trials, effectively expecting to receive a balanced amount of rewards of both types. In that case, the response will follow a binomial distribution (response is always be 0 or 1) with a variance $mean(response) * (1 - mean(response))$. By dividing the measured response variance by this maximal theoretical variance given the emprirical reward bias, we obtain a standardized measure (between 0 and 1) of risk aversion that is independent on the reward preference:

$$riskaversion = var(response) / \Big(mean(response) * \big(1 - mean(response)\big)\Big)$$

Finally, for each participant, the responses were entered in a linear model that included as regressors the hedonic and familiarity ratings of the participant as well as the price and caloric content of each picture. The regression weights therefore indicated the individual drivers of the preference for the food bets.

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Figures

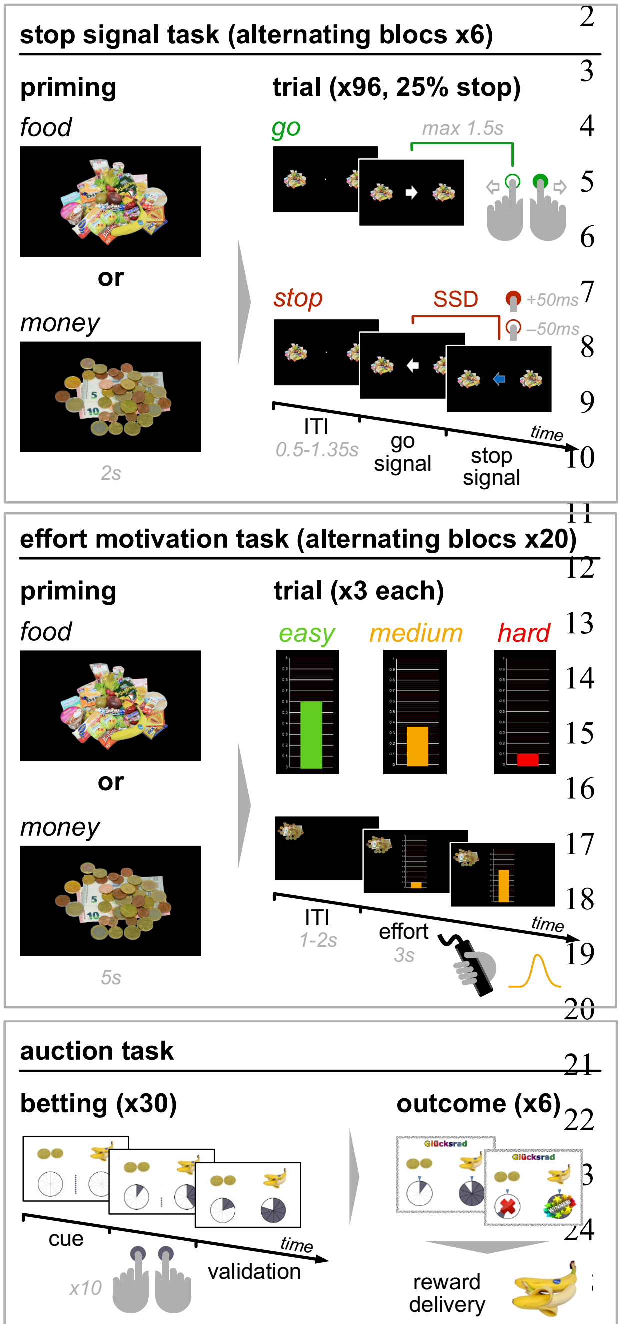

Figure 1: **Experimental design *Top: Stop Signal task*** Each bloc of 96 trials started with a full screen picture of the type of reward at stake. On each trial, a fixation cross first appeared in the center of the screen, flanked by reward cues. Then an white arrow was displayed, prompting the participants to indicate the orientation of the arrow with button presses ("go" condition). In 1/4 of the trials, the arrow turned blue after a variable stop signal delay (SSD). In this "stop" condition, participants were instructed to refrain from responding. The SSD was continuously adjusted to induce a 50% chance of correct response inhibition. ***Middle: Effort Motivation task*** Again, each bloc started with a full screen display of the reward at stake. On each trial, participant could press a hand held dynamometer to raise the level of a gauge on the screen and thus increase their chances of earning the reward. The color of the gauge indicated how hard they had to press to fill the gauge completely (difficulty level). ***Bottom: Auction task*** On each trial, participant could bet a total of 10 tokens on either a monetary reward or a food item of equal value (more tokens = higher chances of winning). The outcome was diplayed once all the bet were set, and both the monetary and food (snacks) rewards were given to participant to consume.

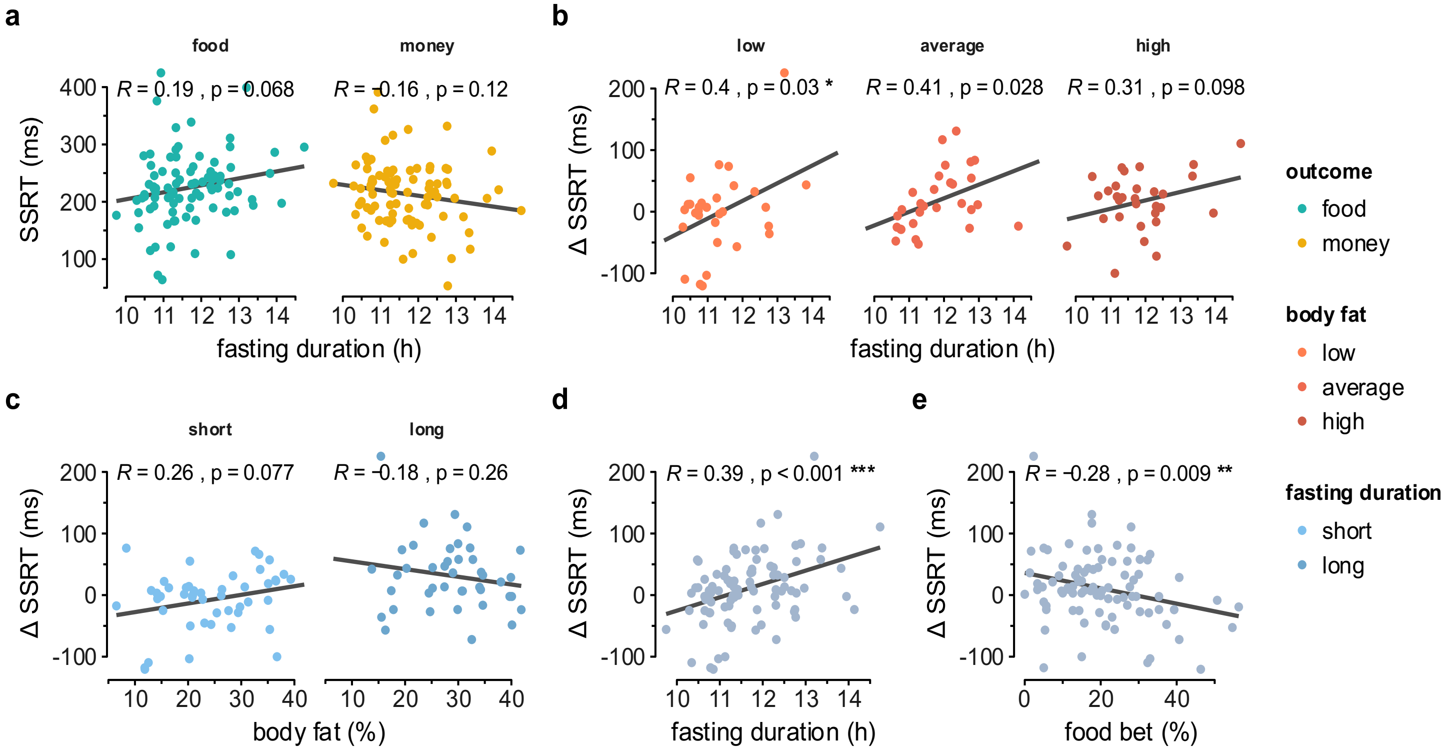

Figure 2: **Impulsive behaviour as quantified by the SSRT measured in the stop signal task.** a) SSRT as a function of fasting duration for food (green) and monetary (yellow) blocs. b-e) Relative impulsivity for food relative to money measured by the difference in SSRT between the two conditions: b) *Δ*SSRT increases with body fat percentage for short (left, light blue) but not for long (right, dark blue) fasting duration (duration split at the median for plotting only). c) *Δ*SSRT increases with fasting duration especially for the lowest (left, light orange), and central (middle, dark orange), compared to the highest (right, red) tercile of body fat percentage. d) *Δ*SSRT increases with fasting duration (same as in c, collapsed across body composition). e) *Δ*SSRT decreases with larger bets toward food items (as opposed to monetary item) in the auction task. All statistics are Pearson correlations and lines best fit linear regression computed for the data showed in each plot.

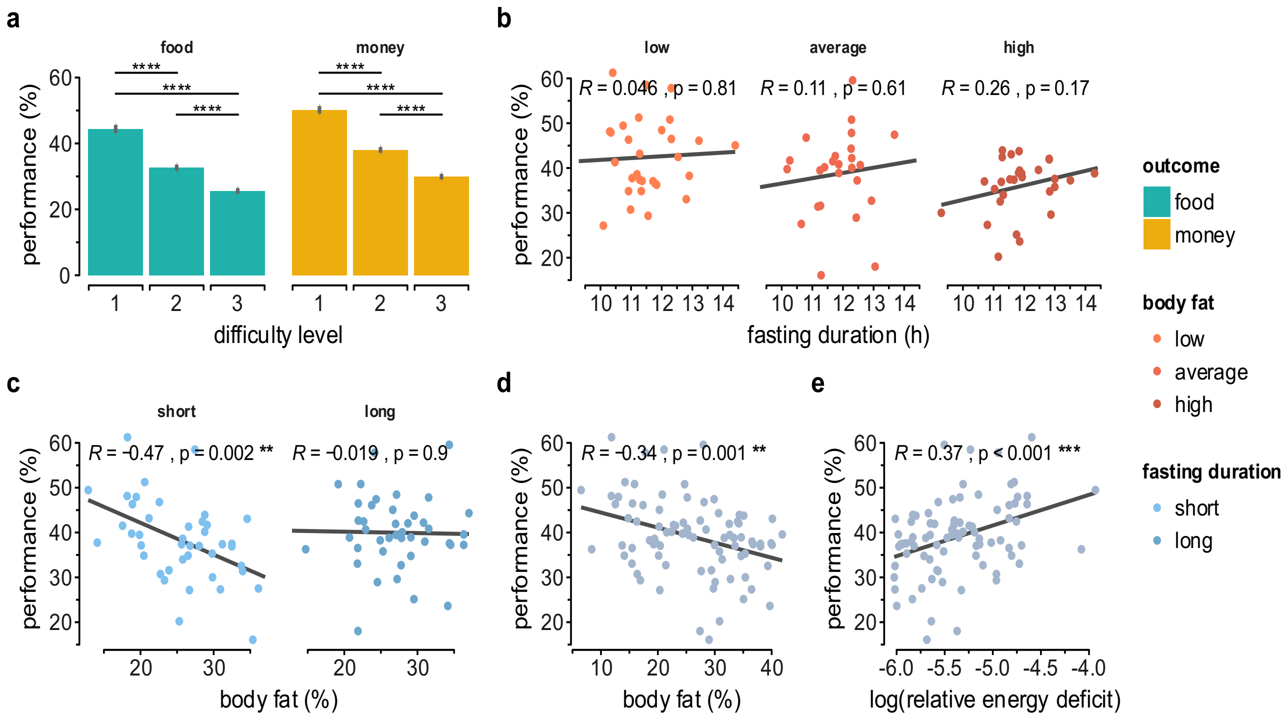

Figure 3: **Results of the incentive motivation task.** a) Average performance for each difficult level for food (green) and monetary (yellow) rewards. Lines are individual averages, bar and error bars represent the group average and standard errors. b) Effort spending decreases with body fat percentage. c) This effect of body composition is driven by participant with shorter fasting duration (left, light blue) and normalises with longer fasting (right, dark blue). d) As body fat percentage increases (low: left, light orange, average: middle, dark orange; high: right, red), effort decreases but fasting gains influence. e) The body composition x fasting interaction is summarized as an effect of relative energy deficit indeuced by fasting. All statistics are Pearson correlations and lines best fit linear regression computed for the data showed in each plot.

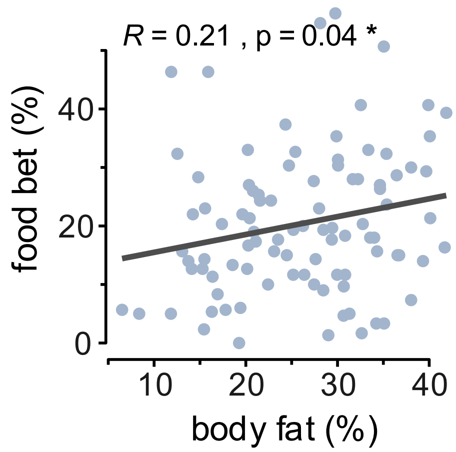

Figure 4: ***Results of the auction task.*** *Willingness to pay for food increases with body fat percentage.*

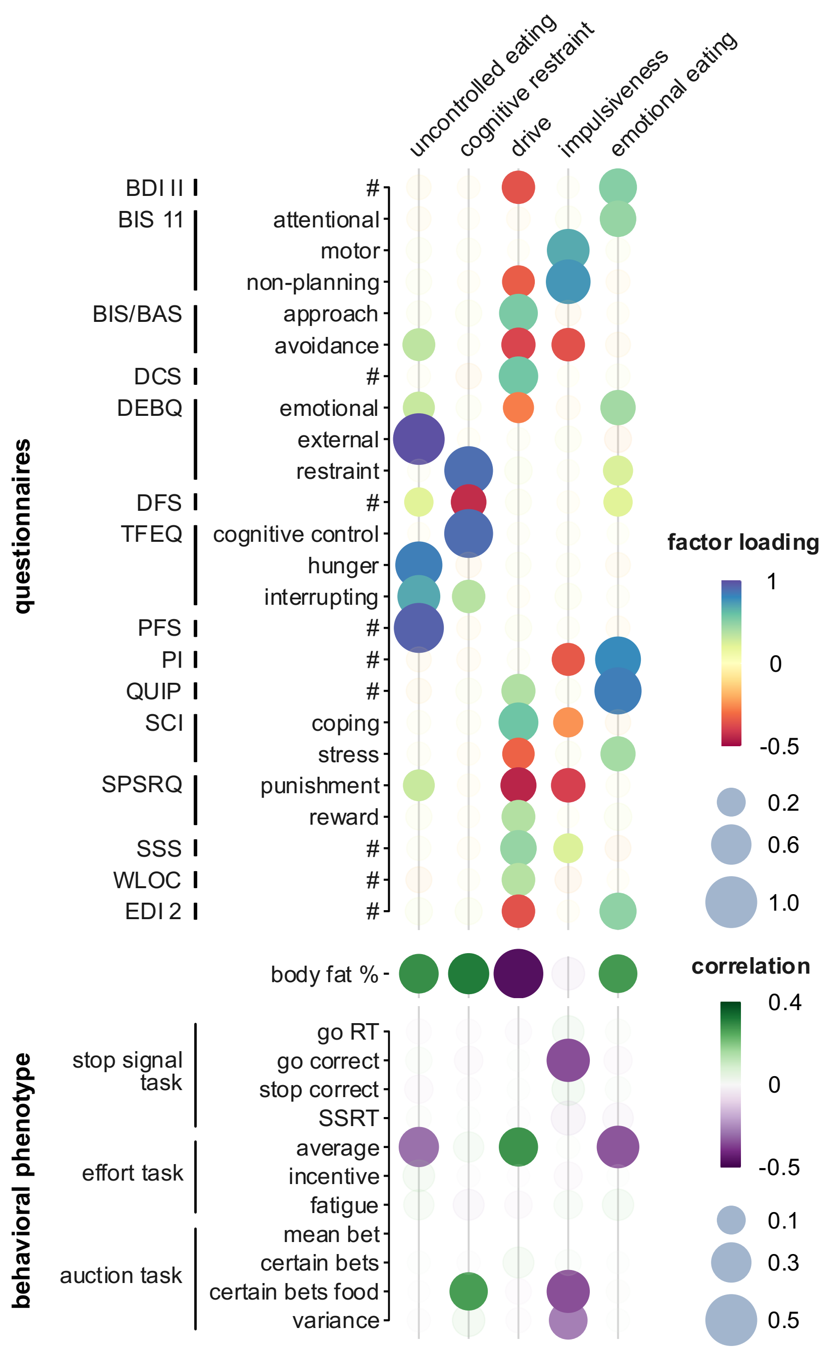

Figure 5: **Factor analysis of the questionnaires Top:** *Each dot represent the loading of each questionnaire scale (lines) on the five identified factors (column).* **Bottom** *Each dot represent the correlation between empirical measures of body composition or behaviour with individual factor scores.*

Tables

Table 1: Questionnaires

Label	Questionnaire	Type	Reference
BIS-11	Barrat Impulsiveness Scale	online	(Hartmann et al., 2011; Stanford et al., 2009)
BDI-2	Beck Depression Inventory	online	(Arnau et al., 2001; Kühner et al., 2007)
BIS/BAS	Behavioral Inhibition and Activation Systems Scales	paper	(Carver & White, 1994; Strobel et al., 2003)
DCS	Desirability of Control Scale	paper	(Burger & Cooper, 1979)
DEBQ	Dutch Eating Behavior Questionnaire	online	(Grunert, 1989; Vanstrien et al., 1986)
DFS	Dietary Fat and free Sugar	online	(Francis & Stevenson, 2013)
EDI2	Eating Disorder Inventroy 2	online	(Garner et al., 1983; Thiel & Paul, 2006)
PFS	Power of Food Scale	online	(Cappelleri et al., 2009; Lowe et al., 2009)

Label	Questionnaire	Type	Reference
PI-WSUR	Padua Inventory - Washington State University Revision	paper	(Burns et al., 1996; Ettelt, 2005)
QUIP-RS	Questionnaire for Impulsive-Compulsive Disorders - Rating Scale	paper	(Probst et al., 2014; Weintraub et al., 2009)
SCI	Stress and Coping Inventory	online	(Satow, 2012)
SPSRQ	Sensitivity to Punishment and Sensitivity to Reward Questionnaire	online	(Torrubia et al., 2001)
SSS-V	Sensation Seeking Scale	paper	(Strobel et al., 2003; Zuckerman et al., 1964)
TFEQ	Three Factors Eating Questionnaire	online	(Pudel & Westenhöfer, 1989; Stunkard & Messick, 1985)
WLOC	Weight of Locus of Control	online	(Holt et al., 2001; Saltzer, 1982)

Supplementary figures

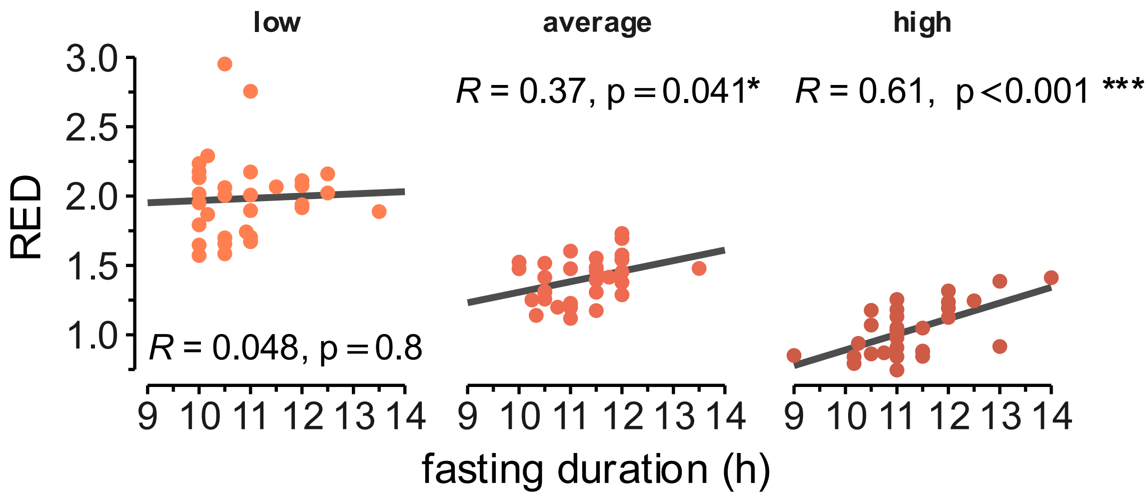

Figure S1: ***Relative energy deficit*** Relative energy deficit as a function of fasting duration for the low (left), average (middle), and high (right) body fat participants.