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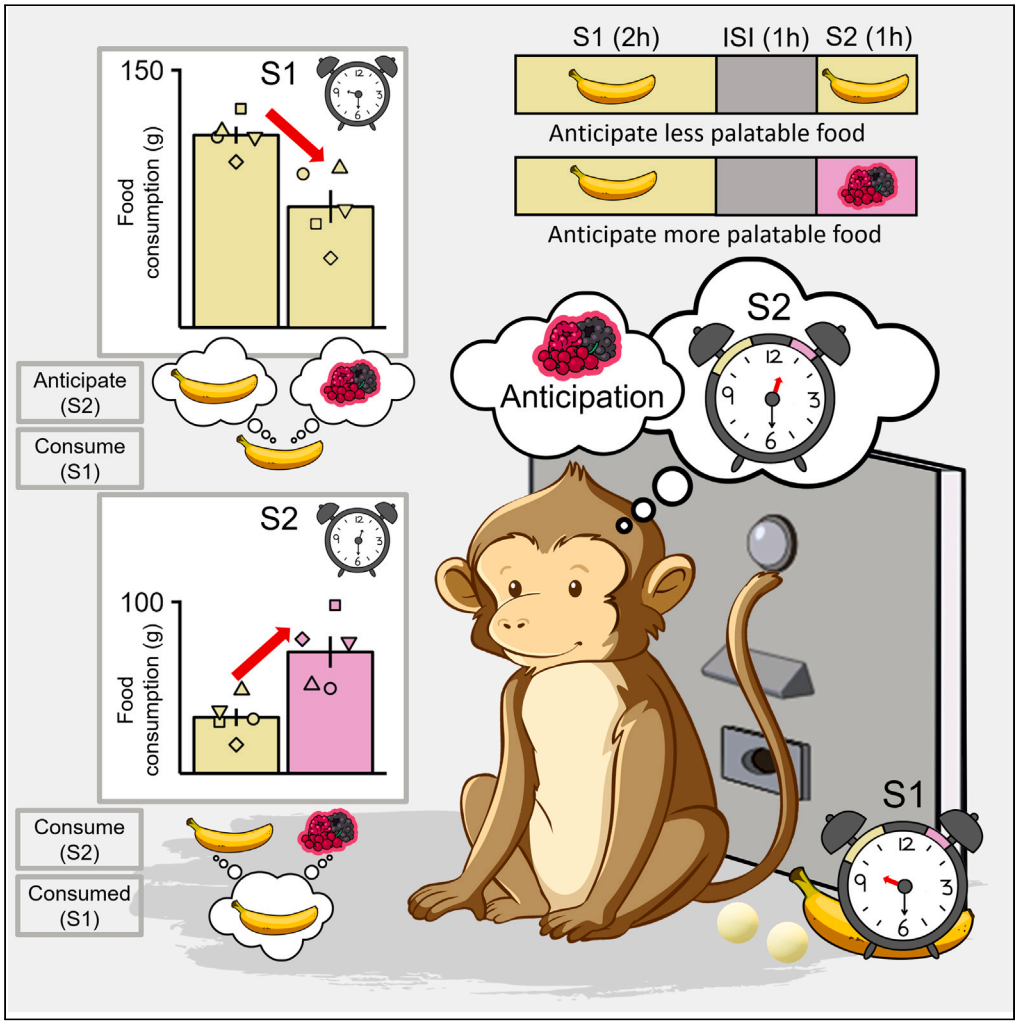

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Highlights

Two-session operant task reveals extended timescale of food anticipation in primates

Macaques decreased food consumption anticipating a more palatable meal 2.5h later

Anticipation of the meal schedule arose after the very first exposure to the task

In the focal condition, responses were withheld 20 min longer relative to control

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Intrinsic anticipatory motives in non-human primate food consumption behavior

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SUMMARY

Future-oriented behavior is regarded as a cornerstone of human cognition. One key phenomenon through which future orientation can be studied is the delay of gratification, when consumption of an immediate reward is withstood to achieve a larger reward later. The delays used in animal delay of gratification paradigms are rather short to be considered relevant for studying human-like future orientation. Here, for the first time, we show that rhesus macaques exhibit human-relevant future orientation downregulating their operant food consumption in anticipation of a nutritionally equivalent but more palatable food with an unprecedentedly long delay of approximately 2.5 h. Importantly, this behavior is not a result of conditioning but intrinsic to the animals. Our results show that the cognitive time horizon of primates, when tested in ecologically valid foraging-like experiments, extends much further into the future than previously considered, opening up new avenues for translational biomedical research.

INTRODUCTION

Regulating behavior with anticipated future events and consequences in mind requires future-oriented cognition, broadly defined as a diverse set of mental processes operating on counterfactual state, action and goal representations involving the sensory, motor, or even abstract domains. The wide range of future-oriented cognitive abilities—self-control, prospective memory and mental time travel, planning, and even foresight—enable individuals to acquire their ultimate goals (such as rewards) more efficiently and are also often regarded as cornerstones of human cognition that make us stand out from the rest of the animal kingdom.[1–4]

One key phenomenon through which future orientation can be studied is the delay of gratification, the ability to inhibit a prepotent response to an immediately available smaller reward to obtain a more valuable outcome in the future. The degree to which animals or humans delay gratification is probed in intertemporal choice, accumulation, and exchange tasks by measuring the maximal value of the anticipation delay—i.e., how far in the future an anticipated event can be put so that the subject still takes it into account in its present behavior.[5–12] Reportedly, in delay of gratification tasks, monkeys (simians excluding apes) refuse to wait more than 40 s for a more valuable reward.[13–15] Interestingly, even great apes have not been reported to be able to wait for rewards to accumulate over time beyond approx. 20 min,[12,16] while, in complex naturalistic tool use task arrangements which did not specifically focus on measuring delay, great apes demonstrated probably the longest (17 h long) anticipation delays in the literature.[17] Relatedly, monkey species that are known to struggle with standard laboratory delay of gratification tasks and fail complex tool use and bartering tasks, still readily appear to make future-oriented decisions in their natural habitats, such as food caching, stalking prey and traveling long distances to good quality feeding sites during foraging.[18]

These field observations imply much longer anticipation delays compared to those measured in the laboratory, which in turn shed doubts on the ecological validity of the laboratory paradigms.[19–21] Even if we also consider supposedly more easily learned and more sensitive foraging-like experimental designs, anticipation delays vary on the timescale of seconds to minutes, leading to the overall conclusion that monkeys have only a short future "time window", incomparable to human decisions with time horizons of days or even longer intervals. With this in mind, we set aside the high-level and abstract criteria[2,22,23] that dominates current scientific debates regarding the existence of future-oriented cognition among apes (and corvids) and focus on the anticipation delay as an experimentally accessible prerequisite for human-like future-oriented cognition. Here, for the first time, we show that in a two-session operant food intake paradigm, rhesus macaques regulate their food consumption in the first daily session contingent on the available information about whether an equicaloric, but more palatable food will or will not be available in the second session 2–2.5 h later. Importantly, the monkeys demonstrated this self-control behavior without any prior conditioning, intrinsically adapting to the dynamics of their own satiation (the process from hunger to satiety

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that regulates energy intake by controlling appetite, resulting in the slowing or stopping of eating),[24] which strongly implies that monkeys are able to anticipate their future physiological needs and the ensuing motivational states (drive states).[25,26] The evidence and theoretical framework presented here complement our present knowledge on the evolutionary history of future-oriented cognition in the primate lineage, and also provide novel methods that are suitable for translational studies of prospective decision-making in the laboratory.

RESULTS

Voluntary operant consumption of two types of food pellets by five adult rhesus macaques was measured in a task comprising two daily sessions (a 2-h Session 1, abbreviated as S1, and a 1-h Session 2, abbreviated as S2, separated by a 1-h break, see Figures 1A and 1B). In a separate preference test, the two pellet types had been selected to have similar caloric value but strongly differing hedonic values (see Figure 1C). Across five baseline weeks and four main study weeks, the meal schedule was kept constant within each week, but may have differed between weeks. The main study weeks covered all four combinations of the two pellet types and the two sessions (Figure 1A, bottom), and the baseline weeks involved meal schedule $b_{S1}v_{S2}$.

Palatability-driven intertemporal choice

Analyzing the four main study weeks, we sought to determine how food consumption in each session depended on food type offered in the current and the other daily session (S1 and S2 meal type effects). More importantly, we also assessed how the observed food consumption

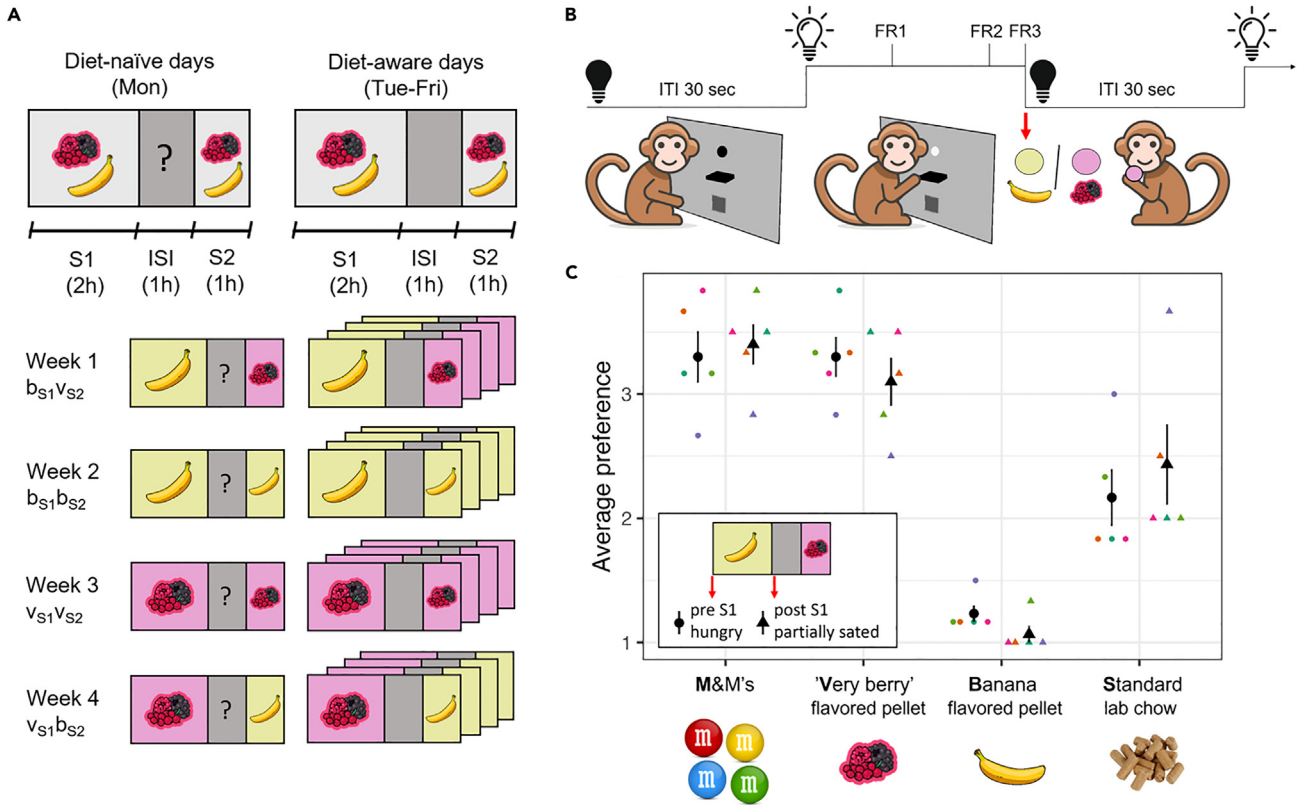

Figure 1. Meal schedules, trial structure and palatability in the food intake paradigm

(A) Daily schedule of the food intake task and meal schedules in the four main study weeks. On each weekday the animals performed the food intake task for 2 experimental sessions per day (top). Within a session, only one type of food was offered: either standard, banana flavored pellets or 'very berry' flavored pellets. Each pellet combination was offered from Mondays to Fridays. On Mondays, the weekly meal schedule could not have been inferred by the animals up to the start of S2, so these days were termed diet-naïve (A, left). Conversely, the meal schedule was unchanged during the remaining (diet-aware) weekdays (A, right). The meal types are indicated by pictograms.

(B) Trial structure of the food intake task. At the beginning of each trial, a cue light switched on, indicating that food items were available upon three consecutive lever presses (fixed ratio 3 reinforcement schedule, FR3). After pellet delivery, the cue light was switched off for a 30-s intertrial interval (IT).

(C) In a food preference test, the pellet used as the more palatable option in the main experiment ('very berry') was strongly preferred to the banana pellets used as the less palatable option. Preference scores were calculated based on data from 6 trials per satiation state (see STAR Methods). 'Very berry' pellets and M&M's were similarly preferred, and they were also the most preferred food items (see Table S1). Colored dots are individual average preference scores for each animal, black dots with whiskers show sample mean and s.e.m.

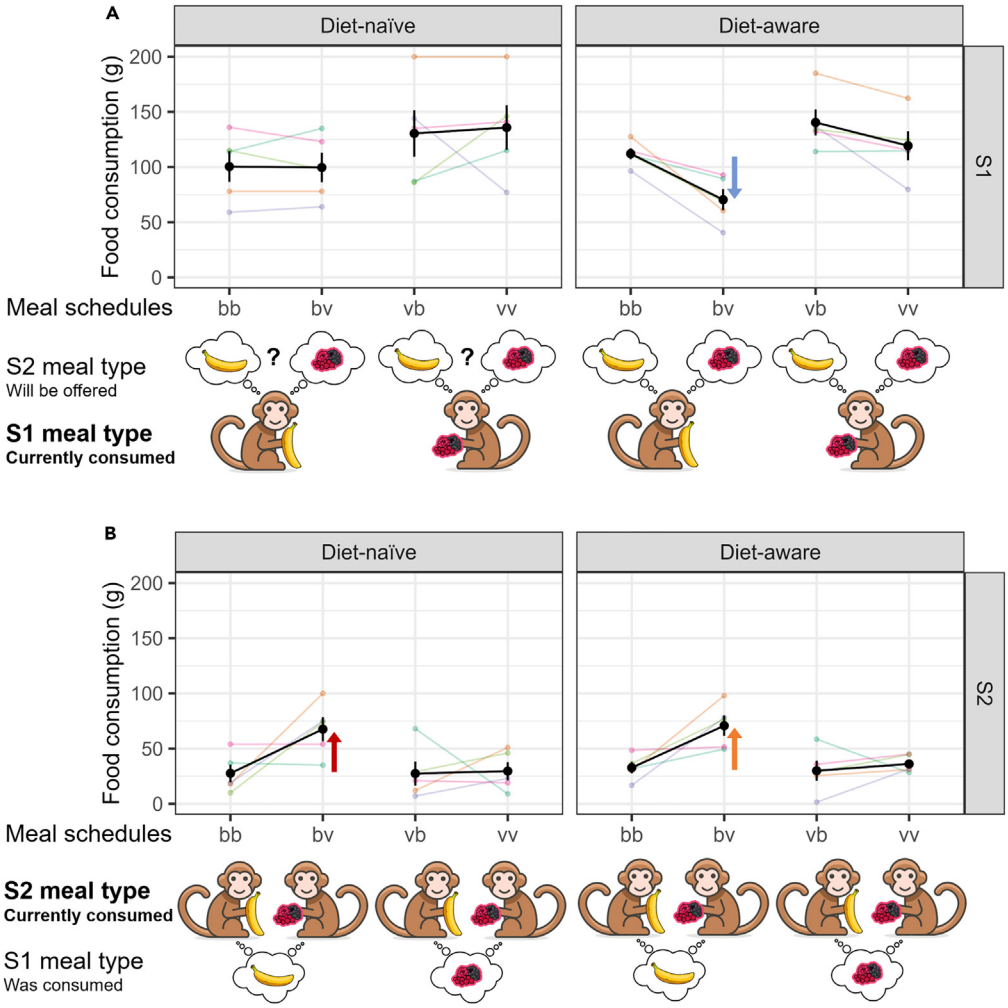

Figure 2. Future palatability outweighs actual palatability in determining food consumption

Food consumption (grams, y axis) is depicted as a function of meal schedules (x axis) in Session 1 (A), Session 2 (B). Left panels, labeled Diet-naïve, show food consumption data from Mondays, when up till the start of S2 animals had not yet been exposed to the weekly food schedule. Right panels, labeled Diet-aware, show data averaged across diet-aware days (Tuesdays to Fridays), when the animals were informed about the weekly feeding schedule. See Figure S1 for data not collapsed across weekdays. Pictograms and labeling below x axes illustrate the currently consumed food type and potential knowledge of the feeding schedule from the point of view of the animals. Colored dots show individual food consumption (g) for each animal, black dots with whiskers show sample mean and s.e.m. Colored arrows illustrate oppositely signed effects of similar magnitude in the $b_{S1}v_{S2}$ condition in S1 (blue arrow) and S2 on diet-aware days (orange arrow), and also in S2 on diet-naïve days (red arrow).

patterns were modulated by whether the animals were already exposed to the weekly meal schedule or not (termed 'Diet awareness', see also Figure 1A). We conducted repeated measures ANOVAs where we pooled diet-aware days (results are from these except otherwise noted) and linear mixed models where the days were kept separately (see STAR Methods).

On average, the animals consumed very similar amounts of the high-palatability and the low-palatability meal in S1: there was only a small, non-significant excess consumption of the more palatable very berry flavored pellets in S1 compared to the banana flavored pellets (S1 meal type: $F_{1,4} = 3.94$, $p = 0.12$), regardless of whether diet-naïve days or diet-aware days were considered (S1 meal type × Diet-awareness: $F_{1,4} = 0.15$, $p = 0.72$; Figure 2A, left).

In contrast, on main study weeks when the more palatable S2 meal was scheduled, food consumption was drastically reduced in S1 from Tuesdays on (termed diet-aware days), compared to weeks with low-palatability S2 meals (S2 meal type × Diet-awareness: $F_{1,4} = 32.53$, $p = 0.005$; Figure 2A, right; mixed model: S2 meal type × Day: $F_{4,64.9} = 4.98$, $p = 0.0015$; S2 meal type × $Day_{diet\text{-}awareness}$ contrast: $t_{65.0} = 3.52$, $p = 0.0008$, see Figure S1). That is, food consumption in S1 depended more strongly on the food offered that week in S2 than the food currently consumed. This modulation of S1 food consumption depending on S2 palatability was completely absent on Mondays (termed diet-naïve days; see Figure 2A, left), when the animals were not yet exposed to the weekly diet schedule. This future palatability effect on diet-aware days was present regardless of the currently consumed pellet type, though it was slightly weaker when the more palatable meal was offered

(future palatability effects on food consumption for diet-aware days, for high-palatability S1 meal, $v_{now}v_{S2}-v_{now}b_{S2} = -21.1 \pm 9.8$ g (mean ± SE); for low-palatability S1 meal, $b_{now}v_{S2}-b_{now}b_{S2} = -41.7 \pm 9.1$ g, interaction contrast comparing the former effects: $F_{1,4} = 5.95$, $p = 0.071$ in the ANOVA, $F_{1,4.99} = 8.07$, $p = 0.036$ in the mixed model for diet-aware days). The observed future palatability effect strengthened from Tuesdays to Fridays (mixed model for S1 food consumption on diet-aware days, S2 meal type × Day: $F_{3,50.2} = 3.05$, $p = 0.037$; S2 meal type × Day_{linear} contrast: $t_{50.0} = -2.44$, $p = 0.018$; see Figure S1 for more details).

Notably, the magnitude of the effect of future palatability on the consumption of the less palatable food in S1 ($b_{now}v_{S2}-b_{now}b_{S2} = -41.7 \pm 9.1$ g, Figure 2A, blue arrow) was very similar to the excess amount of the more palatable food consumed in S2 afterward on diet-aware ($b_{S1}v_{now}-b_{S1}b_{now} = +40 \pm 17.3$ g, Figure 2B, orange arrow), and also on diet-naive days ($b_{S1}v_{now}-b_{S1}b_{now} = +38.1 \pm 12.4$ g, Figure 2B, red arrow). This excess consumption pattern in S2 is supported by a significant S1 meal type × S2 meal type interaction ($F_{1,4} = 12.14$, $p = 0.025$; S1 meal type: $F_{1,4} = 8.53$, $p = 0.043$) that was not modulated by diet-awareness (Diet-awareness × S1 meal type × S2 meal type: $F_{1,4} = 0.72$, $p = 0.444$). Importantly, the excess consumption was clearly not driven solely by the palatability of the presently offered food in S2, but depended on the palatability of the food previously consumed in S1 ($b_{S1}v_{now}-v_{S1}v_{now} = +36.3 \pm 7.4$ g), suggesting a positive contrast effect. S2 food consumption was slightly higher on diet-aware days (Diet-awareness: $F_{1,4} = 8.46$, $p = 0.044$), but otherwise the pattern was remarkably similar between diet-aware and diet-naïve days (no other main effects or interactions were significant, see also Figure 2B). The contrast between decreased S1 and increased S2 consumption as a result of S2 food palatability is also supported by a strong S2 meal type × Diet-awareness × Session interaction in an ANOVA encompassing both sessions ($F_{1,4} = 26.23$, $p = 0.007$).

If changes induced by meal schedules in S1 and S2 food consumption indeed canceled out (S1 decrease 'balancing' the S2 increase, see arrows on Figures 2A and 2B), daily total consumption would be independent of meal schedules on diet-aware days. However, significant meal type effects on the daily total food consumption on diet-aware days (S1 meal type: $F_{1,4} = 9.94$, $p = 0.034$, S2 meal type: $F_{1,4} = 8.39$, $p = 0.044$) imply that the 'balancing' of food consumption was not numerically perfect (Figure 3A). Notwithstanding, in the $b_{S1}b_{S2}$ vs. $b_{S1}v_{S2}$ scenario detailed above, the residual daily total consumption difference ($\Sigma b_{S1}v_{S2}-\Sigma b_{S1}b_{S2}$) was 3.6 ± 4.1 g, which is an order of magnitude smaller than the 40-gram palatability modulations described above, which in turn corresponds to the reallocation of nearly the quarter of the daily total consumption (grand average: 153 ± 9.6 g) across sessions according to the availability pattern of the palatable food. From a neuroeconomic point of view, this relatively stable daily total food consumption can be regarded as a budget constraint that can be aptly visualized by plotting the daily total consumption of the two pellet types against each other under different diet schedule conditions (Figure 3B). We fitted a line using major axis regression for each animal and found that the total daily consumption of the two pellet types was strongly negatively correlated, with slopes around or smaller than −1. This indeed implies a roughly one-to-one trade-off between the two pellet types: consuming one less from the less palatable pellet type was correlated with consumption of 1–1.3 more of the more palatable pellet type. The experimentally set hard limits for food consumption were reached in only 5 out of 100 sessions (see Figure 3B and STAR Methods), so the apparent trade-off was not due to the experiment or instruments, but was set by the animals themselves, since by the end of S2, the animals were sated, having consumed an amount that met their daily caloric requirements (see STAR Methods). This data shows that monkeys regulated their instantaneous food consumption so that they took into account the palatability-driven intertemporal choice situation that was implicitly present in the trade-offs imposed by their own ceiling of satiation, and not by experimentally determined consumption limits.

Inherent expression of the future palatability effect

Our further examination focused on how the above-described future palatability effect arose during seven contiguous weeks right before the first main study week, when the animals were first exposed to worse-now-better-later two-session meal schedules. Before this pre-study period, the animals were completely naive and were only were acclimated to experimental procedures (see STAR Methods for details). The future palatability effect, while most clearly seen when relating to the $b_{S1}b_{S2}$ control condition, can also be captured looking at the differences in food consumption between diet-naïve days and diet-aware days under the $b_{S1}v_{S2}$ meal schedule (i.e., Diet-awareness simple effects). We could assess this effect in the seven initial weeks, including Mondays and Tuesdays from two pilot weeks (PW1 and PW2) when the palatable item in S2 was M&M's ($b_{S1}m_{S2}$ schedule) and five baseline weeks (BW1 to BW5) when the $b_{S1}v_{S2}$ meal schedule was used. As expected based on the main results, S2 food consumption was stable across meal schedule conditions and weeks (no significant effect or interaction; Diet-awareness in S2: $F_{1,4} = 0.001$, $p = 0.98$; Diet awareness×Week: $F_{7,28} = 1.06$, $p = 0.42$; Figures 4A and 4B, bottom rows). More importantly, food consumption in S1 in the $b_{S1}v_{S2}$ study week, baseline and pilot weeks significantly dropped on diet-aware days compared to diet-naïve days (Diet-awareness: $F_{1,4} = 8.71$, $p = 0.042$; Figures 4A and 4B, top rows) in a similar manner across all weeks (Diet awareness× Week: $F_{7,28} = 0.46$, $p = 0.86$; $|t_4| \leq 0.83$, $p \geq 0.45$, uncorrected, for all 7 interaction contrasts comparing the Diet-awareness effect on the study week to each of the baseline and pilot weeks). The effect also did not depend on what the palatable meal was (interaction contrast comparing the average Diet-awareness effect on the five $b_{now}v_{S2}$ baseline weeks to the two $b_{now}m_{S2}$ pilot weeks: $t_4 = 0.456$, $p = 0.67$). Thus, no gradual changes of the S1 Diet-awareness effect in the $b_{now}v_{S2}$ condition were observed, but the effect immediately appeared on the first week and remained consistent across all weeks up to and including the first study week that had the same meal schedule (see Figure 4).

Temporal dynamics of the future palatability effect

To investigate the within-session temporal dynamics of the future palatability-related downregulation of food consumption (FC), we successfully fitted a nonlinear mixture model on each session from the critical $b_{now}v_{S2}$ and the $b_{now}b_{S2}$ conditions of the main study weeks in the case four out of the five animals (see STAR Methods for details), from which ceiling and floor consumption rate parameters (FC_{hi} and FC_{lo}) and two

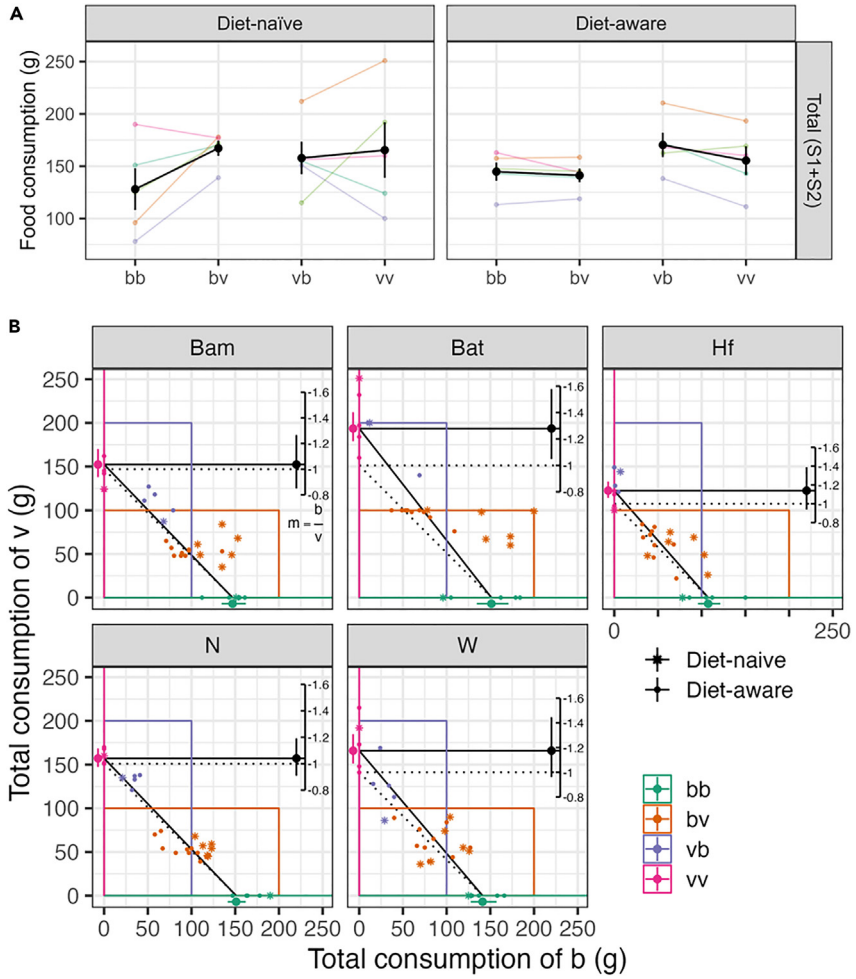

Figure 3. Consumption in S1 is governed by the trade-off between the two pellet types that is imposed by satiation-limited daily food intake

(A) Total food consumption is relatively stable across meal schedule conditions. Total daily food consumption is plotted for the four diet schedules under diet-aware and diet-naïve conditions. Notations of Figure 2 apply.

(B) Daily total consumption of the two pellet types on diet-aware days is strongly negatively correlated across meal schedule conditions, implying a trade-off. For one animal per panel (animal ID in the panel headers), daily total consumption of the palatable very berry pellets ('v') is plotted against the total consumption of the less palatable banana pellets ('b'). Each marker represents daily total consumption on one of the 20 days from the main experiment or the 10 baseline days. Marker colors represents the four meal schedule conditions. Hard consumption limits set by the experimental design are indicated by rectangles colored according to condition. A major axis regression line (solid line) is fitted on the diet-aware days (filled circles; diet-naïve days shown by stars). The slope estimates (with 95% confidence intervals) are shown on the nomogram on the right side of each plot; for comparison the y = -x slope is shown with dotted lines. For two animals, the slope is very close to −1 (animals 'Bam' and 'N'), which implies a one-to-one trade-off between the two pellet types—that is, consuming one further pellet from one type (now) implies consuming one pellet less from the other type (later). For two animals ('Hf' and 'W'), the slope is slightly, for one animal ('Bat') significantly smaller than −1. For these animals, consuming one less from the less palatable pellet type was correlated with consumption of 1.2–1.3 more of the more palatable pellet type.

corresponding temporal parameters (t_{hi} and t_{lo}) were extracted (Figure 5A) and analyzed on the group level (Figures 5B and S4). Intriguingly, only one of the four parameters showed a significant future palatability effect consistent with what we observed in terms of overall S1 food consumption: the time point when food consumption reached the minimum (t_{lo}) was 44 ± 13 min (estimated group-level marginal mean effect ±SE) earlier under high ($b_{now}v_{S2}$) compared to low ($b_{now}b_{S2}$) future palatability on diet-aware days (p_{SS} = 0.047), but not on Mondays (d = 10 ± 17 min, p_{SS} = 0.896, S2 meal type × $Day_{Diet\text{-}awareness}$ contrast in S1: $t_{24.0}$ = 2.404, p = 0.024). The minimum rate that was reached at this point did not differ (S2 meal type × $Day_{Diet\text{-}awareness}$ contrast: $t_{24.0}$ = 0.128, p = 0.899); food consumption started to drop at the same time (S2 meal type × $Day_{Diet\text{-}awareness}$ contrast: $t_{24.0}$ = 1.15, p = 0.260) and from the same plateau rate (S2 meal type × $Day_{Diet\text{-}awareness}$ contrast: $t_{21.0}$ = 0.915, p = 0.370) regardless of day or meal schedule condition. For more details on these models, please refer to Figures S3 and S4. In summary, the future palatability-related downregulation of food consumption occurred after a short, stable initial phase of food intake that was unaffected by the prospect of the more palatable food in S2.

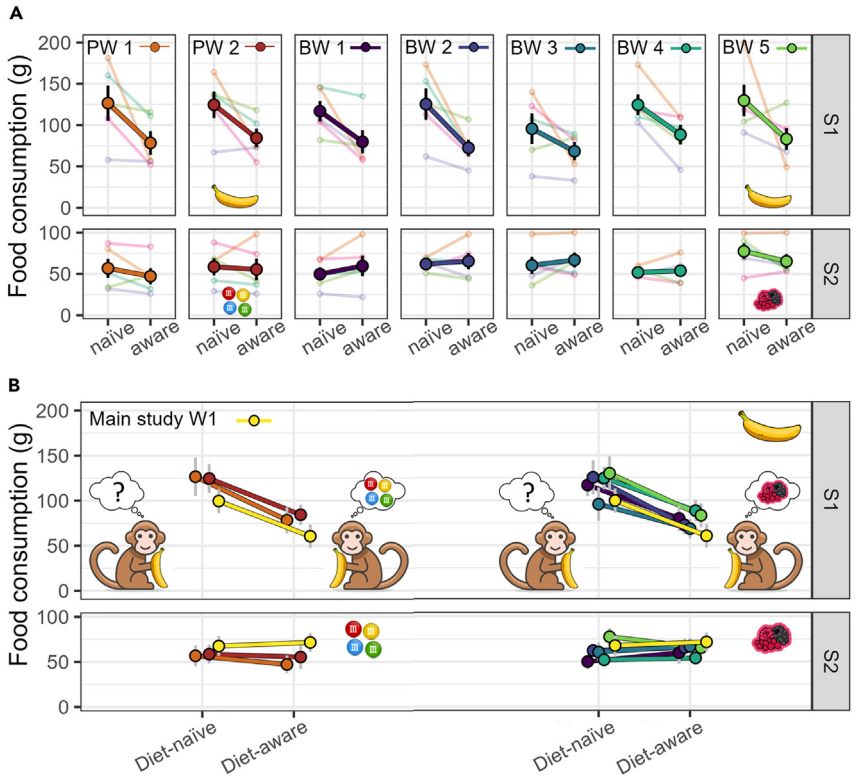

Figure 4. Diet-awareness effects did not arise gradually but appeared upon first exposure to a worse-now-better-later schedule, and also stayed stable and consistent with the main study results across seven preceding weeks

(A) Food consumption of five rhesus macaques on diet-naïve Mondays and diet-aware Tuesdays across two pilot weeks (PW1-2: $b_{S1}m_{S2}$ meal schedule, M&M's as the more palatable S2 meal) and five baseline weeks (BW1-5: $b_{S1}v_{S2}$ meal schedule, 'very berry' as the more palatable S2 meal, identical to one of the main study schedules). In S1, food consumption was higher on Mondays when the animals had not yet been exposed to the weekly feeding schedule, and consistently dropped on Tuesdays (the first Diet-aware day). This pattern was missing in S2, as the meal schedule had been already revealed during the S2 on Mondays. Each panel column shows data from one pilot or baseline week, with S1 data in the top row and S2 data in the bottom row. Colored transparent dots and lines show individual session-wise food consumption (g) for each animal. Large orange/brown (PWs) and purple-to-green (BWs) markers with black outlines denote session-wise group averages, gray whiskers show s.e.m.

(B) Comparison graph depicting food consumption from the two pilot weeks with $b_{S1}m_{S2}$ meal schedule (brown/orange, left), the five baseline weeks with $b_{S1}v_{S2}$ meal schedule (purple to green, right), and the main study week with $b_{S1}v_{S2}$ meal schedule (yellow on both right and left). Notations of panel A apply.

Based on these results, we can estimate the time point within S1 when the palatability of the S2 meal started to influence the food consumption rates. From here on we call the time interval from this point to the start of S2 the *anticipation delay*. On the right panel of Figure 5B, food consumption rates in the $b_{now}v_{S2}$ and the $b_{now}b_{S2}$ conditions appear to diverge approx. at 30 min. More formally, the start of the decreasing phase—the end of the high-consumption plateau, marked t_{hi}—did not significantly differ between the conditions, but the consumption rate started decreasing faster in the $b_{now}v_{S2}$ condition. Based on this, the difference arose between the t_{hi} and t_{lo} of the $b_{now}v_{S2}$ condition (group mean $\pm$ SE: t_{hi} = 27 $\pm$ 8 min, t_{lo} = 54 $\pm$ 12 min), and these temporal parameter estimates can be regarded as the earliest and latest possible time points for the onset of the effect, respectively. This corresponds to an anticipation delay of 2–2.5 h. On Figure S2 we provide further support for this estimate and show individual data for each animal.

Dissociating anticipation and waiting improves measurement of self-control

In traditional tasks measuring delay of gratification, the anticipation delay is conflated with the *per-trial waiting time*, the time during which the animal has to persistently withhold responding to achieve the higher-valued reward. In our study, despite the fact that the better future reward option was not a task-encoded direct and immediate consequence of withholding response during a trial, the animals nevertheless displayed gradually longer per-trial waiting times (from the start of the trial indicated by the cue light, up to completing the FR3 response sequence) in the key $b_{now}v_{S2}$ meal schedule condition compared to the non-contrasting $b_{now}b_{S2}$ condition. Thus, using data from the key meal schedule condition ($b_{now}v_{S2}$) and its control condition ($b_{now}b_{S2}$) from the main study weeks, we could derive future palatability-related trial-wise excess waiting time estimates. Since waiting time is expected to be strongly influenced by current satiation level and expected time until the more palatable food becomes available (i.e., instantaneous anticipation delay), we controlled for either pellets consumed or session time when

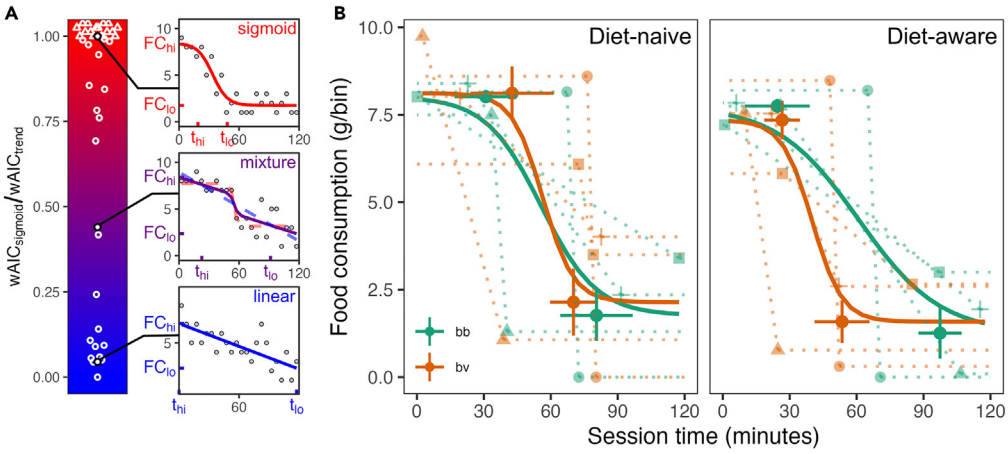

Figure 5. Starting from similar initial levels, mid-session drop in food consumption was accelerated by future palatability on diet-aware but not on diet-naïve days

(A) Individual sessions (white markers) were modeled by mixtures of linear and sigmoid temporal dynamics, with negligible contribution from an intercept-only null model (see STAR Methods). The y axis of the color bar represents the weight of the sigmoid model, thus blue/bottom corresponds to dominantly linear, red/top corresponds to dominantly sigmoid temporal dynamics. 100% sigmoid sessions at the top are jittered above the ceiling level to reveal their numerosity. Three example sessions (marked with black circles) are plotted with bin-wise food consumption (FC) values (gray discs), the fitted curve (solid line colored according to model weights) and for the mixture, component model curves (dashed lines). The parameter estimates FC_{hi} (high plateau/maximum of FC), FC_{lo} (low plateau/minimum of FC), t_{hi} (time when high-FC plateau phase ends) and t_{lo} (time when low-FC plateau phase starts) are marked on these plots at their respective axes. (B) Average temporal dynamics of food consumption in S1 on diet-naïve days (Mondays, left panel) and diet-aware days (Tuesdays to Fridays, right panel). Parameter estimates from the mixture models were summarized across animals and compared between the $b_{S1}b_{S2}$ (green) and $b_{S1}v_{S2}$ (orange) conditions. For diet-aware days, the figure is constructed using parameters averaged over the days. Transparent markers are anchor points [t_{hi}, FC_{hi}] and [t_{lo}, FC_{lo}] for both conditions. Only the time coordinate of the lower points (t_{lo}) on diet-aware days (right panel) showed a strong, significant future palatability effect. Shapes denote individual animals. Dotted lines connecting the anchor points schematically represent temporal dynamics for each animal and meal schedule condition. Larger opaque markers show group averages of parameters and their standard errors, and the solid curves show representative sigmoid curves based on these averaged parameters for all four conditions.

estimating the excess waiting time (see STAR Methods). We found excess trial-wise waiting times ranging from 7 up to 54 min (398–3249 s, average 21 min) when controlling for pellets consumed, and 5 to 56 min (309–3376 s, average 19 min) when controlling for session time (see Figure 6).

To compare our waiting time estimates and the anticipation delay to extant knowledge on waiting and anticipation in animals, we conducted a systematic review of past studies on the delay of gratification using three task types with different avian, rodent, and primate species. As noted above, these tasks provide a combined index of waiting time and anticipation delay (see Figure 6). We found that regardless of the task used, the measured delays were far below the 2–2.5 h of anticipation delay that we observed in this study, in fact, not just for rhesus macaques (2 min)[27] but even for chimpanzees (18 min)[5] and crows (10 min 40 s, see Figure 6).[6] These two latter waiting/anticipation delays were the only ones that were comparable to the average waiting time of approx. 20 min and dwarfed by the maximum of approx. 55 min (see above) in our study.

Rodents needed multiple days of conditioning to show an anticipation effect in the broadly analogous negative anticipatory contrast (NAC) paradigm[28,29] and needed even more conditioning or salient cues to switch between meal schedule conditions.[30] Despite these differences, we looked up maximal anticipation delays from the two NAC studies that specifically probed this variable,[28,29] and found that rats display the NAC effect with an anticipation delay of 35 min (2100 s; see top of Figure 6). While the NAC procedure could in theory yield dissociated anticipation delay and waiting time estimates, unfortunately trial-wise waiting times were not reported in these studies.

To sum up, both trial-wise waiting time estimates and anticipation delays measured in our study far exceeded previous traditional measurements of delay of gratification in a wide range of species.

DISCUSSION

Here we show that rhesus macaques downregulated their current food consumption behavior anticipating a more palatable food option impending 2–2.5 h later in a subsequent feeding session. Importantly, we also showed that this feeding pattern did not arise as a result of gradual learning or conditioning but was present from the very first days when the future palatability condition was introduced, contingent on the potential knowledge of the current week's stable meal schedule. Strikingly, besides this drop in consumption of the less palatable food in the morning sessions (S1s), we observed a comparable excess consumption of the more palatable food in the afternoon sessions (S2s), leading to overall similar daily total food consumption levels that approximated the caloric amount recommended by general veterinary standards remarkably well. We showed this by using a two-session operant food intake task arrangement, similar to that previously used by Flaherty et al.[28,30] in rodents and Williams et al.[31,32] in pigeons in a much shorter timescale and requiring gradual conditioning.

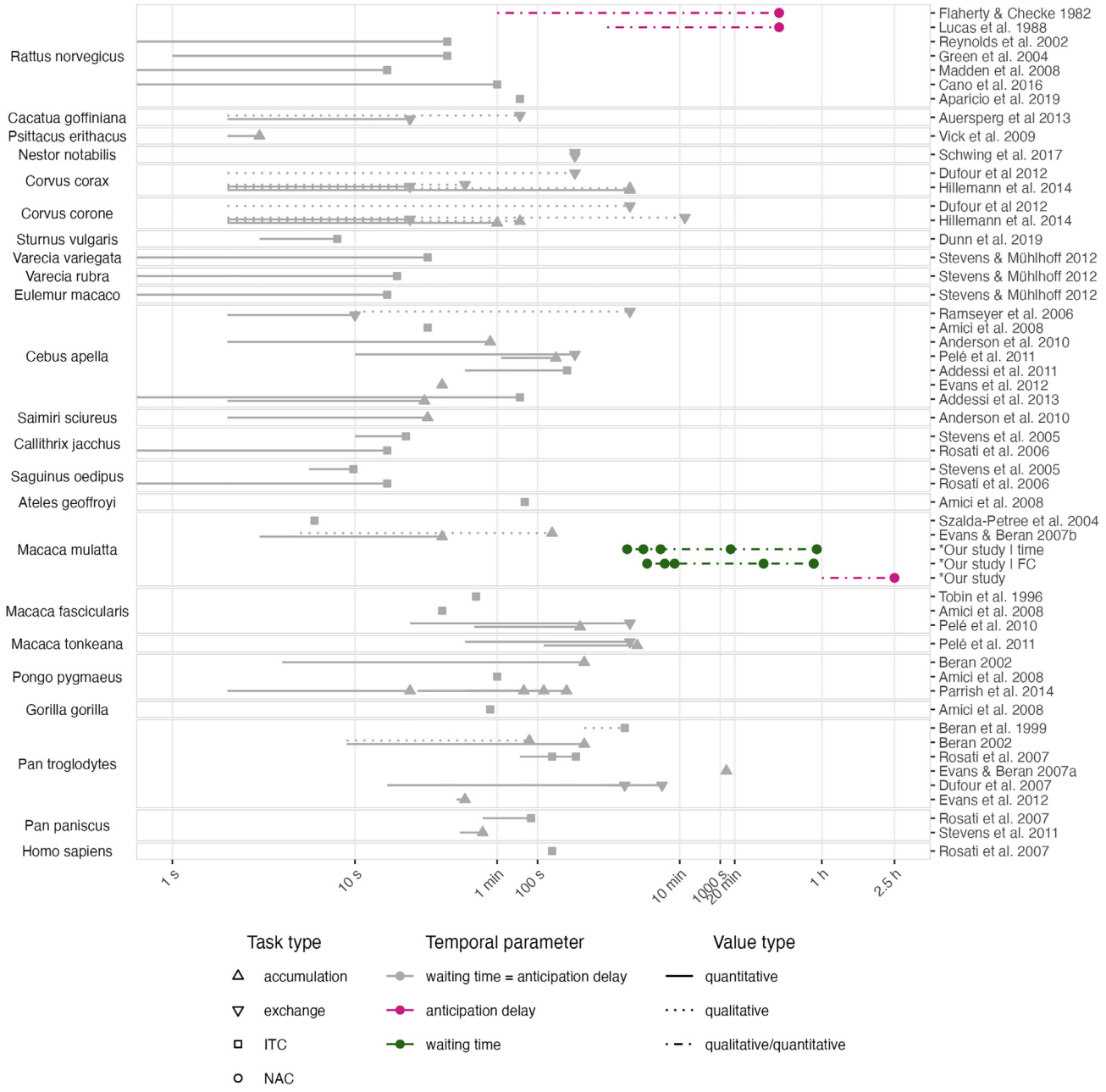

Figure 6. Both trial-wise waiting times and anticipation delay exceeds those measured in previously used tasks in avian, rodent, and primate species

The x axis shows temporal parameters measuring delay of gratification. We compare our results with data from past studies (y axis, right) with a wide range of species (y axis, left). The three lines corresponding to our study show anticipation delays (delay between change in behavior and the anticipated event that was causing it, in violet) and excess trial-wise waiting times attributable to future palatability derived from the key meal schedule condition ($b_{S1}v_{now}$) and its control condition ($b_{S1}b_{now}$), controlling for either pellets consumed (*Our study | FC) or time (*Our study | time). Both parameters largely exceed maximal times from past studies. Delays observed in accumulation (▲), exchange (▼) and ITC (■) tasks provide a combined measure of trial-wise waiting time and anticipation delay (gray color). Anticipation delays (violet color) are shown from two rodent studies (on the top) that varied this parameter in the NAC paradigm (●). Horizontal lines span the range of individual maximal times within each study. Markers show study-level maxima for literature data and individual maxima of each animal for our study. Whether a study employed qualitative or quantitative value differences is marked by line type.

In the rodent literature, an analogous phenomenon has been known as the negative anticipatory contrast (NAC) effect.[30,33] Negative anticipatory contrast refers to the drop of direct consummatory or food-contingent operant behavior for low-valued liquid in a given session (e.g., saccharine solution) that was followed by a high-valued liquid (e.g., sucrose) in a subsequent session. This focal low value/high value NAC

condition is usually compared to a low value/low value (e.g., saccharine-saccharine) control condition with the same time schedule. An important distinction from our paradigm is that rodent NAC experiments typically involve 3–15 min long feeding sessions with only a few seconds of inter-session breaks (usually termed intersolution interval, ISI) between them. Prolonging the ISI has been shown to weaken the NAC effect in rodents, but to our knowledge the highest ISI tested was 32 min,[30] while in our study the ISI equivalent delay was 1 h and the NAC effect was already evident 2–2.5 h before the start of S2 (see Figure 6, violet markers).

Importantly, the less valuable food that predicts the availability of a more valuable food later can itself become a Pavlovian cue and, instead of NAC, entice increased responding. This phenomenon, termed 'induction', occurs in pigeons when the food schedule context is not easily discriminable and/or has not been learned through several sessions of training,[34] and also in rats when the cue signaling the valuable future food source is a flavoring of the liquid consumed in S1.[35] Thus, in pigeons and rats NAC seems to depend on overriding of a Pavlovian response tendency. In pigeons and rats, learning to suppress this hypothesized Pavlovian component is learned throughout several sessions of training, usually with appropriate visual cues.[30,34] A particularly difficult situation for these animals is when different food schedule contexts alternate without external cueing—in a study by Flaherty et al.[35] rats needed extensive training to be able to anticipate S2 in an NAC condition embedded in a day by day alternation with the control condition. Also, while the Flaherty et al.[35] study provided convincing evidence that the NAC in rats is not completely dependent on external cues that signal the impending food schedule, most of the experiments still did involve e.g., visual cues for this purpose.[28,30] In our study, rhesus macaques displayed the future palatability effect—a palatability-based variant of the NAC effect—in an operant task without visual cues or training instantaneously when introduced to the two-session palatability contrast condition. Thus, this behavior is not conditioned but arises endogenously, based on the animals' experience on the previous day, most likely assuming that feeding schedules that are introduced remain stable within the given week. This suggests that rhesus macaques possess the cognitive flexibility that allows both one-shot, 'insight' learning and flexible 're-learning' of food schedules based on generalizable knowledge of usual contingencies in their (lab) environment.

Based on the results of the aforementioned daily alternation paradigm in rats, Flaherty et al.[35] concluded that the effect is not dependent on the preceding day's experience, but the downregulation of feeding is indeed anticipatory in nature. Analogously, we could ask whether the contrast effect that we observed could be driven by S1 being a "downshift" in palatability relative to very berry in the S2 of the previous day — a successive negative contrast (SNC) effect. However, if it was indeed a between-days SNC effect, then we would expect an even stronger SNC effect within the day, since the SNC effect is known to fade with longer time between the two feeding sessions.[33,36,37] Also, our animals were partially sated at the beginning of S2, which could have also facilitated the occurrence of a within-day SNC effect.[38,39] However, we did not observe any within-day SNC effect, since the amount of food consumed in S2 was very similar in the $v_{S1}b_{now}$ and $b_{S1}b_{now}$ meal conditions (see Figure 2B). Based on this, we posit that the observed downregulation of food consumption in the $b_{now}v_{S2}$ condition is probably a within-day NAC effect and not a between-day SNC effect.

Through establishing the boundary conditions for the NAC effect in rats for both consummatory and operant feeding, the possibility that the direct devaluation of the S1 reinforcer in the NAC condition or a response competition confound in the experimental paradigms would explain downregulation of consumption has been convincingly excluded.[33,35] For consummatory behavior in particular, an inhibitory mechanism was conjectured, but attempts to validate this inhibitory account on a neuropharmacological basis have failed.[40] Dominant interpretations of the results from the multitude of rodent and pigeon experiments have largely evaded the following notion: suppression (or inhibition) of a prepotent response with an anticipated future event or goal in mind is fairly close to contemporary definitions of self-control—and, in particular, delay of gratification—in a value-based decision-making framework.[41] Indeed, considering how our results confirm and extend previous results on the delay of gratification in animals and keeping in mind the phylogenetic proximity of monkeys to humans, we argue that this latter interpretation is more than plausible or maybe even parsimonious.

Our task is not an intertemporal choice (ITC) or accumulation type delay of gratification task in the traditional sense. ITC tasks impose a forced choice, while in our study nothing was included in the paradigm to stop the animals from simply consuming all the available reward in S1. Also, the observed decreased food intake in S1 in the future palatability condition was not due to satiety, because it was much lower than the diet-naïve food consumption rate during S1 on Mondays, or during the weekly schedules when the same less palatable meal option was offered in S2. However, the daily total consumption in the four meal schedules was very similar, and the strong negative correlation of consumption of the two pellet types shows that animals indeed allocated food consumption between sessions/pellet types obeying a closely one-to-one trade-off that was due to eventually reaching satiety at the end of S2. Theories of operant conditioning,[42,43] behavioral ecology,[44,45] and neuroeconomics[41] suggest that if the marginal utility (or reinforcement value) of an operandum becomes smaller than the global or ambient marginal utility, then the agent disengages and switches to another (lever or patch of resource in foraging) if available. Since the global marginal utility is an estimate encompassing all possible options in a situation, the dependence of S1 food consumption on the palatability of S2 food strongly suggests that when the animals locally (on the 'molecular' level)[46] decide on the response rate for one pellet type, in the broader (also called 'molar') context, the currently observed behavior can be considered an implied intertemporal choice between two alternatives under endogenously imposed satiety constraints, and the cognitive time horizon of this implied choice encompasses the 3-h period covered by the two experimental sessions. Consequently, we propose that this paradigm can probe future-oriented decision-making, self-control and delay of gratification more effectively than traditionally employed tasks: in our literature review of studies with intertemporal choice (ITC), exchange and accumulation tasks, anticipation delays (the time between the present behavior and the future impending reward that influences it) were far below the 2–2.5 h that we observed in the present study, exceeding even the maximal 1080-s delay times measured earlier in great apes (see also Figure 6).[5]

In traditional delay of gratification tasks, the subjects have to wait throughout the anticipation delay to acquire the larger reward. In our case, though the animals did not wait across the whole period but to some degree engaged with the less palatable reward in S1, the

eventual act behind the decreasing food consumption discussed here was, again, waiting: in each trial, when the cue light switched on again, the animal had the opportunity to withhold the basic Pavlovian response tendency (or Pavlovian responding)[33] to harvest a pellet and exercised self-control, yielding increasing waiting times between pellets. Past research suggests that the waiting time relative to the previous ITI (when an *experimentally determined* 30-s period passed before the next trial) is locally perceivable and also adaptively controllable for the animals,[46,47] and therefore it is a plausible candidate variable for local adjustments of behavior to approximate a globally optimal bundle of daily food consumption. Our estimates of excess waiting times due to future palatability (15–54 min) by far exceeded most delays measured in exchange, accumulation and ITC tasks (Figure 6). We suggest that this 'waiting in small installments' and the dissociation of waiting time and anticipation delay are key features behind the unprecedented sensitivity of our task to assess animal self-control.

Our detailed analysis of the temporal dynamics of food consumption revealed that after an initial stable phase that was similar across meal schedule conditions, the mid-session drop in food consumption rate was steeper in the future palatability condition compared to the control condition. Because of the careful control of extra-experimental reward contingencies, we could infer that the dynamically increasing waiting times and decreasing consumption rates across trials reflect continuous changes in the motivational state of the individual within the session. Specifically, we suggest that the immediate homeostatic needs giving higher present value to the currently consumed food dominated the initial phase, but with gradual satiation the marginal experienced utility of the less palatable food decreased continuously. This is in line with past research showing that food reward valuation and contrast effects are sensitive to food deprivation or satiation state, suggesting that contrast effects are reduced in a food-deprived or hungry state and are amplified by partial satiety.[38,39,48] At the same time, the progressive shortening of the anticipation delay with the passage of time increased the marginal anticipated utility (prospective hedonic value) of the more palatable food. This dynamic shift in the marginal values within the two-session experimental period could unmask delay of gratification that might remain hidden in accumulation experiments with a single trial or a few trials.

The future palatability-related downregulation of S1 feeding is concordant with anticipating the expected *internal* dynamics of satiation: the limiting factor of S2 consumption was not experimentally set but was merely due to the fact that the ability to consume the palatable food in S2 was determined by the animals' residual appetite after S1. In short, the results raise the possibility that the animals were able to factor in their future drive state—residual appetite—beyond the currently experienced state—current hunger/appetite and Pavlovian responding. The Bischof-Köhler hypothesis asserts that animals are generally incapable of putting aside their currently experienced drive state and planning for their future motivational states.[4,22] While apes,[17,49–55] squirrel monkeys[25,26] and corvids[56–60] have previously been shown to exhibit certain evidence of drive state anticipation, for old-world monkeys[61,62] and rhesus macaques[63] in particular, we are the first to provide results that put the Bischof-Köhler hypothesis into question. However, it should be noted that the presently experienced drive state—partial satiety—and its expected instantaneous change induced by consuming the next available pellet—waning hunger—are closely related to the anticipated future drive state—residual appetite—that is relevant to current behavior. We hypothesize that considering the marginal expected utility of the counterfactual more palatable food under the currently experienced change in satiation state is probably sufficient to hold back the animal's responding to the currently available less palatable food. Such mechanism could be facilitated by the fact that the future and present environments were the same, and the operant contingencies during the two sessions were also quite similar. Future research could clarify whether this putative drive state extrapolation mechanism could be a basic process of future-oriented cognition in primates and other species.

Another key finding from the present study is that the animals only downregulated food consumption from Tuesdays on, after they had been exposed to the weekly food schedule on the preceding Monday, and this downregulation pattern was already present at the very first exposure to the worse-now-better-later food schedule. That is, the information that led the animals to withhold their food consumption in S1 had to necessarily arise from explicit or implicit memory based on their experience on the previous day. Also, the way the animals consistently went back to the diet-naïve behavioral pattern every Monday could reflect the notion that a new week could have been perceived by the animals as a *novel context*. The much less likely alternative interpretation is that they forgot the previous week's schedule during the weekend. Recent theories also posit that higher-level cognitive processes are rooted in mechanisms of allostatic or predictive regulation,[64] and the exaptation of such mechanisms can give rise to episodic memory and planning.[17,55,65,66] While there are many open questions related to the present results in the literature around this topic,[2,4,23,67] based on the flexibility and context-sensitivity of the observed behavior, we hypothesize that while in the testing apparatus on the S1 of diet-aware days, the animals recalled an episodic-like memory of the pleasurable experience in the second (S2) session of the previous day. Further research will clarify the exact nature of the memory process that might compete with the Pavlovian response tendency to harvest the currently available food pellet.

The notion that monkeys might be capable of high-level prospective value-based decision-making previously might have appeared as speculative from a conservative behaviorist perspective,[31,33,68] however, through the last two decades, economic principles have been validated in primates and the underlying neurophysiological processes have been characterized using a wide range of methods.[69–72] For example, in a series of studies, Hernádi, Grabenhorst, and Schultz[73,74] have shown that neurons in the amygdala dynamically keep track of critical decision variables during waiting-like ('saving') behavior in an accumulation task. Generally, in the light of such findings about neurocomputational building blocks of value-based future-oriented cognition in animals, basic neural mechanisms of flexible response inhibition that could explain our results are present in monkeys. Past results with very short anticipation delays and waiting times probably reflect a mismatch between the applied experimental design and the behavioral-cognitive repertoire of the species in question, rather than revealing more general limitations of self-control and cognition. Our results not only complement previous knowledge on the continuity of the phylogeny of future-oriented cognition in primates but also provide a novel framework to study future-oriented cognition through the observed

prospective decision-making and delay of gratification in macaques, the most relevant preclinical translational models for basic and applied behavioral neuroscience.

Limitations of the study

Our study involved young adult male animals, which poses a limitation to the generalizability of the results. It will be important in the future to verify the results on female and also on older animals and investigate how sex-specific physiology and age-related conditions modulate the palatability-based anticipatory downregulation of food consumption that we observed in the present study. We did not manipulate the length of the ISI, which, in future studies, could provide important information about the temporal scope of the underlying anticipation process. Another evident step forward is to investigate the underlying neural mechanisms of palatability-based anticipation using pharmacological interventions, electrophysiological or neuroimaging methods.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109459.

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AUTHOR CONTRIBUTIONS

J.I.*: Conceptualization, Methodology, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization; B.K.*: Conceptualization, Methodology, Software, Formal analysis, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization; P.K.: Conceptualization, Methodology, Writing – Review and Editing; B.L.: Resources, Project administration, Funding acquisition, Writing – Review and Editing; I.H.: Conceptualization, Methodology, Resources, Writing – Original Draft, Writing – Review and Editing, Supervision, Project administration, Funding acquisition.

DECLARATION OF INTERESTS

B.L. is employee of Gedeon Richter Plc and K.P. was an employee of Gedeon Richter Plc. during the planning and experimental phase of the study. These do not alter our adherence to journal policies on sharing data and materials. The remaining authors (J.I., B.K., and I.H.) declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Rhesus Macaques (Macaca mulatta)	Grastyán Endre Translational Research Centre, Pécs, HU	N/A
Software and algorithms		
MATLAB	The Mathworks Inc., Natick, Massachusetts, US	RRID:SCR_001622
R 4.1.1	R Core Team[76] https://www.R-project.org/	RRID:SCR_001905
MED PC software for MS Windows	Med Associates, St. Albans, Vermont, US	RRID:SCR_012156
Other		
Product# F0157, Dustless Precision Pellets®,1 gm, Primate Grain-Based Diet, Banana Flavor	Bio-Serv, Inc., Frenchtown, New Jersey, US	N/A
Supreme Mini-Treats™, 1 gm Pellets, Certified, Very Berry Flavor	Bio-Serv, Inc., Frenchtown, New Jersey, US	N/A
Maintenance diet, standard lab chow	Altromin Spezialfutter GmbH & Co, Lage, DE	N/A
M&M's Chocolate Candy	Mars Hungary LP., Budapest, HU	N/A
Modular Intelligence Test System for Primates	Med Associates, St. Albans, Vermont, US	N/A
Wellmed EasyTouch® GCU, ET-301 Multi-Function Monitoring System	Bioptik Technology Inc., Jhunan Township, TW	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, István Hernádi (hernadi.istvan@pte.hu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The data that support the findings of this study are available from the lead contact upon reasonable request.
- Code to reproduce the analyses of this study is available from the lead contact upon reasonable request.
- Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Animals and housing

Five 4-year-old (birth dates: 2011.03-07) pair-housed, pre-trained, healthy male rhesus macaques (*Macaca mulatta*) were used in the experiments. Their body weight was 4.9±0.3 kg and 5.1±0.4 kg (Mean±SEM) at the beginning and at the end of the study, respectively. The home cages are uniformly sized 200 × 100 × 200 cm (length × width × depth) and are equipped with wooden rest areas. Besides natural light from windows, illumination with full-spectrum artificial light was provided for 12 hours each day starting at 7:00 AM. Temperature (24±1°C) and relative humidity (55±10%) of the animal house were kept constant, with continuous airflow.

On experimental days daily food allowance was only offered during the food intake sessions (see section 'Operant food intake paradigm' below). On weekend days (Saturdays and Sundays), animals received their usual dry lab chow with vegetable and fruit supplements. The calorie intake from the pellets consumed during the experimental days and calorie intake from weekend menus were of similar magnitude, and fully satisfied the recommended daily energy requirements of the animals (see section 'Energy intake'). Monkeys had *ad libitum* access to water on every day of the week.

Operant chambers

Training and experimental sessions were conducted in individual, isolated, ventilated and illuminated primate operant conditioning apparatuses which were located in a separate testing room next to the animal house. Each operant chamber was equipped with a response panel (Modular Intelligence Test System for Primates, Med Associates, St. Albans, Vermont, US) and a built-in standard digital camera for real-time video surveillance. Operant response panels were simultaneously controlled with the MED PC software for MS Windows (Med Associates, St. Albans, Vermont, US).

Ethical compliance

All procedures were conducted in the Grastyán Translational Research Center of the University of Pécs. The study was approved by the Department of Animal Health and Food Control of the County Government Offices of the Ministry of Agriculture (ethical permission number: BA02/2000-13/2015). Measures were taken to minimize pain and discomfort of the animals in accordance with the Directive 40/2013 (II.14): "On animal experiments" issued by the Government of Hungary, and the Directive 2010/63/EU "On the protection of animals used for scientific purposes" issued by the European Parliament and the European Council.

METHOD DETAILS

Assessment of food preference

All five subjects performed a simple test to validate their food preference. Animals were tested individually, separated in their home cages. The types of food items tested were as follows: pellets of standard lab chow (Altromin Spezialfutter GmbH & Co, Lage, DE; nutritionally complete, 10 mm, 3.315 kcal/g), banana flavoured pellets (Dustless Precision Pellets®, Bio-Serv, Inc., Frenchtown, New Jersey, US; nutritionally complete, 1 g, 3.35 kcal/pellet), 'very berry' flavoured pellets (Supreme Mini-Treats, Bio-Serv, Inc., Frenchtown, New Jersey, US; nutritionally complete, 1 g, 3.46 kcal/pellet) and M&M's Chocolate Candies (Mars Hungary LP., Budapest, HU; nutritionally incomplete, ~0.91 g, 4.7 kcal/g). M&M's was the food item that our equipment is intended to be used with, but we deemed it nutritionally inadequate for long-term use as the main food in our task. This is why we introduced and tested the banana and very berry flavoured pellets. The lab chow was included in the preference testing because it was the main food of the animals during weekends. In each choice trial, one piece from each of the four types of food items was simultaneously offered to the animal to freely choose from. The animals could take the food items one by one, and the order in which the items were consumed was recorded. We examined the subjects' food preference on the Tuesday and Thursday of baseline week 2. On each day, the first (hungry) preference test session was run before the start of the daily main task session described below. The second (partially sated) preference test session was run after the first session of the daily main task, where banana flavoured pellets were offered. Each preference test session entailed three trials, yielding six trials per satiation state for each animal. The location of the food items was randomized between trials to exclude any side preference.

Two-session operant food intake paradigm

The main task procedure is further referred to as the two-session operant food intake paradigm. In this paradigm, the animals performed a lever pressing task for food pellets, which were selected based on the results of the previously described preference test. At the beginning of each trial, a cue light was switched on, indicating that the animal will receive one food pellet upon three consecutive lever presses (fixed ratio 3 reinforcement schedule, FR3). The cue light was up until the three lever presses were completed which was followed by the delivery of the reward and a 30 sec inter-trial interval. Nutritionally complete one-gram food pellets were offered as the meal in 2 experimental sessions per day, Session 1 (S1) and Session 2 (S2), with a one-hour inter-session interval between them. During the inter-session interval, the subjects were returned to their home cages. S1 lasted for 2h (or until max. 200 pellets were earned) while S2 lasted for 1 h (or until max. 100 pellets were earned). There were five occasions when S1 was 3-9 minutes shorter because of reaching the maximal pellet consumption, and four instances of S2 being 1-4 minutes shorter for the same reason. Every morning, S1 started at approx. 9:30 AM, and S2 started at approx. 12:30 PM.

Within a session, food pellets of only one type were offered: either the standard, banana flavoured pellets (low-palatability meal), or 'very berry' flavoured pellets (high-palatability meal). On experimental days daily food allowance was only offered during the sessions. On the four main study weeks, all possible combinations of the two types of flavoured pellets assigned to the two sessions were tested, resulting in 4 experimental conditions: S1 banana / S2 banana ($b_{S1}b_{S2}$), S1 banana / S2 very berry ($b_{S1}v_{S2}$), S1 very berry / S2 banana ($v_{S1}b_{S2}$), S1 very berry / S2 very berry ($v_{S1}v_{S2}$). Each pellet type combination (meal schedule) was consistently offered for 5 consecutive experimental days, from Mondays to Fridays.

During the entire experimental period, we registered 5 technical errors, caused by the jamming of the pellet dispenser. In these cases, at the end of the affected sessions, we subsequently gave the animals the 'stuck' pellets. There were no external constraints for the animals (e.g., time out) and the delivery of reinforcers was not externally scheduled. No time limit was set for intervals between lever presses, and responding in inter-trial interval periods was also not punished with an extra timeout.

Training and baseline period

Having analysed the data from the four main study weeks, whether the feeding pattern we observed arose gradually or abruptly arose as an important question. Therefore, we decided to analyse as much data as possible from the point when the animals started the two-session

operant task up to the first main study week. This task development and testing period was not planned to involve complete weeks without any interference, but we rather used this data as a semi-observational dataset to support our main results.

The animals were initially naïve: absolutely no cognitive or operant task had been performed by them apart from acclimation to experimental procedures required to introduce the animals to the task environment (e.g., transfer chair training, operant box training). Their first experience in the task environment was with the S1-only version of the task for 8 days. The animals were introduced to the banana and very berry flavoured pellets and M&M's during these eight days.

In the following two weeks that we refer to as 'pilot weeks', the animals were introduced to the two-session operant task with banana pellets were used in S1 and M&M's pellets used in S2. Afterwards, the animals performed the operant food intake task for six consecutive weeks (04.27-05.29.) in the $b_{S1}v_{S2}$ condition (banana flavoured pellet in S1 and very berry pellet in S2). We label these weeks as the 'baseline' weeks. The M&M's pellet type was abandoned because its nutritional profile was not adequate for long-term use as a primary daily food for nonhuman primates, and the banana and very berry flavoured pellets were found to be suitable a) from a veterinary perspective because they are nutritionally complete b) from an experimental perspective because of differential palatability as established in the preference testing (see above) and c) from a procedural point of view as they were found to be compatible with our dispenser system. For consistency, we analysed only Mondays and Tuesdays from baseline and pilot weeks, as medical treatment of some of the animals, and pellet dispenser adjustments were scheduled on later days of those weeks. Data from the week immediately preceding the main study were also excluded for the same reason.

Energy requirements

Juvenile nonhuman primates require more energy per unit of body weight for growth than do adults of their species. For juvenile rhesus macaques, the daily metabolizable energy (ME) intake requirement was determined as 107 $kcal \cdot BWkg^{-1} \cdot d^{-1}$.[75] For the subjects participating in our study, the mean daily ME intake requirement was 519.2 ± 35.1 $kcal \cdot d^{-1}$. The daily ME intake was calculated based on the measured food consumption, the ME of the pellets supplied by the manufacturer and the body weight of the individual animal corresponded to the required daily ME intake in all four meal schedules of the main study weeks ($b_{S1}b_{S2}$: 485.1 ± 29.0 $kcal \cdot d^{-1}$; $b_{S1}v_{S2}$: 480.6 ± 21.9 $kcal \cdot d^{-1}$; $v_{S1}b_{S2}$: 586.1 ± 39.9 $kcal \cdot d^{-1}$; $v_{S1}v_{S2}$: 560.7 ± 43.8 $kcal \cdot d^{-1}$).

QUANTIFICATION AND STATISTICAL ANALYSIS

Data loading and preparation was partly done in MATLAB R2021a (The Mathworks, Natick, MA, USA); analyses and graphics were made in R 4.1.1.[76] Where applicable, statistical tests are two-sided.

Assessment of food preference

In the food preference test, taking a given type of food item as the first, second, third or fourth choice was coded as 4,3,2 or 1 points, respectively. We averaged the points over all 6 trials in each time point (pre-$b_{S1}v_{S2}$ – hungry or post-b_{S1} pre-v_{S2} – partially sated) for each animal to calculate average preference scores, which were analysed separately using Friedman's ANOVA with Durbin-Conover post hoc tests.

Session-wise food consumption analyses

We investigated the total food consumption (g) for each session. The number of pellets delivered was registered by the operant chamber. Leftover pellets were collected from the operant chambers at the end of the sessions and their number was registered manually. Food consumption for each session was calculated by subtracting the number of leftover pellets from the number of pellets delivered. Note that when analysing the amount of food pellets delivered (not excluding the leftovers), the results were compatible with the main results. Also note that when analysing the temporal dynamics of food consumption (see below), we could not subtract the leftover amount since we could not determine the time bin when the given pellet was not consumed.

The food schedule of the actual week was introduced on Mondays, so during the first session of the week the monkeys could not have been aware of what food would be offered to them during the second session. Therefore, data collected on Mondays and the remaining days were analysed separately, labelling Mondays as diet-naïve days and Tuesdays to Fridays as diet-aware days. For the main session-wise food consumption analyses, data from diet-aware days were averaged for each animal. Comparisons contrasting diet-naïve and diet-aware days are labelled as Diet-awareness effects.

As already mentioned in the previous sections, the pellet dispenser was jammed during five of the sessions, and the jammed pellets were in these cases given to the animals by hand at the end of the affected sessions. However, the cessation of reward delivery arguably could have influenced the motivation of the animals. Inspecting the food consumption dynamics of the affected sessions, the motivation drop demonstrably happened in some cases, however, it was not always straightforward to infer a counterfactual food consumption level and pattern that would have been observed without pellet jamming. We tackled this problem by capitalizing on different analysis methods: in the repeated measures ANOVA analysis, we used the consumption data from the jam sessions and regarded them as lower-bound estimates, while we omitted these sessions from the linear mixed model analysis. (The latter can better tolerate missing data.) The concordant results from these analyses ensure that neither inclusion nor exclusion could substantially alter our inferences and conclusions.

The main analyses for S1 and S2 were conducted separately because due to their differing duration, food consumption levels and corresponding variances were quite different between the two sessions, but a control analysis encompassing both S1 and S2 (encoded by an

additional Session factor) was also conducted to reaffirm differing patterns of results between the two sessions. Repeated measures ANOVAs for S1 and S2 food consumption involved the following factors: S1 meal type (b_{S1} or v_{S1}), S2 meal type (b_{S2} or v_{S2}) and Diet-awareness (Diet-naïve or Diet-aware). Note that in the strict sense, the term 'diet-naïve' only applies to S1 on Mondays, since from the start of S2 in the same afternoon, the weekly meal schedule was already revealed to the animals. We nevertheless kept this naming scheme, since comparing Mondays to the remaining weekdays in S2 serves as an important control comparison to the focal S1 – *sensu stricto* – Diet-awareness effect and interactions – comparing the same days, but with no actual difference in potential knowledge about the meal schedule. Also note that for S1 food consumption analyses, S1 meal type effects reflect the presently consumed food, and the S2 meal type factor represents the effect of the type of food that would be consumed hours later. Conversely, for S2 analyses the S2 and S1 meal type effects concern the present and the past, respectively. To emphasise this, we use the labels b_{now} and v_{now} when referring to food consumed in the session currently analysed.

Control analyses using linear mixed models with days of the week kept as separate levels of the Day factor were conducted to ensure that averaging in the main analyses did not mask any contradicting effects. As mentioned above, sessions with technical problems were omitted from these analyses. The models were fitted using the lme4 package (version 1.1-34)[77] with Restricted Maximum Likelihood (REML) estimation. The Satterthwaite method was used to approximate degrees of freedom (lmerTest package, version 3.1-3).[78] The factors were Day (5 levels: Monday, Tuesday, Wednesday, Thursday, Friday), S1 meal type, and S2 meal type. Besides the main effects, all the interactions were included in the fixed effects part of the model. An intercept, the main effects and the interaction of the two meal type factors were included as random terms, with correlations also modelled. To disentangle Diet-awareness effects from generic differences across days of the week, a $Day_{Diet\text{-}awareness}$ contrast was introduced to contrast Mondays to the average of the remaining days, akin to the ANOVA analyses, and the interaction contrasts with the meal type effects were also assessed as contrasts of interest. Besides the above-described model (called Mon-Fri in the legend of Figure S1), an additional (otherwise identical) linear mixed model was also fit excluding Mondays to evaluate the omnibus between-day effects (for Tuesdays to Fridays, called Tue-Fri in the legend of Figure S1) that are orthogonal to the Diet-awareness contrast. In this model, polynomial contrasts were used to assess trends and interactions across weekdays. Detailed results from these models can be read in the legend of Figure S1.

To assess the trade-off between the daily total consumption of the two pellet types, we conducted a major axis regression analysis. For each animal separately, the X variable was the daily total consumption of banana pellets, and the Y variable was the daily total consumption of very berry pellets. All diet-aware days from main study weeks (Tue-Fri) and baseline weeks (Tuesdays) were used. A slope of -1 indicates a perfect one-to-one trade-off between the two pellet types.

To see whether the future palatability effect arose gradually, indicating progressive conditioning or learning, or abruptly, implying insight-like learning, we used data from the five baseline weeks with $b_{S1}v_{S2}$ schedule and two pilot weeks with $b_{S1}m_{S2}$ schedule (M&M's in S2). As also described in the main text, we used the Diet-awareness effect on S1 consumption of banana pellets as a proxy to the future palatability effect (established against the $b_{S1}b_{S2}$ control condition in the main experiment); i.e. the drop of consumption of banana pellets from diet-naïve days (Mondays) to diet-aware days (Tuesdays were available from the baseline and pilot weeks), after the information on the weekly feeding schedule became available to the animals during S2 on Monday. In one pilot week for one animal, the first testing day was Wednesday, so in this case data from Wednesday was used for the diet-naive condition and data from Thursday was used for the diet-aware condition. This data was analysed using repeated measures ANOVA with factors Week (8 levels: two pilot weeks, five baseline weeks and the $b_{S1}v_{S2}$ main study week) and Diet-awareness (2 levels: Diet-naive, Diet-aware, usually Monday and Tuesday, see exception above).

Within-session temporal dynamics of food consumption

In this analysis, we aimed to disentangle when and how the animals decreased their food consumption (FC) within the course of Session 1 in the $b_{now}v_{S2}$ compared to the $b_{now}b_{S2}$ condition. Here we took a two-level analysis approach: on the first level, we used a nonlinear model to capture the temporal dynamics in each session. The parameters capture the way animals started feeding at a high rate at the beginning of the session (FC_{hi}, g/bin) up to a certain time point (t_{hi}, minutes) when the feeding rate started to steadily decrease until reaching a lower plateau rate (FC_{lo}, g/bin; t_{lo}, minutes). The parameters from the individual session fits were carried over to the group-level analyses which were linear mixed models similar to those applied for the consumption data.

Session 1 was divided into 24 five-minute time bins, and food consumption rates were calculated for each S1 of each animal in the two conditions of interest. Visual inspection showed that the temporal patterns of food consumption showed very high variability. Nevertheless, nearly all sessions were characterized by a decreasing trend in food consumption, and the majority of the sessions with a decreasing trend were well fit by a sigmoid function that can be described using the following parameters (see Figure 4A). The animals started feeding at a high rate at the beginning of the session (FC_{hi}, g/bin) up to a certain time point (t_{hi}, minutes) when the feeding rate started to steadily decrease until reaching a lower plateau rate (FC_{lo}, g/bin; t_{lo}, minutes). Sessions with a simple linear decreasing feeding pattern were characterized using the same parameters as if the plateau phases of the sigmoid were missing (using the first and the last time bins for the temporal parameters: t_{hi}=2.5 minutes, t_{lo}=117.5 minutes, FC_{hi} and FC_{lo} estimated based on the linear fit at these time points).

To encompass intermediate cases when both linear and sigmoid fits were substantial, model fits and parameter estimates were obtained from the mixture of these two models, with an additional intercept-only null model. For one subject (Bat), S1 FC temporal dynamics showed an idiosyncratic pattern without a clear trend (the intercept-only null model was the best model for 8 out of 10 sessions), thus all sessions from 'Bat' were excluded from this analysis. The whole modelling procedure commenced as follows:

1. Three models (a sigmoid model denoted by MS, a linear model denoted by M1 and an intercept-only null model denoted by M0) were fit one-by-one to each binned session time series and Akaike weights (based on AICc, sample-size corrected or second-order Akaike

Information Criterion; w_s, w_1 and w_0, respectively) were calculated over this three-model space, based on which an averaged model was calculated (see Figure 4A, left).[79] The data of the first four and two time bins from the Wednesday $b_{now}b_{S2}$ sessions, respectively, were removed for subjects 'Hf' and 'W' to foster model convergence (see Extended Data Figure 2.). The sigmoid submodel was fit using the Levenberg-Marquardt algorithm (nlsLM package 1.2-3)[80] by default and the Gauss-Newton algorithm (nls R function) as a fallback option in case of non-convergence. The linear and the null model was fit using the lm R function.

2. The high level of food consumption at the start of each session (FC_{hi}) and the low level of food consumption at the ends of sessions (FC_{lo}) were calculated based on predictions of the averaged model for the first and the last time bin, respectively. The temporal parameters t_{hi} and t_{lo} were calculated as the weighted average of the temporal parameters obtained from the sigmoid model and the linear model (t_{hi}=2.5 minutes, t_{lo}=117.5 minutes), using the Akaike weights from the previous step (see Figure 4A, right). So, each session was characterized by two temporal and two FC level parameters at the end of the first-level modelling procedure.
3. The first-level parameters were carried on to a second-level (group) analysis. The second-level analysis was very similar to the mixed model analysis of overall food consumption levels. Separate linear mixed models were fit to each of the four parameters with fixed effects factors Day (Mon, Tue, Wed, Thu, Fri), Condition ($b_{now}v_{S2}$ and $b_{now}b_{S2}$) and the Day×Condition interaction. Random terms for the intercepts and the main effects and the correlations between these terms were included in the model. Post hoc tests were conducted for 4 contrasts: simple effect of Condition on Monday, simple effect of Condition on diet-aware days (Tue-Fri), simple effect of Diet-awareness (Mon vs. the average of Tue-Fri) for $b_{now}v_{S2}$ and simple effect of Diet-awareness for $b_{now}b_{S2}$. To adjust for the 4 comparisons, the single-step method was used,[81] and the resulting p-values are denoted by p_{SS} in the manuscript.

The first-level models were specified as follows:

$$M0 : FC_0(t) = b_0$$

$$M1 : FC_1(t) = b_1 + m_1 \cdot t,$$

$$MS : FC_S(t) = FC_{lo}^S + \frac{FC_{hi}^S - FC_{lo}^S}{1+e^{-k\cdot(t-t_s)}}$$

In the sigmoid model MS, t_s marks the inflection point of the sigmoid curve and k is the slope parameter. From t_s and k, the two 'ankle points' of the curve can be calculated as $t_{hi,S}' = t_s + \frac{2}{k}$ and $t_{lo,S}' = t_s - \frac{2}{k}$. Since in some cases this yielded estimates that were outside the bounds of the session (e.g. fitting a time series where only a higher asymptote and the slope phase was present and the lower asymptote phase was missing), in these cases the estimates were taken to be the last (for t_{lo}) and the first time bin (for t_{hi}).

$$t_{hi,S} = \begin{cases} t_{hi,S}', \textit{if } 0 < t_{hi,S}' < 120 \\ 2.5\ \textit{min}, \textit{otherwise} \end{cases}$$

$$t_{lo,S} = \begin{cases} t_{lo,S}', \textit{if } 0 < t_{lo,S}' < 120 \\ 117.5\ \textit{min}, \textit{otherwise} \end{cases}$$

The linear model is always taken to suggest that $t_{hi,1}$=2.5 min and $t_{lo,1}$=117.5 min. The model-weighted estimates for the temporal parameters are calculated as $t_{hi}=w_1\cdot t_{hi,1}+w_s\cdot t_{hi,s}$ and $t_{lo}=w_1\cdot t_{lo,1}+w_s\cdot t_{lo,s}$.

Model-averaged food consumption estimates are calculated as $FC(t) = w_0\cdot FC_0(t) + w_1\cdot FC_1(t) + w_S\cdot FC_S(t)$, yielding ceiling (session start) and floor (session end) food consumption estimates FC_{hi}=FC(2.5 min) and FC_{lo}=max[0 ; FC(117.5 min)]. Note that when the intercept-only null model provides a substantial fit and thus a large model weight, it will pull the estimates toward the mean consumption rate of the session, i.e., introduces shrinkage and practically acts as a simple regularizer in the modelling scheme.

From the group level average temporal parameters and their contrasts we inferred in the Results section that the onset of the future palatability effect was between t_{hi} and t_{lo} of the $b_{now}v_{S2}$ condition. Due to methodological considerations,[82] we deliberately avoided estimating the effect onset using timepoint-by-timepoint (significance) thresholding procedures, and opted to use models that directly estimate temporal parameters of the sessionwise temporal dynamics. However, to support our argument with timepoint-by-timepoint statistics, we calculated crossvalidated relative likelihood of the data given models from the same condition versus models from the other condition. For each time bin (*t*) in each S1 on each diet-aware day of each animal (*s*), we calculated the likelihood of the observed food consumption given the models from all the other days from the same condition. Since the models were fit with a least squares procedure, the likelihood distribution was a Gaussian parametrized with the predicted value as the mean and the standard deviation calculated from residuals. Likelihoods were averaged across days, never using the model that was fit to the data currently assessed. This crossvalidation procedure provides an approximation of the out-of-sample predictive performance. Then, likelihoods were multiplied across the two conditions ($L_{same}(s,t)=L_{bv\text{-}data|bv\text{-}model}(s,t)\cdot L_{bb\text{-}data|bb\text{-}model}(s,t)$). This procedure was repeated with the two conditions exchanged: we calculated the likelihood of the observed food consumption for each animal and time bin given the models from the other condition ($L_{different}(s,t)=L_{bv\text{-}data|bb\text{-}model}(s,t)\cdot L_{bb\text{-}data|bv\text{-}model}(s,t)$). Also analogously, when calculating the 'different' likelihood of a given day of the week, we did not use the model from the same day of the week of the other condition. This ensured that all the likelihoods were calculated based on the same number of models. The log relative likelihood $logL(s,t)= \log(L_{same}(s,t)/ L_{different}(s,t))$ shows how much more likely the data is given models from the same condition versus under models from

the other condition. Positive values of this log relative likelihood reflect more difference between conditions and that models of the two conditions are less exchangeable.

Analysis of waiting times and anticipation delays

We estimated the maximal excess waiting times controlling for either pellets consumed or time elapsed. In each trial, the cue light signalled the availability of the current session's pellet type upon completion of an FR3 response requirement. With decreasing motivation to work and to consume more pellets, the time from cue light onset to pellet delivery – the waiting time – increases, which in turn leads to decreasing food consumption rates. We aimed to derive a conservative estimate of a maximal excess waiting time in the $b_{now}v_{S2}$ future palatability condition compared to the $b_{now}b_{S2}$ control condition for each animal. Since previously we saw that the difference between the two conditions increases across diet-aware weekdays, we used identical days of the week for the calculation (comparing e.g. the Tuesday of the $b_{now}v_{S2}$ week to the Tuesday of the $b_{now}v_{S2}$ week, etc.). We also established that food consumption and the future palatability effect strongly depend on session time, so we aimed to control for session time. In addition, we inferred that the latter time dependence is probably related to satiation, that is related to the pellets consumed up to a given time point, so we derived another estimate of excess waiting times controlling for pellets consumed (approximated by trial number).

To derive the estimated excess waiting time controlling for session time, we did the following. For each trial in the $b_{now}v_{S2}$ condition, we collected the overlapping trials from the corresponding $b_{now}b_{S2}$ control session on the same day of the week and chose the *longest* waiting time as the control waiting time for the current trial. For each $b_{now}v_{S2}$ trial waiting time, we subtracted this control waiting time to yield a differential waiting time. For each subject, the excess waiting time was derived by finding the maximal value among these trial-wise differential waiting times.

To estimate excess waiting times controlling for trial number, the same procedure was used, but the control trial for each $b_{now}v_{S2}$ trial was the trial with the same trial number on the corresponding $b_{now}b_{S2}$ control session on the same day of the week.

We present a literature overview of delay of gratification in three traditional task types in rodent, avian and primate species. Literature search was performed using Google Scholar with keywords 'delay of gratification', 'delayed gratification', 'self-control', 'intertemporal choice', 'accumulation task', 'exchange task'. Our aim was to describe how anticipation metrics differ between species and to reveal gaps in the literature regarding certain species, such as the rhesus macaque. The data from the review is presented in Figure 6, and the references to the studies included in the overview are listed in the Note S1. From each paper, we extracted the maximum tolerated length of delay (by any individual) and whether immediate and future rewards differed in value quantitatively, qualitatively, or potentially along both dimensions (value type). We added two rodent studies using the negative anticipatory contrast (NAC) paradigm that focused on the length of the anticipation delay. In the case of the NAC paradigm, the length of the maximum delay includes the duration of the first session. We can distinguish two types of temporal parameters: anticipation delay (delay between the change in behaviour and the anticipated event that caused it) and waiting time (the time of response inhibition to obtain a higher-valued reward). In our study, both temporal parameters can be measured separately, in contrast to the delay of gratification tasks (anticipation delay = waiting time). The NAC paradigm could potentially also measure these parameters separately, but per-trial waiting times were not reported in the reviewed papers.