Cross-species comparison of human and rodent primary reward consumption under budget constraints

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Abstract

We live in a world of limited resources. Optimal use of resources is therefore of great importance for survival. Previous studies have shown that rodents optimize their allocation of a limited number of operant responses (akin to a finite budget) to trade for food rewards. Here, we propose a novel human cost-benefit decision paradigm translated from an economic choice task initially developed for rodents, to examine human consumption of primary rewards in a budget-constrained consumption scenario. In the first study, heterosexual male participants made effortful presses to obtain the opportunity to watch erotic pictures (task 1: picture task) or drink milk rewards (task 2: milk task) with a limited budget (i.e. finite total amount of presses). Participants adapted their choice allocation when the price (i.e. number of presses required to produce a reward) and the budget changed. We compared our participants' choice pattern to that of rodent consumers performing a matched economic decision task. Our cross-species comparison suggests that humans responded to price and budget changes in a similar way as rat consumers when purchasing milk rewards. However, this was not the case when purchasing the opportunity to watch picture rewards: compared to the milk task and to the rodent task, participants made more internally inconsistent choices in the picture task that failed to comply to the requirements of rational choice theory, despite otherwise identical task structure. We found non-linear changes in arousal state as a function of choice selection of rewards that might potentially underlie the increased choice inconsistency in the picture task. In two control experiments, we replicated our main findings. Our study shows that humans and rodents comply surprisingly well to the predictions of rational choice theory, but that deviations from the rational ideal can be elicited depending on the reward type.

Key Words

primary rewards, effort, budget, cost-benefit, cross-species, behavioral economics, rationality, choice consistency

Introduction

We live in a competitive world: resources are limited, and the clock is ticking. The principle of efficient cost allocation not only matters for species' survival and successful Darwinian fitness maximization, it also lies at the heart of economic choice theory where an optimal decision-making strategy is crucial to maximize utility. Previous research in psychology and neuroscience focused on simple cost-benefit trade-offs, whereas in economic theory as well as in the real world, people's demand for rewards is not only influenced by their costs, but it is also constrained by the available resources at their disposal (i.e. individual income or budget). Existing literature in microeconomics has extensively discussed how limited resources affect consumers' purchasing decisions (Morewedge et al., 2007; Du and Kamakura, 2008; Homburg et al., 2010; Bronner and de Hoog, 2016). Notably, animal experiments, inspired by economic demand theory, have revealed that rodents (Kagel et al., 1981; Kagel et al., 1995; van Wingerden et al., 2015; Hu et al., 2021) and monkeys (Chen et al., 2006) allocate resources adaptively and optimally in response to changes in price and budget constraint. For example, rat consumers have been shown to reduce their demand for a commodity if its price increases, but the reduction in demand, e.g., the demand elasticity, was less pronounced if their income (i.e. budget; here: total number of operant responses in a fixed-ratio schedule) was simultaneously increased as well (reminiscent of the effect of inflation-adjusted income on spending behavior) (Kagel et al., 1995; van Wingerden et al., 2015; Hu et al., 2021). Those findings showed that demand theory does not only apply to human consumers, but it is suitable to describe and predict non-human animal economic choice behavior, too. This suggests the non-trivial possibility that animals have the necessary cognitive capability to process and integrate multi-level information (e.g. prices, reward values, budget constraints) to guide an optimal use of limited resources. The fact that economic demand theory is successful in describing both human and non-human economic choice behavior demonstrates its translational face validity, but it by no means implies that humans and animals use the *same* cognitive decision processes to solve economic choice problems. What is needed for a sound cross-species comparison is a paradigm that keeps the core experimental features constant across species. Establishing such approach is not only essential for understanding complex decision making from an evolutionary perspective, but

also beneficial for complementing and advancing mechanistic neurobiological models of economic choice (Kalenscher and van Wingerden, 2011; Keysers and Gazzola, 2017; Addessi et al., 2020; Barron et al., 2020; Garcia et al., 2021).

To this end, we developed a novel human budget-constrained consumption paradigm that shared the most important characteristics of our rat task (van Wingerden et al., 2015; Hu et al., 2021). In this task, participants made budget-constrained cost-benefit decisions to obtain access to limited amounts of rewards. To minimize procedural differences between the rat and human versions, we controlled two critical parameters: (i) price (i.e., effort requirement) and (ii) commodity (i.e., primary reinforcers). In the rodent task, animals were trained to lever-press (Kagel et al., 1981) or nose-poke (van Wingerden et al., 2015; Hu et al., 2021) to obtain milk rewards with variable prices (i.e. the required number of operants to obtain a fixed unit of reward) and variable budgets (i.e., the total amount of operants available in an experimental session to obtain rewards). In our human version, participants had to engage in a variable number of effortful presses to obtain rewards. Importantly, while the standard microeconomic literature typically operates with monetary costs and secondary reinforcers, our rat version used milk rewards, i.e., primary reinforcers. To parallel the nature of the incentives across tasks and species, we opted for primary reinforcers in our human task as well. More specifically, inspired by previous work on economic choices with primary reinforcers (McClure et al., 2007; Croxson et al., 2009; Prevost et al., 2010; Crockett et al., 2013; Klein-Flugge et al., 2015), we used milk rewards and the opportunity to watch erotic pictures in separate variants of our task. The use of different incentive types allowed us to explore whether and how the kind of commodity matters for human economic decision making (Wilson and Daly, 2004; Ariely and Loewenstein, 2006; Sescousse et al., 2013; De Ridder et al., 2014; Li and Zhang, 2014; Ma and Hu, 2015; Jahedi et al., 2017; Girard et al., 2019; Archambault et al., 2020; Otterbring and Sela, 2020). By unifying the effort and reward format as well as utilizing a similar experimental structure as in the rat task, we aimed to conduct reliable cross-species comparisons, and to evaluate the commonalities and differences in rat versus human economic decision-making.

We first present a replication of our previous findings (van Wingerden et al., 2015; Hu et al., 2021) on the budget-dependent effort allocation and choice adaptation in rodents (Rat Experiment). Then, we illustrate the key features of the human budget task (Study 1 of

Human Experiment) and compare our participants' choice behavior with that of rat consumers. This comparison revealed that participants responded to price and budget changes in a similar way to rats, but only when purchasing milk rewards, not when purchasing the opportunity to watch picture rewards. We further set out to explore the underlying mechanism and found a state-choice-rationality interaction that might drive the behavioral differences when humans traded effort budget for picture and milk rewards. Finally, to validate the results of Study 1, we included two modified versions of the human budget task in which participants obtained twice the amount of milk for each tradeoff in the milk task (Study 2) and received their selected picture reward in a trial-by-trial manner (Study 3) to investigate the effect of milk reward satiation and timing of picture reward consumption on individual behaviors.

Results

In the Rat Experiment (Figure 1A), two batches (batch 1: n = 7, batch 2: n = 10) of rats were trained to choose between chocolate and vanilla milk rewards. They traded instrumental effort (henceforth referred to as the price of a reward, i.e. the number of nose pokes, NPs, necessary to obtain a reward) for rewards while their budget (the total number of NPs available per session that could be distributed between two rewards) was limited. We manipulated the prices of rewards as well as the budget in separate task conditions (uncompensated and compensated budget conditions, see below), and compared the rats' price- and budget-dependent choices to their choices in baseline sessions where the price of either reward was fixed at 2 NPs and the budget was fixed at 80 NPs. In the uncompensated budget condition, the price of chocolate was increased to 4 NPs, relative to baseline, and the price of vanilla was decreased to 1 NP, and we maintained the original budget of 80 NPs as in the baseline condition. The chocolate and vanilla prices in the compensated budget condition were identical to the prices in the uncompensated condition, but we extended the budget to compensate the price changes so that rats could, in theory, obtain the bundle of rewards they obtained at baseline. For example, assume that a rat spends its 80 nose pokes at baseline to purchase 25 units of chocolate and 15 units of vanilla. To keep purchasing this choice bundle after changing the price of chocolate to 4 NPs, and the price of vanilla to 1 NP, the budget would have to be increased to 115 NPs in the compensated budget condition (25 x 4 + 15 x 1 = 115) to compensate for the price changes (see methods for further task details). Animals went through five conditions following an A-B-A-B'-A block design, so that each price-budget condition was preceded and followed by a baseline condition. For each experimental condition, rats were trained in five continuous daily sessions to gradually learn the price and budget. We took the averaged choice data from the last two sessions of each condition assuming that the rats' choice patterns reached a stable state (van Wingerden et al., 2015; Hu et al., 2021).

In the human Study 1 (Figure 1B), heterosexual male participants (n = 60, mean age = 24, SD = 3) were recruited. They were asked to do two tasks, the milk task and the picture task. They came on two separate days, with a minimum three-day interval between tasks. In both tasks, participants were instructed to trade instrumental effort (here: the number of finger

presses on a pedal, PPs; again referred to as the price of a reward) to obtain two types of rewards: milk rewards in the milk task (the same milk used in the rat experiments: chocolate vs. vanilla flavors) or picture rewards in the picture task (the opportunity to watch pictures of faces, “face” and mildly erotic photos with bikini/underwear motives, “body”; the pictures were pre-rated by the participants in a preceding online study, see below). Note that in the milk task, participants obtained either chocolate-flavored or vanilla-flavored milks while in the picture task, they viewed different pictures containing one of the two attractive elements (“face” or “body”) for each selection. Participants went through five experimental conditions with the uncompensated or compensated budget condition sitting in-between each baseline condition, the same A-B-A-B’-A block design as in the rat experiment. In a baseline condition, both milk/picture commodities were equally priced (i.e. identical effort requirement) and participants had a fixed budget of 80 PPs. We used the reward preference revealed at the preceding baseline (i.e. choice proportion of reward selection) to infer which type of reward commodity was preferred and which type was non-preferred in the following budget condition. Subsequently, we increased the price of the preferred reward to 8 PPs and decreased the price of the non-preferred reward to 2 PPs. Importantly, we also manipulated the budget for each budget condition based on the same policy of the rat experiments (see above and methods for details).

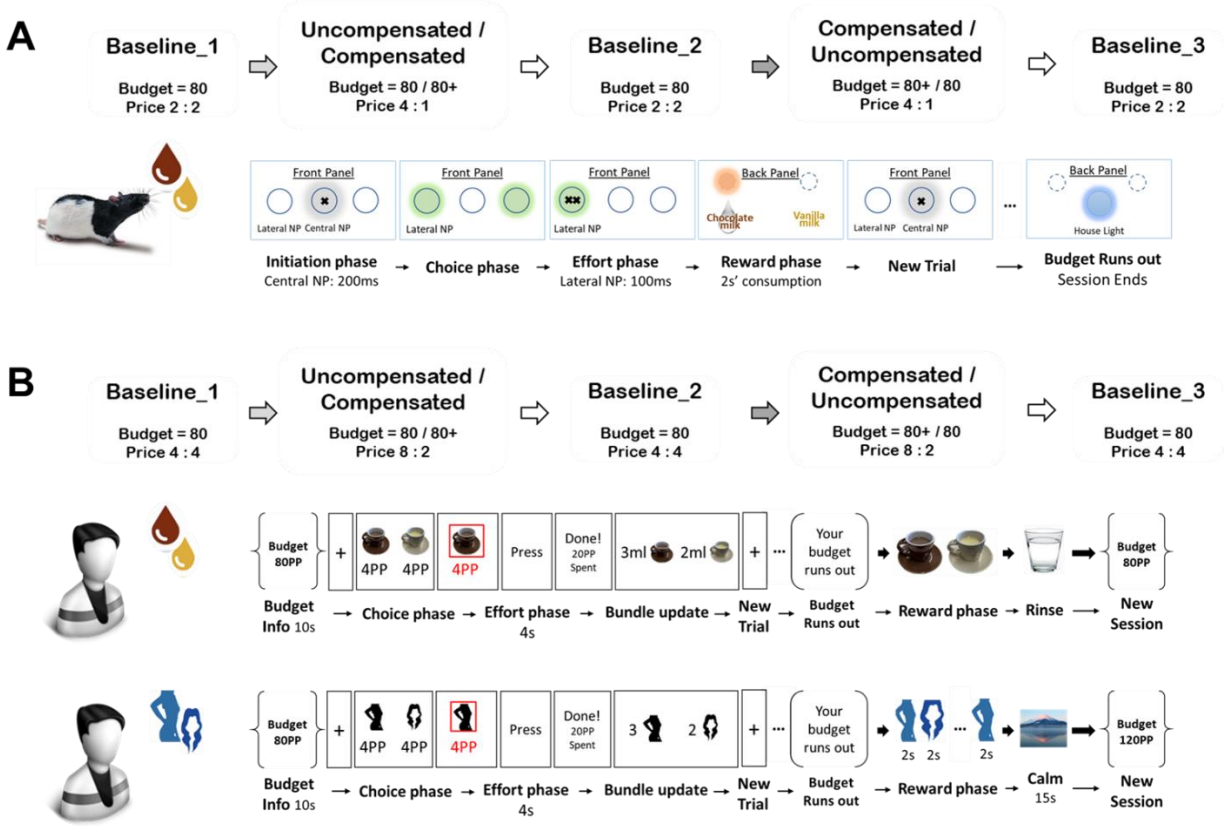

Fig.1 Schematic representation of Rat Experiment (A) and the milk and picture task of Human Study 1 (B). *(A) Rats initiated a trial by making a single nose poke (NP) to the activated central hole (activation indicated by a NP hole light; here: grey color), followed by the activation of both lateral NP holes (green color). Rats were required to meet a condition- and choice-specific fixed ratio requirement, here indicated by the number of crosses, in one of the two lateral NP holes to obtain chocolate or vanilla rewards, delivered at the back panel. Daily session was terminated when the budget was used up, indicated by the illumination of the house light (blue color). The flow chart illustrates the ratio requirement: at baseline, the price for chocolate and vanilla was fixed at two NPs and the budget the rats could spend to 'purchase' chocolate or vanilla was fixed at 80 NPs. In the uncompensated budget condition, the price of preferred milk (typically, chocolate) was increased to 4 NPs, and the price of non-preferred milk (typically vanilla) was decreased to 1 NP, the budget was kept at 80 NPs. In the compensated budget condition, the price change of the rewards was identical to the uncompensated budget condition, but the budget was adjusted following the Slutsky equation (see methods) to compensate the price changes and allow consumption of the baseline bundle of chocolate and vanilla. (B) Humans participated in two similar tasks in which they made pedal presses (PP) with fingers to obtain milk rewards (chocolate vs. vanilla) or the opportunity to view picture rewards (pre-rated pictures of faces, "face" vs. mildly erotic photos with bikini/underwear motives, "body"). The price and budget manipulations were identical to the rat experiment. Both rewards were delivered and consumed after each session ended. In the milk task, milk rewards were served in two milk cups with corresponding colors (chocolate and vanilla). Participants rinsed mouth with a glass of*

water after milk consumption and then proceeded to the next session (e.g. uncompensated budget condition with the same baseline budget, in this given example; see below for details on the session structure). In the picture task, pictures rewards were randomly selected from two categories ("body" and "face") and presented, each for 2 seconds, in the same sequential order as participants made their selections during the budget expenditure. Afterwards, a photo of landscape was shown for 15 seconds as a between-session cue, and the next session started (e.g. compensated budget condition with an extended budget, in this given example). Participants went through five experimental conditions per testing day, one session per condition. They were instructed about the budget size once before each session. Individual reward preference revealed at the preceding baseline was used to infer which commodity was preferred and which one was non-preferred to determine their subsequent prices in each budget condition. The A-B-A-B'-A block design, price ratios and budget manipulation were consistent between the rat and human paradigms to allow direct cross-species comparison on consumption behaviors. The order of the two price/budget conditions ("Compensated" and "Uncompensated") was pseudorandomized across participants. The order of milk and picture tasks was counterbalanced among participants.

Cross-species comparison of the budget effect on reward elasticities

Participants showed a rigid preference when purchasing preferred picture rewards

First, we checked whether manipulating budget and price influenced budget and choice allocations in rats and human participants (Figure 2A-C). A 2 (batch) x 5 (condition) mixed ANOVA on the rats' choices of preferred rewards (which was, typically, chocolate) revealed no significant interaction between the animal batch and condition ($F_{4, 75} = 0.594$, $p = 0.614$, partial $\eta^2 = 0.038$), therefore, we combined the two batches together for further analysis. Consistent with our previous experiments (van Wingerden et al., 2015; Hu et al., 2021), rats could learn the changes of price and budget constraints and significantly adjusted their reward selections to the price changes (all $p < 0.001$ for uncompensated vs. compensated and [uncompensated/compensated] vs. baselines, paired t-test) while their reward preferences remained stable across three baseline conditions (all $p > 0.103$, paired t-test, Figure 2A). For the human Study 1 (Figure 2B-C), we ran a 2 (task: picture vs. milk) x 5 (condition) ANOVA on the choices of preferred reward. We found a main effect of task ($F_{1, 59} = 21.111$, $p < 0.001$, partial $\eta^2 = 0.077$) and condition ($F_{4, 236} = 159.306$, $p < 0.001$, partial $\eta^2 = 0.415$) on choices, as well as a significant interaction of *task x condition* ($F_{4, 236} = 8.618$, $p < 0.001$, partial $\eta^2 = 0.033$). Human participants significantly adjusted their selection of preferred reward to the price and budget change in both tasks (all $p <= 0.002$ for uncompensated vs. compensated and [uncompensated/compensated] vs. baselines, paired

t-tests). They also exhibited a higher baseline selection of preferred reward in the milk task than the picture task (all $p < 0.001$ for the three baselines, paired t-test). Their selection of preferred reward was also higher in the compensated budget condition of the milk task than the picture task ($t = 2.05$, $p = 0.045$, Cohen's $d = 0.265$, 95% CI [0.006, 0.521], paired t-test), but did not differ in the uncompensated budget condition between the two tasks ($t = -0.821$, $p = 0.415$, paired t-test, Cohen's $d = -0.106$, 95% CI [-0.359, 0.148], paired t-test). Together, these revealed a consistent price effect on demands across species and reward tasks.

Interestingly, given the revealed reduced demands for priced commodities in the picture task, the proportion of budget that participants spent on purchasing priced preferred rewards was much higher than the preceding baseline in both budget conditions (uncompensated vs. baseline: $t = 2.977$, $p = 0.004$, Cohen's $d = 0.384$, 95% CI [0.121, 0.645]; compensated vs. baseline: $t = 3.707$, $p < 0.001$, Cohen's $d = 0.479$, 95% CI [0.209, 0.744]; paired t-tests, Figure 2C). In another word, it suggested that participants' genuine preference for preferred rewards remained intact after the price increase in the picture task. Such significant shift in the budget allocation was not present in the rat experiment (uncompensated vs. baseline: $t = -1.671$, $p = 0.114$, Cohen's $d = -0.405$, 95% CI [-0.895, 0.096]; compensated vs. baseline: $t = 1.054$, $p = 0.307$, Cohen's $d = 0.256$, 95% CI [-0.232, 0.735]; pairwise t-tests) or the human version of milk task (uncompensated vs. baseline: $t = -1.585$, $p = 0.118$, Cohen's $d = -0.205$, 95% CI [-0.459, 0.052]; compensated vs. baseline: $t = -1.51$, $p = 0.136$, Cohen's $d = -0.195$, 95% CI [-0.45, 0.061]; pairwise t-tests, Figure 2A-B). These indicated a rigid preference for picture rewards when spending limited budget to purchase priced commodities.

Rat and human consumers exhibit similar reward elasticity patterns in the milk task

Next, we aimed to capture the degree by which individual choices of rewards (Figure 2-figure supplement 1) changed in response to price and budget changes. To this end, we calculated demand elasticity (ε) as an index of price sensitivity, using linear regression on the log-transformed number-of-choices/price-ratio pairs as given by the equation ((Kagel et al., 1981), see also (van Wingerden et al., 2015; Hu et al., 2021)):

$$\log(q_i) = \log(\alpha) + \varepsilon \times log\left(\frac{p_i}{p_j}\right) \quad (1)$$

236 Where q_i indicates the quantity of reward (i) chosen, p_i/p_j indicates the price ratio for
237 reward (i) over reward (j) per price/budget regime and α is a constant. ε denotes the
238 estimated elasticity in demand. We estimated ε individually for preferred and non-preferred
239 reward commodity for the two budget conditions, separately. The negativity/positivity of ε
240 represents the direction of change in demand in response to the price and/or budget changes.
241 The absolute value of ε measures the extent of change in demand compared to the baseline
242 levels. For example, a more negative ε parameter indicates a stronger reduction in demand
243 for rewards after a price increase, or a larger increase in the demand for rewards after a price
244 decrease. A positive ε indicates an increased demand for a more expensive reward, or a
245 reduced demand for a cheaper reward. Economic demand theory predicts a general negative
246 ε if prices go up, indicative of a reduction in demand, and vice versa if prices drop.
247 We, next, determined if demand elasticity in rat and human consumers depended on reward
248 prices and budgets. For the Rat Experiment, we conducted a 2 (budget: compensated vs
249 uncompensated) x 2 (preference: preferred vs non-preferred) ANOVA on demand elasticity
250 (Figure 2D). We found a main effect of preference ($F_{1,16} = 25.381$, $p < 0.001$, partial $\eta^2 = 0.613$)
251 and a significant *budget x preference* interaction ($F_{1,16} = 5.619$, $p = 0.031$, partial $\eta^2 = 0.26$).
252 In the uncompensated budget condition where the budget remained the same as in the
253 preceding baseline, most of the rat consumers reduced their selection of preferred, but now
254 more expensive milk rewards (i.e. price increase from 2 NPs to 4 NPs), and increased their
255 selection of the non-preferred, now cheaper non-preferred rewards (priced dropped from 2
256 NPs to 1NP); the comparison of elasticities of the two rewards revealed no significant
257 difference ($t = 1.744$, $p = 0.1$, Cohen's $d = 0.423$, 95% CI [-0.08, 0.914]), suggesting that
258 demand for the preferred reward decreased in response to the price increase as much as
259 demand for the non-preferred reward increased in response to the price drop. In the
260 compensated budget condition where rats had a larger budget of NPs to spend, they selected
261 more of the preferred, expensive reward compared to the uncompensated budget condition,
262 thus, exhibiting a less negative demand elasticity of preferred reward in the compensated
263 compared to the uncompensated condition ($t = -8.935$, $p < 0.001$, Cohen's $d = -2.167$, 95% CI
264 [-3.04, 1.274]). Such behavioral shifts in response to the budget extension also enlarged the
265 difference between the two reward elasticities in the compensated budget condition ($t = 6.86$,

$p < 0.001$, Cohen's d = 1.664, 95% CI [0.91, 2.396]), but not in the uncompensated budget condition (t = -0.205, p = 0.84, Cohen's d = -0.05, 95% CI [-0.08, 0.914]). Thus, we replicated our previous findings on the budget-dependent choice adaptation in rats (van Wingerden et al., 2015; Hu et al., 2021).

To test whether human participants exhibited similar budget effect on demand elasticity, we performed a three-way ANOVA with budget condition (uncompensated, compensated), task (milk, picture) and preference (preferred commodity, non-preferred commodity) on reward elasticity. We found a main effect of reward type ($F_{1,59} = 11.240$, p = 0.001, partial $\eta^2 = 0.16$), suggesting that participants' demand for milk rewards was much more elastic to the price changes than their demand for picture rewards. We also found a significant *budget x preference* interaction ($F_{1,59} = 62.551$, $p < 0.001$, partial $\eta^2 = 0.515$) and a significant interaction of *preference x task* on demand elasticity ($F_{1,59} = 14.668$, $p < 0.001$, partial $\eta^2 = 0.199$). The three-way interaction of *budget x preference x task* was not significant ($F_{1,59} = 1.557$, p = 0.217, partial $\eta^2 = 0.026$). Therefore, we firstly performed separate 2 (budget: compensated vs. uncompensated) x 2 (preference: preferred vs. non-preferred) ANOVAs on reward elasticity for the milk and picture tasks.

In the milk task (Figure 2E), we found a main effect of preference ($F_{1,59} = 5.892$, p = 0.018, eta square = 0.091) and a significant interaction of *budget x preference* ($F_{1,59} = 31.786$, $p < 0.001$, partial $\eta^2 = 0.35$) on reward elasticity. Same as the rat consumers, participants adapted their choice of milk rewards when having a constrained budget (i.e. uncompensated budget condition) in which their elasticity of preferred milk reward did not differ from non-preferred milk reward (t = -1.668, p = 0.101, Cohen's d = -0.215, 95% CI [-0.47, 0.042]). Similar to the rat consumers, such comparison was significant in the compensated budget condition that the elasticity of non-preferred milk was much more negative than the elasticity of preferred milk (t = -5.325, $p < 0.001$, Cohen's d = -0.687, 95% CI [-0.967, -0.403]). Our participants' elasticity of preferred milk in the compensated budget condition was also much less negative than that of the uncompensated budget condition (t = 7.152, $p < 0.001$, Cohen's d = 0.923, 95% CI [0.618, 1.223]). In addition, their demand for non-preferred reward in the compensated budget condition was more elastic than in the uncompensated condition, too (t = -2.316, p = 0.024, Cohen's d = -0.299, 95% CI [-0.556, -0.039]). Put together, these findings indicated that participants adjusted their demand for milk rewards in

response to the change in the prices (i.e. effort requirement) as well as the size of spendable budget in each session.

Participants' rigid preferences for picture rewards leads to a positive elasticity of demand

The elasticity results in the human milk task suggest a budget-dependent choice behavior when trading effort for milk rewards, just like we observed in the rat task. Both humans and rats tended to reduce their demands for expensive and preferred milks when the budget cap was tight, and relaxed their restricted selection of priced milk rewards when a larger budget was available. In the uncompensated budget condition where the individual budget remained fixed (i.e. 80), the total amount of commodities that individuals can afford (i.e. purchasing power) decreases because of the changes in reward prices. Hence, a price-sensitive consumer should select more of the cheaper rewards to maintain an adequate amount of reward intake, which would result in an increased negative elasticity of demand for the two reward commodities, a phenomenon observed in our rat consumers (van Wingerden et al., 2015; Hu et al., 2021), and in the human milk task. However, this shift to the cheaper option was not found in the picture task.

To examine the effect of price and budget on reward elasticity in the picture task more closely, we ran the same analysis of the milk task and found a main effect of preference ($F_{1,59} = 5.853$, $p = 0.019$, partial $\eta^2 = 0.09$) as well as a significant interaction of *budget x preference* ($F_{1,59} = 61.552$, $p < 0.001$, partial $\eta^2 = 0.511$) on the elasticity of demand for picture rewards (Figure 2F). In line with our observation and in contrast to the rats and humans in the milk task, the elasticity of non-preferred picture reward was much more positive than the elasticity of preferred reward in the uncompensated budget condition ($t = 6.737$, $p < 0.001$, Cohen's d = 0.87, 95% CI [0.569, 1.165]). This suggests that, unlike in the milk task, participants in the picture task *reduced* their selection of non-preferred picture rewards after its price decreased, thus showing a reversed price-effect on demand. Interestingly, we found that this pattern was budget-dependent, as the elasticity of non-preferred reward was much less positive in the compensated budget condition than the uncompensated condition ($t = -3.295$, $p = 0.002$, Cohen's d = - 0.425, 95% CI [-0.688, -0.159]). These findings indicate that the reversed price effect, i.e., the decrease in demand with decreasing prices, was attenuated when having an extended budget to spend. In addition, the elasticity of non-

preferred picture rewards was more negative than the elasticity of preferred rewards in the compensated budget condition ($t = -2.401$, $p = 0.019$, Cohen's $d = -0.31$, 95% CI [-0.568, -0.05]). The elasticities of preferred picture reward significantly differed between the two budget conditions, too ($t = -7.33$, $p < 0.001$, Cohen's $d = -0.946$, 95% CI [-1.249, -0.638]).

Taken together, the choice and elasticity data replicate our previous findings on the price and budget effect on rats' consumption behaviors and further reveal a cross-species similarity in the elasticity pattern of humans and rats who are trading effort for milk rewards with budget constraints. Crucially, the similarity in choice behavior was confined to milk rewards; when trading efforts for picture rewards, participants exhibited a reversed price effect on demand: their demand for the non-preferred pictures *decreased* when their price dropped, and their budget spent on preferred pictures largely increased to maintain an unchanged demand when their price increased.

Additional analysis showing a similar baseline-preference-dependent reward substitution in rats, replicating our previous findings (Hu et al., 2021), and humans in the milk task added further evidence to a cross-species similarity in the adaptive consumption behaviors (Figure 2- figure supplement 1). When consumers experienced a price shock of preferred milk rewards, the pressure of deploying an expensive-to-cheap shift was not equal among individuals, but closely linked to their baseline consumption level. For those who held a higher baseline preference for the preferred milks, they also shifted more heavily from preferred to non-preferred milk reward after the price change. Such behavioral adaptation was present in participants in the picture task when the individual budget was extended to allow the reselection of baseline choice bundle, but not when the spendable resource was scarce (i.e. uncompensated budget condition) where participants showed a larger resistance to the pressure of price increase, thus, led to the positive elasticity of picture rewards.

Though we've found consistent behaviors in rats across batches and experiments, one could argue against the validity of cross-species comparison given the difference in the sample size of human and animal experiment. To examine whether the comparability and discrepancy between humans' and rats' behaviors were driven by a sampling bias, we simulated $n = 1000$ random choice sets given the price regime and budget size of human Study 1 and calculated the demand elasticity of preferred and non-preferred rewards in the two budget conditions (see methods for details of the simulation). We plotted the elasticities of the two reward

358 commodities on a "Elasticity Matrix" for the rats, humans and simulated data (Figure 2-
359 figure supplement 2). The sample size differences between rats and human experiments had
360 little influence on the results in our cross-species comparison. Rather, on the individual level,
361 rat consumers exhibited much less between-subject variability compared to humans in the
362 milk and picture task. This tentatively suggests that rigorous animal models can serve as a
363 benchmark to evaluate humans' economic decision making.
364 To provide additional validations of the results obtained from our novel translated human
365 paradigm, we also present two control experiments (Study 2 and 3) showing the consistency
366 of human consumption strategy of picture and milk rewards (Figure 2- figure supplement 3,
367 see methods for details). Specifically, we found that increasing the value of single units of
368 milk, as well as the total amount of milk intake did not alter the individuals' consumption
369 pattern of milk rewards. Also, the timing and manner of reward consumption did not affect
370 participants' choice pattern of picture rewards. Put together, we concluded that our findings
371 of the distinct strategy of budget and choice allocation regarding the two primary rewards
372 to be a robust and replicable behavioral phenomenon on humans.

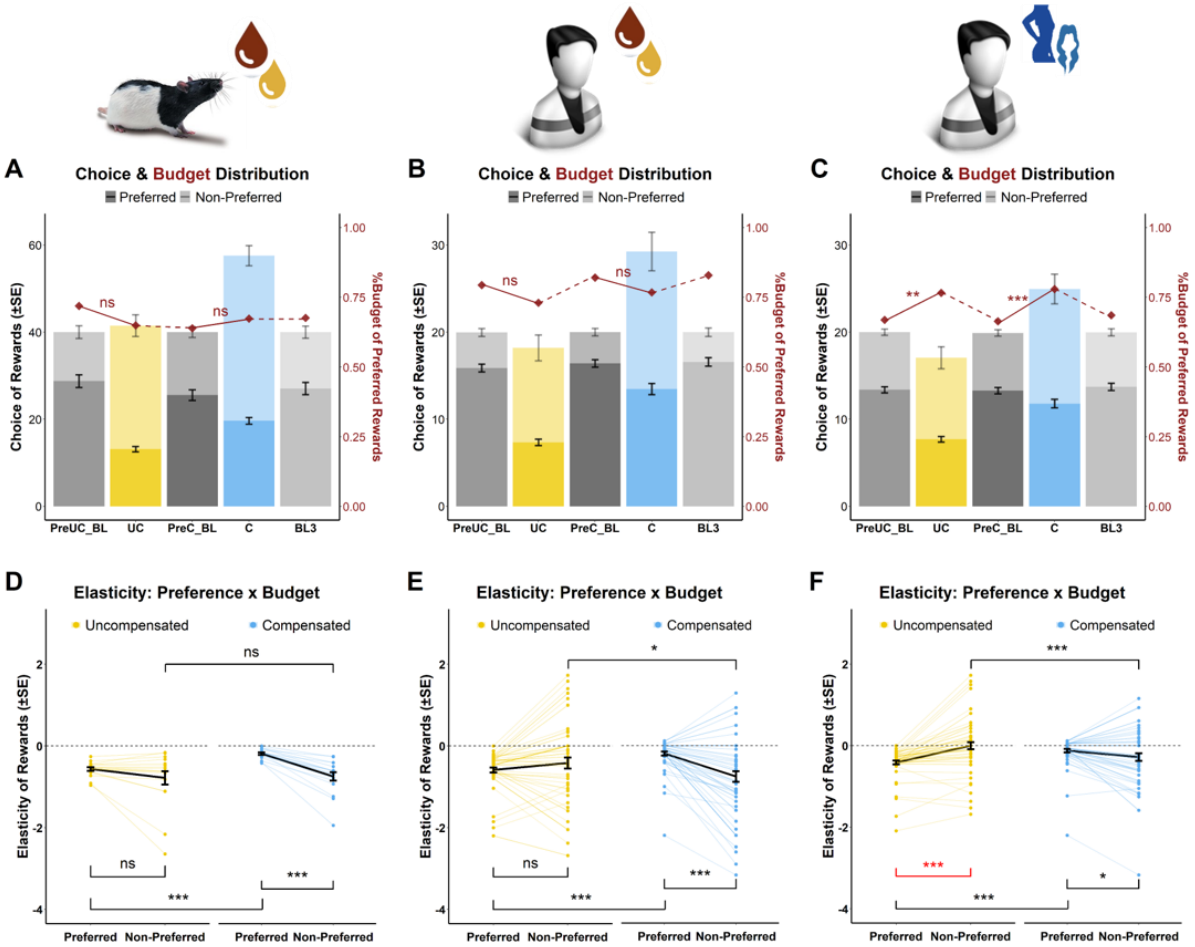

Figure 2 Participants behaved in a similar manner to rat consumers in the milk task, but not in the picture task. *(A-C) Stacked bar plots of choice distribution on preferred and non-preferred rewards (left y-axis) and averaged proportion of budget spent on preferred rewards (right y-axis) across five experimental conditions for rat consumers (A, n= 17) and participants (n = 60) in the milk (B) and picture (C) task. Participants in the picture task significantly increased their budget spent on expensive commodities in both budget conditions, showing a rigid preference for preferred picture rewards. UC: uncompensated budget condition; C: compensated budget condition; PreUC_BL: preceding baseline of uncompensated budget condition; PreC_BL: preceding baseline of compensated budget condition; BL3: the third baseline condition. (D-E) Demand elasticity of preferred and non-preferred rewards in the uncompensated and compensated budget of rat consumers (D) and participants in the milk (E) and picture (F) task. ***: p < 0.001; **: p < 0.01; *: p < 0.05; ns: not significant.*

Figure 2- figure supplement 1 *Baseline-preference-dependent reward substitution in rats and the milk task but not in the picture task.*

Figure 2- figure supplement 2 *Elasticity Matrix: distribution of individual reward substitutions of rats, humans, and simulated data.*

Figure 2- figure supplement 3 *Two control experiment on the effect of reward satiation (Study 2, n = 16) and timing of reward delivery (Study 3, n = 25) on consumption behavior of milk and picture rewards.*

Within-subject comparisons between the milk and picture task

Our comparative approach revealed a similar pattern of demand elasticities and behavioral adaptations in humans in the milk task. This suggests that both species might use a similar decision strategy in the tasks. Interestingly, in the picture task, humans tended to take a different strategy that prioritized their demand for expensive preferred picture rewards, resulting in a reversed price effect on demand. More questions were left open: what could explain the difference in choice behavior between the milk and the picture rewards in humans, despite their similar experimental structures? Did the decision mechanism by which effort and reward was traded-off differ between the two tasks? One probable reason for the difference in choice behavior between tasks is the nature of the primary rewards that are likely linked to different visceral states (i.e. hunger and sexual appetite). One theory (Loewenstein, 2000) posits that utility maximization can be formalized as a function of visceral state (e.g., hunger) and consumption activity (e.g. milk drinking) that would modulate individuals' marginal utility of goods and drive a consequent change in the rate of reward substitution. It also predicts that an instant change in consumption would further mitigate or elevate individual states (e.g., reduce hunger), thus, altering the marginal utility of future rewards. Applied to our task, there might exist a distinct choice-state interaction that accounts for the observed difference in the choice allocation and adaptation in the milk and picture task. Thus, we made the first prediction for our analysis: participants' visceral states changed after the consumption of picture and milk rewards in a reward-dependent way. Importantly, the choice sets generated by self-paced effort-reward trade-offs across sessions allowed us to make estimations on whether participants were making rational choices by analyzing their compliance to consistency criteria in revealed preference theory (Generalized Axiom of Revealed Preference; GARP (Afriat, 1972, 1973; Varian, 1982)). In brief, GARP requires that participants make internally consistent choices. For example, choice chains should be transitive (if option A is chosen over option B, and B is chosen over C, A should also be chosen over C; for details on GARP and consistency, refer to (Glimcher, 2011; Nitsch and Kalenscher, 2020)). For those participants who failed to maximize their utility of consumption, we should observe some degree of GARP violations. If participants' behavior was guided by the choice-state interaction, as the theory predicted (Loewenstein,

2000), the severity of GARP violation should be correlated with individuals' choice pattern in the tasks. Thus, we made our second prediction: participants exhibited a distinct degree of GARP violation in the picture and milk task, which was related to their choice selection of rewards in the two tasks. Furthermore, if there existed a progressive modulation on the utility maximization of future reward consumptions, as the theory predicted (Loewenstein, 2000), the block design of our budget task would also allow us to explore a session-based development of rationality score in related to individual choices. This constitutes the third prediction of our analysis.

Non-linear choice-state correlation in the picture task

To determine the predicted co-dependency of visceral states and choices in the milk and the picture tasks, we collected the participants' subjective rating on their state of general sexual excitement, "how much they like to see" the picture rewards before and after the picture task, and subjective rating on thirst and hunger before and after the milk task. We then ran a Wilcoxon signed-rank test on paired scores (Pre/post, Figure 4A). Participants reported a reduced hunger ($t = -2.565$, $p = 0.013$, Cohen's $d = -0.337$, 95% CI [-0.6, 0.071], pairwise t-tests) and thirst ($t = -6.118$, $p < 0.001$, Cohen's $d = -0.797$, 95% CI [-1.087, 0.501], pairwise t-tests) after participating in the milk task, but an increase in sexual excitement ($t = 6.765$, $p < 0.001$, Cohen's $d = 0.873$, 95% CI [0.573, 1.169], pairwise t-tests) and increased degree of "like to see" ($t = 3.153$, $p = 0.003$, Cohen's $d = 0.407$, 95% CI [0.142, 0.669], pairwise t-tests) after the picture task. We found no significant choice/elasticity – state correlations in the milk task (all $p > 0.167$, Figure 4C). However, we observed a strong negative correlation between the post-experiment score of sexual excitement and the total unit of reward intake (i.e. bundle size, disregarding reward commodity), i.e., participants with higher arousal viewed less pictures in the task, meaning they chose more often the expensive preferred pictures. Notably, this relationship was better approximated by a hyperbolic (R-squared = 0.291, $p < 0.001$, AIC = 489.19, Figure 4B) than a linear function (R-squared = 0.049, $p = 0.05$, AIC = 505.76), indicating a non-linear or *spillover* development of sexual arousal with the consumption of the picture rewards. In addition, the overall bundle size was linearly correlated with the mean elasticity of preferred rewards (R-squared = 0.879, $p < 0.001$,

Figure 4B), suggesting that a more negative elasticity yielded a higher amount of reward intake.

Put together, these findings confirm our first prediction on the state change in the two tasks but reveal a counterintuitive choice-state correlation in the picture task, which can be best depicted by a hyperbolic decay. Specifically, participants who exhibited an elastic demand for expensive pictures and thus, obtained a larger bundle size of rewards, reported a less aroused state after task completion. Those participants who perseverated on selecting the preferred, but costly pictures obtained a smaller number of picture rewards in total and reported higher post-experiment arousal levels. Critically, such correlation was prominent in the participants with a low-to-medium level of arousal state and flattened among highly aroused individuals.

Higher choice consistency in the milk task than the picture task

We counted how many choice bundles, out of the five bundles generated in each session, violated GARP to quantify the severity of economic irrationality in the picture and milk task. To satisfy GARP, individuals must reveal stable preferences in their decisions, as well as act cost efficiently in the pursuit of these (Glimcher, 2011; Nitsch and Kalenscher, 2020). In another word, GARP is satisfied when one participant did not show circularity (e.g. if their choices meet transitivity requirements, see above) in the selected choice sets. If drawing the chosen bundles along the budget lines, one bundle is at least as good as other bundles on the same budget line, and better than bundles that locate underneath its budget line. For example, among the five choice bundles of participant 27 in the picture task (Figure 3E), bundle “BL3” is as good as bundle “preUC_BL” and “preC_BL”, and bundle “C” is better than all other four bundles. Bundle “UC”, underneath the budget line of baseline (the shadow triangle), is worse than the three baseline bundles. However, bundle “BL3” is also not better than bundle “UC” since it locates below the “UC” budget line. Thus, the bundle “UC” and “BL3” constitute two violations of GARP. We found a significant difference in the violation count between the milk and the picture tasks ($p = 0.013$, Wilcoxon signed-rank test, Figure 3D). This indicates that human participants behaved less rationally when consuming picture rewards than milk rewards.

Our previous analysis has demonstrated that an increased arousal state correlated negatively and nonlinearly with the total consumption of picture rewards. To examine whether there existed a link between the consumption of preferred rewards with decision rationality, we ran a Poisson regression on the count of GARP violation against the summed choices of preferred picture or milk rewards. In line with our second prediction, we found a significant positive correlation in the picture task ($z = 3.854$, $p < 0.001$), but not in the milk task ($z = -0.226$, $p = 0.821$). This indicates a choice-rationality correlation in the picture task that a higher violation of choice consistency of GARP was associated with a higher selection of preferred picture rewards.

In addition, we found a strong link between individual elasticity pattern and rationality score in that the difference between the mean elasticity of preferred and non-preferred reward was significantly correlated to the level of choice consistency indexed by the GARP violation count in the picture ($z = -3.489$, $p < 0.001$) and milk ($z = -2.887$, $p = 0.004$) task (Figure 3-figure supplement 1). Briefly speaking, participants who exhibited a more positive elasticity for non-preferred rewards, as compared to their elasticity of preferred rewards, showed a higher level of GARP violations. Such an elasticity-rationality correlation, also existing in Study 3 (Figure 3-figure supplement 2C), verified that our rationality test was not a random result but can truly reveal individual choice patterns.

Early emerged rationality-choice interaction in the picture task, not in the milk task

So far, we tested the first two predictions and found a choice-state and choice-rationality correlation in the picture task, but no indication of significant correlations in the milk task. To explore where there exists a session-wise choice-rationality correlation, we performed a generalized linear model utilizing a Poisson regression on the count of GARP violations against the cumulative choices of preferred rewards, the two tasks (milk vs. picture) and the interaction between the two (Figure 3F). We found a significant interaction between the task and the cumulative choice of preferred rewards on GARP violations that emerged from the beginning of the tasks (Sess-1: $z = -2.898$, $p = 0.004$) and persisted throughout the five progressive sessions (Sess-12: $z = -2.343$, $p = 0.019$; Sess-123: $z = -2.819$, $p = 0.005$; Sess-1234: $z = -2.533$, $p = 0.011$; Sess-12345: $z = -2.254$, $p = 0.019$). Importantly, individuals' selection of preferred rewards in the earliest session was predictive of their count of GARP

violations, and such association remained significant throughout the whole picture task (Sess-1: $z = 3.08$, $p = 0.002$; Sess-12: $z = 4.836$, $p < 0.001$; Sess-123: $z = 3.895$, $p < 0.001$; Sess-1234: $z = 4.427$, $p < 0.001$; Sess-12345, $z = 3.854$, $p < 0.001$). Notably, such prediction was not present in any sessions of the milk task (Sess-1: $z = -1.372$, $p = 0.17$, Sess-12: $z = 0.192$, $p = 0.848$, Sess-123: $z = -0.941$, $p = 0.347$, Sess-1234: $z = -0.003$, $p = 0.998$; Sess-12345, $z = -0.226$, $p = 0.821$).

Note that the individual counts of GARP violations was estimated based on their overall five choice bundles generated through the five experimental sessions of each task. The early-emerged predictive power of preferred reward selections on the choice consistency further supports and adds new evidence to the mechanistic account of irrational behaviors in the picture task. Participants generally expressed a low level of arousal at the beginning of the task (Figure 3A). Their state of arousal was gradually elevated after viewing the collected picture rewards. The elevated state might have probably induced a *projection bias*, a decision bias driven by a focus on the current state, thus, aroused participants failed to adapt their choices to the changing environment (Loewenstein, 1996, 2000; Loewenstein et al., 2003; Kahneman and Thaler, 2006). Such choice-rationality interaction was absent in the milk task across all sessions, suggesting that participants experienced a different or non-significant mechanistic regulation of state and choice on decision rationality when trading effort for the milk rewards.

To conclude, our analysis on human Study 1 provide a mechanistic account of the irrational behaviors in the picture task. We found three pieces of evidence in supporting of a choice-state interaction that drives the irrational behavior during the picture reward consumptions: 1) individuals' post-experimental state of arousal was negatively hyperbolically correlated to their summed collection of picture rewards; 2) a higher selection of preferred rewards was linked to a higher GARP violation; 3) decision rationality can be predicted by the choice of preferred rewards from the earliest session and throughout the whole task.

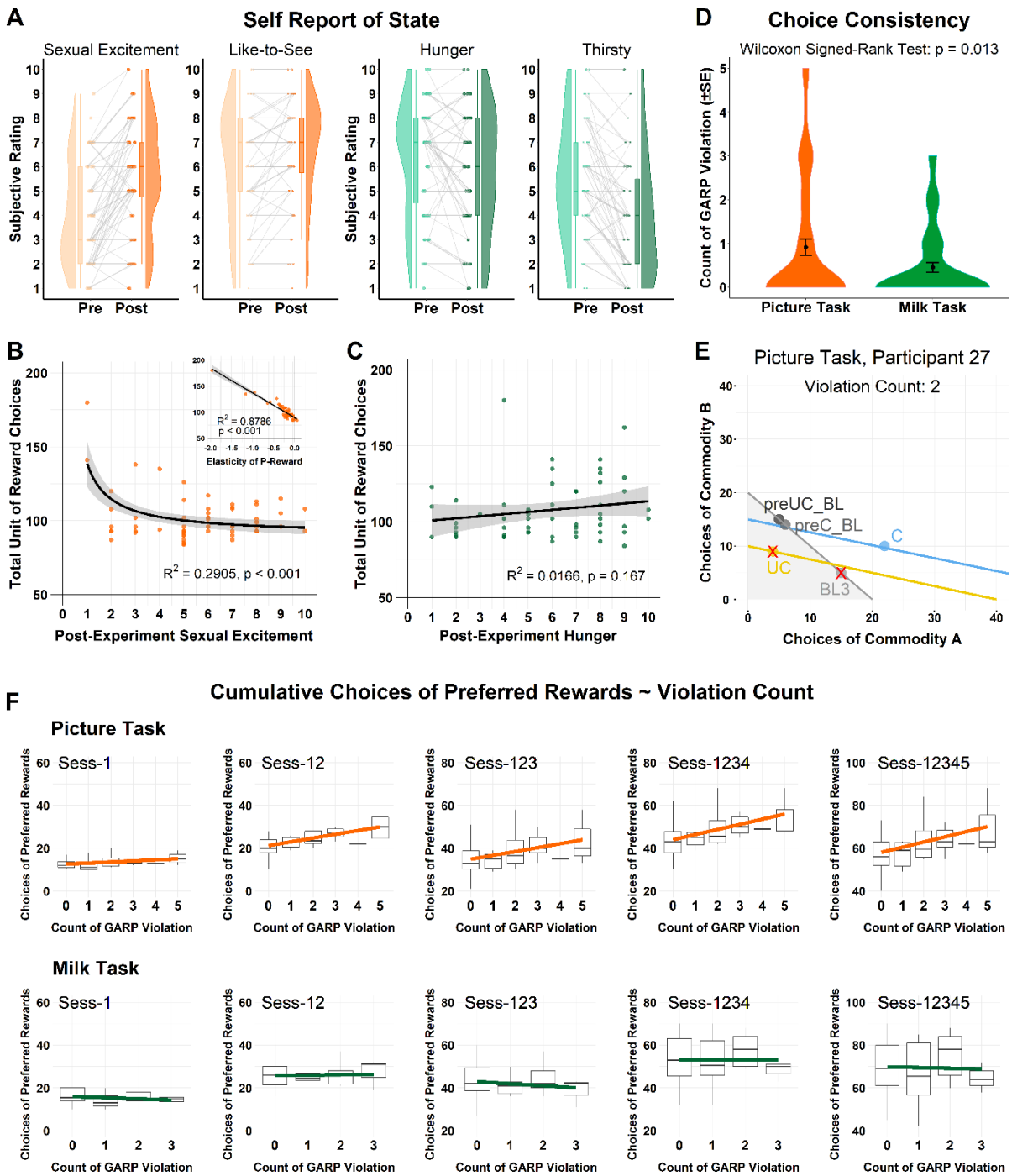

Figure 3 Within-subject comparisons on choice-state-rationality in the picture and milk task of Study 1. *(A) Self-reported scores of sexual excitement, like-to-see, hunger and thirsty before ("Pre") and after ("Post") the experiment. (B) Hyperbolic curve fitting on post-experimental sexual excitement and total amount of reward intake in the picture task. The small figure on the top right plots the linear correlation between elasticity of preferred rewards (P-reward) and total amount of reward intake. (C) Linear regression on post-experimental*

hunger against total amount of reward intake in the milk task. (D) Count of GARP violation, as an index of choice consistency, in the picture and milk task. (E) An example of individual choices generated in the five experimental sessions of the picture task. Red cross indicates the two choice bundles of Participant 27 that violate GARP. (F) Boxplots of the cumulative consumption of preferred rewards against the level of GARP violation across five conditions (i.e. session) in the picture and milk task. preUC_BL: baseline preceding the uncompensated budget condition; preC_BL: baseline preceding the compensated budget condition; BL3: the last baseline condition; UC: uncompensated budget condition; C: compensated budget condition.

Figure 3- figure supplement 1 *(A) Mean elasticity of preferred and non-preferred rewards, plotted against the count of GARP violation in each task. (B) Intra-individual stability in the reward elasticity of picture and milk task.*

550 # Discussion

551 Rodents reveal choice patterns and biases during economic decision making, similar to
552 humans, including regret (Sweis et al., 2018a), sunk-cost sensitivity (Sweis et al., 2018b), risk
553 preference (Constantinople et al., 2019) and inequity aversion (Oberliessen et al., 2016). Our
554 previous studies also showed that rats complied well with the prediction of demand theory
555 in making budget-dependent cost-benefit decisions (van Wingerden et al., 2015; Hu et al.,
556 2021). The central aim of the present study was to develop a parallel human paradigm
557 translated from the rat budget task to investigate humans' budget spending behavior and to
558 conduct reliable cross-species comparisons.

559 In our experiments, both rats and humans made instrumental effort (i.e. nose pokes in rats,
560 and pedal presses in humans) to trade for primary rewards (i.e. milk for rats, milk or erotic
561 pictures for humans). They went through three experimental conditions in which we
562 manipulated effort requirement (i.e. numbers of nose pokes or button presses needed to
563 obtain one unit of reward), and budget (i.e. the total amount of nose pokes or button presses
564 available in a session to spend on rewards). In the baseline conditions, the two reward
565 commodities were equally priced. In-between each baseline was a budget condition (i.e.
566 uncompensated or compensated) where the price of the preferred rewards was doubled,
567 and the price of the non-preferred rewards was halved. In the uncompensated budget
568 condition, the budget was identical to the baseline budget. In the compensated budget
569 condition, the individual budget was increased to compensate for the price change so that
570 animals and humans could afford the same choice bundle chosen and consumed in the
571 preceding baseline condition. The block design, price ratios and budget manipulations were
572 consistent between the rat and human paradigms to allow direct cross-species comparison
573 of consumption behaviors.

574 Previous studies using primary rewards showed a common effort discounting phenomenon
575 in rats and humans (Rudebeck et al., 2006; Prevost et al., 2010; Salamone and Correa, 2018).
576 Here we also observed a price-sensitive choice pattern in both species, reflected by the
577 negative elasticity of preferred rewards, i.e., a drop in demand when the price of a reward
578 increased, and a rise in demand when the price of a reward decreased. Also, our data
579 revealed a consistent budget-dependent effort-reward trade-off across species and reward

type in which the elasticity of preferred rewards was less pronounced in the compensated than the uncompensated budget condition, replicating the budget effect on reward elasticity previously shown in rat consumers (Kagel et al., 1981; van Wingerden et al., 2015; Hu et al., 2021).

In line with our previous finding on the baseline-preference-dependent choice shift after the price/budget change (Hu et al., 2021), we observed a similar adaptive behavior in our rat consumers, as well as in humans in the milk task. This might hint at similarities in the decision strategies employed by both species when utilizing limited budgets to obtain food rewards. Importantly, our human participants' choice pattern in the picture task was different than their choices in the milk task, or the rats' choice in the rodent version of the milk task: participants showed a rigid preference for priced commodity and a reversed price effect on demand: participants *reduced* their selection of the non-preferred rewards when their prices dropped, and their demand for the preferred reward remained insensitive to the rise in price. This decision strategy went along with a higher violation of GARP, suggesting that they made more inconsistent, hence, irrational, choices in the picture task compared to the milk task.

Thus, by developing and running a budget task that was carefully translated from its rodent equivalent, we found a cross-species similarity in choice allocation and strategy adaptation when humans and rats spent limited budget to obtain and consume primary rewards. Crucially, this comparability only holds for the milk tasks, but not for the picture task where participants showed more inconsistent behavior. Thus, the nature of the reward seems to matter for the degree of rationality. There have been concerns regarding a *description-experience gap* when running comparative studies on humans and non-human animals (Hertwig and Erev, 2009; Erev and Roth, 2014; Heilbronner and Hayden, 2016; Lukinova et al., 2019; Monteiro et al., 2020; Garcia et al., 2021). It refers to the discrepancies between choices made in description- versus experience-based paradigms. This methodological gap raises challenges for interpreting shared decision process and/or underlying neural mechanism of similar behavioral phenomenon, for example, risk preference, identified from human and animal experiments using description- or experience-based gambling tasks. Similarly, studies on humans' budget-related purchasing decision making were mostly limited to description-based protocols (Epley et al., 2006; Morewedge et al., 2007; Ulkumen

et al., 2008; Homburg et al., 2010; Stilley et al., 2010; Shah et al., 2015), with a few exceptions in which participants experienced a real-time budget-spending scenario to obtain monetary rewards (Economides et al., 2014; Constantino and Daw, 2015; Seinstra et al., 2018). Our study provides empirical evidence on how the consumption behaviors of humans and rats converge in a decision task involving experienced outcomes, and how the disparities in their choice pattern arise by the types of rewards being consumed.

Our analysis also provides a plausible mechanistic account of the irrationality in the picture task. A severe violation of GARP has been observed in individuals with impaired or less developed cognitive functions (Harbaugh et al., 2001; Camille et al., 2011; Chung et al., 2017) or with a mood disorder (Weinrabe et al., 2020). These findings support the notion that individuals' cognitive limitation or emotional state might contribute to economic irrationality (Kaufman, 1999; Loewenstein, 2000; Pham, 2007; Nitsch and Kalenscher, 2020). Following this line of reasoning, participants indeed reported an increased state of sexual arousal after the picture task and a reduced hunger after the milk consumptions. Importantly, the individual state was found negatively correlated to the total reward selections in the picture task. The decision to view more of the preferred pictures, implying less picture consumptions in total, led to a higher post-experimental state of arousal. In addition, the preference strength for preferred picture rewards predicted decision rationality. Also, the predictive power of cumulative reward selection emerged already in the early sessions and persisted throughout the whole task. These findings are in line with a model (Loewenstein, 1996, 2000) on a mutually regulatory role of elevated state and consumption activity that affects current and future utility maximization of economic behaviors. Unfortunately, not having a direct a direct observation on the development of arousal state, our behavioral analysis cannot conclusively elucidate the causality between state and choice during the reward consumptions. Future studies that measure automatic responses of arousal during the decision process (e.g. pupil dilation) will provide more objective and concrete evidence to address the underlying psychological or neural mechanisms.

Conclusion

We aimed to conduct a sound between-species comparison of economic choice behavior. Our results show that the type of consumed rewards carrying distinct innate values could play a

641 critical role for capturing behavioral parallels in human and non-human animals. We further
642 examined the choice-state correlation that might account for the irrationality in our
643 participants economic choice behaviors. Our translational budget task will allow us to
644 investigate the psychological and neural mechanism of budget-spending behaviors in
645 humans and rats.

Methods

Rat Experiment

Subjects and Rewards

A total number of n = 17 male rats from two batches (batch 1: n = 7, batch 2: n = 10) were included. All rats served as control animals in two separate neurotoxic lesion experiments whose results have not been reported yet. Batch 1 received saline injection in the nucleus accumbens and batch 2 received saline injection in the medial orbitofrontal cortex. Histological verification after the experiments confirmed that no tissue damage occurred in the respective brain regions. All animals weighed between 280-350g at the beginning of the training and had not been used in any previous testing. Rats were housed in a group of three and under a reversed 12:12h light-dark cycle, at a temperature of 22 ± 2 ºC and humidity-controlled (60%) colony room. Throughout the experiment, all animals were food deprived with water available ad libitum in the home cages, and they were kept at 85% of free-feeding body weight. Two flavored soymilks (i.e. chocolate and vanilla) were prepared and further diluted with water (chocolate milk, 2:3 water; vanilla milk, 1:3 water).

Apparatus

Animals were trained in an operant chamber (28 x 23 x 23 cm; Med Associates Inc., Georgia, VM, USA) under red light condition. The front panel of each chamber was equipped with three nose poke units arranged horizontally. All nose poke holes contained photo beams that were able to detect and signal when rats entered the hole with their snouts. On the opposite side of the chamber, the back panel was equipped with one central house light, two reward bottle access holes with infrared photo beams to detect head entry as well as two reward lights located above each access hole. Once the animal met the respective fixed ratio requirement (i.e. a given number of nose pokes), one (forced-choice trials) or two (free-choice trials) reward lights were turned on, and motorized drives lowered the reward dispenser bottle through the hole to make liquid reward accessible for two seconds when head entry into the reward port was detected. The off and on of the house light signals the beginning and ending (i.e. budget went out) of the daily session. Before the sham-lesion surgery, rats were trained in the Skinner box through five steps of shaping procedure with

675 an increased complexity to learn the full structure of the task (see Hu et al., 2021, for details).
676 All inputs, outputs, and events were timestamped, controlled, and recorded by the software
677 MedPC (Med Associates Inc., Georgia, VM, USA), and stored for offline analysis.

678 **Budget and Price Conditions**

679 The structure of the rat budget task was identical to our previous studies (van Wingerden et
680 al., 2015; Hu et al., 2021) and is illustrated in Figure 1A. Rats went through five experimental
681 conditions following an A-B-A-B'-A block design, so that each price-budget condition (B, or
682 B') was preceded and followed by a baseline phase (A). Rats were trained on five consecutive
683 days per block, one session per day, with two days of rest between blocks. The first block
684 was always the baseline condition, followed by a block with a price condition with either
685 compensated or uncompensated budget, followed by the second baseline block, followed by
686 another block with altered reward prices and uncompensated/compensated budget,
687 followed by the third baseline block. The order of the two budget conditions was
688 pseudorandomized and counterbalanced across rats. Before testing in the final task, and
689 before the sham surgery, rats were pre-trained in a five-step shaping procedure (van
690 Wingerden et al., 2015). Rats were allowed to recover for two weeks after surgery before
691 proceeding to the final task.
692 In the baseline phase, each reward had a price of 2 NPs (rats had to keep their nose in the
693 hole for 100ms to count as one NP), and rats had a fixed budget of n=80 NPs they could spend
694 on vanilla or chocolate reward. We measured the baseline demand for chocolate and vanilla
695 milk, given this price and this limited budget. We determined the individually preferred and
696 non-preferred milk at baseline based on the rats' proportion of choices. Next, we changed
697 the price of the non-preferred reward to 1NP, and the price of the preferred reward to 4NPs,
698 and estimated the change in demand for both commodities (i.e. demand elasticity).
699 Importantly, we also manipulated the budget. In the uncompensated budget condition, the
700 budget remained at 80 NPs after implementing the price changes; that is, rats had 80 NPs to
701 spend, as in the baseline sessions. In the compensated budget condition, the budget was
702 compensated following Slutsky's demand equation (Slutsky and Ragusa, 2012) to make sure
703 animal consumers could continue to purchase the same commodity bundle as in the
704 preceding baseline condition. The budget compensation was done independently for each

705 rat, based on their individual baseline choices. For example, assume that a rat spends its 80
706 nose pokes at baseline to purchase 25 units of chocolate and 15 units of vanilla. To keep
707 purchasing this commodity bundle after changing the price of chocolate to 4 NPs, and the
708 price of vanilla to 1 NP, the budget would have to be increased to 115 NPs in the compensated
709 budget condition (25 x 4 + 15 x 1 = 115) to compensate the price changes.

710 **Trial Structure**

711 Each trial began with the activation of the central NP hole on the front panel, indicated by
712 illumination. Rats initiated the trial by making a single NP for 200ms, followed by the
713 activation and illumination of one (in forced-choice trials) or both (in free-choice trials)
714 lateral NP holes. Rats were required to meet a condition- and choice-specific fixed ratio
715 requirement (a variable number of 100ms NP responses; see Budget and Price Conditions
716 above) to obtain a chocolate or vanilla reward. NP responses in one of the two lateral holes
717 yielded chocolate milk reward, delivered in the back panel, responses in the other lateral
718 hole yielded vanilla milk rewards. Rewards were presented for 2s, followed by an intertrial-
719 interval (ITI) of variable duration such that each trial lasted exactly 32 seconds. Central and
720 lateral NP holes were activated for a maximum period of 10s, or until rats responded. Failure
721 to respond within 10s was followed by ITI and a start of a new trial, i.e., re-activation of the
722 central NP hole. The NP side to reward type assignment was counterbalanced across sessions
723 for each rat. Each daily session always started with eight forced-choice trials, four on each
724 side in a pseudorandom order, to allow animals to sample the side-reward assignment and
725 associated ratio requirements, followed by a variable number of free-choice trials. The
726 forced-choice trials were not counted into the available budget in each session; i.e., rats could
727 spend their full session-budget after having completed the forced-choice trials. A session was
728 terminated until the animals spent the entire budget, or after 60 minutes.

729 ## Human Experiments

730 **Participants and Stimuli**

731 Heterosexual male participants were recruited (Study 1: n = 60, mean age = 24, SD = 3; Study
732 2: n = 16, mean age = 23, SD = 2; Study 3: n = 25 , mean age = 23, SD = 2). The sample size of
733 Study 1 was estimated based on the earlier conducted Study 3 with a single picture task.

For the milk task of Study 1 and 2, the same soymilks (i.e. chocolate and vanilla) that were used in the rat experiments were prepared and served in separate cups to the participants. Both flavors contained a comparable level of calories per 100ml (chocolate: 61 kcal, vanilla: 57 kcal). Prior to the milk task, participants were informed not to drink sugared beverages or eat solid food for four hours. Self-reported score (1-10, 1- not at all, 10- very much) of hunger ("How hungry are you at this moment?") and thirst ("How thirsty are you in this moment?") was collected before and after the experiment. Testing of milk task was only arranged around lunch time or in the late afternoon.

For the picture task of Study 1-3, two categories of pictures containing different attractive elements (attractive faces, "face"; or mildly erotic bikini/underwear motives, "body") were prepared with a uniform size of 300 x 400 pixels. All pictures presented in the experiments were retrieved from the internet under open license. As mentioned above, participants needed to online rate all pictures for enjoyableness before being invited to join the laboratory part. Those who rated at least one third of pictures as highly enjoyable were selected to participate in the laboratory tasks. These selection criteria were meant to avoid participants holding an overly strong preference for one category of pictures in the experiment. Participants were also asked to try to refrain from sexual activity one day before the picture task.

Self-reported score (1-10, 1- not at all, 10- very much) of sexual excitement ("How strong is your sexual desire at the moment?") and the degree of "like to see" the pictures ("How much, in general, do you enjoy watching pictures of women with an aesthetic or sexual motive?") was collected before and after the experiment. Each part of the experiment (online rating, picture task and milk task) was separated by at least three days to minimize any learning or carryover effects.

Apparatus

We opted for instrumental effortful presses (Kurniawan et al., 2013; Klein-Flugge et al., 2016; Studer et al., 2019) because a) effortful presses are discrete operant responses similar to the quantifiable instrumental effort requirements of the rat version of our task, and b) they allow a precise manipulations of the price of reward (i.e. number of presses) and the size of the individual budget (i.e. total amount of presses). The instrumental effort in the human

experiment was implemented with a pedal press (PP) using fingers, conceptualized as equal to a button press.

Budget and Price Conditions

Human Study 1-2 (milk and picture rewards)

Human participants came on two separate days, with a minimum three-day interval, for the milk and picture task (Figure 1B). Participants were instructed to trade instrumental effort to obtain milk or picture rewards. For each task, participants completed the five experimental conditions following a following an A-B-A-B'-A block design similar to the animal task, one session per condition, at one time. Briefly, the first, third and last condition was always the baseline condition, in which reward commodities were equally priced at 4 PPs, and individual budget was fixed at the size of 80 PPs. Between baselines were the uncompensated or compensated budget conditions in which the preferred commodity in the preceding baseline became more expensive with a price of 8 PPs and the price of non-preferred commodity was reduced to 2 PPs. In the uncompensated budget condition, the budget remained at 80 PPs. In the compensated budget condition, the individual budget was extended following the Slutsky equation to theoretically maintain participants' baseline consumption level under the new price regime. The order of the uncompensated and compensated conditions, as well as the picture and milk task, were pseudorandomized and counterbalanced across participants.

Human Study 3 (picture rewards only)

In the third study (Figure 2- figure supplement 4E), the block design and price ratio (i.e. 4:4 PP for baselines, 8:2 PP for budget conditions) were the same as in Study 1-2. The only difference is that participants in Study 3 had a doubled amount of budget to spend in each experiment condition. Their baseline and uncompensated budget were 160 PPs and individual compensated budget was extended according to the Slutsky equation.

Trial Structure

Human Study 1-2 (milk and picture rewards)

<u>Practice sessions</u>: Two short practice sessions with an equal price for the two commodities (first practice: 2:2 PP; second practice: 8:8 PP) were implemented before the formal

experiment of each task, serving two purposes: i) to let participants get familiar with the trial structure and experience how budget was consumed, ii) to allow participants to practice on the highest level of effort in the formal task. Note that in the shaping procedure of the rat experiment (see *Apparatus in the Rat Experiment* above) we also trained rats to complete a 4:4 condition before proceeding to the next step.

Picture task: at the beginning of each condition (i.e. session), one sentence (e.g. "Your budget: 80 BPs") was presented for 10 seconds, indicating the size of budget for this session. Each trial started with a fixation cross on the screen, followed by the appearance of two icons representing two categories of the picture rewards with each price (e.g. "4 PP") written below (Figure 1B). The side (i.e., L/R) of each category was randomized across trials. When participants made their choice, the chosen commodity was shortly highlighted and then the effort phase began. In the effort phase, participants pressed buttons to reach the required effort level within four seconds. The length of the effort phase was calibrated in a pilot study to avoid long waiting. If participants were too slow in making their choices or failed to reach the effort requirement within the given time, this trial was considered as missed trial and restarted. When the effort requirement was met, and four seconds had passed, participants received an update of their budget expenditure and the accumulated choice selection of rewards (i.e. updated choice bundle). When the budget expired, participants received the notification at the end of the last trial and proceeded to the reward consumption phase in which picture rewards were displayed for 2 seconds in the same order as participants chose them. For example, if participant A chose to view a body picture in the first trial and then a face picture in the second and third trials, the presentation of pictures followed the same order of "body picture 1 - face picture 1 - face picture 2 - …". After the consumption phase, a photo of Mount Fuji was presented for 15 seconds, and then proceeded to the next experimental condition.

Milk task: The milk task applied the same trial structure as the picture task except that the milks were served in two cups after the session budget expired. Participants had 40 - 60 second to consume the milk rewards, which was similar to the duration of the reward consumption phase in the picture task. After consuming the rewards, they were provided with a cup of water to rinse their mouth and then proceeded to the next condition. In the

milk task of Study 2, instead of getting 1ml for one unit of purchased milk (Study 1), participants received twice the amount (i.e. 2ml) of milk for each purchase.

Human Study 3 (picture rewards only)

In the third study (Figure 2- figure supplement 4E), there were two modifications in the trial structure with respect to the Study 1 and 2: (i) rewards were delivered and consumed in a trial-by-trial manner, i.e., participants viewed a photo of the selected category of picture rewards immediately after their effort exertion phase; (ii) participants received no updates on their selected choice bundle within the session.

Analysis

Elasticity analysis

For elasticity estimation in the rat experiments, the number of choices for each reward in each condition was averaged across the last two sessions, similar to (van Wingerden et al., 2015; Hu et al., 2021). When estimating demand elasticity for participants, we used the raw choices plus one to perform log-transformation. For the ANOVAs on choices and conditions, regression analyses and tests of choice consistency, we used the raw data of individual choices of all conditions and only considered the final consumption bundle (e.g. 16 units of chocolate and 4 units of vanilla) per condition. Choice data and demand elasticity were analyzed using a mixed ANOVA with Bonferroni correction for multiple post-hoc comparisons. Frequentist analysis including ANOVA with repeated measures and post-hoc paired t-test was performed in JASP (JASP Team, 2020). The linear modeling on the elasticity of non-preferred rewards against scaled baseline choice of preferred rewards and the budget conditions (uncompensated and compensated) was performed with a general Gaussian linear regression.

Simulation

To examine whether the comparability and discrepancy in the cross-species behaviors were merely driven by a sampling bias, we generated n = 1000 choice sets following a uniform distribution. Each choice set contained five choice bundles for the five experimental conditions of human study 1. Each choice bundle is referred to a combination of the quantity of two rewards (q_P, q_{NP}), calculated from equation (2), given the fixed budgets (m) and price

regimes of the three baselines ($price_P$: $price_{NP}$ = 4:4) and the two budget conditions ($price_P$: $price_{NP}$ = 8:2):

$$price_P \times q_P + price_{NP} \times q_{NP} = m \quad (2)$$

from which we defined the preferred and non-preferred reward based on the preceding baseline choice and calculated the demand elasticity of each reward commodity in the uncompensated and compensated budget condition.

GARP analysis

To infer individuals' degree of consumption rationality from our participants' choice data, accumulated over each experimental condition, we counted how many choice sets posed a violation of GARP. Wilcoxon signed rank test was performed in R for comparing the count of GARP violation between the picture and milk task, as well as for comparing self-reported score of state before and after each task. The raincloud plots on self-reported state (Figure 3A and Figure 2- figure supplement 4B) were created with 'raincloud plot' R package (Allen et al., 2019). The linear modeling on the counted data of GARP violation against the continuous variable (cumulative choice of preferred rewards) and the categorical variable (picture task vs. milk task) was implanted in a general Poisson linear regression (*glm* function from MASS package, (Ripley et al., 2013)).
The regression on the score of post-experiment sexual excitement against the summed reward intake was estimated by a hyperbolic function with the *glm* function, too.

Data and code sharing

The raw data and analysis scripts are publicly available on the Open Science Framework (https://osf.io/9yqbk/).

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Author contributions

Yue Hu: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft preparation, Writing – review & editing, Visualization, Project administration, Funding acquisition.

Felix Jan Nitsch: Formal analysis, Writing – review & editing.

Marijn van Wingerden: Writing – review & editing.

Tobias Kalenscher: Conceptualization, Software, Resources, Writing – review & editing.

Ethics

Ethics approvals for the human experiments have been obtained from the institutional review board of the Institute of Experimental Psychology, Heinrich-Heine University Düsseldorf. All participants gave their informed consent. The study was conducted in alignment with the declaration of Helsinki. Ethics approvals of animal experiments were granted by the Landesamt für Natur und Verbraucherschutz (LANUV) of Northrhine Westfalia.

Competing interests

The authors declare no competing interests.

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Supplementary Results

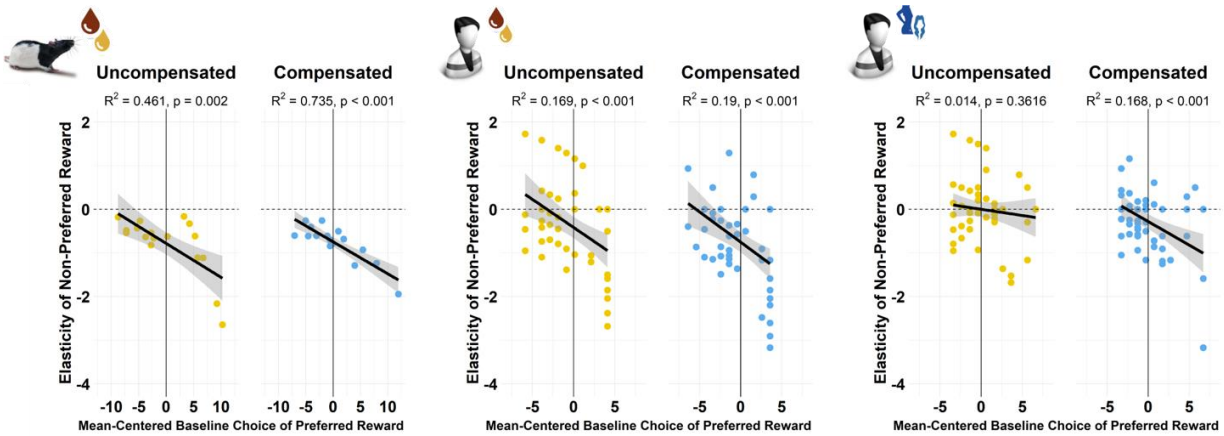


Figure 2- figure supplement 1 *Baseline-preference-dependent reward substitution in rats (A), the milk task (B) but not in the picture task (C). We regressed the elasticity of non-preferred rewards against the scaled baseline choices of preferred rewards, the budget condition and the interaction between the two, for both rats and humans.*

Rat experiment: main effect of baseline choice of preferred reward ($t = -3.843$, $p < 0.001$) on the elasticity of non-preferred reward, but no main effect of budget condition ($t = -0.279$, $p = 0.782$) nor the interaction between the two ($t = -0.181$, $p = 0.857$). Human milk task: main effect of the baseline preference ($t = -3.766$, $p < 0.001$) and a main effect of budget condition ($t = 1.986$, $p = 0.049$) on the elasticity of non-preferred reward, but no significant interaction of the two ($t = 0.19$, $p = 0.849$). Human picture task: main effect of baseline choice of preferred rewards ($t = -3.577$, $p < 0.001$) and budget condition ($t = 2.317$, $p = 0.022$) were significant. Their interaction was a non-significant trend ($t = 1.842$, $p = 0.068$).

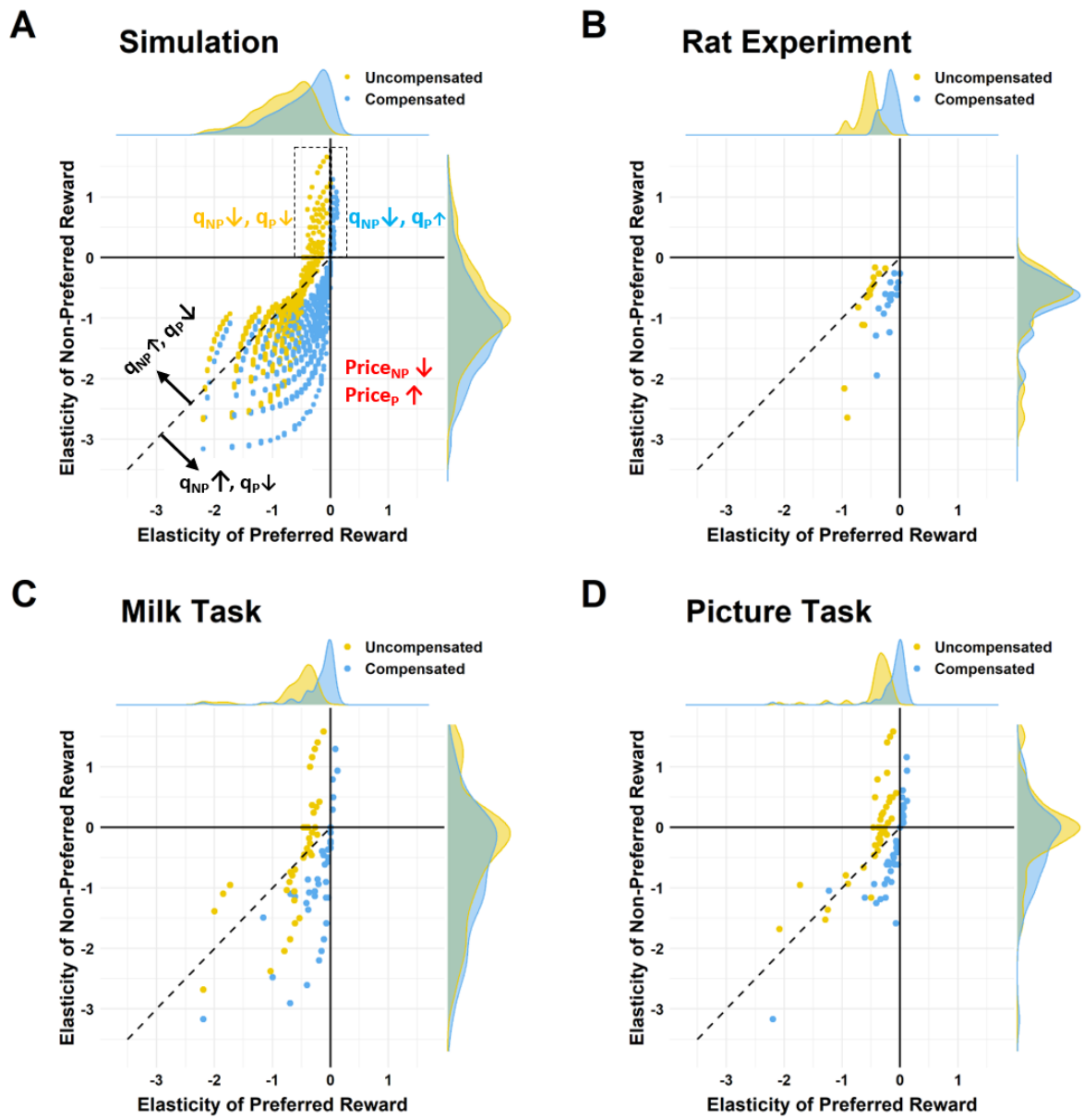
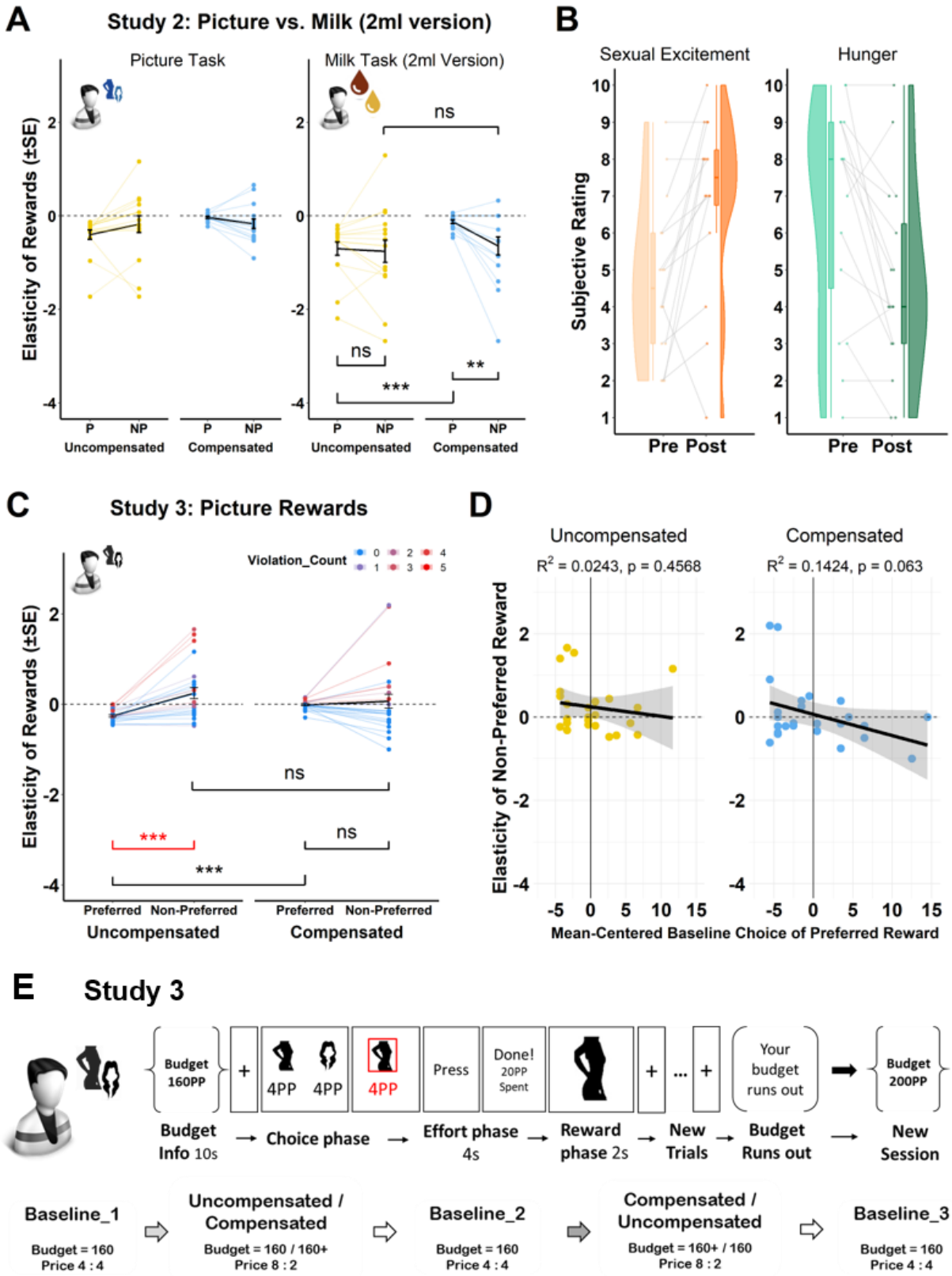


Figure 2- figure supplement 2 *Elasticity Matrix: demand elasticity of preferred and non-preferred rewards in the uncompensated and compensated budget condition of the simulated choice sets (A), Rat Experiment (B), milk task (C) and picture task of Study 1 (D). The position of individual data on the matrix indicates the level and direction of reward substitution after the price change. Dots represent each individual data; on the upper and right side of the matrix is the density plot of the distribution; the dash line indicates the diagonal line (y = x).* $Price_P$*: price of preferred reward;* $Price_{NP}$*: price of non-preferred reward;* q_{Px}*: quantity of preferred reward;* q_{NP}*: quantity of non-preferred reward. Upward arrow indicates an increase in the price or quantity of reward choice, downward arrow indicates a decrease in the price or quantity of reward choice.*

In the uncompensated budget condition, a majority of the simulated sample (854 out of 1000) showed negative elasticities for both rewards, mainly distributed around the diagonal line in the third quadrant of

the matrix. In the compensated condition, more simulated individuals (907/1000) showed negative elasticities for both rewards but drifted towards a reduced negativity of demand for preferred reward (i.e. smaller reduction from the baseline demand) and an increased negative elasticity (i.e. a larger increase from the baseline demand) of non-preferred reward. An approximate proportion of population in rats (17/17) exhibiting the price-sensitive budget-dependent consumption behavior, as well as in humans in the milk task (uncompensated: 47/60, compensated: 53/60). The distribution of individual elasticities in the human picture task shifted away from the third quadrant and more often located in the second (25/60) and first quadrant (16/60) of the matrix where considered as a suboptimal decision strategy in response to the price change and budget constraint.


A
Study 2: Picture vs. Milk (2ml version)
Picture Task
Milk Task (2ml Version)
Elasticity of Rewards (±SE)
ns
ns
***
**
P
NP
Uncompensated
Compensated
B
Sexual Excitement
Hunger
Subjective Rating
Pre
Post
C
Study 3: Picture Rewards
Violation_Count
Elasticity of Rewards (±SE)
ns
***
ns
***
Preferred
Non-Preferred
Uncompensated
Compensated
D
Uncompensated
Compensated
R^2 = 0.0243, p = 0.4568
R^2 = 0.1424, p = 0.063
Elasticity of Non-Preferred Reward
Mean-Centered Baseline Choice of Preferred Reward
E
Study 3
Budget 160PP
4PP
4PP
4PP
Press
Done! 20PP Spent
Your budget runs out
Budget 200PP
Budget Info 10s
Choice phase
Effort phase 4s
Reward phase 2s
New Trials
Budget Runs out
New Session
Baseline_1
Budget = 160
Price 4 : 4
Uncompensated / Compensated
Budget = 160 / 160+
Price 8 : 2
Baseline_2
Budget = 160
Price 4 : 4
Compensated / Uncompensated
Budget = 160+ / 160
Price 8 : 2
Baseline_3
Budget = 160
Price 4 : 4

1068 ***Figure 2- figure supplement 3*** *Two control experiment on the effect of reward satiation (Study 2, n = 16)*
1069 *and timing of reward delivery (Study 3, n = 25) on consumption behavior of milk and picture rewards. (A-B)*
1070 *Study2: demand elasticity of rewards and self-reported scores of sexual desire and hunger before ("Pre") and after*
1071 *("Post") the task. In Study 2, each unit of purchase would yield the doubled amount (i.e. 2ml) of milk compared to*
1072 *the milk task of Study 1 (i.e. 1ml for each unit), while the picture task remained the same. (C-D) Study 3: demand*
1073 *elasticity of preferred and non-preferred rewards, plotted against the count of GARP violation, and correlations*
1074 *between the scaled baseline choice of preferred rewards and elasticity of non-preferred rewards in the two budget*
1075 *conditions. (E) Schematic representation of Study 3 in which picture rewards were delivered and consumed in a*
1076 *trial-by-trial manner, that participants viewed a photo of the selected category of picture rewards, for example,*
1077 *body shape of bikini/underwear models, immediately after their effort exertion phase. P: preferred rewards; NP:*
1078 *non-preferred rewards; ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$; ns: not significant.*
1079 *Study2: Participants reported a decrease in hunger after the milk task ($p = 0.008$, Wilcoxon signed-rank test),*
1080 *and an increased sexual excitement after the picture task ($p = 0.006$, Wilcoxon signed-rank test). A similar*
1081 *three-way ANOVA yielded a main effect of budget ($F_{1,15} = 10.753$, $p = 0.005$, partial $\eta 2 = 0.418$), a marginally*
1082 *significant main effect of task ($F_{1,15} = 4.347$, $p = 0.055$, partial $\eta 2 = 0.225$), a significant budget x preference*
1083 *interaction ($F_{1,15} = 8.827$, $p = 0.01$, partial $\eta 2 = 0.37$) and a marginally significant interaction of preference x*
1084 *task on demand elasticity ($F_{1,15} = 3.998$, $p = 0.064$, partial $\eta 2 = 0.21$). The three-way interaction of budget x*
1085 *preference x task was not significant ($F_{1,15} = 0.197$, $p = 0.664$, partial $\eta 2 = 0.013$). In the milk task, we found*
1086 *a main effect of budget ($F_{1,15} = 6.318$, $p = 0.024$, partial $\eta 2 = 0.296$), a marginally significant main effect of*
1087 *preference ($F_{1,15} = 4.3$, $p = 0.056$, partial $\eta 2 = 0.223$) and an interaction of budget x preference on reward*
1088 *elasticities ($F_{1,15} = 6.341$, $p = 0.024$, partial $\eta 2 = 0.297$). In the picture task, the interaction of budget x*
1089 *preference revealed a tendency towards significance ($F_{1,15} = 3.817$, $p = 0.07$, partial $\eta 2 = 0.203$).*
1090 *Study 3: A two-way ANOVA yielded a main effect of preference ($F_{1,24} = 8.137$, $p = 0.009$, partial $\eta 2 = 0.253$)*
1091 *and an interaction of budget x preference ($F_{1,24} = 9.802$, $p = 0.005$, partial $\eta 2 = 0.29$) on reward elasticities.*
1092 *Importantly, we replicated our finding in the picture task of Study 1 that the elasticity of non-preferred*
1093 *rewards in the uncompensated budget condition was much more positive than the elasticity of preferred*
1094 *rewards ($t = -4.733$, $p < 0.001$, Cohen's $d = -0.947$). Such comparison was not significant in the compensated*
1095 *budget condition ($t = -0.578$, $p = 0.569$, Cohen's $d = -0.116$). We also found a reduced negative elasticity of*
1096 *preferred reward in the compensated budget condition as compared to the uncompensated condition ($t = -$*
1097 *11.077, $p < 0.001$, Cohen's $d = -2.215$). The elasticity of non-preferred rewards did not differ between the two*
1098 *budget conditions ($t = 1.29$, $p = 0.209$, Cohen's $d = 0.258$). Also, the differences between the two reward*
1099 *elasticities in the two budget conditions were reflected with the count of GARP violation (both $p < 0.01$).*

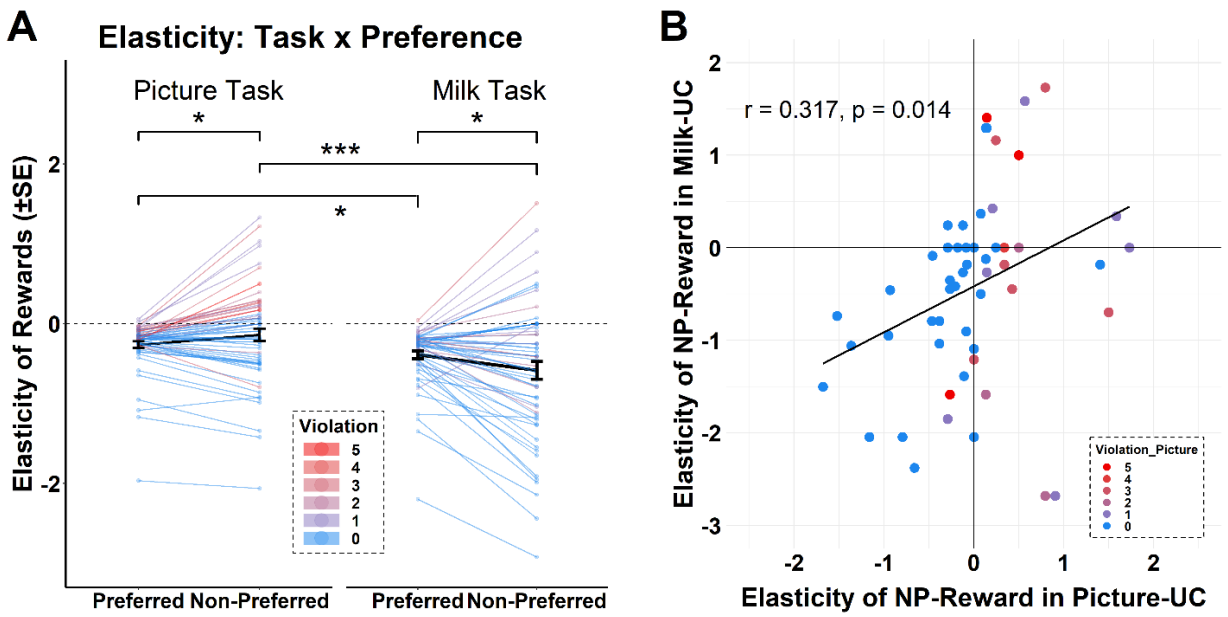


Figure 3- figure supplement 1 *(A) Mean elasticity of preferred and non-preferred rewards in the two tasks, plotted against the count of GARP violation in each task. (B) Intra-individual stability in the reward elasticity of picture and milk task: correlation of non-preferred reward elasticity in the uncompensated budget condition in the picture and milk task, plotting against the count of GARP violation in the picture task. NP-Reward: non-preferred reward; UC: uncompensated budget condition. ***: p < 0.001, *: p < 0.05.*