Title: Neural substrates underlying the expectation of rewards resulting from effortful exertion

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Abstract: Expectations as a reference point shape our decisions to motivate effortful activity. Despite the important role of reference points in human performance, little is known about how the brain processes expectations to guide motivated exertion. Participants completed a reward-based effort task in an MRI scanner. During each trial, participants were presented with a risky option that would either result in a fixed monetary payment, regardless of their effort exertion, or a piece-rate payment where the payment was proportional to the amount of effort exerted. We found that participants exerted more effort as the fixed payment increased, suggesting that the fixed payment influenced the reference point for effort exertion. The strength of this reference-dependent behavior was correlated with neural activity in the ventral striatum, which was significantly modulated by the deviation from the payoff to reward expectations after effort exertion. Our results suggest that value-related brain areas, particularly the ventral striatum, encode expectations of reward as a reference point to motivate effort exertion.

One-Sentence Summary: Value-related brain areas process reward expectations and how we evaluate outcomes based on that.

Main Text:

Introduction

Imagine you worked overtime, expecting a $2,000 bonus at the end of the month. Your colleague, on the other hand, expected only $1,000 as a bonus. At the end of the month, both of you instead received $1,500 as a bonus. Although you received the same bonus, you might feel dissatisfied and that you lost $500, while your colleague might feel better about the result of earning an unexpected $500. Individuals often evaluate outcomes in relation to their expectations. In this view, reward expectations can be a reference point that motivates effortful activity. These reference-dependent preferences are the core foundation of prospect theory (*1*, *2*).

Many field experiments consistently have observed that reward expectations, influencing outcome evaluation, drive effortful activity (*3*–*7*). For instance, taxi drivers determine their work hours based on self-determined daily expected income and hours worked (*3*), while professional athletes play more vigorously if they expect to win a game based on prior experience (*4*). Although field experiments have revealed expectation-based reference-dependent behavior in various situations, how reward expectations differentially influence effortful activity across individuals remains to be studied.

Despite the fundamental role of reference points in human performance during effortful activity, little is known about how the brain encodes expectations to guide motivated exertion. Previous neuroimaging studies investigating reference-dependent valuation in market transactions found that reference-dependent value uniquely modulated neural activity in the ventral striatum (VS) (*8*). This modulation also predicted individual variability in the degree of reference-dependent preferences (*8*). Further, the level of satisfaction from the outcome relative to external reference during the market transaction was reflected by the anterior cingulate cortex

(ACC) (*9*). Activity in both the VS and ACC is strongly associated with reward-based decision-making. Specifically, neural activity in the VS tracks subjective values of decision stimuli (*10*), reward expectations (*11*), preference (*12*, *13*), and deviations from the outcome to reward expectation (i.e., reward prediction error) (*11*, *14–16*). On the other hand, neural activity in the ACC modulates error processing (*17*) and predicting outcomes (*18*) specifically during effort exertion. Although these studies hint at the idea that reference-dependent effortful activity might involve neural activity in the VS and ACC, this has not been directly confirmed.

In this study, we investigated the neurobiology of reference-dependent effort exertion and inter-individual variability of the influence of reward expectations in motivating effort exertion using functional magnetic resonance imaging (fMRI). Participants performed an effort task with risky options in an MRI scanner. For each trial, participants were presented with a risky option that would either result in a fixed monetary payment, regardless of their effort exertion, or a piece-rate payment where the payment was proportional to the amount of effort exerted, which occurred with an equal probability. We manipulated the fixed payment option so that participants had different reward expectations by exogenous monetary variation for each trial. Participants freely determined how strongly they would grip a hand dynamometer given the risky option. The outcome payoff was realized at the end of each trial, which allowed us to examine how the brain would process the evaluation of realized outcomes in relation to reward expectations as a reference point.

We hypothesized that individuals would exert effort with respect to the exogenously varied monetary expectation (i.e., exogenous expectation). We predicted that neural activity in the VS would be modulated by the magnitude of exogenous expectation when fixed payment was presented. We also hypothesized that neural activity in the VS would be modulated by the degree of the outcome evaluation relative to reward expectations. Lastly, we hypothesized that

neural activity in the VS would explain the inter-individual variability in the degree of reference-dependent effort exertion behavior.

Our results demonstrate that exogenous reward expectations influenced effortful exertion. The VS and the ventromedial prefrontal cortex (vmPFC) encoded these expectations and neural activity in the VS tracked the expectation-based evaluation of an outcome after effort exertion such that the activity in the VS was modulated by the degree of positive deviations (i.e., satisfaction) when the payoff after effort exertion was better than expected. Importantly, we identified that the VS was associated with individual variability in the amount of effort exertion as a function of exogenous reward expectations. Overall, our results shed light on the neural mechanisms of expectation-based, reference-dependent preferences resulting from effort exertion, and particularly, that the VS plays a key role in tracking the inter-individual differences in the degree of reference dependence in effortful activity.

Results

34 participants (24 ± 7 years, 17 F) performed a reward-based effort task in the fMRI scanner (Fig 1A). We excluded four participants who did not follow the instructions during the *Training* phase and three additional participants for excessive head motion. Therefore, we analyzed a total of 30 and 27 participants for behavior and neuroimaging data, respectively. Participants practiced the associations between effort exertion and reward (*Training*, Fig 1B), and then were tested for their understanding of these associations (*Recall*, Fig 1C). Following the *Training* and *Recall* phases, participants were presented with a risky option (*Test*) that would either result in a fixed monetary payment, regardless of their effort exertion, or a piece-rate payment where the payment was in proportion to the amount of effort exerted during each *Test*

trial (Fig 1D) (*19*). Each option had an equal probability of occurring and the fixed payment ranged from 25 cents to 4 dollars in increments of 25 cents, thus allowing participants to have different trial-to-trial reward expectations. Effort exertion allowed us to observe participants' preference for the fixed payment, enabling us to investigate reference-dependent effort exertion. The actual payoff was revealed after the risky options were presented and individuals had an opportunity to exert effort. Following the test in the fMRI scanner, participants completed 140 trials of an economic choice task (Fig 1A) (*20*). Using this economic choice task, we estimated each participant's degree of loss aversion (Supplementary Material).

Given the varied reward expectations manipulated by fixed payment, we measured individuals' effort exertion as an expression of their preference. Individuals can utilize two potential strategies: 1) exert equal effort to the amount required for the fixed payment, minimizing the cost of effort while maximizing reward (*19*), or 2) exert maximum effort disregarding the exogenous variation in the fixed payment to maximize reward (Fig 1E). We found that participants exerted more effort as the fixed payment increased, suggesting that exogenous variation in the fixed payment influenced the reference point for effort exertion ($t = 7.28$, $p < 0.001$, Fig 1F). However, there was considerable inter-individual variability in effort exertion based on the fixed payment values (Fig 1G). Although this behavioral variance is thought to stem from individual differences in loss aversion (*5*, *19*, *21*), we found no correlation between each participant's loss aversion parameter estimated using the incentive preference task and their effort exertion as a function of the fixed payment ($p = 0.60$, Supplementary Fig 3). In summary, fixed payment as exogenous expectations of reward partially shaped effortful activity.

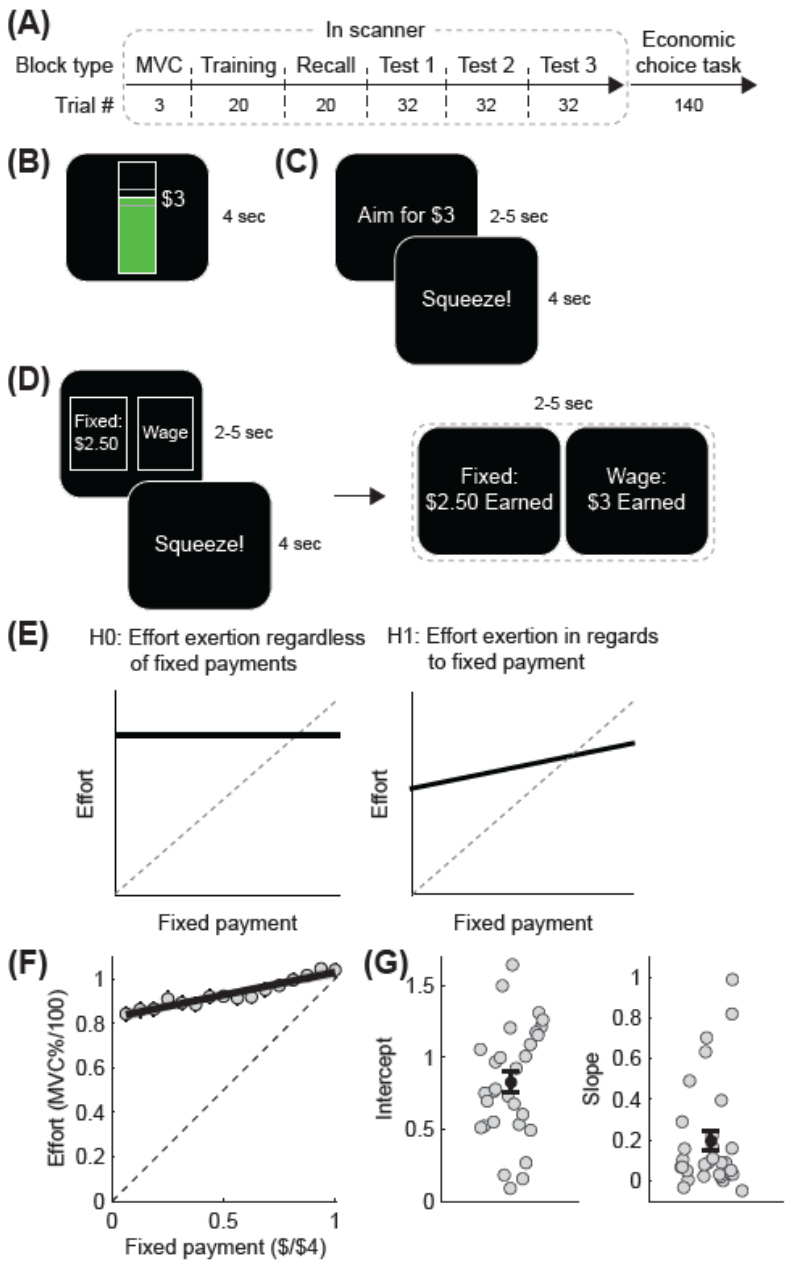

Fig. 1. Experimental design and behavioral results. (A) Experimental protocol. Participants' maximum voluntary contraction (MVC) was measured to normalize each individual's strength for the effort task. (B) Screens of the *Training* phase that participants viewed in the scanner. Force measured by a hand dynamometer was real-time reflected as an interactive bar in the thermometer with a target monetary reward range. Screens of the (C) *Recall* and (D) *Test* phase that participants viewed in the scanner. (E) Behavior hypothesis schematics. If participants were exogenous reference-independent, they would exert constant effort regardless of the fixed payment. In contrast, if participants were reference-dependent, they would exert effort in regard to the fixed payment. (F) Individual and group fit of effort exertion as a function of the fixed payment. Both effort and fixed payment were normalized to 1 to be 100 effort units and $4, respectively. The gray points and shaded areas represent the mean and standard error of effort exertion across participants for each fixed payment, and the

yellow line represents the average fit across all participants. The dotted line is a unity line. (G) Intercept and slope from the individual regression models. Gray points are individual data, and the black points and whiskers are the mean and standard error across participants.

We then examined regions of the brain that encode exogenous reward expectations and process preferences based on these expectations when the outcome of the risky option (i.e., either the fixed payment or their piece-rate payment) was revealed. We constructed a single general linear model (GLM) that included 1) the time of presentation with a parametric modulator of the magnitude of fixed payment as exogenous expectations and 2) the time of outcome with a parametric modulator of outcome preferences based on reward expectations. Since the reward expectations have changed from the fixed payment alone to a combination of fixed payment and effort exerted, we computed the expected value as updated reward expectations, which was a linear combination of fixed payment and effort exertion with equal probabilistic weights (0.5 × Fixed payment + 0.5 × Piece-rate payment). Then, the outcome preferences were computed as the deviations between the actual outcome received and the updated reward expectations.

The ventral striatum played a significant role in the process of exogenous effort-based reward expectations and the outcome evaluations based on those expectations. At the time of presentation, we found that exogenous reward expectations (i.e., Fixed payment) were positively scaled in the left VS ($p<0.005$ cluster-corrected, k=187, peak MNI coordinate = [-16, 10, -6]) and bilateral anterior insula (aI, peak [-32, 24, 0] for left, [36, 18, -6] for right) (Fig 2A, B). The activity in the VS was consistent with our hypothesis and previous literature, which has shown that the VS plays a crucial role in signaling reward and motivation (*10*, *11*, *22*). Moreover, at the time of outcome, we found significant activity in the bilateral VS ($p < 0.005$, k=20, peak = [-10, 12, -4] for left, [16, 6, -8] for right). This activity was positively scaled with outcome preferences, in which the payoff was better than expected (Fig 2C, D). The VS processes reward

prediction error (*11*, *14–16*), which is consistent with our findings of scaling with the deviation between the actual outcome and the reward expectations. Additionally, we found significant BOLD activity in the anterior cingulate cortex (ACC, peak = [6, 40, 4]) and right anterior insula (peak = [36, 16, -4]). Together, these results may shed light on the role of VS in encoding preferences with respect to reward expectations.

Lastly, we investigated whether neural activity could explain the behavioral variance in reference-dependent effort exertion by correlating the whole brain neural activity with individual coefficient estimates from the behavioral model of effort exertion as a function of fixed payments. We found that individuals who were more influenced by the fixed payment (i.e., more reference-dependent) exhibited stronger associations between the NAcc activity and positive experience of preferences based on reward expectations ($p<0.005$ cluster-corrected, $k=143$, peak = [-10, 14, -8]) (Fig 2E, F). Therefore, neural activity in the left VS not only tracked the positive preferences relative to reward expectations but also explained the inter-individual variability in the degree of influence that external referents had on participants' reference-dependent effort exertion.

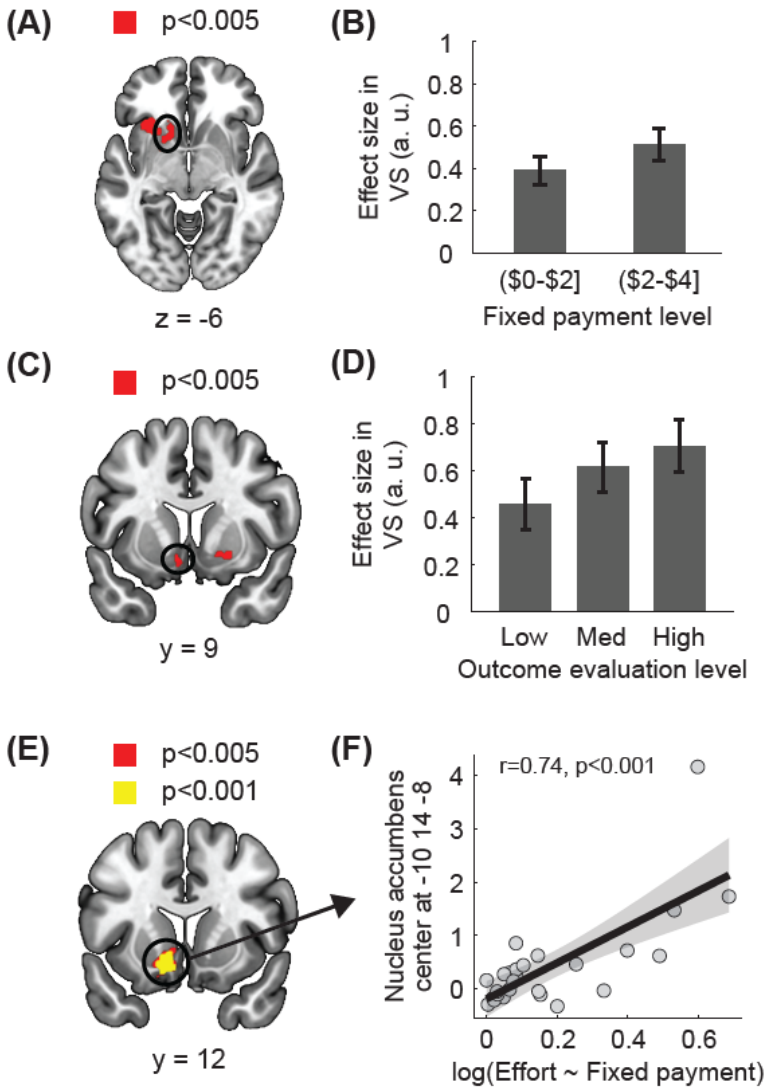

Fig. 2. Brain activities during Presentation and Outcome evaluation. (A) Whole-brain results with a threshold at voxel-wise p<0.005 cluster-corrected with k=187. There was significant neural activity in the left VS (peak = [-16, 10, -6]) and bilateral aI (peak = [-32, 24, 0] for left, [36, 18, -6] for right), positively modulated by the fixed payment. (B) Effect size in the right VS (5mm sphere centered at [-13, 17, -8]) for low ($0.25-$2) and high ($2.25-$4) fixed payments. This was illustrative only and was not used for statistical inference. (C) Whole-brain results with a threshold at voxel-wise p<0.005 and k=20. There was significant neural activity in the bilateral VS (left peak = [-10, 12, -4], right peak = [16, 6, -8]), aI (peak = [36, 16, -4]). (D) Effect size in the bilateral VS (5mm sphere centered at [-6, 7, -13] for left and [21, 7, -10] for right) for low, medium, and high deviations of the outcome from the reward expectations. This was illustrative only and was not used for statistical inference. (E) Whole-brain results with a threshold at voxel-wise p<0.005 cluster-corrected with k=143. There was significant activity in the left VS, specifically, the nucleus accumbens, associated with the degree of reference-dependent effort exertion (peak = [-10, 14, -8]). (F) Neural activity in the nucleus accumbens was significantly correlated with individual differences in reference-dependent tendency during effortful activity, estimated as the log of the slope from the individual regression model (r=0.74, p<0.001).

To ensure that the amount of effort exertion was due to the fixed payment as exogenous expectations of reward, we additionally tested potential confounding factors such as physical fatiguability (i.e., trial number), the history of reward, the history of outcome type (i.e., fixed or wage payment as outcome), and the history of effort exertion. We found no significant effects of physical fatiguability, history of reward, and history of outcome type (Supplementary Fig 4). However, there was a significant effect of the history of effort exertion ($t = 12.08$, $p < 0.001$, Supplementary Fig 4). Specifically, individuals exerted proportionally more effort at the subsequent trial than the previous trial, but as individuals exerted effort greater than on average 94 effort units at the previous trial, they exerted lesser effort at the subsequent trial. Interestingly, this association between previous and subsequent effort exertion was negatively correlated with the degree of reference-dependent effort exertion ($r = -0.47$, $p = 0.008$, Supplementary Fig 5). This negative association may infer that individuals utilize different balance between fixed payment and effort as their reference points. Further, this degree of the history effect of effort was also explained by the ventral putamen modulated by the outcome evaluation ($p<0.005$, $k=20$, peak = [-24, 12, 0]) (Fig 3A, B). This suggests that regardless of which reference points (fixed payment or effort) were utilized in this reference-dependent effort exertion, the ventral striatum may encode the reference point utilized by individuals.

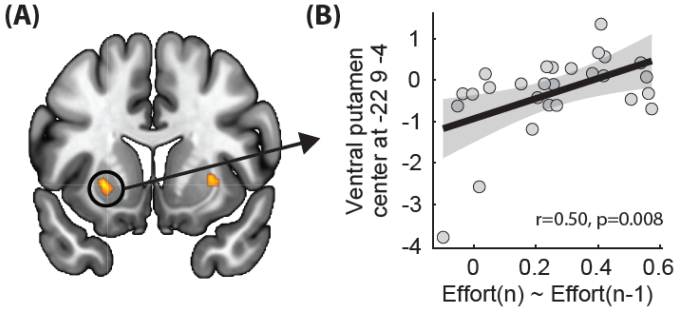

Fig. 6. Correlation between the history effect of effort exertion and brain regions modulated by the difference between outcomes and expectations. (A) Whole-brain results with a threshold at voxel-wise $p<0.005$ cluster-corrected with $k=20$. There was significant activity in the left VS, specifically, the ventral putamen, associated with the degree of history

effects of effort exertion (peak = [-24, 12, 0]). (B) Neural activity in the ventral striatum was significantly correlated with individual differences in effort exertion based on the previous effort, estimated as the slope from the individual regression model (r=0.50, p=0.008).

Discussion

Expectations play an essential role in daily decisions for effortful activities, but little is known about what determines these expectations and how human brains compute this relationship. Therefore, we aimed to understand whether effortful activities are shaped by reward expectations and whether this relationship modulates neural activity in value regions of the brain. We hypothesized that 1) reward expectations would positively influence effort exertion, 2) the VS would encode both reward expectations and deviations of the outcome from the expectations, and 3) the VS would explain the individual differences in the degree of expectation-based, reference-dependent effort exertion. By providing risky options with varying degrees of reward expectations, we were able to demonstrate that individuals partially account for the explicitly manipulated expectation to guide effortful activity. These exogenous reward expectations were encoded in the VS, which is the region of the brain that typically processes value and reward, and aI, which encodes risk. Similarly, when evaluating outcomes, deviations of preferences relative to the internal representation of reward and effort expectations were encoded in the nucleus accumbens, anterior insula, as well as ACC. Specifically, neural activity in these areas was greater during *better-than-expected* outcomes. Critically, the VS further explained inter-individual variability in reference-dependent effort exertion, suggesting that the VS has a key role in encoding and computing gains and losses that take expectations as the reference point.

The externally manipulated reference point (i.e., fixed payment) partially influenced the effortful activity. This was consistent with previous studies that the average effort was generally higher than the externally manipulated reference point (*19*, *23*). The expectation-based model of

preferences predicts that individuals have a high probability of stopping exerting effort when the marginal returns of effort are equal or similar to the reference point and the subjective aversiveness to losses influences this stopping point (*5*, *19*, *21*, *24*). However, our study found no significant association between reference-dependent effort exertion and loss aversion. This might be because our participants determined how much effort might be worth given the fixed payment based on a balance between reward and cost of effort. Therefore, loss aversion estimated by a monetary choice task may not fully reflect effort preferences (*25*). Alternatively, this might be partially due to our study design. Participants performed the economic choice task, in which we derived subjective loss aversion after they completed the effort-based task in the MRI scanner. This might have shifted the level of loss aversion due to possible fatigue (*26*). It will be of interest to investigate other factors such as individuals' susceptibility to fatigue or the level of weekly vigorous exercise that could contribute to the individual variability in reference-dependence during effortful activity.

Although the effort exertion behavior on average is generally consistent with the previous research, our participants favored earning monetary rewards more than minimizing effort. A previous study found that there is a significant likelihood to stop working when the marginal cost of effort (i.e., piece-rate payment) is greater than exogenous expectations (i.e., fixed payment) (*19*). Unlike this study, our participants were likely to exert more effort than the effort required for the fixed payment. The difference between the previous study and ours is the type of effort cost. In the previous study, the cost of the effort was time, which participants could choose to work as long as they wanted to increase the possible payoff if the piece-rate payment option was selected. On the other hand, in our study, the cost of the effort was physical forces. Although effort can be manipulated in both ways (time and physical force), physical force as an effort cost is recoverable while time as an effort cost is irrecoverable in that participants permanently lose

the time spent during the experiment. This sense of recoverability may motivate our participants more to temporarily sacrifice their efforts to increase potential payouts. Future research can investigate how the difference in effort cost domains influence reference-dependent behavior.

Consistent with our hypothesis, neural activity in the VS was positively modulated by the magnitude of exogenous reward expectations at the time of presentation. The VS is a well-known structure in the value circuit encoding reward and motivation signals (*11*, *27*). Combining the previous findings and our results, the role of VS may be processing reward expectations to provide motivation signals to other areas of the brain, or different subsections of the VS may involve slightly different processing of reward, reward expectations, and motivation. Although the dissociation of these roles in the VS was not the purpose of our study, a future investigation may identify potential subsections of the VS processing different components of the decision-making.

In addition to VS, we observed that aI was positively modulated by the magnitude of reward expectations. As previous literature suggested, aI not only tracks the formation of expectations resulting from a combination of reward and effort (*28*) but also encodes risk associated with the trial (*29*, *30*). Although our task provided equal uncertainty for all trials (i.e., 50/50 chance to receive fixed or wage payment), individuals may perceive the risk of the exogenous reference as greater when the reference was higher, indicating that higher expectations (i.e., higher reference) may reflect higher risk as well. Overall, our results provide additional insights that the VS and aI play a primary role in encoding expectations of reward associated with future effort and aI in their perceived risk in the form of reward expectations.

Moreover, our study uncovered brain regions that preferentially encoded deviations between effort-based reward expectations and final payoff. The neural activity in the VS, ACC,

240 and aI positively tracked a trial-by-trial divergence of payoff from expectation (i.e., expected value of reward and effort). Interestingly, the activity in the VS also explained the inter-individual variability in the degree of reference-dependent preferences. This is consistent with the previous finding that the striatal activity predicted deviations from the outcome to subjective evaluations of a product during market transactions (*8*). The subjective evaluation of products
245 indicates each individual's expected valuation, reflecting their "reference" expectation. They further found that the VS activity explained between-subject variability in participants' reference-dependent computation of value (*8*). The ACC and aI often show a close link with the VS, forming a reward-related circuit (*31*) and encoding values of reward prediction error (*28*). Particularly, a recent meta-analysis identified functional connectivity between pregenual ACC,
250 which is precisely the significant ACC region in our study, aI, and the VS that were associated with decision-making and reward tasks (*32*). As such, our findings may hint that the value network encodes positive experiences of outcomes based on effort-based reward expectations beyond the domain of reward and market transaction.

It is of note that the history of effort exertion significantly influenced the subsequent
255 effort exertion. This history effect of effort was negatively correlated with the degree of expectation-based, reference-dependent effort exertion. One possibility of this negative correlation is that individuals differently balance the weight of the reward expectations as a point of reference and the history of effort such that if reward expectations are prioritized, then the weight of the history of effort is balanced and vice versa. Neural activity in the ventral putamen
260 further explained the degree of history effect of effort exertion. This indicates that the ventral striatum in general might play a significant role in tracking individual differences in outcome preferences based on some anchor point, whether the point is from the reward expectations or the history of effort.

In conclusion, our study demonstrates that reward expectations partially shape effort exertion. Moreover, the VS plays a primary role in encoding reward expectations and evaluating the outcome based on reward expectations resulting from effort exertion. Specifically, the VS and aI track expectations of reward for future effort, and the typical value network including the VS, ACC, and aI reflects satisfying outcomes relative to expectations, but critically, the VS is positively associated with inter-individual variability in reference-dependent effort exertion. The tighter link for encoding *better-than-expected* outcomes in the VS was positively associated with individual variability in the degree of reference-dependent effort exertion, indicating an important role of the VS in integrating positive experience with initial expectations.

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Materials and Methods

Participants

34 healthy, right-handed young adults (17 female, mean and SD age = 24 ± 7 years) participated in the study. Four participants were excluded from the behavioral analysis due to 1) a lack of understanding of effort-reward associations and 2) more than 50% failed trials during the *Test*. Three additional participants were excluded from the neuroimaging analysis due to excessive head movement. The excessive head movement was defined as 1) mean framewise displacement (FD) was greater than 1 mm or 2) the number of outlier frames, which was determined by FD greater than 1 mm, were greater than 43 frames (approximately 2 minutes of the 11-minute scan). Therefore, the final behavioral and neuroimaging analyses included a total of 30 and 27 participants, respectively. We prescreened all participants to exclude those with a prior history of neurological or psychiatric illness. The Johns Hopkins School of Medicine Institutional Review Board approved this study, and all participants provided written informed consent.

Experimental Design

Before the experiment, we informed the participants that they would receive a fixed show-up fee of $25 and earn more money based on 10 randomly selected trials at the end of the fMRI session. After the fMRI session, we would endow participants with $25 prior to a monetary choice task and they would either earn or lose money from the endowed $25 based on one randomly selected choice at the end of the task. We revealed the total amount of compensation at the end of the experiment to minimize the effect of different status quo for the monetary choice task.

Reference-dependent Preferences Task When participants arrived at the laboratory, they read an experiment instruction package that guided them through the fMRI session. The fMRI experiment began with acquiring participants' maximum voluntary contraction (MVC, Fig 1A). They held the hand-held dynamometer in their dominant hand and squeezed as hard as possible when cued for three consecutive repetitions. Their MVC was calculated as an average maximum force over three repetitions and the force level was converted into effort, which was defined as force relative to MVC that 0 effort corresponded to no exertion while 100 effort corresponded to 80% of the participant's MVC.

Following that, participants performed a *Training* phase to train them in an understanding of the associations between the effort and a monetary payment (Fig 1B). This phase consisted of a total of 20 trials with 5 trials for each target payment from $1 to $4 in increments of $1 in a randomized order. Each trial started with a fixation cross (2-10 s) and Get Ready screen (1-2 s), followed by a training task (4 s) with an interactive vertical bar that filled up with a red bar until participants reached the target range (defined as ±2.5 effort levels of the target, corresponding to $0.25) by gripping the hand dynamometer, which then turned into a green bar. Participants were instructed to reach the target range as fast as possible and maintain the bar within the target range until they stopped seeing the bar.

Next, participants performed a *Recall* phase to test their understanding of the associations between the effort and its corresponding payment (Fig 1C). In this phase, participants viewed a

target reward (2-5 s) prior to the grip cue instead of the interactive vertical bar. We also did not provide the outcome of the associations (success or failure) for this phase. The number of trials was the same as the *Training* phase.

Lastly, participants performed a *Test* phase, consisting of 3 blocks of 32 trials in each block (Fig 1D). At the time of *Presentation*, each trial displayed two possible payments: 1) Fixed payment and 2) Wage payment with a 50/50 change for each payment. Fixed payment varied from $0.25 to $4 in increments of $0.25 and corresponded to a fixed amount of payment regardless of the effort exertion. The fixed payment was presented in a pseudo-randomized order, such that a set of 16 consecutive trials consisted of the full range of fixed payments in a randomized order. Wage payment corresponded to piece-rate payment in proportion to the amount of effort exerted. Participants did not actively select one payment, but rather they gripped the dynamometer to the amount worth for them. The computer program randomly selected one of the two payments, but the outcome was revealed after the effort exertion (*Outcome*). Participants were instructed to grip the dynamometer as quickly as possible and as hard as they wished and maintain the grip until they viewed the outcome. If participants failed to initiate gripping quickly enough (approximately 1 s) or maintain the grip within the 2.5 standard deviations of the last three seconds, that trial was considered a missed trial, and we did not include that in our final analyses. We computed piece-rate payment using the last two seconds of effort exertion in the case that Wage payment was selected.

Monetary Choice Task (Prospect Theory Task) At the completion of the fMRI session, participants received $25 as an endowment and read another instruction package for the monetary choice task outside of the scanner (Fig 1A). They were instructed that they could use the money to pay any potential losses that they may experience. They performed a series of gambles, which involved choosing between flipping a coin in which they had a 50/50 chance of winning or losing an amount of money; or a sure option in which the outcome is certain and occurs with 100% probability (*20*). If participants missed a choice within 4 seconds, the trial was considered a missed trial, and they lost $1 for each missed trial.

Experimental Setup

Presentation of visual stimuli and data acquisition for the experiment was achieved using custom MATLAB 2020b (MathWorks, Natick, MA) scripts using the *Psychtoolbox* Version 3 (Kleiner et al 2007). A hand clench dynamometer (TSD121B-MRI, BIOPAC Systems, Inc., Goleta, CA) was used to record the exerted grip force. Force signals were amplified 1000 times (DA100C, BIOPAC Systems, Inc., Goleta, CA) and sampled at 1,000Hz (NI-DAQ card, Model PCIe-6321, National Instruments, Austin, TX).

MRI Protocol MR images were acquired with a 3 Tesla Philips Achieva Quasar X-series MRI scanner and radio frequency coil located at the F.M. Kirby Research Center for Functional Brain Imaging at the Kennedy Krieger Institute. We collected high-resolution structural images using a standard magnetization-prepared rapid gradient echo (MPRAGE) pulse sequence, providing full brain coverage at a resolution of 1 mm × 1 mm × 1 mm. Functional images were acquired using an echo-planar imaging (FE EPI) pulse sequence (TR = 2800 ms, TE = 30 ms, FOV = 240 mm, flip angle = 70°) at an angle of 30° from the anterior commissure–posterior commissure (AC–PC) axis, which reduced signal dropout in the orbitofrontal cortex. Forty-eight slices were acquired at a resolution of 3 mm × 3 mm × 2 mm, providing whole-brain coverage.

We obtained a total of five runs of the functional images, consisting of *Training*, *Recall*, and three *Test* phases.

Data Analysis

Reference-dependent Effort Exertion Behavioral Analysis We tested the hypothesis that individuals would exert effort in reference to fixed payment using a linear mixed-effect model (LME) analysis. We also included trial numbers in the model as a proxy of physical fatiguability to confirm that the effort exertion was driven by the exogenous referent (fixed payment), not by physical fatiguability (trial numbers). Therefore, the dependent variable was effort exerted and the independent variables were fixed payment, trial numbers, and interaction between them with a random intercept of the participants.

Incentive Preference Task Analysis We used a 2-parameter model with a maximum likelihood procedure to estimate participants' loss aversion in a similar manner described by (*20*, *25*). We expressed the expected utility, U, of a mixed gamble as

$$U(G, L, S) = (0.5G + 0.5\lambda L) - S \tag{1}$$

where G, L, and S are the monetary value of gain, loss, and sure options, respectively, and λ represents the degree of a participant's loss aversion. The probability of choosing the gamble option for the *k*th trial is expressed as the softmax function as

$$P_k(U(G, L, S)) = 1/[1 + \exp\big(-\tau U(G, L, S)\big)] \tag{2}$$

where k = 1:140 and τ denotes a temperature parameter, corresponding to the stochasticity of a participant's choice (τ = 0 corresponds to random choice). The free parameters were estimated using a maximum likelihood function.

$$\sum_{k}^{140} y_k log\left(P_k\big(U(G, L, S)\big)\right) + (1 - y_k) log\left(1 - P_k\big(U(G, L, S)\big)\right) \tag{3}$$

y_k represents participant response $y \in \{0,1\}$ where y = 1 indicates that participant chose a gamble.

Image Processing and fMRI Statistical Analysis We used the SPM12 (Wellcome Trust Centre for Neuroimaging, Institute of Neurology, London, UK) software package to analyze the fMRI data. Functional images were 1) applied with a slice-timing correction, 2) realigned to the first image to reduce the effects of head movement, 3) normalized to the Montreal Neurological Institute (MNI) template, and 4) smoothed using a 3D Gaussian kernel (5 mm at full-width half maximum) to account for anatomical differences between participants.

The primary aim of the neuroimaging analysis was to identify regions of the brain that encode preferences based on a reference point. Thus, we generated first-level, voxel-wise statistical parametric maps for each participant using general linear models (GLMs) with two conditions (*Presentation and Outcome*). The *Presentation* was modeled with a block-based design to account for our experimental design that allowed participants to decide how much effort they would exert at any time within the entire period of the *Presentation*. This condition

included trial-by-trial fixed payment as exogenous reward expectation as parametric modulators. The *Outcome* was modeled with an event-related design and included the trial-by-trial difference between actual outcomes and expected value (0.5 × Fixed payment + 0.5 × Piece-rate payment) as parametric modulators, respectively. Further, we included missed trials and outlier trials (mean effort exertion ± 2 × standard deviation of effort exertion) as separate nuisance regressors. Head motion parameters derived from the affine part of the realignment procedure during preprocessing were also modeled as separate nuisance regressors. In addition, we calculated FD based on the head motion parameters as an additional nuisance regressor (*33*). If there existed frames that were 1 mm or higher FD, we created temporal masks of the data to specify frames to ignore during analysis. These temporal masks were included as nuisance regressors. Finally, we created contrasts with the above parametric modulators for each GLM per participant.

We performed second-level analyses using independent t-tests with the first-level contrasts. We set the initial criteria for significant results at $p < 0.005$ and cluster size (k) of 20 voxels. If the activity map further survived cluster correction, we presented the cluster-corrected results. For the VS as an *a priori* interest, we confirmed the results with a small-voxel correction (SVC) using a 5 mm sphere mask of the bilateral VS obtained from Neurosynth using a search term of *reward anticipation* (left center = [-10, 6, -8], right center = [12, 12, -12]). Moreover, we investigated whether individual differences in reference-dependent effort exertion or loss aversion were correlated with the regions of the brain that encode reference-dependent effort exertion by including the slope estimate of the effort exertion as a function of fixed payment or λ (subjective loss aversion), respectively, as a covariate in the second-level analyses.

Potential Confounding Variable Analysis We additionally tested potential confounding factors for (1) physical fatiguability, (2) history of reward (3) history of outcome type, and (4) history of effort exertion using LME analysis for each variable. The independent variable for each model was (1) trial numbers, (2) the magnitude of reward in the previous trial, (3) the type of outcome in the previous trial (either fixed or wage payment), and (4) the magnitude of effort exertion in the previous trial. The dependent variable was an effort at the current trial for all models.

Because the history of effort exertion was significant, we performed a Pearson's correlation between individual differences in the history of effort exertion and reference-dependent effort exertion. Moreover, we used the individual differences in the history of effort exertion as an additional covariate in the second-level analysis on SPM.

Supplementary Text

Reward-effort Associations during *Training* and *Recall* Phase

Participants had a good understanding of the reward-effort associations after practice (**Fig. S1**). We compared effort exertion for a given fixed payment between the *Training* and *Recall* phases to confirm that individuals were able to exert correct effort for fixed payment without visual feedback during *Recall*. A linear mixed-effects model revealed that there was no significant difference in effort exertion between the *Training* and *Recall* phases ($t = 0.72$, $p = 0.47$), demonstrating that effort exertion without visual feedback was similar to exertion with visual feedback.

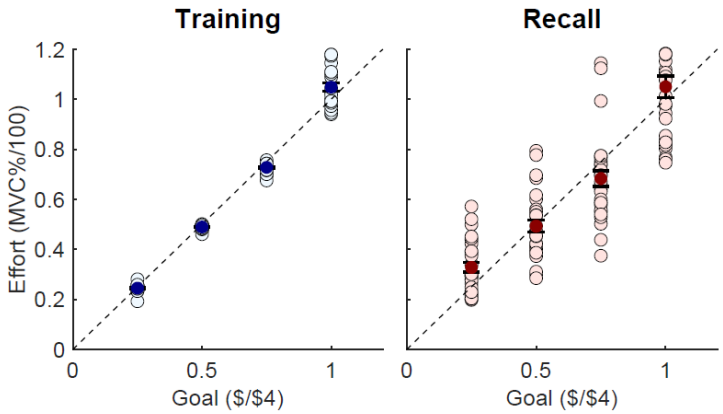

Fig. S1.
Effort exertion as a function of goal payment during the *Training* and *Recall* phases. Both the goal payment and effort exertion were normalized to 1 by dividing the maximum unit. The lighter points represent individual data points for effort exertion and the darker points represent means of effort exertion for each goal payment. The black error bars represent the standard error of the mean. The dotted line is a unity line.

Loss Aversion Measured by Incentive Preference Task

We used maximum likelihood to estimate participants' loss aversion λ and temperature parameter τ. We excluded participants 1) if they made less than five choices for one of the options and 2) if τ is less than 0.001 (inconsistent or random choices), resulting in a total of 25 out of 30 participants. The majority of participants showed some degree of loss aversion (n = 22, median [Q1-Q3]: 1.45 [1.13-1.92], **Fig. S2**) with median τ [Q1-Q3] of 1.33 [0.73-2.12]. Because λ had a non-normal distribution, we log-transformed λ for correlation analysis to test if the degree of loss aversion would explain individual differences in reference-dependent effort exertion (r = -0.21, p = 0.33, **Fig. S3**).

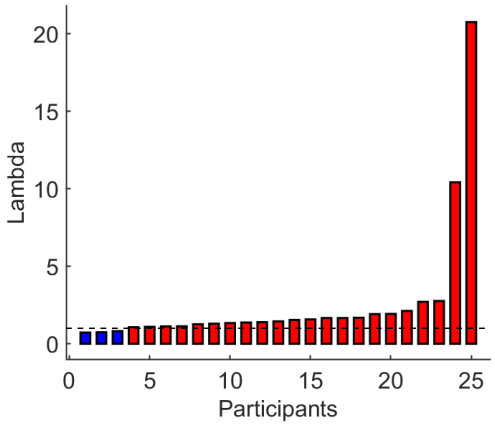

Fig. S2.
Individual λ estimated from the maximum likelihood procedures. λ > 1 indicates loss aversion (red), λ = 1 indicates loss neural (dotted line), and λ < 1 indicates no loss aversion (blue).

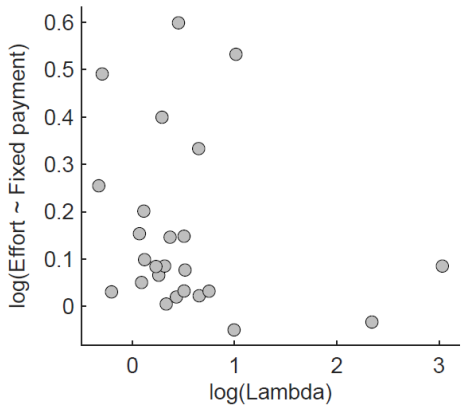

Fig. S3.
Correlation between reference-dependent effort exertion and the degree of loss aversion. Due to the non-normality of the estimations, we log-transformed both variables. Each data point represents a participant.

Potential Confounding Factors

LME analyses exhibited that physical fatiguability, history of reward, and history of outcome type were not significantly associated with effort exertion (Fig. S4). However, there was a significant effort in the history of effort exertion ($t = 12.08$, $p < 0.001$, Fig. S4). The individual difference in the degree of the history effect of effort was negatively correlated with individual differences in reference-dependent tendency of effort exertion ($r = -0.47$, $p = 0.008$, Fig. S5).

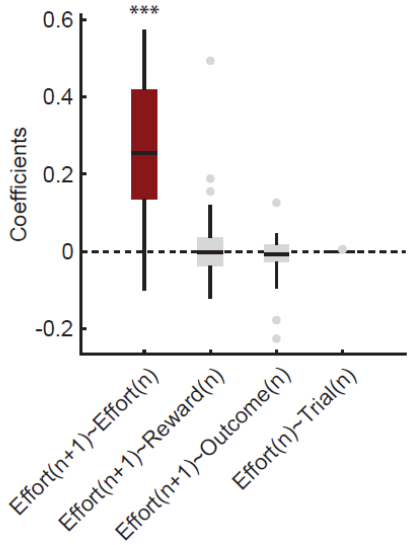

Fig. S4.
Coefficients from regression models for potential confounds. The range of the box represents the 25th and 75th percentile of the data and the black horizontal line inside the box represents the median over all participants. Whiskers represent the minimum and maximum range. Single data points outside of the whiskers are outliers that are lesser or greater than the 1.5x value of the box range.

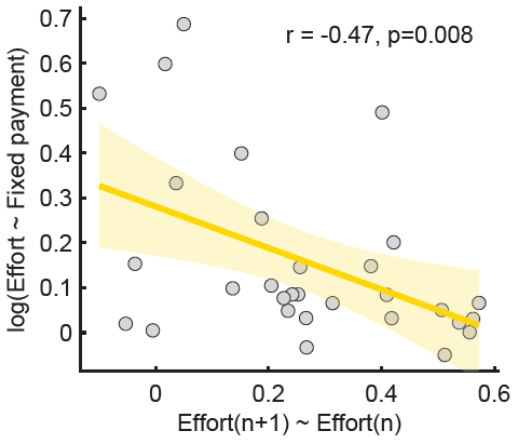

Fig. S5.

Correlation between the effort of effort history on the subsequent effort exertion and reference-dependent effort exertion. Due to the non-normality of the estimations, we log-transformed reference-dependent effort exertion. Each data point represents a participant. The yellow line and shade represent the fitted line and standard error of the mean from the regression model.

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