



# Cognitive and neural bases of visual-context-guided decision-making

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## ABSTRACT

Humans adjust their behavioral strategies based on feedback, a process that may depend on intrinsic preferences and contextual factors such as visual salience. In this study, we hypothesized that decision-making based on visual salience is influenced by habitual and goal-directed processes, which can be evidenced by changes in attention and subjective valuation systems. To test this hypothesis, we conducted a series of studies to investigate the behavioral and neural mechanisms underlying visual salience-driven decision-making. We first established the baseline behavioral strategy without salience in Experiment 1 ( $n = 21$ ). We then highlighted the utility or performance dimension of the chosen outcome using colors in Experiment 2 ( $n = 30$ ). We demonstrated that the difference in staying frequency increased along the salient dimension, confirming a salience effect. Furthermore, the salience effect was abolished when directional information was removed in Experiment 3 ( $n = 28$ ), suggesting that the salience effect is feedback-specific. To generalize our findings, we replicated the feedback-specific salience effects using eye-tracking and text emphasis. The fixation differences between the chosen and unchosen values were enhanced along the feedback-specific salient dimension in Experiment 4 ( $n = 48$ ) but unchanged after removing feedback-specific information in Experiment 5 ( $n = 32$ ). Moreover, the staying frequency was correlated with fixation properties, confirming that salience guides attention deployment. Lastly, our neuroimaging study (Experiment 6,  $n = 25$ ) showed that the striatum subregions encoded salience-based outcome evaluation, while the vmPFC encoded salience-based behavioral adjustments. The connectivity of the vmPFC-ventral striatum accounted for individual differences in utility-driven, whereas the vmPFC-dmPFC for performance-driven behavioral adjustments. Together, our results provide a neurocognitive account of how task-irrelevant visual salience drives decision-making by involving attention and the frontal-striatal valuation systems.

**Public significance statement:** Humans may use the current outcome to make behavior adjustments. How this occurs may depend on stable individual preferences and contextual factors, such as visual salience. Under the hypothesis that visual salience determines attention and subsequently modulates subjective valuation, we investigated the underlying behavioral and neural bases of visual-context-guided outcome evaluation and behavioral adjustments. Our findings suggest that the reward system is orchestrated by visual context and highlight the critical role of attention and the frontal-striatal neural circuit in visual-context-guided decision-making that may involve habitual and goal-directed processes.

## 1. Introduction

Humans adjust their future behaviors based on the outcome of their current actions, which can be from the utility (e.g., gain or loss), performance (e.g., correct or incorrect choice), or both. One of the well-established behavioral strategies deployed during outcome-based adjustments is to stay with the same option as the current one on the subsequent trial after rewarded/correct feedback but switch to the alternative

choice after non-rewarded/incorrect feedback (Cavanagh et al., 2010; Chau et al., 2014; Cohen and Ranganath, 2007; Rudebeck et al., 2013). In other words, humans follow the win-stay loss-shift (WSLS) or correct-stay incorrect-shift (CSIS) strategy to adjust their behavior. These actions may reflect our spontaneous thoughts and habitual preference and can be influenced by contextual factors such as salient texts or colors. However, how humans learn about contextual influences that further guide decision processes is yet to be determined. Under the hypothesis

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that visual salience-driven decisions may automatically recruit attention and subjective valuation systems, we examined the behavioral and neural bases of visual salience-guided outcome evaluation and behavioral adjustments.

The visual salience-driven valuation and decision-making may reflect how bottom-up visual attention interacts with the internal system by integrating habitual and goal-directed learning processes. The deployment of attentional gain selectively emphasizes forward connections and links with inner beliefs to plan the next move (Itti and Koch, 2001; Parr and Friston, 2019). Specifically, emphasizing a specific aspect of outcomes increases behavioral switching along the salient outcome dimension, even if such salient information is redundant (Sun and Wang, 2020; Sun et al., 2020). The ventral striatum and ventromedial prefrontal cortex (vmPFC) are well known for their functions in value-based outcome evaluation and action selection, which further guide goal-directed and habitual decisions (Bartra et al., 2013; Gläscher et al., 2009; Lebreton et al., 2009; Lim et al., 2011; Rangel and Hare, 2010). Individual variations in goal-directed and habitual reinforcement learning can be explained by the anatomical connectivity in the frontostriatal circuit, specifically the vmPFC and medial striatum (Piray et al., 2016). A recent meta-analysis has revealed that the medial prefrontal cortex, particularly the vmPFC, is involved in goal-directed learning, while the dorsal striatum is implicated in habitual learning, and the ventral striatum plays a role in both types of learning (Huang et al., 2020). Building on these findings, we hypothesize that salient visual context can potentially influence the allocation of attention during outcome evaluation and subsequently guide behavioral adjustments by engaging the subregions of the striatum and vmPFC.

The striatum, with its dissociable functions in the ventral and dorsal portions, has been implicated in salience processing in numerous human neuroimaging and non-human neurophysiology studies (Cooper and Knutson, 2008; Zaehle et al., 2013; Zink et al., 2006, 2004, 2003). Our previous electroencephalogram (EEG) studies have revealed that the feedback-related negativity (FRN) and P300 are influenced by the salience of feedback (Sun and Wang, 2020; Sun et al., 2020). The FRN is originated from the rostral anterior cingulate cortex, which is close to the vmPFC (Nieuwenhuis et al., 2005; Walsh and Anderson, 2012), and the FRN amplitude is positively correlated with fluctuations in the blood-oxygen-level-dependent (BOLD) signals of the ventral striatum and medial prefrontal cortex (mPFC) (Carlson et al., 2011). In addition, the P300 is related to the ventral striatum BOLD response (Pfabigan et al., 2014). These source localization and neuroimaging findings suggest that the striatum and mPFC are involved in processing feedback that is sensitive to salience. Furthermore, these findings indirectly link the striatum and mPFC to the valuation and decision-making processes that are modulated by salience.

To directly examine these links, we employed a simple gambling task where participants chose between two options and quantified the frequency that participants stayed with the same option or switched to an alternative option after observing the feedback. Building on our prior EEG studies that employed *text* emphasis for salience modulation (Sun and Wang, 2020; Sun et al., 2020), in this study, we further examined the attentional deployment and frontal-striatal connectivity during the salience modulation process in separate experiments. Critically, we highlighted either the utility (win or loss) or performance (correct or incorrect) dimension of the *chosen* outcome. We found that the difference in staying frequency was enlarged along the highlighted dimension. When using non-specific salience emphasis of the outcome (i.e., only the utility or performance dimension was emphasized but not the specific outcome), such salience effect was abolished. Moreover, the salience-guided behavioral pattern could be explained by the fixation difference between chosen and unchosen values under specific but not non-specific salience manipulation. We also investigated the neural mechanisms underlying this salience-guided decision-making process using functional magnetic resonance imaging (fMRI). Our findings

suggested that the subregions of the striatum were involved in salience-based outcome evaluation, while the ventromedial prefrontal cortex (vmPFC) was implicated in salience-based behavioral adjustments. Furthermore, the functional connectivity between the vmPFC and the striatum (when utility was emphasized) or dorsomedial prefrontal cortex (dmPFC) (when performance was emphasized) accounted for individual differences in salience-guided outcome-specific behavioral adjustments.

## 2. Materials and methods

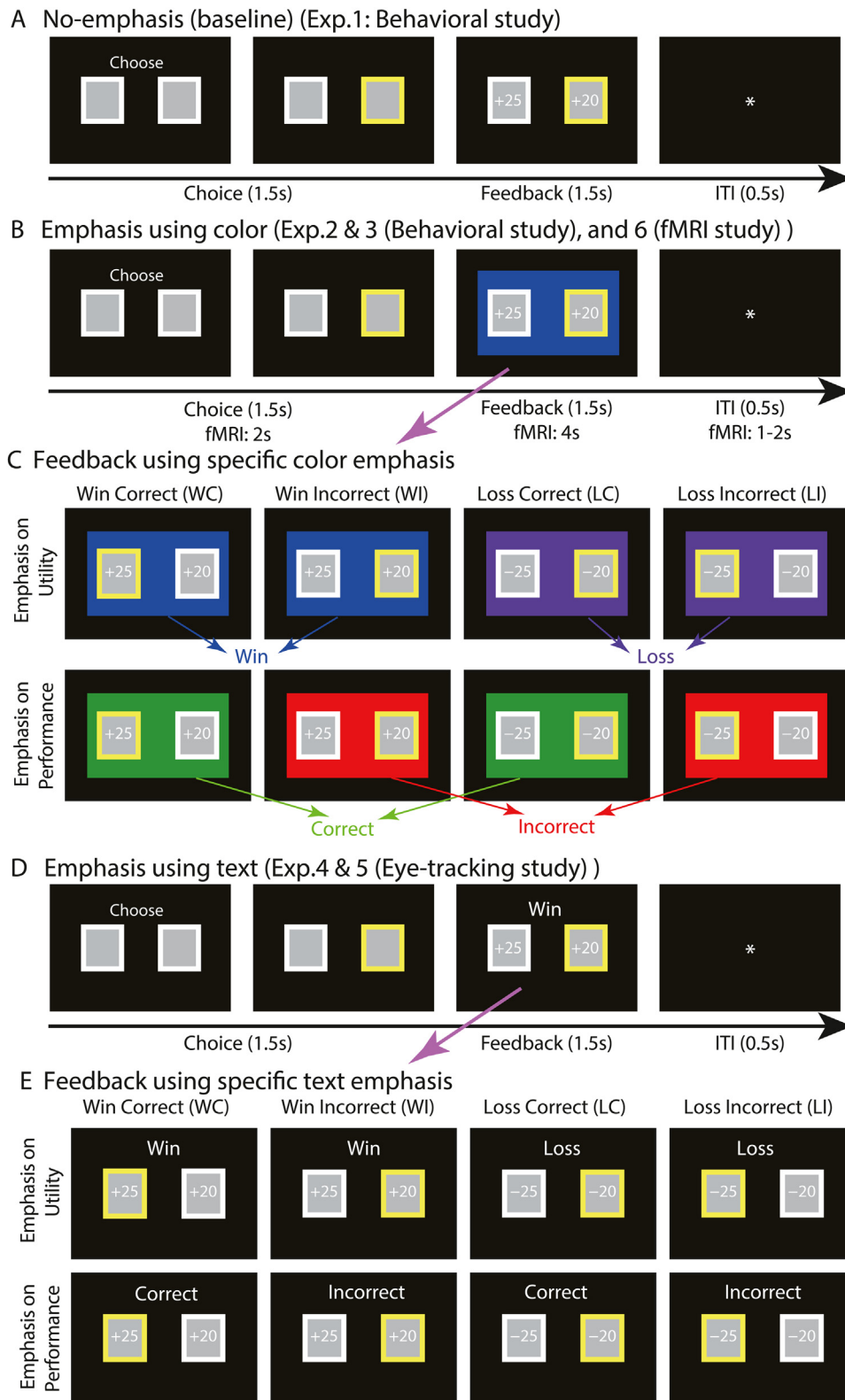
We closely followed the procedures from our previous work (Sun and Wang, 2020; Sun et al., 2020), with appropriate variations noted, and replicated Experiment 1 with more participants. The main differences between the previous work and this study are the salience manipulation and behavioral generalization (*color* in Experiment 2&3&6 vs. *text* in Experiment 4&5), salience-driven attention deployment using eye-tracking (Experiment 4&5), and salience-driven neural correlates using fMRI (Experiment 6). This study was not preregistered.

In Experiment 1, we established the baseline behavior by using no salience emphasis, which was reported in our prior work (Sun and Wang, 2020; Sun et al., 2020). In Experiment 2, we used informative color emphasis highlighting a specific dimension of the chosen outcome, e.g., correct or incorrect. In Experiment 3, we used uninformative color emphasis that only highlights the dimension to attend to without directional information, e.g., performance dimension. In Experiment 4 and 5, we replicated our behavioral findings in Experiment 2 and Experiment 3 using informative and non-informative text emphasis, respectively. Further, we demonstrated salience-guided attention deployment with simultaneous eye movements recording. Finally, in Experiment 6, we delineated the neural correlates of salience-guided outcome evaluation and behavioral adjustments using fMRI.

### 2.1. Participants

Twenty-one participants (12 females/9 males; mean age  $\pm$  SD:  $22.46 \pm 1.83$  years) participated in Experiment 1 (Behavioral study with *no* emphasis). Thirty participants (25 females/5 males;  $21.53 \pm 2.24$  years) participated in Experiment 2 (Behavioral study with *specific color* emphasis). Twenty-eight participants (17 females/11 males;  $20.89 \pm 2.45$  years) participated in Experiment 3 (Behavioral study with *non-specific color* emphasis). Sixty-two participants were recruited for Experiment 4 (Eye-tracking study with *specific text* emphasis). Fourteen eye-tracking participants from Experiment 4 were dropped from further analysis due to the high rejection rate of trials ( $>17\%$ ), including trials in which responses were initiated too quickly ( $<100$  ms) during the choosing period and those in which the fixation duration for either of the two cards is less than 100 ms. The remaining eye-tracking participants were 48 (31 females/17 males;  $20.63 \pm 2.88$  years) for Experiment 4. Thirty-eight participants were recruited for Experiment 5 (Eye-tracking study with *non-specific text* emphasis). Six participants from Experiment 5 were excluded due to the low proportion of validated trials, leaving 32 (17 females/15 males;  $20.90 \pm 2.11$  years) for Experiment 5. Twenty-eight participants participated in Experiment 6 (fMRI study with *specific color* emphasis), and 3 of them were dropped from further analysis due to strong head motions ( $>3$  mm, in x, y, and z-axis), leaving 25 participants (17 females/8 males;  $22.15 \pm 2.40$  years). All participants are Chinese and were recruited by advertisement. The demographic information about gender, age, education levels, and major was collected via an online registration form with a short answer. All participants reported no neurological or psychiatric disorders. All participants provided written informed consent, and the research protocols were approved by the Institutional Review Board of South China Normal University. All participants were told that they could discontinue participation at any time.





**Fig. 1.** Task and stimuli. (A) Task structure for Experiment 1. Participants were presented with two gambling cards and then were asked to choose one. The chosen card was highlighted in yellow. Then the outcomes associated with the chosen and unchosen cards were shown, followed by an inter-trial interval. (B) Task procedure for Experiment 2, 3, and 6. A colored rectangle (e.g., blue for the “Win”) was used to emphasize a specific outcome and task dimension. (C) In Experiment 2 (specific color emphasis), four types of colored emphasis were used (e.g., blue for the win, purple for loss, green for correct, and red for incorrect). In Experiment 3 (non-specific color emphasis), four colors (e.g., red/green for utility and blue/purple for performance) were used but the same color was assigned for different types of utility (win/loss) or performance (correct/incorrect). (D) Task procedure in Experiment 4 and 5. A non-colored text (e.g., “Win”) was used to indicate the emphasized dimension. (E) In Experiment 4 (specific text emphasis), participants were explicitly told the association between the texts and chosen outcome (e.g., “+” for Win, “-” for Loss, “a larger reward or a smaller penalty” for Correct, and “a smaller reward or a larger penalty” for Incorrect). In Experiment 5 (non-specific text emphasis), a similar procedure as Experiment 4 was performed except that a non-specific outcome message (“Win or Loss”, “Correct or Incorrect”) about the emphasized dimension was displayed above the outcomes.

## 2.2. Stimuli and procedure

We employed a well-established paradigm to study the behavioral adjustment (Sun and Wang, 2020; Sun et al., 2020). Participants were presented with two gambling cards (rough visual angle  $15^\circ \times 8^\circ$ ). Then they were asked to choose one by pressing the “F” (for the left card) or

“J” (for the right card) button within 1.5 s using the keyboard (Fig. 1A, B, D; 2 s for fMRI experiment, “1” (for the left card) or “3” (for the right card) button). Participants were informed that they were too slow if they failed to respond within this time window. The chosen card was highlighted by a yellow box for 1.5 s (2 seconds for the fMRI experiment). Subsequently, the outcomes associated with both cards were presented



for 1.5 s (4 seconds for the fMRI experiment). The inter-trial interval (ITI) is 0.5 s for behavioral experiments (jittered randomly with a uniform distribution between 1 and 2 s for the fMRI experiment). The task was implemented in E-prime 2.0 (Psychology Software Tools, Inc. Pittsburgh, PA, USA, [www.pstnet.com/e-prime](http://www.pstnet.com/e-prime)).

The chosen card yields either a reward or a penalty (Fig. 1C, E). The comparison between the chosen outcome and the unchosen outcome indicates that the choice is either correct (i.e., chosen outcome is better than the unchosen outcome) or incorrect. The four combinations were explicitly explained to participants (see Fig. 1C, E for examples). Unbeknownst to participants, all outcomes were predetermined and pseudo-randomized across conditions. The value of the chosen card was randomly selected from a uniform distribution ranging from  $-40\text{¥}$  to  $+40\text{¥}$  (about \$6). The value of the unchosen card was also randomly selected with the constraint that the absolute difference between the chosen and unchosen outcomes was between  $2\text{¥}$  and  $20\text{¥}$  (\$0.3 to \$3). Participants were told their goal was to maximize their rewards, and they were free to use any strategies. Participants were informed that one randomly selected trial would be implemented on top of their base payment of  $60\text{¥}$  (about \$9). Participants did ten practice trials before proceeding to the formal testing.

### 2.3. Salience manipulation

Each participant underwent two sessions. In Experiment 1 (Fig. 1A), both sessions were the same and had no salience emphasis. This baseline condition has been reported in our previous study (Sun and Wang, 2020; Sun et al., 2020). In Experiment 2–6, each session had a different salience manipulation (emphasizing one of the task aspects using either *color* (Fig. 1B, Experiment 2, 3, and 6) or *texts* (Fig. 1D, Experiment 4 and 5). For example, to emphasize utility (win/loss) or performance (correct/incorrect), a colored rectangle (i.e., highlight) was displayed around the outcomes of the cards (Fig. 1B), or a non-colored text was displayed above the outcomes of the cards (Fig. 1D). In Experiment 2, the highlight was specific to the outcome. The meaning of colors was explained to participants (e.g., blue for the win, purple for loss, green for correct, and red for incorrect; see Fig. 1C for examples, corresponding to Fig. 1B), and colors were randomly assigned to each outcome across participants. However, in Experiment 3, two colors (e.g., red/green for utility and blue/purple for performance) were presented randomly for each session. Participants were told that when red/green was presented, they should pay attention to the utility (i.e., win/loss) dimension of the outcomes. In contrast, when blue/purple was presented, they should pay attention to the performance (i.e., correct/error) dimension. Compared to Experiment 2, the highlight in Experiment 3 only reminded participants which dimension they should focus on without providing directional information about the chosen outcome.

Except for the *color* emphasis (perceptual salience), two independent behavioral experiments using *text* emphasis (semantic salience) were performed to quantify the attentional deployment combined with simultaneous eye movements recorded in Experiment 4 and 5 (Fig. 1D). In Experiment 4, participants were explicitly told the association between the texts and chosen outcome (e.g., “+” for Win, “−” for Loss, “larger positive value or smaller negative value” for Correct, and “larger negative value or smaller positive value” for Incorrect; see Fig. 1E for examples, corresponding to Fig. 1D). In Experiment 5, a similar procedure as Experiment 4 was performed except that a non-specific highlight message about the emphasis dimension (“Win or Loss”, “Correct or Incorrect”) was displayed. Lastly, a similar procedure as Experiment 3 (Fig. 1B) was performed to demonstrate the functional role of a frontal-striatal circuit in salience-guided outcome evaluation and behavioral adjustments combined with fMRI.

The colors were counterbalanced across participants for Experiment 2, 3, and 6 across two sessions (salience emphasis) and outcomes. Each session consisted of 2 blocks of 80 trials each for the behavioral study (Experiment 2 and 3), two blocks of 60 trials each for the eye-tracking

study (Experiment 4 and 5), and two blocks of 50 trials each for the fMRI study (Experiment 6). There was a short break between two blocks.

### 2.4. Subjective rating

After the Eye-tracking and fMRI experiment, participants were debriefed and required to indicate how satisfied and surprised they felt for the 8 examples of outcomes (WL, WI, LC, and LI for each session) using an 11-point analog Likert scale (0 = not at all, 10 = very intensely).

### 2.5. Eye-tracking data acquisition and analysis

Participants' eye movements were recorded with a head-supported contactless infrared-based video-camera EyeLink 1000 System (SR Research Ltd). Monocular data was captured at a sampling rate of 1000 Hz. Participants were seated in a dimly lit and sound-attenuated room at a viewing distance of 60 cm from a 20-inch Lenovo CRT display (with  $1024 \times 768$  screen resolution). Saccade was detected when there was a deflection larger than  $0.1^\circ$ , with a minimum velocity of  $30^\circ/\text{s}$  and a minimum acceleration of  $8000^\circ/\text{s}$ . Fixations were defined as periods without saccades, with a resolution of  $5 \mu\text{m}$  ( $0.005 \text{ mm}$ ). We focused on eye movement data in two regions of interest (ROIs) (the two rectangles for the two cards) within the 1.5 s after the stimuli presentation.

### 2.6. Statistics

A salience (utility vs. performance)  $\times$  utility (win vs. loss trials)  $\times$  performance (correct vs. incorrect trials) repeated-measures ANOVA was performed separately on staying frequency, fixation duration, and subjective ratings. Greenhouse-Geisser corrections were used when sphericity was violated.

### 2.7. MRI data acquisition and analysis

MRI scanning was conducted on a 3-Tesla Siemens Tim Trio scanner using a standard 12-channel head coil. Echo-planar T2\*-weighted imaging (EPI) data was acquired with the following parameters: 32 oblique axial slices; 3.9 mm thickness; 3 mm in-plane resolution; repetition time (TR) = 2150 ms; echo time (TE) = 30 ms; flip angle =  $90^\circ$ ; FOV = 112 mm. T1-weighted images were acquired at a resolution of  $1 \times 1 \times 1 \text{ mm}$ .

Functional MRI data were processed using SPM12 ([www.fil.ion.ucl.ac.uk/spm/](http://www.fil.ion.ucl.ac.uk/spm/)). The first five volumes were discarded to account for stabilization. EPI images were slice-timing corrected and then realigned to the first scan by rigid-body transformations to correct for head movements. The data were smoothed with a Gaussian kernel of full-width-half maximum 6 mm and co-registered and normalized to the T1 MNI 152 template (Montreal Neurological Institute, International Consortium for Brain Mapping). High-pass temporal filtering with a cutoff of 128 s was applied to remove low-frequency drifts in the signal.

To investigate the neural activities related to outcome evaluation, we constructed a general linear model (GLM) at the onset of outcome evaluation with a factorial design (win vs. loss  $\times$  correct vs. incorrect) for each salience emphasis. The values of the chosen and unchosen cards were modeled as parametric modulators (see Fig. S6 and Table S1). In addition, six head-motion parameters were modeled as regressors of no interest. The second-level group analysis applied a random-effects statistical model on the contrast images (Penny and Holmes, 2007). For whole-brain analysis, activations were reported if they survived  $P < 0.001$  uncorrected, cluster size  $k > 20$ .

To further test our hypothesis (Delgado et al., 2003; Lim et al., 2011; O'Doherty et al., 2004; Oyama et al., 2015), we conducted a region-of-interest (ROI) analysis. Three ROIs, including Caudate, Putamen, and Nucleus Accumbens (NAcc) were obtained from the WFU PickAtlas (<http://fmri.wfubmc.edu/software/PickAtlas>). For ROI analysis, activations were reported if they survived  $P < 0.05$  family-wise error (FWE) after small volume correction (SVC) at the voxel level.



To investigate the neural activities related to behavioral adjustment, we used an event-related design and constructed another GLM at the onset of outcome evaluation with a factorial design (win vs. loss X correct vs. incorrect X stay vs. switch) separately for each emphasis. Eight conditions were included in the GLM as regressors depending on the category of outcome (win, loss, correct, incorrect) and subsequent behavioral choice (stay or switch): stay win, stay loss, stay correct, and stay incorrect, switch win, switch loss, switch correct, switch incorrect. In addition, six head-motion parameters defined by the realignment were added to the model as regressors of no interest. Notably, to study the effect of salience modulation, in the first-level analysis, we used the contrast of [Stay(W–L) – Switch(W–L)] and [Stay(C–I) – Switch(C–I)] for both salience emphases, which could reveal whether salience-emphasized task dimension (i.e., [Stay(W–L) – Switch(W–L)] congruent with the emphasis on utility and [Stay(C–I) – Switch(C–I)] congruent with the emphasis on performance) could elicit a stronger neural response. The putamen, caudate, NAcc, and vmPFC were defined as ROIs for this analysis (Huang et al., 2020; Zink et al., 2006, 2004, 2003).

Lastly, a psychophysiological interaction (PPI) analysis was conducted. The physiological connectivity between two brain regions could also vary with the psychological context, known as the psychophysiological interaction (PPI) (Friston et al., 1997). We placed the seed in the vmPFC and used the contrast [Stay(W–L) – Switch(W–L)] for emphasis on utility and [Stay(C–I) – Switch(C–I)] for emphasis on performance to identify brain regions that showed differential connectivity in response to salience. The first GLM was then performed with three regressors (1) the main effect of vmPFC activity (estimated volume of interest signals from a 6-mm-radius sphere), (2) the main effect of the behavioral effect, and (3) the interaction effect between the vmPFC and the behavioral effect (PPI.ppi).

### 3. Results

#### 3.1. Behavior: salience emphasis modulated behavioral strategy

To investigate the impact of feedback and salience emphasis on participants' decision-making strategies, we analyzed the frequency of choosing a same card in the subsequent trial. The staying/switching frequency can index the behavioral strategies. Prior studies on reinforcement learning have consistently shown that individuals tend to stick with the same option after a gain, but opt for a different choice after a loss or suboptimal decision (Cavanagh et al., 2010; Cohen and Ranganath, 2007). Here, we explored whether salience manipulation could alter the frequency of choosing the same option repeatedly.

We first established the baseline performance in Experiment 1 among 21 subjects (Fig. 2A), where we did not have any salience emphasis. Participants tended to stick with the same option more frequently following correct trials than incorrect trials (two-tailed paired *t*-test:  $t(20) = 4.24$ ,  $P < 0.001$ , Cohen's  $d = 0.94$ ). However, there was no significant difference between win and loss trials ( $t(20) = 1.49$ ,  $P = 0.14$ ,  $d = 0.33$ ).

We next included salience modulation in Experiment 2 (Fig. 2B). The difference in staying frequency following win vs. loss (W–L) trials was congruent with the emphasis on utility and was thus salient when the utility was emphasized. This was confirmed by a significant interaction between salience emphasis and utility ( $F(1, 29) = 9.11$ ,  $P = 0.0053$ ,  $\eta_p^2 = 0.24$ ). Indeed, participants stay more frequently following win trials (mean  $\pm$  SD:  $53.57\% \pm 15.53\%$ ) than loss trials ( $41.52\% \pm 17.38\%$ ) when the utility was emphasized ( $t(29) = 4.17$ ,  $P = 2.52 \times 10^{-4}$ ,  $d = 0.77$ ; see Supplementary Fig. S1A, B for absolute staying frequency), which was significantly stronger than the W–L effect in the no emphasis condition. However, this was not the case when performance was emphasized ( $t(29) = 1.94$ ,  $P = 0.061$ ,  $d = 0.36$ ), suggesting that emphasis on utility specifically increased staying frequency following win trials.

On the other hand, the difference in staying frequency following correct vs. incorrect (C – I) trials was congruent with the emphasis on performance and was thus salient when performance was emphasized. An

interaction between salience and performance was also observed ( $F(1, 29) = 4.10$ ,  $P = 0.05$ ,  $\eta_p^2 = 0.13$ ): although participants stayed more frequently following correct trials than incorrect trials when either utility ( $25.36\% \pm 29.81\%$ ;  $t(29) = 4.07$ ,  $P = 3.31 \times 10^{-4}$ ,  $d = 0.76$ ) or performance ( $14.60\% \pm 19.64\%$ ;  $t(29) = 4.66$ ,  $P = 6.52 \times 10^{-5}$ ,  $d = 0.87$ ) was emphasized, the difference was more significant when performance was highlighted ( $t(29) = -2.03$ ,  $P = 0.05$ ,  $d = -0.38$ ), which was significantly stronger than the C–I effect in the no emphasis condition. Our results suggest that salience emphasis can increase the difference for the congruent (thus salient) task aspect. Therefore, adjustment of behavior (shown in staying frequency) can be modulated by salience emphasis.

In addition, no difference in staying frequency was found for the first half vs. second half of the trials (four-way repeated-measure ANOVA of salience X utility X performance X group (first vs. second): no effects involving the group was significant  $P_s > 0.05$ , suggesting that participants didn't show any significant improvement throughout the experiment.

Lastly, we analyzed response times (RT) for behavioral adjustment. No significant difference in RT was found when participants made either stay or switch choices (all  $P_s > 0.05$ ), indicating an equal response effort that was not influenced by salience or outcome.

#### 3.2. Behavior: non-specific salience emphasis did not modulate behavioral strategy

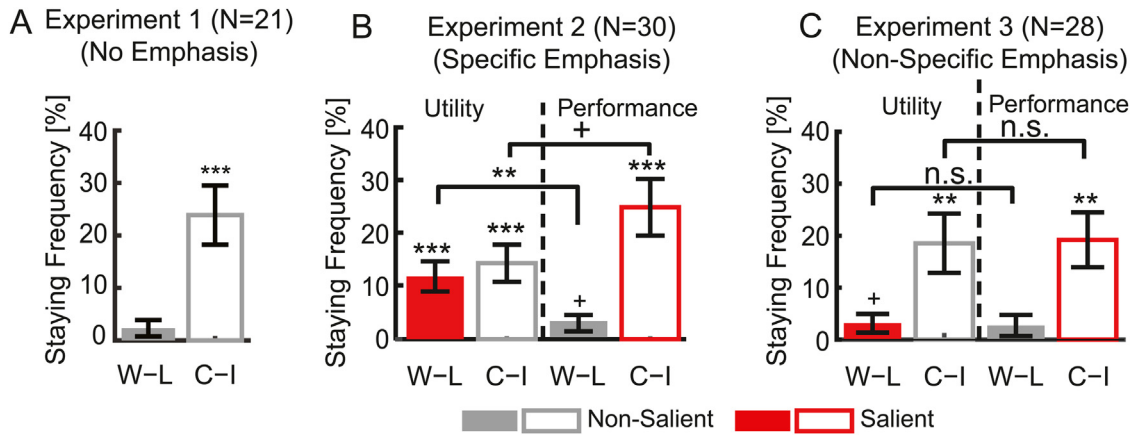
To test whether salience emphasis had to be specific about the chosen outcome, we conducted Experiment 3 with non-specific salience emphasis—only the dimension of the emphasis (utility or performance) was indicated to participants, but not the trial-by-trial specific emphasis on the chosen outcome. Here, we found that salience modulation was abolished (Fig. 2C): we found no significant interaction between salience and utility ( $F(1, 27) = 0.039$ ,  $P = 0.844$ ,  $\eta_p^2 = 0.001$ ; see Supplementary Fig. S1C, D for absolute staying frequency). Specifically, we found no significant difference in staying frequency between win and loss trials when either utility or performance was emphasized (both  $P_s > 0.1$ ), similar to Experiment 1 (Fig. 2A). On the other hand, no significant interaction between salience and performance was found ( $F(1, 27) = 0.035$ ,  $P = 0.852$ ,  $\eta_p^2 = 0.001$ , although participants stayed more frequently after correct trials than incorrect trials when either utility ( $19.82\% \pm 31.72\%$ ) or performance ( $21.39\% \pm 29.75\%$ ) was emphasized. Therefore, when salience emphasis was not specific to the outcome, there was no significant difference between different salience emphases. Our results suggest that non-specific salience emphasis did not modulate behavioral strategies.

#### 3.3. Eye-movement results: salience enhanced the fixation difference along the salient dimension

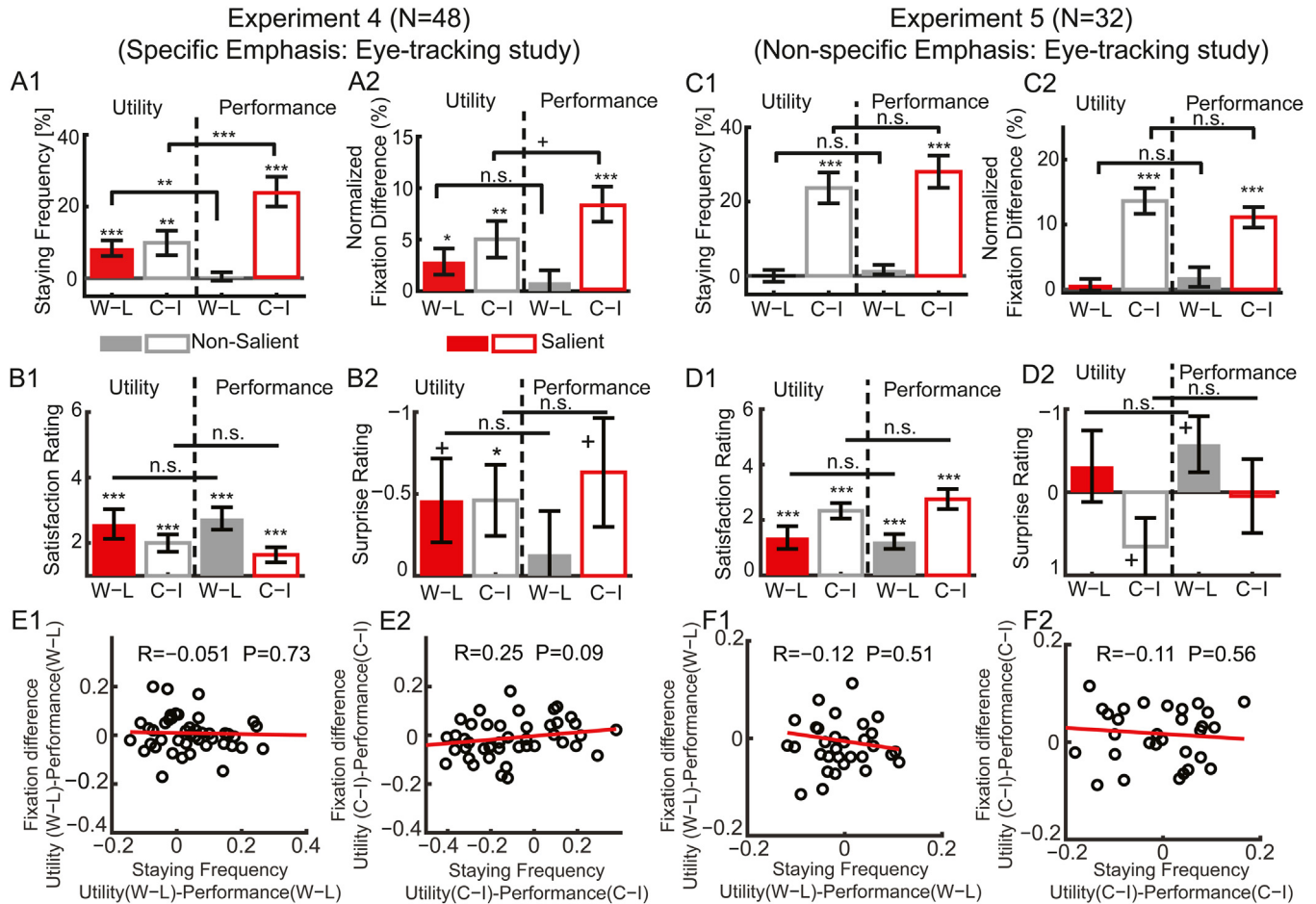
To generalize our behavioral findings, we first replicated our behavioral result in Experiment 2 (color emphasis) with an independent sample of 48 eye-tracking participants in Experiment 4 (text emphasis). Specifically, we identified a significant interaction between salience and utility ( $F(1, 47) = 11.33$ ,  $P = 0.002$ ,  $\eta_p^2 = 0.90$ , Fig. 3A1). When utility was emphasized, participants stayed more frequently following win trials than loss trials ( $t(47) = 3.83$ ,  $P < 0.001$ ,  $d = 0.55$ ; see Supplementary Fig. S1E, F for absolute staying frequency), but not when performance was emphasized ( $t(47) = 0.45$ ,  $P = 0.65$ ,  $d = 0.06$ ). In addition, the difference between the two emphases was significant:  $t(47) = 3.36$ ,  $P = 0.001$ ,  $\eta_p^2 = 0.49$ .

In addition, we identified a significant interaction between salience and performance ( $F(1, 47) = 16.67$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.98$ , Fig. 3A1). Participants stayed more frequently following correct than incorrect trials when either utility ( $t(47) = 2.87$ ,  $P = 0.007$ ,  $d = 0.41$ ) or performance ( $t(47) = 5.84$ ,  $P < 0.001$ ,  $d = 0.85$ ) was emphasized. Furthermore, the difference was enhanced along the salient dimension:  $t(47) = -4.08$ ,  $P < 0.001$ ,  $d = -0.59$ .





**Fig. 2.** Behavioral results for Experiment 1 to 3. (A) Experiment 1. When there was no salience emphasis, participants stayed more frequently following correct trials than incorrect trials, but there was no significant difference between win and loss trials. The y-axis shows the percentage of trials participants stayed with the same choices in the next trial. (B) Experiment 2. Specific salience emphasis increased the difference in staying frequency congruent to the emphasized dimension. (C) Experiment 3. Non-specific salience emphasis did not increase the difference in staying frequency congruent to the emphasized dimension. W-L: win-loss; C-I: correct–incorrect. Error bars denote one SEM across participants. Asterisk indicates a significant difference using two-tailed one-sample *t*-test: +:  $P < 0.1$ , \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , and \*\*\*:  $P < 0.001$ . n.s.: not significant. Red: congruent / salient. Gray: incongruent / non-salient. Solid bars denote win–loss, whereas open bars denote correct–incorrect.



**Fig. 3.** Behavioral and eye-tracking results for Experiment 4 and 5. (A1–A2) Specific salience emphasis increased the difference in staying frequency and fixation difference along the emphasized dimension. (B1–B2) Specific salience didn't change satisfaction and surprise ratings. (C1–C2) Non-specific salience emphasis did not increase the difference in staying frequency and fixation difference along the emphasized dimension. (D1–D2) Non-specific salience didn't change satisfaction and surprise ratings along the emphasized dimension. (E1–E2) Correlations between fixation difference and staying patterns in specific emphasis. (F1–F2) Nonsignificant correlations in the non-specific emphasis conditions. W-L: win-loss; C-I: correct–incorrect. Error bars denote one SEM across participants. Asterisk indicates a significant difference using two-tailed one-sample *t*-test: +:  $P < 0.1$ , \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , and \*\*\*:  $P < 0.001$ . n.s.: not significant. Red: congruent / salient. Gray: incongruent / non-salient. Solid bars denote win–loss whereas open bars denote correct–incorrect.



Notably, we observed qualitatively similar results between Experiment 2 (Fig. 3A1) and 4 (Fig. 2B) (two-tailed two-sample *t*-test; all *Ps* > 0.2). As a result, we validate our findings regarding the impact of salience emphasis on behavioral staying by conducting a separate study with an independent group of participants. Furthermore, we extended the scope of our research by examining the effects of different emphasis manipulations, such as color and text, and found that our results were consistent across both methods.

We then investigated the fixation difference between chosen and unchosen cards to quantify the attentional deployment during outcome evaluation. We first checked the total fixation duration during outcome evaluation and found no significant differences across different outcomes (see Supplementary Fig. S2A1, B1). Subsequently, a divisive normalization technique was implemented to derive the normalized fixation discrepancy between the two cards. This entailed dividing the relative fixation differences (chosen – unchosen) by the total fixation of both cards.

A qualitatively similar pattern of fixation deployment (Fig. 3A2) was observed as the behavioral strategies (Fig. 3A1). Specifically, the normalized fixation difference was enhanced after trials with win feedback compared to loss when the utility was emphasized (*t* (47) = 2.26, *P* = 0.028, *d* = 0.33; see Supplementary Fig. S2A2 and A3 for absolute changes), but not when performance was emphasized (*t* (47) = 0.75, *P* = 0.55, *d* = 0.10, see Supplementary Fig. S2B2 and B3 for absolute changes). However, the difference between the two emphasizes didn't reach significance: *t* (47) = 1.11, *P* = 0.27, *d* = 0.16), which was also indicated by the non-significant interaction between salience and utility (*F* (1, 47) = 1.23, *P* = 0.27,  $\eta_p^2$  = 0.19, Fig. 3A2).

Moreover, the normalized fixation difference was enhanced after trials with correct feedback compared to incorrect when either utility (*t* (47) = 2.83, *P* = 0.007, *d* = 0.41) or performance (*t* (47) = 5.84, *P* < 0.001, *d* = 0.85) was emphasized. A marginally significant difference between the two emphasizes was observed: *t* (47) = -1.71, *P* = 0.09, *d* = -0.25), which was also indicated by a weak interaction between salience and performance (*F* (1, 47) = 2.95, *P* = 0.09,  $\eta_p^2$  = 0.39, Fig. 3A2).

Notably, emphasizing "win-loss" does not necessarily require individuals to actively disregard the unselected option. It may, however, influence their attentional allocation towards the chosen or unchosen outcome (see Supplementary Fig. S3). When focusing on utility, participants tended to allocate more attention towards the utility dimension of the chosen outcome, resulting in a disparity in fixation between the chosen and unchosen outcomes that slightly differ from focusing on performance (see Supplementary Fig. S3A3, B3). When focusing on performance, participants tended to allocate more attention toward the performance dimension of the chosen outcome, resulting in a disparity in fixation between the chosen and unchosen outcomes that significantly differ from focusing on utility (see Supplementary Fig. S3A3, B3).

Besides behavioral strategies and attentional properties, we also investigated the subjective pleasantness and surprise ratings for each experimental condition in Experiment 4. As expected; participants were more satisfied in win trials than in loss trials and more satisfied in correct trials than in incorrect trials when either utility or performance was emphasized (Fig. 3B1; three-way repeated-measure ANOVA of salience X utility X performance: main effect of utility: *F*(1, 37) = 54.01, *P* < 0.001,  $\eta_p^2$  = 1.0; main effect of performance: *F*(1, 37) = 81.04, *P* < 0.001,  $\eta_p^2$  = 1.0). However, no significant interaction effects were observed between salience and utility or performance (all *Ps* > 0.2). For the self-reported surprise, participants were more satisfied in correct trials than in incorrect trials (Fig. 3B2; three-way repeated-measure ANOVA of salience X utility X performance: main effect of performance: *F* (1, 37) = 5.41, *P* = 0.026,  $\eta_p^2$  = 0.62). No significant main effect of utility (*F* (1, 37) = 2.49, *P* = 0.12,  $\eta_p^2$  = 0.33) or interactions (Fig. 3B2; all *Ps* > 0.1) were found. Therefore, the salience-guided behavioral adjustments cannot be attributed to the difference in subjective feelings towards outcomes.

Lastly, we analyzed response times (RT) for behavioral adjustment. No significant difference in RT was found when participants made a switching choice under two emphases (see Supplementary Fig. S4A1-A3; all *Ps* > 0.1). Interestingly, when participants made a staying choice, they exhibited post-error slowing after receiving incorrect feedback under performance emphasis but were quicker after receiving correct feedback under utility emphasis, as manifested by a significant interaction between salience and performance (*F* (1,47) = 5.52, *P* = 0.023,  $\eta_p^2$  = 0.63) (see Supplementary Fig. S4B1-B3).

#### 3.4. Eye-movement results: non-specific salience didn't modulate the fixation deployment

Similarly, we replicated our behavioral findings in Experiment 3 using an independent group of 32 eye-tracking subjects in Experiment 5. We found that salience modulation was abolished when the emphasis was non-specific (Fig. 3C1). Specifically, no significant interaction between salience and utility (*F* (1, 31) = 0.58, *P* = 0.45,  $\eta_p^2$  = 0.11; see Supplementary Fig. S1G, H for absolute staying frequency) and no significant main effect of valence (*F* (1, 31) = 0.70, *P* = 0.40,  $\eta_p^2$  = 0.12) on staying frequency was observed. Although participants stayed more frequently after correct trials than incorrect trials (main effect of performance: (*F* (1, 31) = 46.01, *P* < 0.001,  $\eta_p^2$  = 1), no significant interaction was found between salience and performance (*F* (1, 31) = 1.41, *P* = 0.24,  $\eta_p^2$  = 0.21). Again, our results suggest that non-specific salience emphasis did not modulate behavioral strategy. Notably, we observed qualitatively similar results between Experiment 5 (Fig. 3C1) and 3 (Fig. 2C) (two-tailed two-sample *t*-test; all *Ps* > 0.2).

We then investigated the fixation difference between chosen and unchosen values. A qualitatively similar pattern of fixation deployment (Fig. 3C2) was observed as the behavioral staying in Experiment 5 (Fig. 3C1). Specifically, the normalized fixation difference was unchanged between trials with win and loss feedback (main effect of utility: *F* (1, 31) = 2.55, *P* = 0.12,  $\eta_p^2$  = 0.34; see Fig. S2C2-D3 for absolute changes). Moreover, there was no significant interaction between salience and utility (*F* (1, 31) = 0.40, *P* = 0.52,  $\eta_p^2$  = 0.09, Fig. 3C2). Although the normalized fixation difference was enhanced after trials with correct feedback compared to incorrect (main effect of performance: *F* (1, 31) = 58.73, *P* < 0.001,  $\eta_p^2$  = 1), no significant difference between two emphasizes was observed (*F* (1, 31) = 2.66, *P* = 0.11,  $\eta_p^2$  = 0.35, Fig. 3C2).

Next, we investigated the subjective pleasantness and surprise ratings for each experimental condition. Similar to the findings in Experiment 4, participants were more satisfied in win trials than in loss trials and more satisfied in correct trials than in incorrect trials when either utility or performance was emphasized (Fig. 3D1; three-way repeated-measure ANOVA of salience X utility X performance: main effect of utility: *F*(1, 31) = 17.58, *P* < 0.001,  $\eta_p^2$  = 0.98; main effect of performance: *F*(1, 31) = 69.03, *P* < 0.001,  $\eta_p^2$  = 1.0). However, no significant interaction effects were observed between salience and utility or performance (all *Ps* > 0.1). For the self-reported surprise, no significant main effects or interactions were found (Fig. 3B2; all *Ps* > 0.1). Overall, we have observed similar results in subjective feelings regardless of the specification of outcomes that are also independent of behavioral strategies.

Lastly, we analyzed response times (RT) for behavioral adjustment. No significant difference in RT was found when participants made either switch (Fig. S4C1-C3; all *Ps* > 0.47) or stay (see Supplementary Fig. S4D1-D3; all *Ps* > 0.43) choices, indicating an equal response effort that was not influenced by salience or outcome.

#### 3.5. Eye-movement results: behavioral strategy was correlated with attention deployment

We have identified similar patterns of behavioral strategy and attentional deployment. To explore the role of attention in salience effects,



we conducted a Pearson correlation analysis to examine the relationship between behavioral staying and attentional deployment for each condition.

When emphasizing utility, the staying difference along the salient utility dimension (W–L) was positively correlated with the normalized fixation difference (Chosen–Unchosen) under the same dimension (W–L) (see Supplementary Fig. S5A1;  $r = 0.29$ ,  $P = 0.046$ ). Moreover, the staying difference along the non-salient performance dimension (C–I) was positively correlated with the normalized fixation difference (Chosen–Unchosen) under the same dimension (C–I) (see Supplementary Fig. S5A2;  $r = 0.4$ ,  $P = 0.005$ ).

When emphasizing performance, the staying difference along the salient performance dimension (C–I) was positively correlated with the normalized fixation difference (Chosen–Unchosen) under the same dimension (C–I) (see Supplementary Fig. S5A4;  $r = 0.33$ ,  $P = 0.023$ ). However, no correlation was identified between the staying difference along the non-salient utility dimension (W–L) and the normalized fixation difference (Chosen–Unchosen) under the same dimension (W–L) (see Supplementary Fig. S5A3;  $r = -0.19$ ,  $P = 0.2$ ). Altogether, our results support that specific feedback modulated attention deployment and further guided behavioral adjustments.

Notably, no direct correlation was observed between salient utility-modulated fixation difference [Utility (W–L) – Performance (W–L)] and salient utility-modulated behavioral staying [Utility (W–L) – Performance (W–L)] (Fig. 3E1;  $r = -0.05$ ,  $P = 0.73$ ). Moreover, only a marginally significant correlation was observed for salient performance-modulated fixation difference [Utility (C–I) – Performance (C–I)] and salient performance-modulated behavioral staying [Utility (C–I) – Performance (C–I)] (Fig. 3E2;  $r = 0.25$ ,  $P = 0.09$ ). These findings may suggest that salience-guided fixation deployment did not have a direct influence on the utilization of salience-guided behavioral strategies. Alternatively, it is possible that salience-guided fixation deployment did not completely account for the differences in salience-guided behavioral strategies, although we have observed direct evidence of salience guiding the allocation of attention.

Moreover, no significant correlation between behavioral difference and attentional deployment was identified under the non-specific salience emphasis (Fig. 3F1–F2: all  $P$  values  $> 0.5$ ; Supplementary Fig. S5B1–B4, all  $P$  values  $> 0.2$ ).

Lastly, a general linear mixed model was applied to predict the behavioral strategy by utilizing chosen value, unchosen value, and normalized fixation difference as independent variables for each subject. We have identified a significant role of chosen value, unchosen value, and normalized fixation difference on the behavioral strategy when either utility (see Supplementary, Fig. S5C1) or performance (Fig. S5C2) was emphasized. However, no significant effect of normalized fixation difference was identified when the emphasis was non-specific (see Supplementary Fig. S5D1, D2).

### 3.6. Replication in the fMRI study

Notably, we further replicated the salience effect using color emphasis by an independent sample of 25 fMRI participants (Experiment 6). Qualitatively, the same results were observed (Fig. 4A): when the utility was emphasized, participants stayed more frequently following win trials ( $52.85\% \pm 12.16\%$ ) than loss trials ( $44.35\% \pm 16.73\%$ ;  $t(24) = 2.76$ ,  $P = 0.011$ ,  $d = 0.56$ ; see Supplementary Fig. S11, J for absolute staying frequency), but not when performance was emphasized ( $t(24) = 0.30$ ,  $P = 0.76$ ,  $d = 0.06$ ; interaction:  $F(1, 24) = 5.12$ ,  $P = 0.033$ ,  $\eta_p^2 = 0.58$ ). In addition, participants stayed more frequently following correct than incorrect trials when either utility ( $9.97\% \pm 22.53\%$ ;  $t(24) = 2.21$ ,  $P = 0.03$ ,  $d = 0.45$ ) or performance ( $16.12\% \pm 24.92\%$ ;  $t(24) = 3.23$ ,  $P = 0.004$ ,  $d = 0.66$ ) was emphasized (the difference between two emphases:  $t(24) = -1.60$ ,  $P = 0.12$ ,  $d = -0.33$ ). Notably, we observed qualitatively similar results between Experiment 2 and 6 for each condition (two-tailed two-sample  $t$ -test; all  $P$ s  $> 0.2$ ).

Similarly, we investigated subjective pleasantness and surprise ratings of outcomes in fMRI participants. As expected, participants were more satisfied in win trials than in loss trials and more satisfied in correct trials than in incorrect trials when either utility or performance was emphasized (Fig. 4B; three-way repeated-measure ANOVA of salience X utility X performance: main effect of utility:  $F(1, 24) = 116.18$ ,  $P = 1.11 \times 10^{-10}$ ,  $\eta_p^2 = 1.0$ ; main effect of performance:  $F(1, 24) = 49.30$ ,  $P = 2.92 \times 10^{-7}$ ,  $\eta_p^2 = 1.0$ ). However, no significant interactions were observed between salience, utility, or performance (all  $P$ s  $> 0.1$ ). Likewise, for the self-reported surprise, no significant main effects or interactions were found (all  $P$ s  $> 0.1$ ). Therefore, the salience-guided behavioral adjustments cannot be attributed to the difference in subjective feelings towards outcomes.

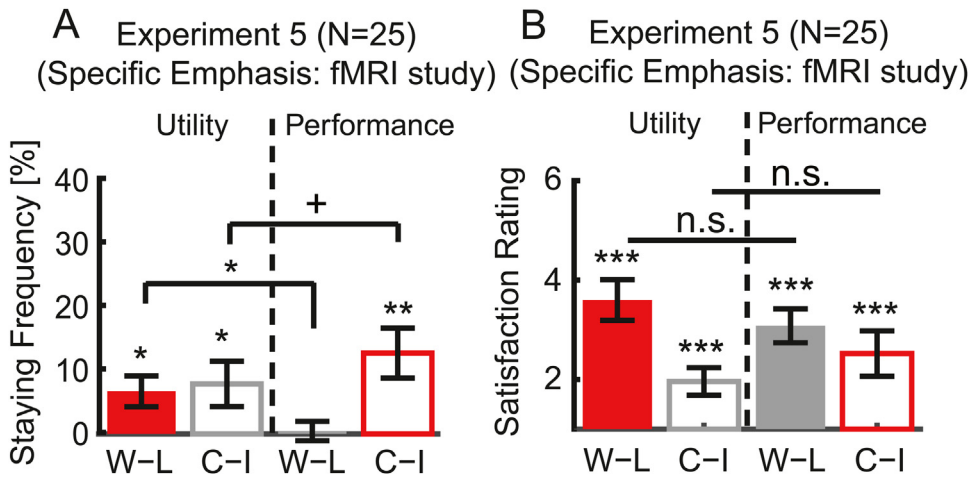
### 3.7. fMRI: the striatum subregions encoded salience-modulated outcome evaluation

We next investigated the neural substrates underlying this behavior. The striatum showed significantly stronger activity associated with the win versus loss outcome when either utility (Fig. 5A) or performance (Fig. 5B) was emphasized (see Table 1 and Supplementary Table S1 for complete statistics). Furthermore, the difference between win vs. loss outcomes became larger when the utility was emphasized (congruent and salient) compared with when performance (incongruent and non-salient) was emphasized, suggesting that the congruent and thus salient task aspect could enhance the striatum's coding of utility. To test the statistical significance of the salience effect on neural activity, we conducted an ROI analysis (see Methods for choice of ROIs) in the striatum subregions. We found that the dorsal striatum (particularly the left caudate) had a stronger activity for win–loss when the utility was emphasized than when performance was emphasized (Fig. 5E; peak: Montreal Neurological Institute (MNI) coordinate:  $x = -12$ ,  $y = 18$ ,  $z = 3$ , 10 voxels, FWE  $P < 0.05$ , small volume corrected (SVC); Fig. 5G; two-tailed one-sample  $t$ -test against 0: utility:  $t(24) = 4.50$ ,  $P = 1.45 \times 10^{-4}$ ,  $d = 0.91$ ; performance:  $t(24) = 2.87$ ,  $P = 0.008$ ,  $d = 0.58$ ; two-tailed paired  $t$ -test between two emphases:  $t(24) = 1.80$ ,  $P = 0.08$ ,  $d = 0.37$ ; see also Table 1), suggesting the left caudate selectively encoded salience-modulated utility information.

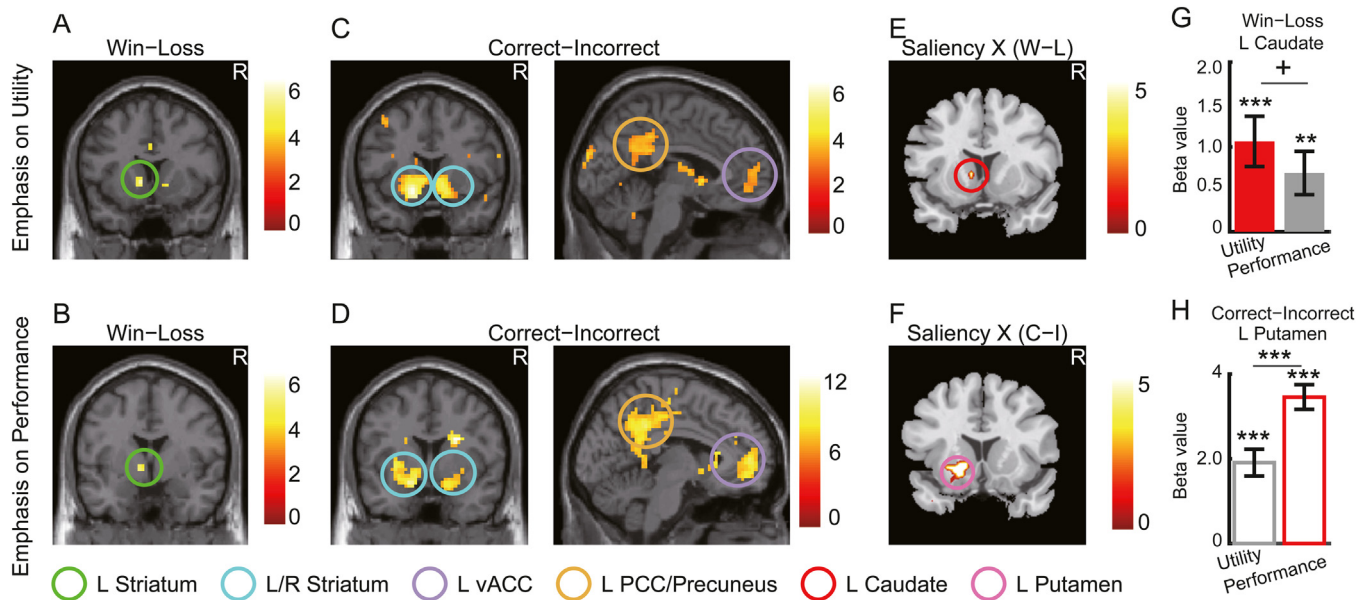
Similarly, the striatum also showed significantly stronger activity associated with the correct versus incorrect outcome when either utility (Fig. 5C) or performance (Fig. 5D) was emphasized (see Table 1 and Supplementary Table S1 for complete statistics). Other activated brain regions included the ventral medial prefrontal cortex (vmPFC). However, the difference between correct vs. incorrect outcomes became larger in the striatum when performance was emphasized that involved both the dorsal (left caudate) and ventral (bilateral putamen) striatum, suggesting that the congruent and thus salient task aspect could enhance the coding of performance as represented by both ventral and dorsal striatum. ROI analysis further confirmed the results and revealed a significant difference between salience emphases (the left putamen; Fig. 5F; peak:  $x = -18$ ,  $y = 12$ ,  $z = -6$ ,  $Z = 3.68$ , 27 voxels, FWE  $P < 0.05$ , SVC; Fig. 5H; two-tailed paired  $t$ -test between two emphases:  $t(24) = 4.51$ ,  $P = 1.41 \times 10^{-4}$ ,  $d = 0.92$ ; see also Table 1). Therefore, both ventral and dorsal striatum encoded salience-modulated performance information.

It is worth noting that no significant correlation was observed between the neural response from the striatum (left caudate or putamen) and the corresponding behavioral staying under salience manipulation. Moreover, although the above analyses were performed categorically (i.e., win, loss, correct, incorrect), we repeated our analyses using parametric effects on outcome difference (i.e., using actual payoff values), and we derived qualitatively the same results (see Supplementary Fig. S7 and Table S2). Together, our results suggested that the striatum encoded utility and performance and could be modulated by salience emphasis. This was in accordance with behavior (Fig. 4) and might explain salience-modulated behavioral adjustment, a point we will elucidate next.





**Fig. 4.** Behavioral results for fMRI study. (A) Experiment 6. (fMRI participants) replicated the results from Experiment 2 (behavioral participants). (B) Satisfaction rating from fMRI participants. W-L: win-loss; C-I: correct-incorrect. Error bars denote one SEM across participants. Asterisk indicates a significant difference using two-tailed one-sample *t*-test: +:  $P < 0.1$ , \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , and \*\*\*:  $P < 0.001$ . n.s.: not significant. Red: congruent / salient. Gray: incongruent / non-salient. Solid bars denote win-loss, whereas open bars denote correct-incorrect.



**Fig. 5.** Saliency-modulated outcome evaluation. (A) When the utility was emphasized, the left caudate ( $x = -9, y = 12, z = 0$ ) encoded utility (win-loss). (B) When the performance was emphasized, the left striatum ( $x = -9, y = -3, z = -3$ ) also encoded utility (win-loss). (C, D) Both the left and right striatum encoded performance (correct-incorrect) when either utility (C) or performance (D) was emphasized. (E) The left caudate ( $x = -12, y = 18, z = -3$ ) encoded the interaction between saliency and utility (win-loss). (F) The left putamen ( $x = -18, y = 12, z = -6$ ) encoded the interaction between saliency and performance (correct-incorrect). (G, H) Parameter estimate (beta values). The left bar shows parameter estimates for emphasis on utility, and the right bar shows parameter estimates for emphasis on performance. The bars show the average beta values of all voxels from the ROI. Red: congruent / salient. Gray: incongruent / non-salient. Solid bars denote win-loss whereas open bars denote correct-incorrect. The generated statistical parametric map was superimposed on anatomical sections of the standardized MNI T1-weighted brain template. Images are in neurological format with participants left on the image left. L: left, R: right. Activations were shown at  $P < 0.001$  uncorrected. Asterisk indicates a significant difference using a two-tailed one-sample *t*-test: \*\*:  $P < 0.01$ . \*\*\*:  $P < 0.001$ .

### 3.8. fMRI: the vmPFC encoded saliency-modulated behavioral adjustment

We next investigated the brain regions that may encode behavioral adjustment following outcome evaluation under saliency modulation, which corresponded to our observed behavior (Fig. 4). We identified the brain regions that were activated under the contrasts of [Stay(W-L) - Switch(W-L)] and [Stay(C-I) - Switch(C-I)] for both saliency manipulations. Interestingly, the vmPFC was activated during behavioral staying following utility and performance information but showed a stronger response following information congruent with the saliency manipulation (Fig. 6A-F). ROI analysis further confirmed the results and revealed a significant difference between saliency-modulated behavioral adjustment (the vmPFC; Fig. 6E; peak:  $x = -15, y = 42, z = 0$ ,  $Z = 3.52$ , 6 voxels, FWE  $P < 0.05$ , SVC; Fig. 6F; peak:  $x = 3, y = 54, z = 0$ ,

$Z = 3.84$ , 22 voxels, FWE  $P < 0.05$ , SVC). Therefore, the vmPFC represents saliency-driven behavioral adjustments.

### 3.9. fMRI: behavioral adjustment modulated functional connectivity between the vmPFC and NACC/DMPFC

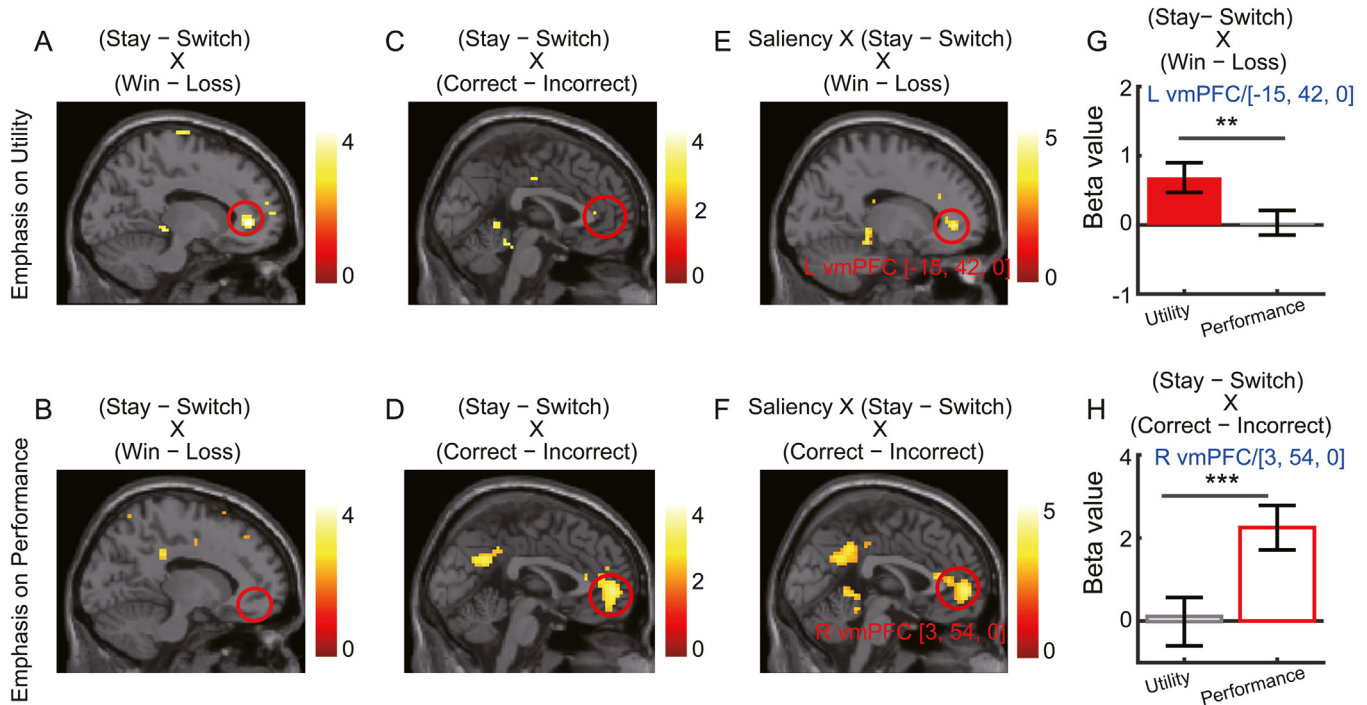
Lastly, to further explore whether the vmPFC was functionally connected with other brain regions and whether such connectivity could be modulated by saliency-modulated behavioral adjustment, we performed a classical PPI analysis with the vmPFC (utility: MNI peak:  $x = -15, y = 42, z = 0$ ; performance:  $x = 3, y = 54, z = 0$ ) as the seed and the signals from a 6-mm-radius sphere around the seed as a volume of interest (VOI). However, no brain regions were significantly activated and showed connectivity with the vmPFC under two emphases.



**Table 1**

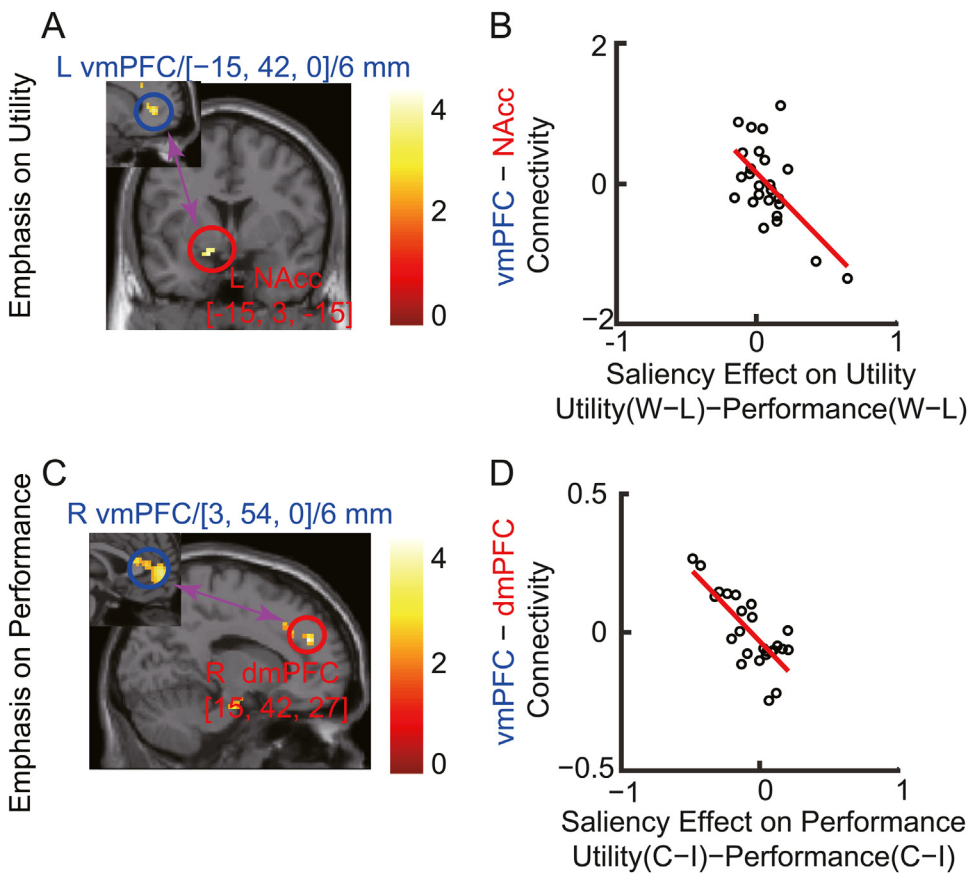
Brain areas are modulated by salience-modulated outcome evaluation and behavioral adjustment. All values are  $P < 0.001$  uncorrected at the peak voxel level. \* indicates  $P < 0.05$  and \*\* indicates  $P < 0.01$  family-wise error (FWE) after small volume correction (SVC).

|                                   | Contrast  | Brain Region<br>Salience-modulated outcome evaluation | Z-score                 | Peak Coordinate MNI (X Y Z) |               |               | Volume (voxel) |
|-----------------------------------|---|---|-------------------------|-----------------------------|---------------|---------------|----------------|
| Saliency X Utility                | Utility (W–L)<br>–<br>Performance (W–L)                                     | L Caudate head*                                       | 2.98*                   | –12                         | 18            | –3            | 2              |
| Saliency X Performance            | Utility (C–I)<br>–<br>Performance (C–I)                                     | L Caudate*<br>L Putamen*<br>R Putamen*                | 3.40*<br>3.43*<br>3.39* | –18<br>–18<br>27            | 21<br>12<br>0 | 9<br>–6<br>–6 | 3<br>5<br>5    |
| Saliency X Utility X Strategy     | Utility (Stay – Switch) X (W–L)<br>–<br>Performance (Stay – Switch) X (W–L) | L vACC*   | 3.52*                   | –15                         | 42            | 0             | 5              |
| Saliency X Performance X Strategy | Utility (Stay – Switch) X (C–I)<br>–<br>Performance (Stay – Switch) X (C–I) | R vmPFC*  | 3.84*                   | 3                           | 54            | 0             | 22             |
| Saliency X Utility X Strategy     | Utility (Stay – Switch) X (W–L)<br>–<br>Performance (Stay – Switch) X (W–L) | “High order” PPI Results                              |                         |                             |               |               |                |
|                                   |   | L Nucleus Accumbens**                                 | 3.28**                  | –15                         | 3             | –15           | 5              |
| Saliency X Performance X Strategy | Utility (Stay – Switch) X (C–I)<br>–<br>Performance (Stay – Switch) X (C–I) | R dmPFC/Middle Frontal Gyrus**                        | 4.55**                  | 15                          | 42            | 27            | 12             |



**Fig. 6.** Salience-modulated behavioral adjustment. (A, B) When utility was emphasized, the left vmPFC was activated under behavioral adjustment following utility information [Stay(W–L) – Switch(W–L)]. At the same time, no brain regions showed any significant activation when performance was emphasized. (C, D) When the performance was emphasized, the behavioral adjustment following the performance information [Stay(C – I) – Switch(C – I)] involved the right vmPFC. (E, F) The interaction between salience and utility-based behavioral staying and performance-based behavioral staying. (G, H) Beta values in vmPFC show the interaction between salience and behavioral staying. The generated statistical parametric map was superimposed on anatomical sections of the standardized MNI T1-weighted brain template. Images are in neurological format with participants left on the image left. L: left, R: right. Activations were shown at  $P < 0.005$  uncorrected. Asterisk indicates a significant difference: \*\*\*:  $P < 0.001$ . Each dot shows an average beta value of all voxels from the ROI.





**Fig. 7.** Regional activity on behavioral adjustment and high-order PPI results. (A) When utility was emphasized, the left vmPFC ( $x = -15$ ,  $y = 42$ ,  $z = 0$ ) encoded behavioral adjustment following utility feedback, and its connectivity to nucleus accumbens (NAcc) ( $x = -15$ ,  $y = 3$ ,  $z = -15$ ) was negatively modulated salience-guided behavioral adjustments. W-L: win-loss; C-I: correct-incorrect. Activations were shown at  $P < 0.005$  uncorrected. (B) When the performance was emphasized, the right vmPFC ( $x = 15$ ,  $y = 42$ ,  $z = 27$ ) encoded behavioral adjustment following performance feedback, and its connectivity to dmPFC ( $x = 15$ ,  $y = 54$ ,  $z = 0$ ) was negatively modulated by the behavioral adjustments. W-L: win-loss; C-I: correct-incorrect. Activations were shown at  $P < 0.005$  uncorrected.

A further “high-order” PPI model was constructed in which the salience-guided behavioral staying after utility or performance from each participant was put into one vector to capture brain regions that may respond to the main contrast of PPI.ppi generated from the primary PPI model. This is indeed a regression model aimed to pinpoint the areas that had functional connections with the vmPFC, and additionally, their connectivity was modulated by the degree of behavioral staying under each salience manipulation. We found that the left vmPFC was co-activated with the left NAcc (Fig. 7A; MNI peak:  $x = -15$ ,  $y = 3$ ,  $z = -15$ ,  $Z = 3.28$ , 5 voxels, FWE  $P < 0.01$ , SVC) when emphasizing on utility. A Pearson correlation analysis further confirmed a high inter-participant negative correlation between the strength of vmPFC-NAcc connectivity and the behavioral staying following utility (Fig. 7B). Moreover, the right vmPFC was co-activated with the right dmPFC (Fig. 7C; peak:  $x = 15$ ,  $y = 42$ ,  $z = 27$ ,  $Z = 4.55$ , 12 voxels, FWE  $P < 0.01$ , SVC) when emphasizing on performance. A Pearson correlation analysis further confirmed a high inter-participant negative correlation between the strength of vmPFC-dmPFC connectivity and the behavioral staying following performance (Fig. 7D). Together, our results indicated that the frontostriatal neural circuit could be modulated by salience-driven behavioral adjustment.

#### 4. Discussion

This study investigated the cognitive and neural bases of visual contexts guided decision-making. Consistent with our hypothesis, participants showed salience-modulated behavioral adjustment in experiments that had a specific association between visual salience and outcome but not in experiments where the association between visual salience and outcome was non-specific. These findings suggested that salience emphasis exerted influences through specific mapping of bottom-up visual cues with feedback that guided the allocation of attention and

further modulated behavioral strategies. The striatum subregions encoded salience-based outcome evaluation, while the vmPFC encoded salience-based behavioral adjustment. The functional connectivity of vmPFC-NAcc accounted for the inter-individual difference in utility-driven behavioral adjustment. In contrast, the functional connectivity of vmPFC-dmPFC accounted for the interindividual difference in performance-driven behavioral adjustment. Altogether, our study indicates that behavioral adjustment is influenced by the salient visual context that is specific to the content of feedback. This is achieved by modifying the weighting of outcome information during the evaluation process as revealed by attention deployment and the frontal-striatal valuation system.

##### 4.1. Non-salience or non-specific salience and decision making

The baseline behavior without emphasis is intriguing as the participants exhibited little behavioral switching in response to the win/loss dimension (Fig. 2A), which is similar to the results obtained under conditions with non-specific emphasis (Fig. 2C). Previous research has shown that the FRN is stronger following a loss than a win (Gehring and Willoughby, 2002; Nieuwenhuis et al., 2004), and there is increased activation in the striatum after reward compared to non-reward feedback, even without emphasis (Carlson et al., 2011; Pfabigan et al., 2014). However, in our study, participants were more sensitive to correct/incorrect feedback as they provided direct evidence of whether the previous choice was optimal or not. Therefore, participants might think that the win/loss feedback was less behaviorally relevant because the win/loss dimension could not be influenced by choices.

##### 4.2. Visual salience and decision making

Traditional decision-making studies typically present participants with options that are well-balanced in visual salience to rule out con-



founding variables from the low-level sensory perception. However, options in real-world situations rarely appear in a visual vacuum. For example, an aircraft pilot must interpret data from the instrument panels and the surrounding environment to make a successful landing after weighing the importance of the information. Our study mainly conveys that visual salience interplays with value-based decision-making. In line with this viewpoint, it has been demonstrated that perceptual salience competes with the expected value, and both influence the saccadic endpoint within an object (Krajebich et al., 2010; Schütz et al., 2012; Towal et al., 2013). Moreover, motivationally salient stimuli, such as items previously associated with rewards, can bias visual attention and subsequent decision strategy (Hickey et al., 2010). Similarly, socially salient stimuli (i.e., facial attractiveness) can bias attention and influence personal preference (Park et al., 2010; Shimojo et al., 2003). A reward-associated distractor can change saccade trajectories even when participants expect this object and try to ignore it (Hickey and van Zoest, 2012).

Additionally, manipulating the relative level of visual attention between two alternative options can influence subsequent choices (Armell et al., 2008). Similar to our present findings, behavioral economic studies have suggested that deemphasizing a stock's purchase price can substantially reduce stockers' propensity to sell risky assets with capital gains (Frydman and Rangel, 2014). However, the above-mentioned salience modulation could be confounded by the simple demand characteristics effect, where individuals pay more (or less) attention to the emphasized (or non-emphasized) dimension. Our results have further extended previous studies by showing that outcome salience, even when it is redundant in nature, has an impact on subsequent decisions, which is different from the effect of the demanding characteristics, given that only specific (vs. general) emphasis for the directional information of feedback contributes to the behavioral adjustments. We have further shown that the specificity of salience modulation can exert an impact on subsequent choices as guided by attention deployment. Although no linear correlation was observed between salience-guided attention and behavioral adjustment at an individual level, a similar pattern between attention deployment and behavioral adjustment was generally identified at a group level that was also modulated along the salient dimension.

#### 4.3. The striatum subregions encode salience-modulated outcome evaluation

Our neuroimaging results have revealed that the striatum subregions were involved in both utility (i.e., dorsal striatum: the caudate) and performance (both dorsal and ventral striatum: bilateral caudate, putamen, and NAcc) evaluation, and their activities were further modulated by salience emphasis. The human striatum has long been implicated in value-based decision-making, and significantly activated by the positive versus negative feedback (Becker et al., 2014). However, it has been argued that the striatum is not only engaged in reward processing but also encodes stimulus salience (Delgado, 2007; Guitart-Masip et al., 2010; Jensen et al., 2003; Oyama et al., 2015; Zaehle et al., 2013; Zink et al., 2006, 2004, 2003). In particular, the ventral striatum is shown to be modulated by both value and visual salience (Litt et al., 2011), and it encodes attention-guided relative-value signals (Lim et al., 2011), anticipated aversive stimuli (Jensen et al., 2003), salient non-rewarding stimuli (Zink et al., 2003), and salient prediction errors (Metereau and Dreher, 2013). The striatum's importance in salience processing has been consistently demonstrated by our findings.

Moreover, the dorsal striatum represents visual salience-based outcome evaluation regardless of the dimension (utility or performance) of information (dimension-general). In contrast, the ventral striatum only represents salience-based performance information (dimension-specific). This is in line with the studies on goal-directed (model-based) and habitual (model-free) processes, in which the ventral striatum is involved in both processes. In contrast, the dorsal striatum is only ac-

tivated in the habitual (model-free) process (Huang et al., 2020). Our findings indicate that dimension-general emphasis, whether on utility or performance, can influence the habitual learning process and trigger automatic outcome evaluation through the recruitment of the dorsal striatum. In contrast, performance-specific outcome evaluation may be more goal-directed than utility-specific outcome evaluation, as evidenced by the activation of the ventral striatum, which represents a model-based learning process. Our research has contributed to the neurocognitive comprehension of salience-based outcome evaluation by demonstrating that the evaluation of salience may be contingent on the precision of feedback and its interaction with goal-directed and habitual learning mechanisms.

Another line of evidence from human EEG studies has identified two ERP components, the FRN and the P300, that are sensitive to the reward-based outcome evaluation (Cohen and Ranganath, 2007; Gehring and Willoughby, 2002; Nieuwenhuis et al., 2004; Yeung and Sanfey, 2004) and are modulated by salience manipulation (Sun and Wang, 2020; Sun et al., 2020). The FRN discriminates monetary outcomes with different salience levels that are rendered by levels of perceptual noise, suggesting an interaction between stimulus salience and the value computation (Lou et al., 2015). Source localization has indicated that the FRN originates from cortical regions such as the medial frontal gyrus that receive dopaminergic projections from the basal ganglia (including the striatum) and reflects activity in the mesocorticolimbic reward circuits (Becker et al., 2014; Carlson et al., 2011; Delgado et al., 2003; Knutson et al., 2003; Nieuwenhuis et al., 2005). A simultaneous EEG-fMRI study showed that surprise-like salience signals are directly projected to the source region of the FRN (Hauser et al., 2014). The P300 is often elicited by rare or novel stimuli, that may reflect unexpected changes in the sensory environment that are sufficiently salient to enter the awareness (Pinheiro et al., 2015). Multi-modal neuroimaging research showed that the P300 was significantly correlated with the activity in the striatum (Pfabigan et al., 2014; Pogarell et al., 2011). The above-mentioned neuroimaging and electrophysiology studies have consistently indicated a role of the striatum in salience processing. Taken together, our present findings have verified the function of the striatum in integrating subjective value and visual salience and highlighted the functional dissociations of the striatum subregions in salience-based specific outcome evaluation.

#### 4.4. The striatum and prefrontal cortex encode salience-modulated behavioral adjustment

Our fMRI results demonstrated a crucial role of the vmPFC in salience-guided strategic behavioral adjustment. Our study is thus among the first to identify the critical role of vmPFC in salience-driven decision-making. These findings are in line with previous evidence suggesting that the vmPFC is involved in the interplay of goal-directed and habitual learning (Piray et al., 2016), as well as the transition from goal-directed to habitual control of actions (Gremel and Costa, 2013). Moreover, a growing body of neuroimaging research and meta-analyses have revealed the pivotal function of the prefrontal cortex in guiding goal-directed instrumental decision-making (Huang et al., 2020; Valentin et al., 2007) and avoidance learning (Kim et al., 2006), and encoding abstract rules in intricate choices (O'doherty et al., 2007). Despite the established role of the striatum and vmPFC in value computation (Bartra et al., 2013; Rangel et al., 2008), which could be modulated by self-control or selective attention (Hare et al., 2009, 2011), our study is the first to reveal the functional significance of the vmPFC in salience-guided behavioral adjustment.

Moreover, high-order PPI analysis suggested that activity in the vmPFC was functionally correlated with the NAcc (for utility emphasis) and dmPFC (for performance emphasis). The connectivity in both pathways further explained the interindividual variations in staying frequency under different salience manipulation. Notably, the encoding of feedback-guided behavioral adjustments differed between the



vmPFC and dmPFC. The vmPFC encoded both utility- and performance-guided adjustments and was influenced by salience manipulation, while the dmPFC only encoded performance-guided adjustments after salience manipulation. The findings suggest that the vmPFC may have a dimension-general role in salience-modulated decision-making, encompassing both utility and performance. Meanwhile, the dmPFC may have a dimension-specific role in performance-based salience processing. The dissociable functions of vmPFC and dmPFC in encoding salience-based dimension-general versus dimension-specific behavioral adjustment are akin to the dissociable roles of the dorsal and ventral striatum in general and performance-based outcome evaluation, respectively. Altogether, our results demonstrated a crucial role of the frontal-striatal circuit in encoding salience-driven outcome evaluation and behavioral adjustments, pointing that the salience-driven process may integrate both top-down goal-directed and bottom-up habitual learning processes (Gremel and Costa, 2013; Huang et al., 2020; Piray et al., 2016; Redgrave et al., 2010).

Lastly, the putamen in the ventral striatum was found to be responsible for salience-based outcome evaluation, while the NAcc in the same region was responsible for salience-based behavioral adjustment. On the other hand, the caudate in the dorsal striatum was only involved in salience-based outcome evaluation. This highlights the functional separation of striatum subregions in distinguishing decision stages (i.e., outcome evaluation or action), with the ventral striatum playing a crucial role in integrating both processes, as suggested by (Bartra et al., 2013).

Notably, the phenomenon of goal-directed behavioral adjustment has also been studied using single neuron recordings among human and non-human animals. For instance, Isoda and Hikosaka's research found that the presupplementary motor area (pre-SMA) neurons in the medial frontal cortex marks behavioral switching from automatic to volitionally controlled action in monkeys (Isoda and Hikosaka, 2007), see also (Nachev et al., 2008) for review. However, the pre-SMA region was not found in our fMRI results, possibly due to differences in task design. Isoda and Hikosaka's study involved training monkeys to perform a saccadic eye movement task that required the suppression of an automatic and enhancement of a controlled action (Isoda and Hikosaka, 2007). While these regions may be involved in switching between actions, they may not be influenced by salience manipulation. In another study by Isoda et al., the movement neurons in the superior colliculus were found to encode reward-guided saccadic switching behaviors (Isoda and Hikosaka, 2008). Nonetheless, the influence of visual salience on these neurons remains uncertain. Among humans, it has been demonstrated that behavioral switching is a result of performance monitoring, with post-error slowing being a prominent form of behavioral adjustment as observed in Fu et al.'s study that involves the neurons from the human medial frontal cortex (Fu et al., 2019) as well as in other reviews (Fu et al., 2023; Kennerley et al., 2006; Shenhav et al., 2013; Ullsperger et al., 2014). However, in our study, post-error slowing was only evident when participants repeated the same option under emphasis on performance, possibly due to cognitive suppression of intuitive switching behaviors (i.e., switching after an error). The dorsal anterior cingulate cortex (dACC) has also been linked to goal-directed behavioral adjustments, particularly in terms of behavioral switching after errors, as demonstrated in Fu et al.'s study (Fu et al., 2019). Our study validated this finding by showing that participants made adjustments following performance information that triggered the engagement of dmPFC/dACC. Moreover, we extended these findings by revealing that the dmPFC was linked to the vmPFC, and that their connectivity was also subject to the influence of salience manipulation.

#### 4.5. Limitations and future directions

First, in our present study, there was no inherent statistical structure to the task, and therefore participants could not learn the distribution of outcomes from feedback. Such a design may exacerbate the visual contexts guided decision-making, in which the participants only

adjusted their decisions along with the salient dimension and the feedback from the most immediate trial. Although our findings may explain how salience influences the attention and subjective valuation systems that further strengthen salience-guided behavioral adjustment, it is still unclear where the default behavior comes from. Further studies may answer these questions independently under a non-salience condition. Second, despite our efforts to gauge individuals' subjective feelings towards outcomes and establish a correlation between attention and behavioral adjustment, the precise nature of the interplay between attention, motivation, and emotion (namely satisfaction and disappointment) remains unclear. Furthermore, it is uncertain how these factors interact with stable personality traits to determine individual differences in behavioral strategies. Future research may delve into the potential components that generate variations in learning behaviors. Last, in our present study, visual salience exerted its effect by explicitly instructing participants to pay attention to certain aspects of reward feedback. The salience cues were thus not endogenous because specific verbal or non-verbal instructions had been provided to them. As a result, they were considered motivational salience due to their intrinsic properties or behavioral significance, as mentioned by Zink et al. (2004). Salience can also be manipulated by other means, such as the amount of time participants fixate on an item (Armell et al., 2008), the amount of information revealed to participants (Frydman and Rangel, 2014), or visual contrasts (Moher et al., 2015). While our research has yielded encouraging results in some contexts, it remains to be tested whether these findings can be generalized to situations where salience is endogenously determined. Additionally, it is worth exploring how our results can inform interventions targeting irrational behaviors, such as overspending, or addictive behaviors, such as tobacco or food addiction, through both explicit (e.g., emphasizing certain information) and implicit modulation techniques (e.g., using neurofeedback to manipulate attention).

## 5. Conclusion

In conclusion, our behavioral studies have revealed that specific visual salience modulates behavioral strategies based on feedback evaluation. Furthermore, our eye-tracking studies have established a crucial role of attention in salience-driven outcome evaluation, and how attention may guide subsequent behavioral adjustments. Lastly, our fMRI results identified the neural correlates of visual-context-guided decision-making, pinpointing the role of the striatum and vmPFC in encoding salience-modulated outcome evaluation and behavioral adjustment. Our findings suggest that the reward system is orchestrated by visual salience and highlight the critical role of attention and the frontal-striatal circuit in visual salience-guided behavioral adjustment. These findings may update the theoretical framework and provide insights into the understanding of visual-context-guided decision-making and subjective valuation. Such salience modulation can be utilized in real-life situations like casinos, marketing, and policymaking to nudge individuals' choices.

## Data and code availability statement

The data and codes used in this study are publicly available on OSF (<https://osf.io/ud7yc/>).

## Declaration of Competing Interest

The authors have no conflicts of interest to declare.

## Credit authorship contribution statement

**Sai Sun:** Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Hongbo Yu:** Writing – original draft, Writing – review & editing. **Shuo Wang:** Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review & editing, Supervision. **Rongjun Yu:**



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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2023.120170](https://doi.org/10.1016/j.neuroimage.2023.120170).

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