


Motor activation in cue-guided behavior: Neural evidence from human Pavlovian-to-instrumental transfer (PIT)

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ARTICLE INFO

Keywords:

Pavlovian-to-instrumental transfer (PIT) task
Sensorimotor integration
Motor system
Functional MRI
Reward learning
Action motivation

ABSTRACT

In everyday life, our behavior is often guided by environmental cues that predict rewarding or aversive outcomes. The Pavlovian-to-Instrumental Transfer (PIT) paradigm provides a framework for examining how conditioned stimuli (CS) influence instrumental actions (R) associated with specific outcomes (O). Two distinct mechanisms have been identified: specific PIT, where a cue selectively invigorates the action linked to the same outcome, and general PIT, where reward-predictive cues non-selectively enhance response vigor. Theoretical accounts propose that specific PIT depends on the reactivation of learned action representations by sensory-specific cues, yet it remains unclear whether such reactivation occurs during passive cue exposure (Pavlovian phase) and how it evolves across learning. Using fMRI ($N = 31$), we investigated cue-evoked neural activity during two Pavlovian learning phases, before and after instrumental learning, in a four-phase PIT paradigm. Behaviorally, participants showed robust specific and general PIT effects in the transfer phase. At the neural level, general PIT-related cues engaged occipito-temporal visual and associative regions early in learning, whereas specific PIT-related cues recruited fronto-parietal, premotor, sensorimotor and striatal regions (MFG, IPS, PMC/M1/S1, caudate, putamen) after instrumental learning. These findings indicate that Pavlovian cues dynamically engage motor and sensorimotor systems following action–outcome learning, consistent with outcome-mediated retrieval of learned action representations even in the absence of overt movement. Together, the results refine theoretical models of PIT by demonstrating learning-dependent modulation of corticostriatal circuits during passive cue processing.

1. Introduction

Imagine walking along a busy street, searching for your favorite restaurant. Among the many signs, a familiar logo immediately catches your eye, guiding your movement toward your favorite restaurant. Such environmental cues can greatly facilitate goal-directed behavior by signaling potential rewards in our surroundings. However, these same cues can also bias our actions in unintended ways, a cue-guided behavior

known as Pavlovian bias (Holmes et al., 2010; Cartoni et al., 2016). Pavlovian bias arises when conditioned stimuli (CS), through repeated associations with rewarding or aversive outcomes, acquire motivational and predictive significance, thereby biasing instrumental action (Dickinson and Balleine, 1990; Dolan and Dayan, 2013; Ceceli and Tricomi, 2018). This reflects interactions between the Pavlovian system, which encodes stimulus–outcome associations, and the instrumental system, which governs action–outcome learning (Dayan and Balleine,

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<https://doi.org/10.1016/j.neuroimage.2026.121874>

Received 30 December 2025; Received in revised form 2 March 2026; Accepted 23 March 2026

Available online 23 March 2026

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2002; Guitart-Masip et al., 2014). While such interaction is often adaptive, enabling rapid detection of environmental opportunities, it can also become maladaptive when cue-driven responses are difficult to suppress or no longer appropriate (Garbusow et al., 2022; Heck et al., 2024), as seen in addiction and compulsive disorders, where reward-predictive cues elicit strong motivational tendencies even in the absence of actual reward (Dong et al., 2020; Krypotos and Engelhard, 2020; Doñamayor et al., 2021). Understanding how Pavlovian cues shape instrumental action is therefore essential for elucidating the neural mechanisms underlying both adaptive and maladaptive control of cue-guided behavior.

A well-established paradigm to investigate these mechanisms is the Pavlovian-to-Instrumental Transfer (PIT) task. Originally developed in animal research (Estes, 1948; Lovibond, 1983), PIT has since been adapted to human behavioral and neuroimaging studies (Holmes et al., 2010; Cartoni et al., 2016; Garofalo et al., 2021; Badioli et al., 2024). PIT tasks typically include Pavlovian cue–outcome learning (CS–O), instrumental response–outcome learning (R–O), and a transfer phase in which cues are presented during instrumental responding under extinction, allowing measurement of how cues bias action selection or vigor (CS–R). Two forms of PIT have been identified. In specific PIT, a cue selectively enhances the action associated with the same outcome, reflecting outcome-specific motivational processes that link sensory representations of the expected reward to specific actions (Badioli et al., 2024). This effect has been associated with corticostriatal regions such as ventrolateral putamen, caudate and premotor areas (Bray et al., 2008; Talmi et al., 2008; Prevost et al., 2012; Garofalo et al., 2021; Mahlberg et al., 2021). In contrast, general PIT reflects nonspecific invigoration of responding by reward-predictive cues and engages broader motivational circuitry, including the ventral striatum and midbrain pathways (Mahlberg et al., 2021). Both animal (Hall et al., 2001; Yin et al., 2004; Corbit and Balleine, 2005; Corbit et al., 2007) and human neuroimaging studies supports the involvement of partly dissociable neural circuits in these two forms of PIT. However, most human PIT studies have focused on the transfer phase and subcortical regions, leaving open whether cortical motor and sensorimotor systems are also involved, and critically, whether such recruitment already occurs during Pavlovian learning, before action execution.

Beyond this distinction, theoretical accounts suggest that specific PIT reflects a goal-directed process in which Pavlovian cues retrieve sensory-specific outcome representations that bias instrumental action selection (Jahanshahi et al., 2015; Morris et al., 2015; Balleine and O’Doherty, 2010; Garofalo et al., 2021; Mahlberg et al., 2021). In contrast, general PIT has traditionally been characterized as a habitual or energizing process (Holmes et al., 2010; Cartoni et al., 2016). Consistent with this distinction, neuroimaging evidence points to partly dissociable corticostriatal circuits: goal-directed control engages vmPFC–caudate pathways, whereas motivational invigoration involves putamen–premotor networks (van Steenbergen et al., 2017). Despite these differences, both forms of PIT ultimately influence motor execution, suggesting that the motor system is not a passive recipient of motivational signals but actively transforms value signals into action plans. This aligns with theories proposing that Pavlovian cues modulate sensorimotor control and action selection (Dickinson and Pérez, 2018; Wit and Dickinson, 2009), as well as ideomotor accounts positing that outcome representations can automatically activate their associated motor programs (Shin et al., 2010).

This raises a central question: do Pavlovian cues recruit motor representations even when no movement is required? If so, such recruitment might not necessarily reflect overt motor preparation or imminent execution. Rather, it might indicate the engagement of action-related neural processes within motor and sensorimotor systems, including outcome-specific motor coding and preparatory motor states that link predicted outcomes to potential responses. Supporting this view, Mendelsohn et al. (2014) showed that motivationally salient cues modulate connectivity between ventral striatum and motor cortex during motor

imagery, indicating that value-related cues can evoke internal motor representations (Mendelsohn et al., 2014). More recently, Finotti et al. (2025) demonstrated that reward-predictive cues evoke early (~300–500 ms) lateralized beta desynchronization over premotor regions during Specific PIT related cues processing, prior to action execution in transfer phase. Together, these findings suggest that Pavlovian cues can reactivate action-related motor representations linked to the predicted rewards. However, it remains unclear whether such motor recruitment already emerges during Pavlovian learning phase, after instrumental contingencies have been established, but when cues are merely observed and action execution is not required. If motivational value becomes embedded within the motor system, cue-evoked activation should emerge not only during transfer, but already during Pavlovian learning following instrumental acquisition. Demonstrating such learning-dependent recruitment would provide direct neural evidence that outcome-predictive cues engage action-related representations through shared outcome-response chains, even in the absence of overt behavior.

The present fMRI study examined whether motor and sensorimotor regions are engaged during the Pavlovian learning phase, how this activation evolves across learning, and how it differs between cues related to general and specific PIT. To address these questions, we used a four-phase PIT paradigm, in which participants first learned CS–O associations (CS1 -> O1, CS2 -> O2, CS3 -> O3, CS- -> O-), then instrumental R–O contingencies (R1 -> O1, R2 -> O2), followed by a second Pavlovian phase and a transfer test under nominal extinction (see Methods). Critically, because cue–action associations were never directly trained, any cue-driven motor activation observed during the second Pavlovian phase would reflect outcome-mediated integration across learning phases rather than direct stimulus–response retrieval. We first tested general and specific PIT effects at the whole brain level. A Go/No-Go functional localizer then identified subject-specific motor and premotor regions of interest (ROIs) to test for motor hypothesis in Specific PIT. We hypothesized that: i) both general and specific PIT effects would be observed behaviorally during the transfer phase; at the whole-brain level, ii) the general PIT related cue (CS3), compared to non-rewarded cue (CS-), would engage motivational-related circuits during Pavlovian learning, with learning-dependent modulation across phases following the establishment of instrumental contingencies; iii) the specific PIT related cues (CS1, CS2), compared to general PIT cue (CS3), would recruit motor and sensorimotor regions during Pavlovian 2, after instrumental learning; and iv) If motor activation contributes to specific PIT, ROI analyses should reveal lateralized motor activity, in which cues associated with left-hand responses (CS1) elicit greater activation in right motor areas, and vice versa for the right-hand cue (CS2).

2. Methods

2.1. Participants

Thirty-eight right-handed participants were recruited from the student population of South China Normal University. One participant did not complete the experiment due to physical discomfort during scanning. After data preprocessing, six participants were excluded (see exclusion criteria in MRI data acquisition and preprocessing), resulting in a final sample of 31 participants (mean age = 20.36 years, $SD = 2.36$, 15 female). Female and male participants did not differ significantly in age (females: $M = 19.93$ years, $SD = 2.40$; males: $M = 20.75$ years, $SD = 2.32$; $t(29) = -0.96$, $p = 0.34$). All participants provided written informed consent and completed MRI safety screening prior to participation. Inclusion criteria required right-handedness, normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders or psychotropic medication use. Participants were pre-screened to ensure they were not dieting and were asked to refrain from eating at least 2 h before the experimental session (water

permitted). The study was approved by the Ethics Committee of South China Normal University (reference number: SCNU-BRR-2021-023). All ethical regulations relevant to human participants were followed. Participants received monetary compensation of 135 CNY and food snacks after the experiment.

2.2. Reward selection and stimuli

To ensure individually motivating outcomes, participants completed an online reward rating task one day prior to the experimental session. They rated 18 snack items (3 savory, 15 sweet) on a nine-point Likert scale (1 = not at all; 9 = very much) based on subjective liking. For each participant, three snacks (O1, O2, O3) were selected that were both highly liked and equally valued. These snacks served as individualized food rewards during the experiment, and their corresponding images were used as visual stimuli in all tasks.

2.3. Experimental procedure

At the start of the experimental session, the three selected snacks were placed on a table to reinforce motivation. If participant expressed a

strong preference for one snacks over the others, it was replaced with a comparable alternative when necessary. Participants were informed that the experiment would take place inside the MRI scanner and that they would receive an amount of food proportional to the number of snack images presented during the task phases. The session consisted of three main tasks (Fig.1a): i) a Go/No-Go functional localizer; ii) a reward rating task; and iii) a four-phase Pavlovian-to-Instrumental Transfer (PIT) task.

2.3.1. Go/No-Go functional localizer task

The functional localizer was adapted from cue-based Go/No-Go paradigms and motor-preparation studies showing that preparatory cues recruit neural systems supporting motor readiness and proactive inhibition (Simmonds et al., 2008; Hong et al., 2017; Svoboda and Li, 2018; Ficarella and Battelli, 2019; Schimel et al., 2024). Each trial began with a circle, square, or cross cue presented at the center of the screen, signaling preparation for a specific response: circle = right-hand response; square = left-hand response; cross = no-response (baseline). Cues remained onscreen for 4000 ms, during which participants prepared (but did not execute) the indicated action. A Go signal (requiring the prepared response) or No-Go signal (blank screen) followed for 800

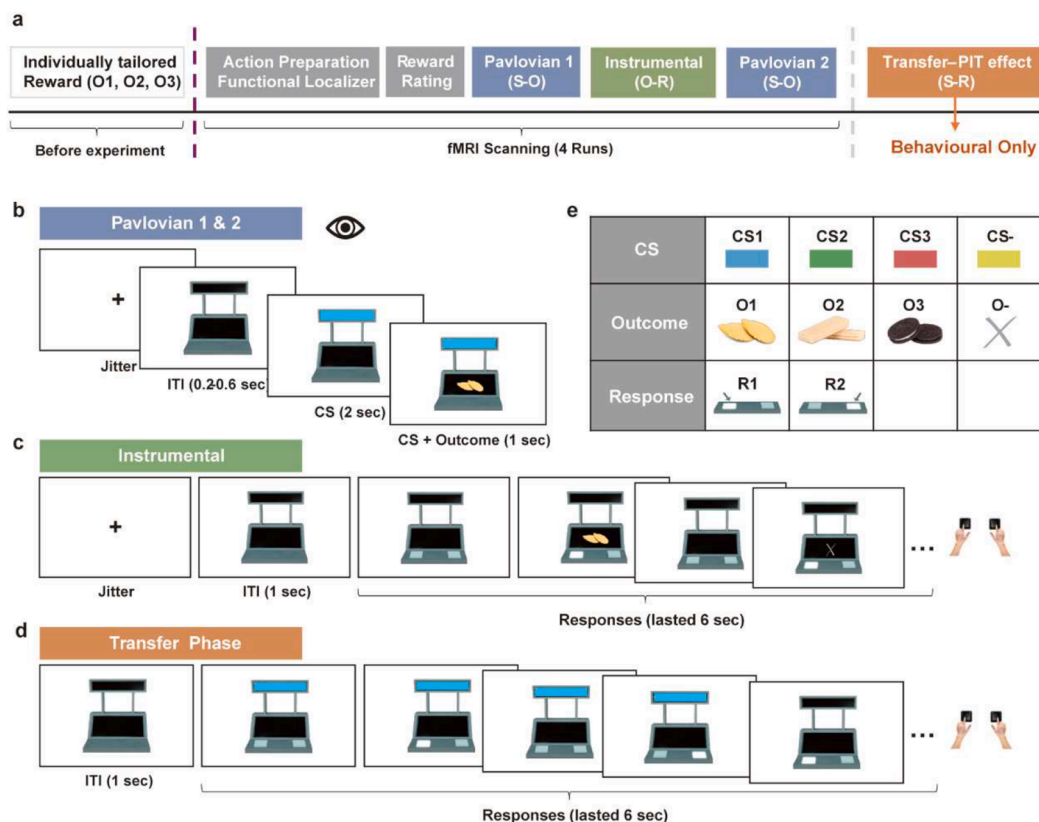


Fig. 1. Experimental procedure and design. *Note.* **a**) *Experimental procedure.* The day before the experiment, all participants completed an online reward selection questionnaire to individually tailor the food rewards used during the study. On the experimental day, participants fasted for 2 h prior to arrival. The experiment consisted of four fMRI runs: (1) a Go/No-Go functional localizer to identify the action preparation brain network (see Methods). Before the Pavlovian-to-Instrumental Transfer (PIT) task, participants rated their current liking and wanting for each reward, as well as their hunger level. The remaining runs included: (2) Pavlovian 1 (stimulus–outcome; S–O), (3) Instrumental (outcome–response; O–R), and (4) Pavlovian 2 (S–O). Finally, participants completed a Transfer phase (PIT effect; S–R), which was conducted behaviorally. **b**) *Pavlovian phases 1 and 2.* Participant were instructed that the slot machine’s buttons were broken, meaning they could not press to win. But each time a food reward appeared on the middle screen of the slot machine, it indicated that they had “won” that reward. Participants simply observed during this phase, learning the association between the colored cues (conditioned stimuli, CS) and specific food outcomes. **c**) *Instrumental phase.* Participants were told that the slot machine buttons were now repaired and that they could press to win snacks. Each trial lasted 6 s, during which they could press as many times as they liked, but only one key (left or right) per trial. Each key was associated with a specific food reward or a non-rewarded outcome (X). **d**) *Transfer phase.* Participants were instructed that they could press to win again, but the slot machine’s middle screen was now broken, so the outcomes were not visible. Each trial again lasted 6 s, and participants could freely press the left or right key as often as they wished. **e**) *Example of conditions.* Food rewards shown here are examples; in the actual experiment, reward types were individually tailored based on each participant’s subjective ratings of liking, ensuring matched reward value across individuals. R1 = left key; R2 = right key.

ms. Participants executed the cued response on Go trials or withheld action on No-Go trials. Inter-trial intervals consisted of a fixation cross (pseudo-logarithmic jitter distribution: mean \approx 2700 ms; 50% short durations of 200, 800, 1400, or 2000 ms, 33.3% intermediate durations of 2600, 3200, 3800, or 4400 ms, 16.7% long durations of 5000, 5600, 6200, or 6800 ms), identical across MRI runs. Participants completed two blocks of 53 trials each (106 trials total): 16 Go and 90 No-Go trials, equally distributed across cue types (30 left-hand, 30 right-hand, 30 baseline). Accuracy feedback was provided at the end of each block, followed by a short self-paced break.

2.3.2. Reward rating

After the Go/No-Go task, participants rated their current liking (“How much do you like to eat it usually?”) and wanting (“How much do you want to eat it right now?”) for the three selected snacks using a nine-point Likert scale (1–9). They also rated their current hunger level to ensure comparable motivation toward food rewards prior to the PIT task.

2.3.3. Pavlovian-to-instrumental transfer (PIT) task

The PIT task assessed the influence of Pavlovian cues on instrumental actions and comprised four phases, following a procedure adapted from [Finotti et al. \(2025\)](#). Participants were told that they would interact with a virtual slot machine to win snack rewards. Each phase began with task-specific instructions explaining how the slot machine operated (see [Fig. 1](#)).

Pavlovian Phase 1. Participants were instructed that the slot machine buttons were broken, so they could not press to win. However, each time a food image appeared on the lower screen, they won it. When an “X” appeared, no reward was delivered. Throughout this phase, participants formed the association between four color cues (conditioned stimuli; CS) and their respective outcomes (O). Three cues (CS1, CS2, CS3) were predicted one of the three individually tailored snack rewards (O1, O2, O3) with an 80% contingency. In the remaining trials, these cues were followed by the non-rewarding outcome (O-; an “X”). A fourth cue (CS-) was consistently associated with O-. Each trial began with a fixation cross presented with a pseudo-logarithmic jitter (200–6800 ms; mean \approx 2700 ms), followed by a slot machine without buttons (0.2–0.6 s). The upper screen of the slot machine then lighted up one of the CS cues (2 s), followed by the corresponding outcome (1 s). Participants completed three blocks of 40 randomized trials each (10 per CS; 120 total). After each mini-block, a contingency awareness check assessed cue–outcome knowledge (e.g., “Which food did you win with this color?”). Participants responded using key presses (1–4), with the key–outcome mapping (O1, O2, O3, O-) randomized across blocks.

Instrumental learning phase. Participants were told that the slot machine buttons had been repaired and that they could now press to win snacks. At the beginning of each trial, they chose whether to press the left (R1) or right (R2) button. Only one button could be pressed per trial, but participants could press it repeatedly within a 6-s response window. Each button press produced immediate feedback: R1 actions yielded O1, and R2 actions yielded O2 on 25% of presses, with the remaining presses resulting in O-. Each trial began with a fixation cross presented with a pseudo-logarithmic jitter (200–6800 ms; mean \approx 2700 ms), followed by a 1-s slot machine display before the buttons appeared. Each press triggered an outcome shown for 1-s, during which no further responses could be made. Participants first completed six practice trials (no rewards), followed by two blocks of 40 trials (80 total). After each block, similarly an instrumental contingency check assessed action–outcome knowledge (e.g., “Which food did you win with this button?”).

Pavlovian Phase 2. Participants then performed a second Pavlovian phase, identical to Pavlovian phase 1. This phase was designed to examine changes in brain activity resulting from instrumental learning compared to Pavlovian 1.

Transfer phase (PIT effect). Finally, participants completed a transfer phase to assess the influence of Pavlovian cues on instrumental

action in the absence of reward delivery. They were instructed that the slot machine buttons could again be pressed to win snacks, but that the lower screen was broken, so the outcomes would not be visible. They were also told that presses might still lead to snack rewards, maintaining task engagement under nominal extinction. This nominal extinction procedure follows common practice in human PIT paradigms and has been shown to reliably produce transfer effects while maintaining participant engagement ([Badioli et al., 2024](#)). Each trial began with a 1-s presentation of the slot machine without buttons. When the buttons appeared, the upper screen simultaneously displayed one of the four CS cues for 6 s. Participants could freely press the left or right button as often as they wished. No outcomes were shown to prevent further learning. The transfer phase consisted of six blocks of eight trials (48 trials total), with 12 trials per CS condition. Behavioral data were collected inside the scanner, although no fMRI data were acquired during this phase.

2.4. Data acquisition and preprocessing

All tasks and stimuli were programmed and presented in OpenSesame v3.2 ([Mathôt et al., 2012](#)). Functional MRI data were acquired at the fMRI center of South China Normal University using a Siemens Trio 3T scanner (Siemens, Erlangen, Germany) equipped with a 20-channel head coil. Functional blood-oxygenation-level-dependent (BOLD) images were collected using a T2*-weighted echo-planar imaging (EPI) sequence consisting of 62 axial slices acquired in ascending order and oriented along the anterior commissure–posterior commissure (AC–PC) plane (voxel size = $2 \times 2 \times 2$ mm³; slice thickness = 2 mm; interslice gap = 15%; repetition time [TR] = 2000 ms; echo time [TE] = 30 ms; flip angle = 90°; field of view [FOV] = 224 mm). Data were collected across four functional runs per participant. To correct for magnetic field inhomogeneities, a gradient echo field map was acquired prior to the EPI scans (TE1 = 4.92 ms; TE2 = 7.38 ms). A high-resolution T1-weighted anatomical image was acquired using a magnetization-prepared rapid gradient-echo (MPRAGE) protocol at the end of the functional runs (voxel size = $0.5 \times 0.5 \times 1$ mm³; TR = 2530 ms; TE = 1.94 ms; flip angle = 7°; slice thickness = 1.0 mm; FOV = 256 mm).

Preprocessing of functional MRI data was conducted using SPM12 (Statistical Parametric Mapping; Wellcome Trust Centre for Neuroimaging, University College London, London, UK). Raw DICOM (Digital Imaging and Communications in Medicine) images were first converted to NIFTI (Neuroimaging Informatics Technology Initiative) format. To correct for spatial distortions caused by magnetic field inhomogeneities, voxel displacement maps (VDMs) were generated using the FieldMap toolbox ([Hutton et al., 2002](#); [Ashburner, 2007](#)). VDMs were derived from the phase-difference and magnitude field map images and were aligned to the first volume of each of the four functional runs as well as the subject’s T1-weighted anatomical image. Functional images were then slice-timing corrected to account for between-slice acquisition differences, followed by realignment to the mean functional image of the first run to correct for head motion. Unwarping was performed using subject-specific VDMs to correct for susceptibility-by-movement interactions. All functional volumes were then normalized to Montreal Neurological Institute (MNI) space via unified segmentation of the co-registered structural image and resampled to $2 \times 2 \times 2$ mm voxel resolution. Finally, the normalized images were spatially smoothed using an 8 mm full-width at half-maximum (FWHM) Gaussian kernel. Six participants were excluded due to excessive motion (>3 mm translation or >3° rotation). No significant differences in mean head motion, quantified as framewise displacement of the head, were observed across Pavlovian phases or CS conditions (all $ps > 0.17$).

2.5. Behavioral data analysis and statistics

Behavioral data were analyzed using both frequentist and Bayesian statistical approaches in JASP v0.95.1 ([Love et al., 2019](#)). Statistical

significance was determined at $p < 0.05$, with Bonferroni correction applied when applicable. Depending on the comparisons, repeated-measures analyses of variance (RM-ANOVAs), one-sample t -tests or Pearson correlations were performed. When sphericity assumptions were violated, Greenhouse–Geisser corrections were applied. Effect sizes were reported using partial eta-squared (η_p^2) for ANOVAs, Cohen's d for t -tests, and Pearson's r for correlations. Bayesian analysis were conducted to quantify evidence for the alternative hypothesis (H_1) related to the null hypothesis (H_0) using the Bayes Factor (BF_{10}), defined as $p(\text{data}|H_1)/p(\text{data}|H_0)$ (Kruschke, 2021). A BF_{10} between 1/3 and 3 indicates inconclusive evidence, while values > 3 or $< 1/3$ provide increasing support for H_1 or H_0 , respectively. For example, $BF_{10} = 10$ implies the data are 10 times more likely under H_1 than H_0 , whereas $BF_{10} = 0.05$ implies the data are 20 times more likely under H_0 than H_1 , providing strong support for the null (Marsman and Wagenmakers, 2017). Default prior distributions implemented in JASP were used, depending on the statistical test.

2.6. MRI data analysis

2.6.1. Univariate whole-brain analyses

To identify brain activation patterns during the functional localizer and PIT task, we employed a general linear modeling (GLM) approach across analyses. At the first-level, experimental regressors were modeled as boxcar functions and convolved with a canonical hemodynamic response function (HRF). A high-pass filter with a 128-s cut-off was applied to remove low-frequency drifts. Six head motion parameters (translation and rotation) were entered as nuisance regressors to account for motion-related variance.

Go/No-Go Functional Localizer. The Go/No-Go task was modeled to identify regions involved in action preparation. The first-level GLM included: 1–3) Correct prepared No-Go trials (Prepare-Left, Prepare-Right, Prepare-None), modeled at cue onset (duration = 4 s); 4) Correct prepared Go trials (cue onset); 5–6) Correct Go button-press regressors for left- (L) and right-hand (R) responses, modeled as impulses (duration = 0 s) at response time; 7) Incorrect trials (cue onset); and six motion parameters. To identify the action preparation network, hemispheric regions of interest (ROIs) were mapped using contralateral contrasts: Left ROIs $\rightarrow R > L$; Right ROIs $\rightarrow L > R$. For bilateral ROIs, the contrast $(L + R) > (2 \times \text{None})$ was used. (See Supplementary Materials and Definition of ROIs)

Instrumental Phase. The instrumental conditioning phase was modeled separately to identify regions involved in instrumental learning. The first-level GLM included: 1) Action-Left, modeled at the trial onset (trial duration); 2) Parametric modulator (Left): number of left responses; 3) Action-Right (same as regressor 1); 4) Parametric modulator (Right): number of right responses; 5) Instrumental question screen (Q); 6–7) Button-press regressors for left- and right-hand responses (impulses duration = 0 s); 8) Incorrect trials (simultaneous presses both hands; included only if present); and plus six motion parameters. Lateralized contrasts ($L > R$; $R > L$) were used to identify instrumental learning related regions (See Supplementary Materials and Definition of ROIs).

Pavlovian Phases 1 and 2. Event-related GLMs examined cue-evoked neural activity during Pavlovian learning. Pavlovian 1 and Pavlovian 2 were modeled as separate sessions with identical regressors. Each session included: 1–4) four CS–outcome events (CS1, CS2, CS3, CS–), modeled at the slot machine onset (duration = slot-machine + CS presentation + outcome presentation); 5) Pavlovian question screen (Q); 6–7) Left- and right-hand button presses (impulse duration = 0 s); and six motion parameters (Two session in total of 26 regressors).

To identify brain regions sensitive to action-specific and motivational properties of cues, the following contrasts were computed for each Pavlovian phase. The general PIT effect was defined as $CS3 > CS-$, capturing motivational priming relative to a non-rewarded cue. The specific PIT effect was defined as $(CS1 + CS2) > (2 \times CS3)$ assessing

action-specific versus general motivational signals. Hand-specific PIT was examined using $CS1 > CS3$ (left-hand) and $CS2 > CS3$ (right-hand) contrasts. $CS1 > CS2$ and $CS2 > CS1$ contrasts were used to test lateralized cue-action associations. Exploratory analyses also included $CS1 > CS-$ and $CS2 > CS-$ to capture general motivational contributions of specific CSs. Learning-related changes were tested using Pavlovian phase interactions ($Pav1 > Pav2$; $Pav2 > Pav1$) for each contrast.

Statistical inference. For whole brain analysis, first-level contrast images were entered into second-level one-sample t -tests. Whole-brain results were thresholded at $p < 0.001$ (uncorrected) with cluster-level FWE correction at $p < 0.05$ with minimum cluster size $k = 20$ determined in SPM. Exploratory findings were reported at $p < 0.001$ (uncorrected) only when spatially extended and located within regions consistent with a priori hypotheses.

2.6.2. Subject-specific functional regions of interest (fROIs)

Definition of fROIs. Subject-specific fROIs were defined using a functionally constrained, anatomically guided approach (Fedorenko et al., 2011; Nieto-Castañón and Fedorenko, 2012; Abassi and Papeo, 2024; Munin et al., 2025). This procedure combined group-level anatomical masks with subject-specific functional activation patterns to account for inter-individual variability and localization of functionally relevant regions. For each participant and ROI, the a priori anatomical mask was resliced to the participant's first-level contrast t -map and used as a spatial constraint to identify activated voxels within masks. Within each anatomical mask, activated voxels of the relevant contrast were identified at $p < 0.05$ (uncorrected), ranked by t -value, and up to $N = 100$ voxels per ROI were retained. If fewer than 100 voxels survived, the threshold was relaxed to $p < 0.10$. On average, ROIs contained 86.9 ± 26.4 (SD) voxels. ROIs with fewer than 10 voxels were excluded from further analyses (2.8%; $n = 13$ across subjects). If a hemispheric ROI failed to meet inclusion criteria, a mirrored substitute was generated from the contralateral homologue by reflecting across the midline. Mirroring was applied to 11.6% of lateralized ROIs ($n = 36$ across subjects). All fROIs were defined using an independent Go/No-Go localizer and the instrumental learning phase, without consulting any Pavlovian learning-related contrasts. Voxel selection was performed once per participant based solely on these independent contrasts, and the same voxel sets were used to extract PSC values for both Pavlovian phases. This ensured full independence between ROI definition and subsequent hypothesis testing, thereby avoiding circularity.

Motor-Preparation ROIs. Bilateral ROIs were selected a priori based on previous literature demonstrating their involvement in visuomotor preparation and motor planning. We targeted fronto-parietal network including the premotor cortex (PMC), primary motor cortex (M1), primary somatosensory cortex (S1), anterior intraparietal sulcus (aIPS), anterior inferior parietal lobule (aiPL), pre-supplementary motor area (pre-SMA), and supplementary motor area proper (SMA-proper). Briefly, PMC supports stimulus–response mapping and motor planning (Hoshi and Tanji, 2007); M1 and S1 encode action-specific preparation and the anticipated sensory consequences of action (Gale et al., 2021; Sun et al., 2015); The aIPS contributes to visuomotor transformations underlying goal-directed actions (Hamilton and Grafton, 2006; Tunik et al., 2007; Wolynski et al., 2009), while the aiPL supports higher-order sensorimotor integration and the representation of motor intentions (Fogassi and Luppino, 2005; Desmurget and Sirigu, 2012; Rizzolatti et al., 2006). The pre-SMA support voluntary action selection and inhibition, whereas SMA-proper contributes to the initiation and execution of self-generated movements (Coull et al., 2016). Cortical masks were derived from the Jülich (JuBrain) cytoarchitectonic atlas (maximum-probability maps, v3.0) in MNI space. ROI definitions were as follows: PMC = $6d1/6d2/6d3$; M1 = Areas 4a/4p; S1 = $3a/3b/1/2$; aSPL/IPS = $hIP1-hIP3$; aiPL = $PFt/PFop/PF/PFm$; pre-SMA = Area 6mr (bilateral); SMA-proper = Area 6mc (bilateral). For lateralized motor-preparation ROIs (Go/No-Go localizer), left hemispheric ROIs were identified using $R > L$ contrasts and right hemispheric ROIs using L

> R. For midline regions (pre-SMA and SMA-proper), the contrast ($L + R$) > ($2 \times \text{None}$) was used.

Instrumental-Learning ROIs. Subcortical ROIs included the caudate nucleus, putamen, and thalamus, selected a priori based on their well-established roles in goal-directed learning and sensorimotor control (Bradfield and Balleine, 2017). The anterior caudate nucleus integrates performance-related information and cognitive control demands during goal-directed action–outcome learning (Grahn et al., 2008), whereas the putamen tracks stimulus–response associations during instrumental learning (Brovelli et al., 2011). The thalamus serves as an integration hub for cortico-striatal signaling, supporting adaptive motor control and the coordination of action plans (Haber and Calzavara, 2009). Anatomical masks were defined using the Harvard–Oxford subcortical atlas (max-probability, 25% threshold) in MNI space. Hemisphere-specific contrasts ($L > R$; $R > L$) were used to capture lateralized activation patterns during instrumental learning.

ROI Analysis and Statistical Inference. For each subject, percent signal change (PSC) values were extracted from the defined ROIs during Pavlovian Phase 1 and Phase 2 using MarsBaR (Brett et al., 2002). PSC values were analyzed using repeated-measures ANOVAs in R using the *afex* package, including within-subject factors of Pavlovian Phase, CS conditions, ROIs, and Hemisphere. The specific ANOVA structure varied according to ROIs grouping and hypothesis tested. As in the behavioral analyses, both frequentist and Bayesian statistics were reported. Post-hoc analyses were performed using the *emmeans* package (Lenth and Piaskowski, 2026). Hypothesis-driven contrasts were specified to test cue-related effects relevant to specific and general PIT (e.g., CS1 vs. CS2, CS1 vs. CS3, CS2 vs. CS3, CS3 vs. CS–). These contrasts were evaluated within relevant levels of Pavlovian Phase, ROI, and Hemisphere. For each predefined contrast type, p-values were first computed without adjustment and then corrected using Bonferroni correction across all corresponding tests within that contrast family to control the family-wise error rate. Only Bonferroni-corrected p-values are reported.

3. Results

3.1. Behavioral results

3.1.1. Reward liking and wanting

To ensure that the three selected rewarding outcomes (O1, O2, O3) were similarly valued, we conducted one-way ANOVAs on liking and wanting scores obtained on the experimental day prior to the PIT task. Liking ratings did not significantly differ across outcomes (O1: $M = 6.77$, $SD = 1.26$; O2: $M = 6.39$, $SD = 1.48$; O3: $M = 6.58$, $SD = 1.39$; $F_{(2,60)} = 2.517$, $p = 0.089$, $\eta_p^2 = 0.077$, $BF_{10} = 0.675$). Similarly, wanting ratings showed no significant differences (O1: $M = 6.45$, $SD = 1.57$; O2: $M = 6.32$, $SD = 1.78$; O3: $M = 6.29$, $SD = 1.58$; $F_{(2,60)} = 0.560$, $p = 0.574$, $\eta_p^2 = 0.018$, $BF_{10} = 0.150$). Participants also hunger level above the midpoint of the scale ($M = 5.65$, $SD = 1.68$; one sample $t(30) = 2.133$, $p = 0.021$, Cohen's $d = 0.383$, $BF_{10} = 2.689$), indicating adequate motivation toward the food rewards. Together, these results support the methodological effectiveness of the individualized reward selection procedure, ensuring that outcome values were comparable across the rewards used in the PIT task.

3.1.2. Explicit measures of Pavlovian and instrumental contingency

During Pavlovian phase 1, all participants ($N = 31$) reached the learning criterion by the second block, with 100% accuracy in answering the cue–outcome associations. Accuracy remained at ceiling in the third block, with an overall accuracy of 99.2% across the three blocks. The same pattern was observed in Pavlovian Phase 2, in which all participants again achieved 100% accuracy by the third block, with an overall accuracy of 99.5%. During the instrumental phase, all participants reached the learning criterion by the second block (100% accuracy on the contingency questions), and overall accuracy across both blocks was 91.9%. Together, these results confirmed that participants acquired

explicit knowledge of the Pavlovian and instrumental contingencies.

3.1.3. Response bias of instrumental phase

The average number of total responses during the Instrumental phase was 283.87 ($SD = 41.64$, Range = [184, 347]). To assess whether participants had a response bias between the two instrumental actions (R1 = Left, R2 = Right), we compared the number of R1 and R2 presses using a paired-samples *t*-test. No significant differences observed (R1: $M = 147.58$, $SD = 36.66$; R2: $M = 136.29$, $SD = 36.485$; $t_{(31)} = 1.045$, $p = 0.304$, Cohen's $d = 0.188$, $BF_{10} = 0.316$). The Bayes factor indicates moderate evidence in favor of the null hypothesis, suggesting no response bias and comparable learning of the R1→O1 and R2→O2 contingencies.

3.1.4. Transfer phase

Number of responses. To examine how CS cues biased action selection, we conducted a repeated-measures ANOVA on the number of responses with factors CS Cue (CS1, CS2, CS3, CS–) and Response (R1, R2). There were a significant main effects of CS cue ($F_{(1.56, 46.68)} = 5.572$, $p = 0.011$, $\eta_p^2 = 0.157$; $BF_{10} = 3.575 \times 10^{+6}$) and Response ($F_{(1, 30)} = 22.00$, $p < 0.001$, $\eta_p^2 = 0.423$; $BF_{10} = 2.239 \times 10^{+7}$). A significant interaction between CS cue and Response was also observed ($F_{(3,90)} = 9.852$, $p < 0.001$, $\eta_p^2 = 0.247$; $BF_{10} = 1.608 \times 10^{+7}$). As shown in Fig. 2a, post-hoc comparisons revealed a significant left-hand response bias in the CS1 condition (R1: $M = 141.00$, $SD = 67.79$; R2: $M = 95.90$, $SD = 72.59$; $t = 2.833$, $p = 0.005$, Cohen's $d = 0.671$), and a significant right-hand response bias in the CS2 condition (R1: $M = 76.87$, $SD = 52.91$; R2: $M = 158.58$, $SD = 80.32$; $t = -5.134$, $p < 0.001$, Cohen's $d = -1.215$). A similar right-hand bias was also observed under the CS3 condition, likely reflecting right-hand dominance (R1: $M = 95.36$, $SD = 60.23$; R2: $M = 144.39$, $SD = 76.26$; $t = -3.081$, $p = 0.003$, Cohen's $d = -0.729$). No significant response bias was found under CS– (R1: $M = 85.10$, $SD = 56.54$; R2: $M = 105.90$, $SD = 66.50$; $t = -1.307$, $p = 0.194$, Cohen's $d = -0.309$). These results provide behavioral evidence of specific transfer, where CS1 and CS2 biased action toward their associated responses, and also reveal a hand-dominance effect under CS3.

Specific and general PIT effects. To quantify specific PIT, we calculate the proportion of congruent responses ($CS1_{R1} + CS2_{R2}$) and incongruent responses ($CS1_{R2} + CS2_{R1}$) relative to the total number of responses ($CS1_{R1+R2} + CS2_{R1+R2}$) separately. Because congruent and incongruent responses are complementary and sum to 1 within each participant, specific PIT was tested using a one-sample *t*-test against chance level (0.5) on the proportion of congruent responses. As shown in Fig. 2b, the proportion of congruent responses was significantly higher than chance (Congruent: $M = 0.64$, $SD = 0.17$; $t_{(30)} = 4.563$, $p < 0.001$, Cohen's $d = 0.820$, 95%CI = [0.471, ∞]; $BF_{10} = 632.260$). The Bayes factor indicates strong evidence in favor of the alternative hypothesis, confirming a robust specific PIT effect. The complementary incongruent proportion ($M = 0.36$, $SD = 0.17$) reflects the same deviation from chance in the opposite direction. To quantify general PIT, we computed the proportion of responses during CS3 ($CS3_{R1+R2}$) and CS– (CS_{-R1+R2}), relative to the total number of response during CS3 and CS– trials ($CS3_{R1+R2} + CS_{-R1+R2}$). We again performed a one-sample *t*-test against 0.5 on the CS3 proportion. As shown in Fig. 2c, response vigor was significantly greater than chance under CS3 (CS3: $M = 0.57$, $SD = 0.16$; CS–: $M = 0.44$, $SD = 0.16$; $t_{(30)} = 2.300$, $p = 0.014$, Cohen's $d = 0.413$, 95%CI = [0.102, ∞]; $BF_{10} = 3.648$). The Bayes factor provides moderate evidence in favor of the alternative hypothesis, supporting the presence of a general PIT effect. Although general PIT is typically quantified using an outcome-independent cue (CS3 vs. CS–), motivational invigoration may also appear under outcome-specific cues (CS1 and CS2) due to their shared association with reward. Using the same one-sample *t*-test approach against chance, both CS1 ($t_{(30)} = 2.267$, $p = 0.015$, Cohen's $d = 0.407$; $BF_{10} = 3.433$) and CS2 ($t_{(30)} = 2.270$, $p = 0.015$, Cohen's $d = 0.408$; $BF_{10} = 3.451$) showed significant deviations from chances, with moderate evidence for the alternative hypothesis, indicating that outcome-specific cues also exert a general motivational influence, consistent with prior work (Degni et al., 2024; Finotti et al., 2025).

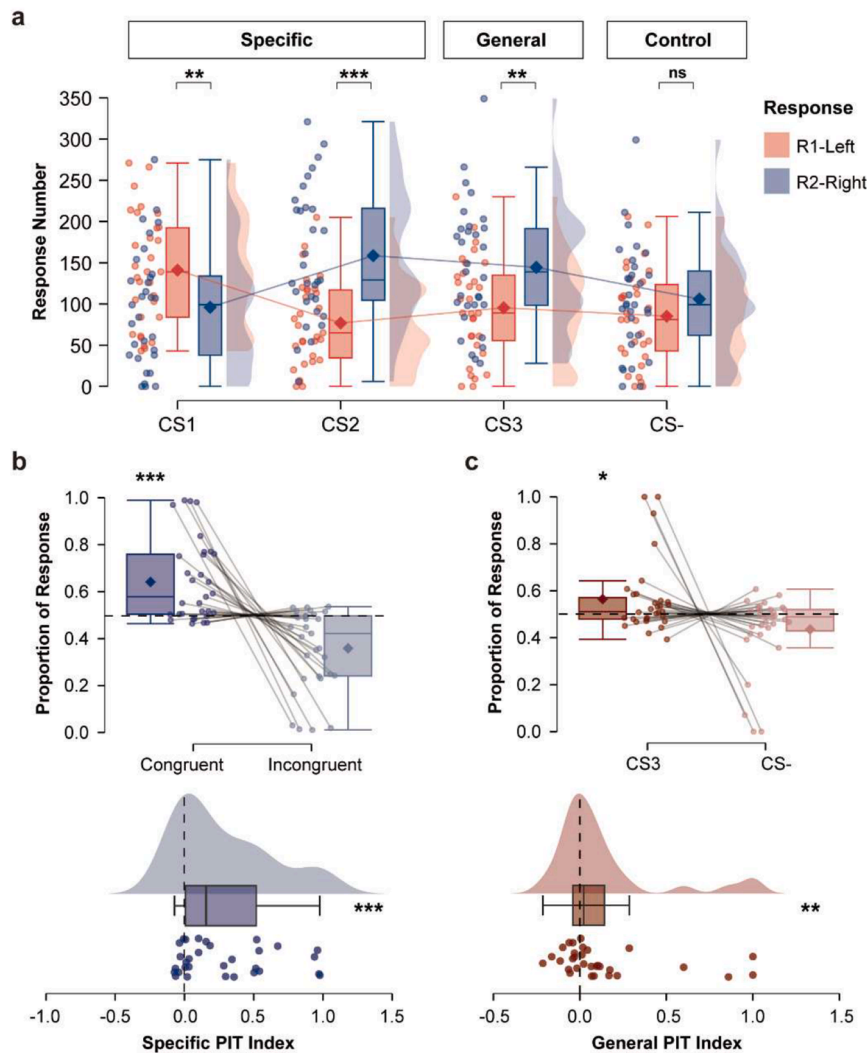


Fig. 2. Behavioral results of Pavlovian-to-instrumental transfer (PIT) Effect. *Note.* **a.** Response bias as a function of CS cue type. "Specific" refers to reward-predictive cues (CS1 and CS2) showing a specific transfer effect; "General" reflects the general transfer condition (CS3); and "Control" refers to the non-rewarded condition (CS-). **b.** Upper panel: Proportion of congruent and incongruent responses under CS1 and CS2. Because these proportions are complementary and sum to 1, the specific PIT effect was tested as deviation from chance (0.5) of the congruent proportion (dashed line). Lower panel: The specific PIT index [(Congruent – Incongruent) / total responses] reflects bias toward the response associated with the same reward (positive values indicate congruent bias). **c.** Upper panel: Proportion of responses under CS3 relative to CS-. As these proportions are complementary, general PIT was tested as deviation from chance (0.5) of the CS3 proportion. Lower panel: The general PIT index [(CS3 – CS-) / total responses] reflects cue-induced response invigoration (positive values indicate enhanced responding under CS3). Box plots display the median and interquartile range (IQR); whiskers extend to $1.5 \times$ IQR. Diamond markers indicate the mean. Asterisks indicate significance levels: * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$. ns indicate non-significant results.

Specific and general PIT indices. For subsequent fMRI analysis, we computed two behavioral indices. The specific PIT index was calculated as: (Congruent responses) – (Incongruent responses) divided by the total number of responses under CS1 and CS2, reflecting the degree to which participants favored the response previously associated with the same reward. A one-sample t -test against zero confirmed a significant bias toward congruent responses ($t_{(30)} = 4.563$, $p < 0.001$, Cohen's $d = 0.820$; $BF_{10} = 316.151$), validating a robust specific transfer (Fig. 2b). The general PIT index was defined as: (CS3 responses) – (CS- responses) divided by the total number of responses across both conditions, capturing the extent to which a reward-associated cue (CS3) invigorates action relative to a neutral cue (CS-). This index was also significantly greater than zero ($t_{(30)} = 2.300$, $p = 0.014$, Cohen's $d = 0.413$; $BF_{10} = 1.856$), validating the behavioral index of general transfer (Fig. 2c). No significant correlation was found between the specific and general PIT indices (Pearson's $r = 0.213$, $p = 0.249$; $BF_{10} = 0.421$), suggesting that these two effects may rely on distinct mechanisms and operate independently at the behavioral level.

3.2. Whole-brain neural results

3.2.1. Baseline Pavlovian learning effect (Pavlovian 1)

We first examined the baseline effects of Pavlovian learning during Pavlovian phase 1. Since all three CS+ cues (CS1, CS2, CS3) were associated with equally valued outcomes, we expected them to recruit comparable neural responses relative to CS- cue. As shown in Fig. 3a, each [CS+ > CS-] contrast revealed overlapping activation in visual occipitotemporal regions (including fusiform gyrus and V4), as well as in fronto-parietal areas such as inferior and middle frontal gyri (IFG, MFG), intraparietal sulcus (IPS), and pre-supplementary motor area (pre-SMA) (see Table S1 for full results). These effects were consistent across the three CS+ cues. When examining the combined contrast [CS1+CS2+CS3 > 3CS-], we observed a similar activation pattern, with additional significant clusters in the bilateral dorsal Insula. Together, these findings indicate that the three CS cues elicited broadly comparable activation patterns during early Pavlovian learning.

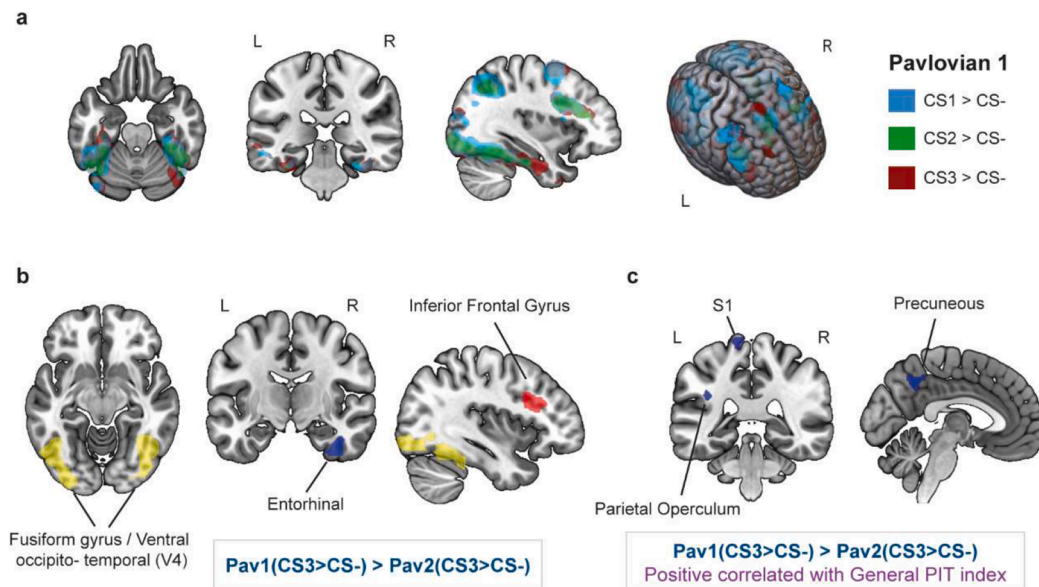


Fig. 3. Neural results of baseline Pavlovian learning and general PIT. *Note.* **a.** *Baseline Pavlovian learning effect (Pavlovian 1).* Increased activation for CS+ cues (CS1, CS2, CS3) relative to CS-, observed in the fusiform gyrus (FG), ventral occipitotemporal cortex (V4), inferior and middle frontal gyri (IFG/MFG), intraparietal sulcus (IPS), dorsal insula, and pre-SMA. The effect was consistent across all CS+ cues ($p_{FWE} < 0.05$, see Table S1). **b.** *General PIT effect.* Whole-brain contrasts of CS3 > CS- ($p_{FWE} < 0.05$) revealed stronger activation in Pavlovian 1 compared to Pavlovian 2. Significant clusters included the FG and V4, entorhinal cortex, and IFG. No significant clusters were found for Pavlovian 2 > Pavlovian 1, indicating a decline in general PIT-related activation as learning stabilized. **c.** *Group-level regression analysis of General PIT.* Neural activation for [Pavlovian 1 (CS3 > CS-) > Pavlovian 2 (CS3 > CS-)] positively correlated with individual behavioral general PIT indices. Exploratory analyses ($p < 0.001$ uncorrected) revealed positive correlations in the primary somatosensory cortex (S1), parietal operculum, and precuneus, suggesting that these regions track individual differences in the behavioral expression of general PIT (See Table S2).

3.2.2. General PIT effect (CS3)

We next examined neural response engaged by the general PIT-related cue (CS3) during Pavlovian learning. The contrast [CS3 > CS-] was used to identify reward-predictive cue responses relative to a non-rewarded CS- cue. Learning-related modulation was assessed by comparing Pavlovian Phase 1 and Pavlovian Phase 2. To test whether CS3-related processing changed following instrumental learning, we computed the interaction contrast [Pavlovian 1 (CS3 > CS-) > Pavlovian 2 (CS3 > CS-)]. This analysis revealed significant clusters in bilateral fusiform gyrus (FG) and ventral occipitotemporal cortex (VOTC), extending into the inferior frontal gyrus (IFG) and right entorhinal cortex ($p_{FWE} < 0.05$; $k = 198$; Fig. 3b and Table S2). No significant clusters were observed in the reverse comparison [Pavlovian 2 > Pavlovian 1]. To further identify brain regions tracking individual variability in general PIT strength, we conducted a group-level regression analysis in which the behavioral general PIT index was entered as a between-subject covariate for the same interaction contrast. An exploratory uncorrected analysis ($p < 0.001$, see Fig. 3c and Table S2) revealed positive correlations in the left postcentral gyrus (S1; $x = -10$, $y = -38$, $z = 78$; $T = 4.34$), parietal operculum (-40 , -36 , 28 ; $T = 5.44$), and precuneus (-4 , -54 , 42 ; $T = 4.73$), although this association should be interpreted with caution. Together, these findings indicate that neural responses to general PIT-related cues are modulated following instrumental learning, particularly within occipitotemporal regions. While responses to CS3 appear reduced in Pavlovian Phase 2 relative to Phase 1, these changes likely reflect a learning-dependent reweighting of cue relevance.

3.2.3. Specific PIT effect (CS1, CS2)

Our main hypothesis concerned the specific PIT effect, predicted to emerge after instrumental contingencies were learned. Specifically, we examined whether action-specific Pavlovian cues (CS1, CS2) would evoke stronger responses in motor and sensorimotor regions during Pavlovian 2 compared with Pavlovian 1. To test this, we examined the contrasts [Pavlovian 2 (CS1 > CS3) > Pavlovian 1 (CS1 > CS3)],

[Pavlovian 2 (CS2 > CS3) > Pavlovian 1 (CS2 > CS3)], and [Pavlovian 2 (CS1 + CS2 > 2 × CS3) > Pavlovian 1 (CS1 + CS2 > 2 × CS3)]. No clusters survived whole-brain correction for the direct contrasts. However, group-level regression analysis revealed that neural activity covaried with individual differences in specific PIT strength. As shown in Fig. 4a, for the contrast [Pavlovian 2 (CS1 > CS3) > Pavlovian 1 (CS1 > CS3)], significant positive correlations emerged in the bilateral middle frontal gyrus (MFG) and IPS ($p_{FWE} < 0.05$). Exploratory uncorrected effects were found in the left primary sensorimotor cortex (M1/S1) ($k = 119$, peak MNI: $x = -28$, $y = -32$, $z = 56$, $t = 4.32$, $p_{uncor} < 0.001$), suggesting that stronger behavioral PIT expression was associated with recruitment of frontal-parietal and sensorimotor regions. No significant clusters were found for the [CS2 > CS3] contrast. An exploratory contrast, [Pavlovian 2 (CS1 + CS2 > 2 × CS3) > Pavlovian 1 (CS1 + CS2 > 2 × CS3)], revealed additional activation in the right IPS ($k = 94$, $t = 4.60$, $p_{uncor} < 0.001$). Overlap between specific and general PIT regression maps (Fig. 4b) showed largely distinct activation patterns, suggesting the view that these two forms of PIT may recruit partially distinct cortical networks. However, because this comparison includes exploratory maps, this dissociation should be interpreted cautiously.

To test whether specific PIT involved lateralized motor coding at the whole-brain level, we compared [CS1 > CS2] and [CS2 > CS1] contrasts. No significant clusters were found during Pavlovian 1. During Pavlovian 2, exploratory results ($p_{uncor} < 0.001$) revealed bilateral caudate activations for [CS2 > CS1] (left: $x = -6$, $y = 12$, $z = 4$; right: $x = 8$, $y = 16$, $z = 8$; $t = 6.49/4.94$; Fig. 4c). A similar interaction pattern was observed from exploratory analyses for the interaction contrast [Pavlovian 2 (CS2 > CS1) > Pavlovian 1 (CS2 > CS1)], which showed clusters in right caudate, pre-SMA, and fusiform/V4 regions. ($p_{uncor} < 0.001$). (see Supplementary Results and Table S3). Together, these results suggest that the specific PIT expression relates to increased engagement of fronto-parietal regions, particularly MFG and IPS, and may involve sensorimotor processing. Evidence for direct motor cortex or lateralized motor recruitment at the whole-brain level was limited, and the observed subcortical effects, including caudate activation,

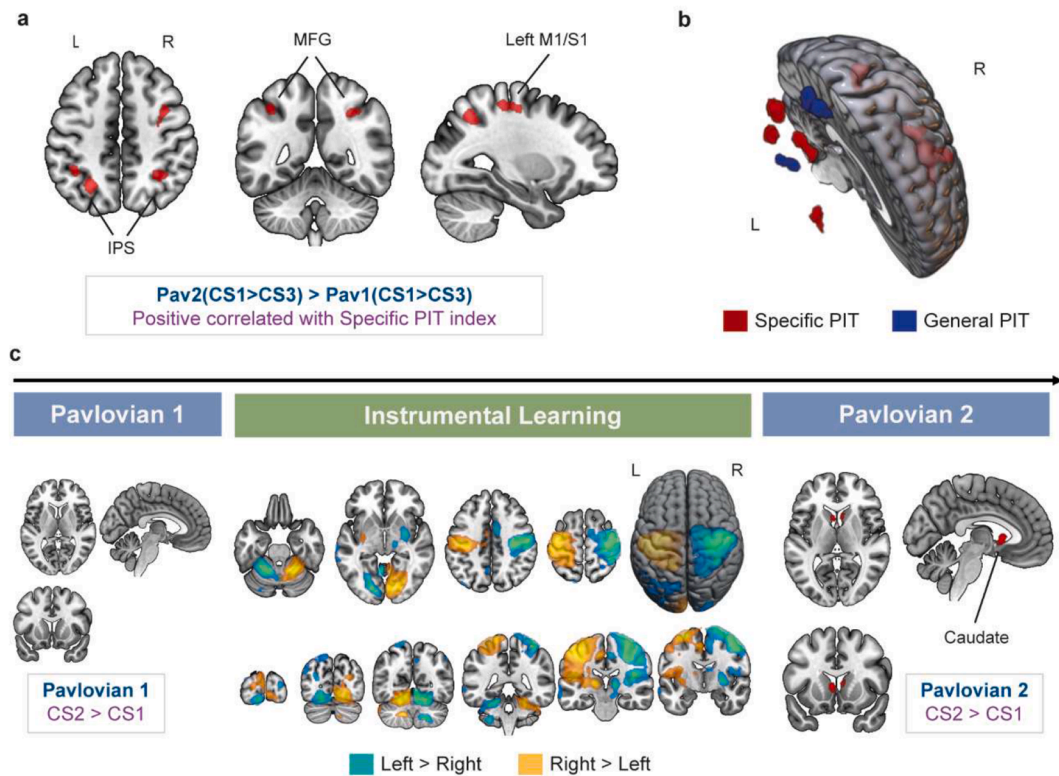


Fig. 4. Neural Results of Specific PIT. *Note.* **a.** Group-level regression analysis of the specific PIT effect. Neural activation for the contrast [Pavlovian 2 (CS1 > CS3) > Pavlovian 1 (CS1 > CS3)] positively correlated with individual behavioral specific PIT indices. Significant correlations were observed in the MFG and IPS ($p_{\text{FWE}} < 0.05$), as well as in the primary motor and somatosensory cortices (M1/S1) at an exploratory threshold ($p < 0.001$, uncorrected), indicating that these regions track individual variability in the behavioral expression of the specific PIT effect (See Table S3). **b.** Overlap between specific and general PIT regression maps. Overlapping activation maps revealed distinct cortical networks underlying specific and general PIT effects. **c.** Lateralization analysis of specific PIT before and after instrumental learning. No significant clusters were found during Pavlovian 1, whereas a significant caudate cluster emerged during Pavlovian 2 for the contrast [CS2 > CS1] ($p_{\text{uncor}} < 0.001$). During the instrumental learning phase, we also observed robust bilateral activations were observed across cerebellar, sensorimotor, and parietal regions, consistent with recruitment of the action-execution network (see Supplementary Results and Table S4).

should be interpreted cautiously. Nonetheless, the pattern aligns with the view that specific PIT involves the integration of sensory–motor and motivational representations, supporting the goal-directed accounts of PIT.

3.3. ROI approach results

3.3.1. Motor-Preparation network

Our primary hypothesis was that specific PIT would engage the motor system in an action-specific and lateralized manner, such that Pavlovian cues associated with left- or right-hand actions (CS1, CS2) would preferentially recruit contralateral motor regions. To directly test this hypothesis, we conducted a hypothesis-driven ROI analysis within an independently defined motor-preparation network derived from the Go/NoGo localizer (see Fig. S1). The localizer robustly activated the canonical fronto–parietal motor circuit involved in action selection and preparation (see Supplementary Results, Table S5 and Fig. 5). Based on this activation pattern and prior literature, seven bilateral regions were defined as the anatomical mask for subject-specific functional ROIs (fROIs; Fig. 5a), including the anterior inferior parietal lobule (aIPL), anterior intraparietal sulcus (aIPS), premotor cortex (PMC), primary somatosensory cortex (S1), primary motor cortex (M1), pre-supplementary motor area (pre-SMA), and supplementary motor area proper (SMA-proper).

Percent signal change (PSC) values were extracted for each Pavlovian phase (Pavlovian 1, Pavlovian 2) and cue condition (CS1, CS2, CS3, CS–) and entered into repeated-measures ANOVAs (see Table S6). The full factorial model revealed a significant interaction of

Hemisphere (Left, Right) \times ROIs (aIPL, aIPS, PMC, S1, M1) \times Pavlovian \times Cue ($F_{(6,16, 184.91)} = 4.41$, $p < 0.001$, $\eta^2_p = 0.128$; $\text{BF}_{10} = 2.027 \times 10^{+7}$), indicating that cue-related activation differed across hemispheres, ROIs, and learning phase. Significant three-way interactions of Pavlovian \times CS \times Hemisphere ($F_{(1,95, 58.47)} = 17.87$, $p < 0.001$, $\eta^2_p = 0.373$, $\text{BF}_{10} = 3.609 \times 10^{+6}$) and CS \times Hemisphere \times ROIs ($F_{(6,19, 185.80)} = 5.03$, $p < 0.001$, $\eta^2_p = 0.143$, $\text{BF}_{10} = 50,034.878$) further suggested that the cue-related lateralization varied across motor-preparation regions and was modulated by learning phase.

Post hoc analyses supported our directional hypotheses (Fig. 5b). During Pavlovian 2, the left-hand cue (CS1) evoked greater activation than CS3 in the right PMC ($t = 3.854$, $p = 0.011$, Cohen's $d = 1.856$) and bilaterally in the aIPS (L: $t = 3.829$, $p = 0.012$, Cohen's $d = 1.281$; R: $t = 3.788$, $p = 0.014$, Cohen's $d = 1.231$). Conversely, the right-hand cue (CS2) elicited stronger activation than CS3 in the left M1 ($t = -3.411$, $p = 0.037$, Cohen's $d = -1.306$) and S1 ($t = -4.272$, $p = 0.004$, Cohen's $d = -1.729$), as well as the right PMC ($t = 3.880$, $p = 0.011$, Cohen's $d = 1.072$). Although the [CS2 > CS3] contrast did not yield significant clusters at the whole-brain level, significant motor activations were observed within predefined motor ROIs, reflecting the increased sensitivity of ROI analyses to detect spatially constrained effects. Direct CS1–CS2 comparisons (Fig. 5c) revealed hemispheric asymmetries, with greater PSC for CS1 in the left PMC, M1, and S1, and bilateral effects in the aIPS ($p < 0.05$). In contrast, CS2 elicited inhibitory activation in the left PMC, M1, and S1 relative to the right hemisphere ($p < 0.05$), consistent with hemisphere-specific suppression of contralateral motor regions involved in right-hand dominance control. Notably, CS1 showed stronger positive BOLD responses, whereas CS2 elicited negative PSC

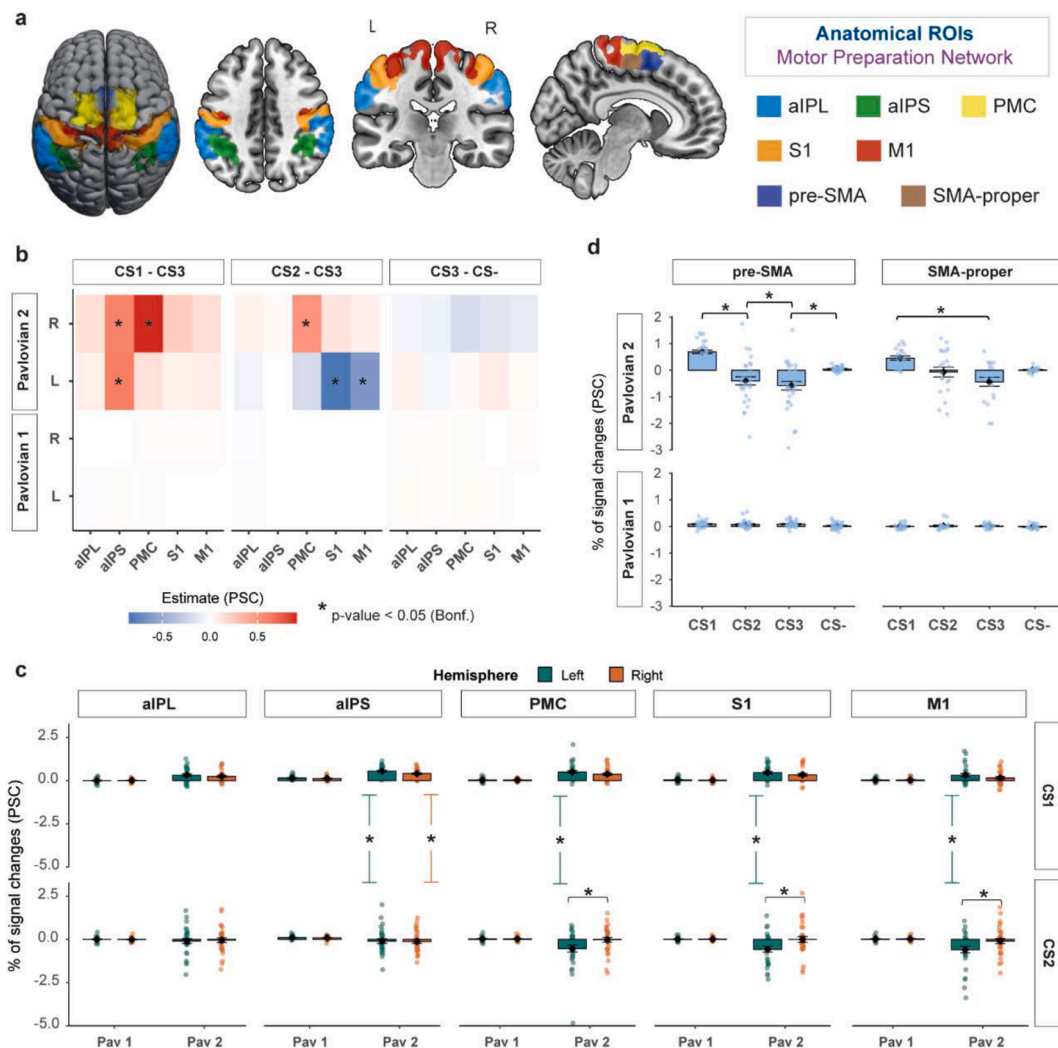


Fig. 5. fROI results for the motor-preparation network. *Note.* **a.** Anatomical regions of interest (ROIs) constituting the motor-preparation network (S1, M1, PMC, aIPL, aIPS, pre-SMA, SMA-proper). These anatomical masks were used as constraints to define subject-specific functional ROIs (fROIs) based on activation patterns from the Go/NoGo localizer. **b.** % of signal change (PSC) extracted from each ROI and hemisphere during Pavlovian Phases 1 and 2, showing cue-related differences between specific PIT cues (CS1, CS2) and the general cue (CS3). Warm colors indicate positive PSC estimates, and cool colors indicate negative PSC estimates. **c.** Lateralized cue contrasts (CS1 vs CS2) reveal hemispheric asymmetries across motor-preparation ROIs, with stronger activation in left-hemisphere motor regions during Pavlovian 2. Notably, CS2 (the right-hand cue) elicited inhibitory activation in the left hemisphere, indicating hemisphere-specific suppression associated with contralateral motor control. **d.** PSC values from the midline pre-SMA and SMA-proper show cue-selective increases for specific PIT cues (CS1, CS2) relative to CS3 during Pavlovian 2. Asterisks indicate Bonferroni-corrected significance ($p < 0.05$); lack of asterisks denotes non-significant effects. Error bars represent SEM, and diamonds indicate the group mean. Green lines indicate significant CS1–CS2 differences in the left hemisphere, and orange lines indicate corresponding right-hemisphere effects.

values. This lateralized pattern suggests differential modulation of motor system dynamics across cue conditions, potentially influenced by participants' right-handedness and associated left-hemisphere motor dominance. No effects were found for [CS3 > CS-] contrast, nor during Pavlovian 1, confirming that action-specific motor representation emerged only after instrumental learning.

A separate ANOVA focusing on medial motor ROIs (pre-SMA, SMA-proper, see Table S7) was conducted as these regions represent anatomically distinct medial motor subdivisions with different roles in action planning and execution. This analysis revealed a significant Pavlovian \times CS \times ROIs interaction ($F_{(1.72, 32.70)} = 7.52, p = 0.003, \eta^2_p = 0.283; BF_{10} = 44,630.242$). During Pavlovian 2, the pre-SMA showed cue-selective increases for CS1 and CS2 relative to CS3 ($p < 0.05$), while SMA-proper displayed a more restricted pattern with increased activation for CS1 compared to CS3 (Fig. 5d). Neither region showed cue-related effects during Pavlovian 1. These results suggest that pre-SMA is sensitive to both specific and general PIT cues, whereas SMA-proper

is preferentially engaged by specific PIT cues.

Overall, our ROI analyses support a motor activation of specific PIT, showing that cortical motor-preparation regions differentiate action-specific Pavlovian cues after instrumental learning, revealing hemisphere-biased cue selectivity and supporting a mechanistic account in which Pavlovian cues gain access to motor representations underlying the expression of specific PIT.

3.3.2. Instrumental learning ROIs

Considering the whole-brain evidence of caudate involvement during specific PIT (CS1 > CS2) and theoretical accounts linking dorsal striatal circuits to goal-directed action control, we next examined whether subcortical regions engaged during instrumental learning showed cue-dependent modulation during the Pavlovian phases. To this end, percent signal change (PSC) values were extracted from bilateral thalamus, putamen, and caudate ROIs defined from the instrumental learning phase (Fig. 6a), and analyzed using a repeated-measures

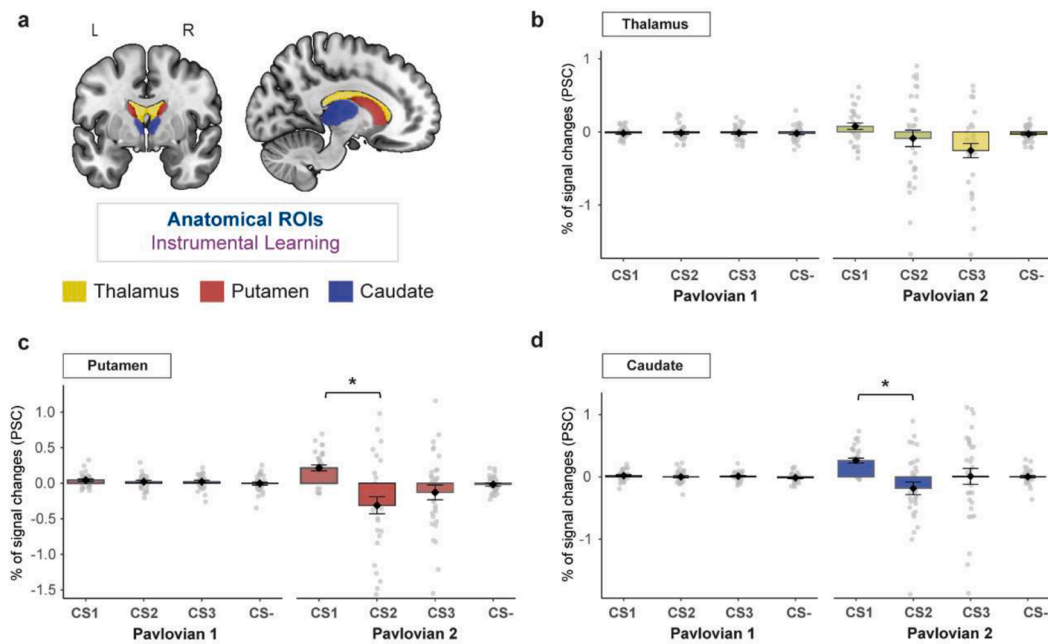


Fig. 6. Subcortical ROI results: goal-directed components of the PIT effect. *Note.* **a.** Anatomical regions of interest (ROIs) used to constrain subject-specific fROIs derived from the Instrumental Learning phase, including the thalamus, putamen, and caudate. These anatomical masks were used as constraints to define subject-specific functional ROIs (fROIs) based on activation patterns from the Instrumental learning phase. **b.** Thalamus showed no significant cue-related modulation across phases. **c–d.** In contrast, both the putamen and caudate displayed significant differences between CS1 and CS2 during Pavlovian 2. Asterisks indicate Bonferroni-corrected significance ($p < 0.05$); lack of asterisks denotes non-significant effects. Error bars represent SEM, and diamonds indicate the group mean.

ANOVA with factors Pavlovian Phase (Pavlovian 1, Pavlovian 2), Cue (CS1, CS2, CS3, CS-), and ROIs.

As shown in Table S8, the analysis revealed a significant main effect of Cue ($F_{(2.15, 62.21)} = 6.73, p = 0.002, \eta^2_p = 0.188; BF_{10} = 206.696$), as well as a significant Pavlovian \times Cue interaction ($F_{(2.06, 59.86)} = 5.91, p = 0.004, \eta^2_p = 0.169; BF_{10} = 18.032$), indicating that cue-related differences changed following instrumental learning. The three-way interaction of Pavlovian Phase \times Cue \times ROI did not reach significance ($F_{(3.22, 93.41)} = 1.92, p = 0.128, \eta^2_p = 0.062; BF_{10} = 0.411$). Given our a priori interest in learning-dependent cue modulation and the caudate effects observed at the whole-brain level, we conducted exploratory simple main-effects analyses within each Pavlovian phase. No cue-related differences were observed during Pavlovian 1 ($p \geq 0.983$). In contrast, during Pavlovian 2, significant cue effects emerged in the caudate ($F = 4.673, p = 0.004$), putamen ($F = 7.630, p < 0.001$), and thalamus ($F = 3.425, p = 0.021$). Post hoc comparisons (Fig. 6b–d) showed greater activation for [CS1 > CS2] in both the putamen ($t = 3.495, p = 0.009$, Cohen's $d = 1.629$) and caudate ($t = 3.407, p = 0.012$, Cohen's $d = 1.295$). No differences were observed for CS3 relative to CS- in either Pavlovian phase.

Together, these results indicate that cue-related modulation within subcortical regions emerges only after instrumental contingencies are established. Differentiation of specific PIT cues was most evident in dorsal striatal regions, consistent with their involvement in action–outcome encoding, supporting the goal-directed account of specific PIT.

4. Discussion

The present study investigated how Pavlovian cues engage motor and sensorimotor systems during learning, and how such neural activity relates to specific and general PIT. Our primary hypothesis focused on the motor involvement in outcome-specific PIT, predicting that Pavlovian cues linked to instrumental actions would recruit motor and sensorimotor systems even during passive cue exposure.

4.1. Motor activation in specific PIT

Behaviorally, participants exhibited robust specific PIT, selectively biasing actions congruent with learned cue–action associations (CS1→R1; CS2→R2). Consistent with our hypothesis, ROI analyses based on independently defined regions implicated in motor preparation, including IPS, PMC, M1, S1 and pre-SMA, revealed action-specific cue modulation during Pavlovian Phase 2. Whole-brain analyses, although partially exploratory, provided converging evidence of frontoparietal involvement (e.g., MFG, IPS and M1/S1). Importantly, these effects were absent during Pavlovian Phase 1, indicating that cue-specific motor engagement emerged only after action–outcome contingencies had been established.

At the whole-brain level, the engagement of MFG and IPS aligns with their roles in goal-directed control and visuomotor transformation (Morris et al., 2015; van Steenbergen et al., 2017). In particular, the aIPS has been implicated in mapping perceptual input onto motor commands (Hamilton and Grafton, 2006; Tunik et al., 2007; Wolynski et al., 2009), and premotor cortex involvement supports the recruitment of motor planning. Concurrent M1 and S1 activity is consistent with cue-evoked reactivation of learned motor representations and anticipated sensory consequences. Although the M1/S1 effects at the whole-brain level were observed at an uncorrected threshold, the independently defined ROI analysis demonstrated lateralized sensorimotor activation corresponding to learned hand-response mappings. CS1 preferentially modulated right PMC and bilateral aIPS, whereas CS2 modulated left M1/S1 and right PMC. Importantly, the negative PSC values observed for CS2 in left PMC/M1/S1 likely reflect suppression of competing motor representations. Given that all participants were right-handed and instructed to withhold responses during Pavlovian phases, CS2 (associated with right-hand responses) may have reactivated dominant-hand motor representations while concurrently engaging inhibitory control mechanisms to prevent overt movement, consistent with hemisphere-specific suppression of contralateral motor regions (Duque and Ivry, 2009; Duque et al., 2010; Greenhouse et al., 2015). Notably, these effects were observed in contrasts relative to CS3 (CS1 > CS3; CS2 > CS3). Although

CS3 was never associated with a specific response, it may reflect generalized right-hand dominance-related motor readiness, given that all participants were right-handed and a significant right-hand response bias was observed at the behavioral level. While hemispheric asymmetries may have been amplified by hand dominance, the differential modulation relative to CS3 indicates that dominance alone is unlikely to account for the observed pattern. Rather, the pattern supports cue-driven modulation of motor systems that interacts with intrinsic motor dominance. When directly comparing CS1 and CS2, the stronger left-hemisphere modulation is consistent right-handed dominance in motor planning (Hervé et al., 2013; Ocklenburg and Güntürkün, 2024; Tzourio-Mazoyer and Seghier, 2016), suggesting that hand-dominance may have amplified, but not generated the observed lateralized effects alone.

Critically, none of these effects were present during Pavlovian 1, demonstrating that Pavlovian cues gain access to motor circuits only after action–outcome learning. Because cue–action associations were never directly learned, this learning-dependent emergence supports the interpretation that cues access motor representations indirectly via outcome–action associations established during instrumental learning, rather than through direct stimulus–response retrieval. Importantly, this motor engagement should not be equated with full motor preparation for imminent execution. Participants were explicitly instructed to withhold responses, making overt preparation unlikely. Instead, this activity may reflect retrieval and partial activation of learned action representations associated with specific outcomes (Mendelsohn et al., 2014). Nevertheless, cue-evoked motor and sensorimotor activation may also reflect a combination of process, including attentional prioritization of behaviorally relevant stimuli, generalized motor readiness, and retrieval of learned action representations (Calderon et al., 2018). These interpretations are not mutually exclusive, as attentional prioritization and motor readiness may facilitate the retrieval of action-relevant information during specific PIT. Although the present design cannot fully dissociate these components, the outcome-specific differentiation between CS1 and CS2, emerging only after instrumental learning, argues against a purely nonspecific arousal or attentional account. This interpretation is consistent with recent EEG evidence showing lateralized motor activation during specific but not general PIT (Finotti et al., 2025), reinforcing the view that specific PIT involves cue-driven engagement of motor systems beyond a general increase in motivational arousal.

Subcortically, ROI analyses showed that the caudate and putamen differentiated CS1 and CS2, but not CS3 and CS–, indicating that these regions encoded specific cue–action associations rather than general motivational value. At the whole-brain level, exploratory uncorrected contrasts revealed caudate activation differentiating CS1 and CS2; however, these effects did not survive correction for multiple comparisons and should therefore be interpreted cautiously. The anterior caudate supports goal-directed action–outcome retrieval (Grahn et al., 2008; Jahanshahi et al., 2015; Morris et al., 2015), while the putamen contributes to stimulus–response execution (Brovelli et al., 2011). This pattern broadly aligns with basal ganglia models proposing that dorso-medial striatum mediates outcome-specific transfer (Corbit and Balleine, 2005; Corbit et al., 2007; Holmes et al., 2010; Prevost et al., 2012), although fine-grained striatal dissociation was not the primary focus of the present study.

Together, these findings support theoretical accounts proposing that specific PIT reflects cue-triggered retrieval of learned action representations (Balleine and O’Doherty, 2010; Garofalo et al., 2021; Mahlberg et al., 2021) through motor–sensorimotor control circuits (Hamilton and Grafton, 2006; Mendelsohn et al., 2014; van Steenbergen et al., 2017), thereby biasing potential responses rather than directly initiating movement execution. Within contemporary computational frameworks, specific PIT is conceptualized as the retrieval of outcome-specific value representations that bias action-selection processes implemented in corticostriatal circuits responsible for goal-directed action selection

(Balleine and O’Doherty, 2010; Dayan and Balleine, 2002). In this view, Pavlovian cues reactivate learned action–outcome associations or stored action policies, thereby increasing the expected value of a particular action and lowering its decision threshold during subsequent response selection, without necessarily initiating overt motor preparation. This interpretation is also consistent with ideomotor accounts, which propose that sensory-specific outcome representations are bidirectionally linked to their associated motor encoding (Wit and Dickinson, 2009; Shin et al., 2010; Dickinson and Pérez, 2018). Thus, cue-evoked motor activity during the Pavlovian phase likely reflects representational activation within motor-preparatory systems rather than direct preparation of imminent movement execution.

4.2. General PIT and Pavlovian associative learning

We also examined the neural responses associated with general PIT. Behaviorally, CS3 significantly increased response vigor compared to CS–, confirming a robust general PIT effect. At the neural level, general PIT-related cue engagement (CS3 > CS–) during early Pavlovian learning was observed in the fusiform gyrus (FG), ventral visual area V4, entorhinal cortex, and inferior frontal gyrus (IFG). The FG and V4 activation aligns with evidence that visual associative regions are sensitive not only to perceptual features but also to the motivational relevance of stimuli, supporting increased attentional prioritization and perceptual salience for reward-predictive cues (Price et al., 2003; Krawczyk et al., 2007; Shultz and McCarthy, 2012; Adamson and Troiani, 2018). Engagement of the entorhinal cortex, implicated its role in linking sensory input to predictive outcome representations (Sugase-Miyamoto and Richmond, 2007; Schultz et al., 2015; Sosa and Giocomo, 2021; Grienberger and Magee, 2022; Barnaveli et al., 2025), support the early cue–value learning during general PIT. The involvement of IFG aligns with its established role in action inhibition and the motivational effects of salient cues (Aron et al., 2014; Gershman et al., 2021; Pool et al., 2023). Notably, ventral striatum and vmPFC were not prominently engaged, consistent with evidence that Pavlovian learning without instrumental control does not necessarily recruit ventral striatal reward signals (Beyer et al., 2026). Exploratory correlations linking general PIT strength with somatosensory and parietal regions (S1, parietal operculum) may reflect increased behavioral readiness. However, these effects did not survive correction and should be interpreted with caution.

Critically, CS3-related activation was attenuated in Pavlovian Phase 2 following instrumental learning. This modulation cannot be attributed to simple cue exposure, as none of the CS cues were directly presented during instrumental learning. Rather, instrumental learning established action–outcome contingencies linking O1 and O2 to specific responses, thereby increasing the functional relevance of CS1 and CS2 within the action system. In contrast, CS3 remained outcome-associated but did not acquire action relevance. From this perspective, the reduction in CS3-related activity likely reflects learning-dependent reweighting of cue processing after instrumental acquisition, whereby neural resources are preferentially allocated to cues that can guide specific actions. This interpretation is further supported by the absence of significant activation in the reverse contrast [Pavlovian 2 (CS3 > CS–) > Pavlovian 1 (CS3 > CS–)], arguing against a novelty-based increase in CS3 salience due to reduced exposure to O3 during instrumental learning. Moreover, ROI analyses indicated stable CS– responses across phases, suggesting that the observed interaction primarily reflects modulation of CS3 rather than changes in baseline activity.

Together, these findings suggest that general PIT primarily relies on perceptual and associative learning-related regions encoding cue salience and predictive value, rather than direct action-specific recruitment. Although attentional prioritization likely contributes to both general and specific PIT, the absence of comparable motor and dorsal striatal engagement for CS3 argues against a purely attentional explanation for the action-specific neural effects observed during

specific PIT, further supporting a dissociation between general and specific PIT (Holmes et al., 2010; Cartoni et al., 2016). Moreover, the attenuation of CS3-related activation from Pavlovian Phase 1 to Phase 2 likely reflects learning-dependent reorganization of cue processing following instrumental acquisition. Once action–outcome contingencies are established, cues capable of guiding specific actions may gain functional priority within the action system, whereas cues lacking action relevance, such as CS3, remain primarily encoded at a perceptual–associative level (den Ouden et al., 2009).

4.3. Implications and limitations

The present findings demonstrate how motivational learning shapes neural activity across perceptual, associative, and motor systems. The observation of lateralized motor activation during passive cue exposure provides neural evidence that Pavlovian cues can engage motor systems even in the absence of overt action. Importantly, such engagement likely reflect a combination of processes, including attentional allocation to behaviorally relevant cues, generalized motor readiness, and retrieval of learned action representations. Although the present design does not allow these components to be fully disentangled, the learning-dependent emergence of lateralized motor activation argues against a purely nonspecific attentional or arousal-based account. At the same time, because all participants were right-handed, intrinsic dominance-related biases may have contributed to hemispheric asymmetries, and future studies including left-handed or mixed-handed samples would help clarify this issue.

Several limitations must be acknowledged. First, the sample size ($N = 31$) is modest for fMRI research and may limit generalizability. Sensitivity analyses indicated that the present design had 90% power to detect effects of approximately $f = 0.30$ for the behavioral interaction (observed $f = 0.57$) and $f = 0.14$ for the primary ROI-level fMRI interaction (observed $f = 0.38$), under conservative assumptions ($r = 0.30$; $\epsilon = 0.50$). However, power estimates based on observed effect sizes may overestimate true sensitivity, and whole-brain fMRI analyses require larger samples due to increased variability and multiple-comparison correction. Accordingly, neural findings, particularly whole-brain effects, should be interpreted cautiously, and replication in larger samples will be important. Second, several whole-brain findings associated with both general and specific PIT were observed only at an uncorrected threshold. In addition, we did not perform non-parametric permutation-based inference for whole-brain analyses, therefore these results should be interpreted cautiously. Furthermore, fROI definition involved threshold relaxation and hemispheric mirroring to increase sensitivity, which may reduce functional specificity. Future studies using stricter or fully independent ROI definitions will be important for validating hemispheric effects. Third, although average hunger levels of participants were above the midpoint of the scale and did not correlate with PIT behavioral effects, hunger ratings were not included as covariates. Residual variability in motivational state may therefore have contributed to variability in PIT effects. Extending PIT paradigms to aversive outcomes or non-food rewards will help clarify the generalizability of the present findings. Fourth, neural activity was not measured during the transfer phase, limiting direct comparison between passive cue-exposure during learning and cue preprocessing before action execution. Although behavioral results suggest sustained task engagement, time-related factors such as fatigue, fluctuations in attention, or subtle shifts in subjective reward value across learning phases cannot be fully excluded and may have contributed to phase-related differences. Finally, the observed motor-related activations cannot fully distinguish retrieval of action-specific representations from more general preparatory or attentional states. Experimental designs that orthogonalize attentional relevance and action specificity, or that manipulate response mappings independently of cue–outcome associations, would help clarify the representational content of cue-evoked motor activity.

5. Conclusion

Our study provides convergent evidence that Pavlovian cues influence action not only through general motivational arousal but also, at least in part, through engagement of indirectly learned motor representations. The lateralized, action-related activation observed after instrumental learning indicates that cues access motor circuits via outcome-mediated integration across learning phases, even when no overt response is required. Rather than reflecting direct motor preparation, this engagement is consistent with retrieval of learned action representations within corticostriatal circuits. By demonstrating that cue-driven value signals can modulate motor and sensorimotor systems during passive processing, the present study refines theoretical models of Pavlovian-to-Instrumental Transfer. These results suggest that motivational cues shape goal-directed behavior not merely by energizing responses, but by biasing action-selection systems through learned outcome–action associations. Together, this work advances our understanding of the neural mechanism underlying adaptive and maladaptive cue-driven behaviors.

Data and code availability

Data and code supporting this study are available on OSF at <https://osf.io/3tdnq/>. This includes the experimental materials, analysis code, behavioral data, and extracted neural data used in the analyses. The project was pre-registered at <https://osf.io/dy3hw>. The raw neural dataset can be obtained from the corresponding author, Lara Bardi, upon reasonable request.

CRediT authorship contribution statement

Yulong Huang: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Chen Qu:** Writing – review & editing, Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **Valeria Gazzola:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Sara Garofalo:** Writing – review & editing, Supervision, Software, Project administration, Methodology, Funding acquisition, Conceptualization. **Francesca Starita:** Writing – review & editing, Funding acquisition, Conceptualization. **Ruth M. Krebs:** Writing – review & editing, Supervision, Methodology. **Luigi A.E. Degni:** Writing – review & editing, Software, Conceptualization. **Junjie Wei:** Writing – review & editing, Methodology. **Gianluca Finotti:** Writing – review & editing, Conceptualization. **Giuseppe di Pellegrino:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Michel Desmurget:** Writing – review & editing, Funding acquisition, Conceptualization. **Angela Sirigu:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Lara Bardi:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Siying Li and Qingxia Liu for their assistance with data collection. This work was supported by the following grants: (1) The Program for National Natural Science Foundation of China (grant number: 32171019), the MOE Project of Key Research Institute of

Humanities and Social Sciences in Universities (grant number: 22JJD190004), and Research Center for Brain Cognition and Human Development, Guangdong, China (grant number: 2024B0303390003) to Chen Qu. (2) European Union's Horizon 2020 Framework Programme for Research and Innovation FLAG-ERA JTC 2019 (Human Brain Project SGA3), and Italian Ministry of University (MUR), with the project titled "The Motor-way to Decision Making" (MoDeM; Grant Agreement No. 945539, CUP J32F20000870001). (3) Bijzonder Onderzoeksfonds UGent (BOF starting grant, Special Research Fund, Ghent University, grant number: BOF/STA/202309/012) to Lara Bardi.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2026.121874](https://doi.org/10.1016/j.neuroimage.2026.121874).

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