The role of corticostriatal systems in speech category learning

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Corticostriatal speech category learning

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Abstract

One of the most difficult category learning problems for humans is learning non-native speech categories. While feedback-based category training can benefit speech learning, the mechanisms underlying these benefits are unclear. In this fMRI study, we investigated neural and computational mechanisms underlying feedback-dependent speech category learning in adults. Positive feedback activated a large corticostriatal network including the dorsolateral prefrontal cortex, inferior parietal lobule, middle temporal gyrus, caudate, putamen, and the ventral striatum. Successful learning of non-native speech categories was contingent upon the activity of domain-general category learning systems: the fast-learning reflective system, involving dorsolateral prefrontal cortex that develops and tests explicit rules based on the feedback content, and the slow-learning reflexive system, involving the putamen in which the stimuli are implicitly associated with category responses based on the reward value in feedback. Computational modeling of response strategies revealed significant use of reflective strategies early in training and greater use of reflexive strategies later in learning. Reflexive strategy use was associated with increased activation in the putamen. Our results demonstrate a critical role for the reflexive corticostriatal learning system as a function of response strategy and proficiency during speech category learning.
Introduction

What neural mechanisms underlie language acquisition in adulthood? Learning speech sounds of a new language is argued to be a difficult category learning problem in adulthood. For instance, native Japanese speakers find it difficult to learn to categorize English /r/ vs. /l/ sounds (Iverson et al. 2003). This difficulty is likely due to the high variability and multidimensional nature of speech categories (Hillenbrand et al. 1995; Jongman et al. 2000; Vallabha et al. 2007; Holt and Lotto 2008, 2010). Adequate feedback can significantly enhance speech category learning in adults (McCandliss et al. 2002; McClelland and Patterson 2002; Norris et al. 2003; Goudbeek et al. 2008). Trial-by-trial feedback is therefore ubiquitously used in speech training paradigms. However, little is known about the neural mechanisms underlying feedback-based error reduction in speech learning (Holt and Lotto 2008, 2010). Understanding the neural mechanisms underlying feedback-based learning is critical because subtle variations in feedback characteristics can significantly modulate speech learning rates (Chandrasekaran et al. 2013). Furthermore, it would contribute to our general knowledge of the neural mechanisms involved in learning a second language.

Outside the speech domain, previous research examining visual category learning has identified at least two partially dissociable neural systems that process feedback: a reflective system, wherein processing is under conscious control, and a reflexive system that is not under conscious control (Ashby and Alfonso-Reese 1998; Poldrack and Packard 2003; Ashby and Ennis 2006; Nomura et al. 2007; Seger and Miller 2010). The reflective system, as also referred to as the rule-based learning system in the literature, uses working memory and executive attention to develop and test verbalizable rules based on feedback (Maddox and Ashby 2004). It relies on an executive corticostriatal loop that primarily involves the dorsolateral prefrontal cortex (DLPFC), head of the caudate nucleus, the anterior cingulate cortex and the hippocampus. These brain regions contribute to the generation, selection, and maintenance of verbalizable rules. In contrast, the reflexive learning system, which has also been referred to as the procedural-based learning system, is not consciously penetrable, non-verbalizable, and operates by associating perception with actions that lead to immediate reward (Maddox and Chandrasekaran, 2014). During reflexive learning, a single medium-spiny neuron in the
striatum implicitly associates an abstract motoric response with a group of sensory cells. Learning occurs within cortical–striatal synapses, wherein plasticity is facilitated by a reinforcement signal from the ventral striatum (Ashby and Ennis 2006; Seger 2008). A recent study examining visual category learning showed that the putamen is critical to reflexive learning (Waldschmidt and Ashby 2011). Animal research has shown that both the reflective and reflexive circuitries receive direct input from several auditory regions (Reale and Imig 1983; Yeterian and Pandya 1998). While the role of the reflexive auditory loop has been extensively studied (Romanski et al. 1999; Rauschecker and Scott 2009), much less is known about the role of the reflexive learning system in speech processing.

In the current study, we examined the hypothesis that optimal speech category learning is mediated by the neural circuitry underlying the reflexive learning system. We hypothesized that explicit, reflective learning of speech categories is difficult due to the multidimensional nature and high variability of speech categories. In addition, dimensions underlying speech categories are integral and often difficult to verbalize (Lisker 1986; Hillenbrand et al. 1995; Jongman et al. 2000; Vallabha et al. 2007; Holt and Lotto 2008, 2010). Integral dimensions stimuli, by definition, are difficult to attend selectively (Shepard 1964; Garners 1974; Ashby 1992). Indeed, when the mode of stimulus presentation and the nature of the trial-by-trial feedback were manipulated in a recent behavioral study examining speech learning (Chandrasekaran et al. 2013), learning was enhanced under conditions that were previously shown to augment reflexive learning in the visual domain (Maddox et al. 2003; Maddox et al. 2008). Computational modeling of behavioral data collected in a similar learning paradigm revealed that optimal speech category learning is associated with initial use of reflective strategies followed by a transition to the use of reflexive computational strategies (Maddox and Chandrasekaran 2014).

Despite this growing body of evidence that suggest that speech category learning is reflexive, there currently is no neural evidence of the relative role of the two learning systems in speech categorization. To this end, we employ a combination of behavioral, neural, and computational modeling methods to evaluate the mechanisms underlying feedback-dependent speech category learning. Specifically, we predict that optimal
speech category learning will be associated with increased processing in the putamen, which is hypothesized to be involved in a ‘motor loop’ that implicitly associates stimuli with category responses within the motor cortex. We used an individual differences approach as well as computational modeling to assess the mechanistic link between learning and computations within the domain-general learning systems. Adult native speakers of English (N = 23) learned novel speech categories (Mandarin tone categories, Figure 1) while blood oxygenation level dependent (BOLD) responses were collected. Participants made a category response to each stimulus, which resulted in positive or negative feedback. Neural activation during stimulus presentation and feedback processing were separately estimated using an optimized rapid event-related design. Behavioral accuracies were calculated and decision-bound models were applied at the individual participant level to provide a window onto cognitive processing and the computational strategies employed at different stages of category learning.

Materials and Methods

Participants

Native speakers of American English (age: 18-35; n = 25; 14 female) were recruited from the University of Texas at Austin community. Participants self-reported as right-handed and passed a hearing screening examination (pure tone thresholds < 25 dB HL at 1, 2, and 4 kHz). Further, participants had no prior exposure to a tonal language, as determined by an abbreviated form of the LEAP-Q (Marian et al. 2007). Potential participants were excluded if they reported a current or past history of a major psychiatric condition, neurological disorders, hearing disorders, head trauma, or use of psychoactive drugs or psychotropic medication. Data from two male participants were excluded from all analyses due to file corruption and an incidental finding on the structural scan. The University of Texas at Austin IRB approved the experimental protocol.

Materials
Natural exemplars (N = 40) of the four Mandarin tones (high-flat, low-rising, high-falling, low-dipping) were produced in citation form by two native Mandarin speakers (originally from Beijing; 1 female) in the context of five monosyllabic Mandarin Chinese words (/bu/, /di/, /lu/, /ma/, /mi/). These syllables were chosen because they also exist in the American English inventory (Alexander et al. 2005). The stimuli were normalized for RMS amplitude of 70 dB and duration of 0.4 s (Alexander et al. 2005; Wong et al. 2009; Perrachione et al. 2011). Five independent native speakers correctly identified the four tones (>95%) and rated the stimuli as highly natural.

Procedures

Participants performed a category learning task in the scanner while listening to the speech sounds presented through headphones. Visual stimuli including the instructions and feedback were displayed via the in-scanner projector visible using a mirror attached onto the head coil. Participants were equipped with a two-button response box in each hand. Prior to scanning, participants underwent a brief training procedure in which they familiarized themselves with the association of keys to four possible responses. Tone learning procedures closely followed a previous study on visual category learning in the scanner (Nomura et al. 2007). The experiment consisted of 6 contiguous scans, or “learning blocks”. Prior to each block, participants were instructed to attend to the fixation cross on the screen. During each trial, an auditory stimulus was presented for 445 ms. Participants were instructed to categorize the sound into one of four categories. They were encouraged to guess even if they did not know the answer. Following a jittered stimulus-feedback interval, corrective feedback (“RIGHT” vs. “WRONG”) was displayed for 750 ms. If the participant failed to respond within the 2 s following stimulus onset, the response did not register and a cautionary feedback display was presented (“TIME”; Figure 1). Each stimulus was presented once within each block. The presentation order of the stimuli was pseudorandomized into a sequence common for all participants but different across learning blocks.

Scan Parameters
The participants were scanned using the Siemens Magnetom Skyra 3T MRI scanner at the Imaging Research Center of the University of Texas at Austin. High-resolution whole-brain T1-weighted anatomical images were obtained via MPRAGE sequence (TR = 2.53 s; TE = 3.37 ms; FOV = 25 cm; 256x256 matrix; 1x1 mm voxels; 176 axial slices; slice thickness = 1 mm; distance factor = 0%). T2*-weighted whole-brain blood oxygen level dependent (BOLD) images were obtained using a gradient-echo multi-band EPI pulse sequence (flip angle = 60°; TR = 1.8 s; 166 repetitions; TE = 30 ms; FOV = 25 cm; 128x128 matrix; 2x2 mm voxels; 36 axial slices; slice thickness = 2 mm; distance factor = 50%) using GRAPPA with an acceleration factor of 2. To separately estimate neural responses to the stimulus from the response to the feedback, the stimulus-feedback and feedback-stimulus intervals were randomly jittered using samples from a uniform distribution (stimulus-feedback: 2 to 4 s; feedback-stimulus: 1 to 3 s; Figure 1; Dale 1999; Liu et al. 2001; Birn et al. 2002).

Behavioral analysis

Accuracy

Each participant's response on each trial was coded as “correct” or “incorrect,” with the missed trials also being coded as incorrect. A mixed logit analysis was conducted to estimate the log odds of producing a correct response, using the lmer program (Bates et al. 2012). The fixed effect of interest was the number of the block (1-6) mean-centered to 0 (-2.5, -1.5, -0.5, 0.5, 1.5, 2.5). The model was corrected for by-participant random slopes for each block and the random intercept for each block.

Model fitting approach

The model fitting approach closely followed the methodology published in Maddox and Chandrasekaran (2014) and in other applications to speech and in vision (Maddox 2002; Maddox and Filoteo 2011; Maddox et al. 2013; Chandrasekaran et al.
2014; Maddox et al. 2014). We fit each model on a block-by-block basis separately to the data from each participant to circumvent misleading results from interpreting fits to aggregate data (Estes 1956; Ashby et al. 1994; Maddox 1999). We assumed that the two-dimensional space (pitch height vs. pitch direction) displayed in Figure 1 accurately describes the perceptual representation of the stimuli. Note that previous multidimensional scaling studies suggest that these two dimensions explain a significant percentage of variance (Chandrasekaran et al. 2007). Based on the results from our earlier work (Maddox & Chandrasekaran, 2014) we also assumed that participants applied category learning strategies separately to the male and female perceptual spaces (Figure 1). We explored three classes of models: reflexive, reflective, and a random responder model. The model parameters were estimated using maximum likelihood procedures (Wickens 1982; Ashby 1992) and model fits were compared using Akaike weights to determine the best fitting model for each participant in each block of trials (Wagenmakers and Farrell 2004).

The reflexive learning system was modeled using the Striatal Pattern Classifier (SPC; Ashby and Alfonso-Reese 1998; Maddox et al. 2002; Seger and Cincotta 2005; Ashby and Ennis 2006; Nomura et al. 2007). The model reflects the many-to-one mapping from the primary and secondary auditory cortices along the superior temporal gyrus to the striatum (Yeterian and Pandya 1998), where a low-resolution map of the perceptual space is represented among different striatal units. Category learning involves associating each category label with a cluster of striatal (medium spiny) neurons (Hikosaka et al. 1989; Wilson 1995; Arnauld et al. 1996; Yeterian and Pandya 1998; Ashby and Ennis 2006). We model this association by assuming that each category is represented by a striatal “unit” in the pitch height-pitch direction space. The SPC assumed four striatal units in the two dimensional pitch height-pitch direction space for the male speakers and a separate four striatal units in the pitch height-pitch direction space for the female speakers. The SPC contained six free parameters in each space: five that determine the location of the units, and one that represents the noise associated with the placement of the striatal units. The versions of SPC have already been applied in an

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1 Modeling analyses were also conducted using the Bayes Information Criterion (BIC). In every case the results mirrored those reported with AIC. We provide the results using BIC in the supplementary materials.
artificial auditory category learning task (Maddox et al. 2006), vowel categorization task (Maddox et al. 2002), and Mandarin lexical tone learning (Maddox et al. 2013; Maddox et al. 2014). It is important to note that the SPC is a computational model inspired by what is known about the neurobiology of the striatum. Because of this fact, the striatal “units” are hypothetical and could be interpreted within the language of other computational models (e.g., as “prototypes” in a multiple-prototype model like SUSTAIN; Love et al. 2004).

A series of unidimensional reflective models were also fit to the data. The unidimensional reflective models assumed that the participant set three criteria along the pitch height or pitch direction dimension, ignoring the other dimension. The unidimensional height model assumed that the three criteria along the pitch height dimension were used to separate the stimuli into low, medium-low, medium-high or high pitch height, each of these being associated with one of the tone categories, while ignoring the pitch direction dimension. Although a large number of versions of this model are possible, we explored the eight variants of the model that made the most reasonable assumptions regarding the assignment of category labels to the four response regions. Using the convention that the first, second, third and fourth category labels are associated with low, medium-low, medium-high and high pitch height, respectively, the 8 variants were: 3214, 3412, 3241, 3421, 2314, 4312, 2341, and 4321. The unidimensional direction model assumed that the three criteria along the pitch direction dimension were used to separate the stimuli into low, medium-low, medium-high or high pitch direction, each of these being associated with one of the tone categories, while ignoring the pitch height dimension. Although a large number of versions of this model are possible, we explored the two variants of the model that made the most reasonable assumptions regarding the assignment of category labels to the four response regions. Using the convention that the first, second, third and fourth category labels are associated with low, medium-low, medium-high and high pitch direction, respectively, the 2 variants were: 4312 and 4132. The unidimensional models each contained four free parameters in each space: three criteria and one noise parameter. The random responder model assumed a fixed probability of responding tone 1, tone 2, tone 3, and tone 4, allowing for response biases. The model had three free parameters in each space to reflect the predicted
probability of responding ‘1,’ ‘2,’ or ‘3’, the probability of responding ‘4’ being equal to one minus the sum of the other three.

Finally, a more complex conjunctive reflective model was also considered in a secondary analysis. In previous behavioral pilot work, we elicited verbal descriptions of the four categories after the category learning task. No participant reported a conjunctive reflective strategy, although several described unidimensional strategies. However, since a conjunctive model is theoretically possible, we conducted a separate analysis using this model as a possibility. The model assumed that the two criteria along the pitch direction dimension are used to separate the stimuli into falling, flat or rising pitch direction. Falling pitch height items are classified as tone category 4 and rising pitch height items as tone 2. If an item is classified as flat pitch height, the pitch height dimension is examined. The single criterion along the pitch height dimension is used to separate the stimuli into low and high pitch height. Stimuli that have flat pitch direction and high pitch height are classified as tone 1 and flat pitch direction items of low pitch direction as tone 3. This model contained four free parameters in each space: three criteria and one noise parameter. Inclusion of this model did not alter the main findings of the study, and therefore we only present the findings of this secondary analysis as supplementary materials.

To assess the strategy selection by participants over the course of learning blocks, a linear mixed effects analysis was applied to the set of best fitting models per block for each participant (Bates et al. 2012). Mean-centered block numbers were included as the dependent variable, with the best fitting strategy being the fixed effects (the reflexive model as the reference), corrected for by-participant random intercepts. Finally, an analysis was run to examine whether reflexive strategy use was associated with better learning than non-reflexive strategies. The dependent variable was trial-by-trial accuracy. The fixed effects were the mean-centered block numbers and whether the participant was using a reflexive strategy. The model was corrected for a random intercept of each participant, as well as the random slope of block by strategy interaction for each participant.

fMRI preprocessing
fMRI data were analyzed using FMRIB's Software Library Version 5.0 (Smith et al. 2004; Woolrich et al. 2009; Jenkinson et al. 2012). BOLD images were motion corrected using MCFLIRT (Jenkinson et al. 2002). All images were brain-extracted using BET (Smith 2002; Jenkinson et al. 2005). Registration to the high-resolution anatomical image (df = 6) and the MNI 152 template (df = 12; Grabner et al. 2006) was conducted using FLIRT (Jenkinson and Smith 2001; Jenkinson et al. 2002). Six separate block-wise first-level analysis were run within-subject. The following pre-statistics processing were applied: spatial smoothing using a Gaussian kernel (FWHM = 5 mm); grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight line fitting; $\sigma = 50.0$ s). Each event was modeled as an impulse convolved with a canonical double-gamma hemodynamic response function (phase = 0 s). Motion estimates were modeled as nuisance covariates. Temporal derivative of each event regressor, including the motion estimates, was added. Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Smith et al. 2004). The events of interest were stimulus, response and feedback, which were further subdivided according to the accuracy valence: correct, incorrect, and missed. The missed trials were separately modeled and treated as nuisance variables.

Whole brain analysis

First-level analysis results were committed to second-level analysis using fixed effects with three regressors: group average, mean-centered block numbering, and mean-centered accuracy per block per participant. The latter two regressors were included as nuisance variables to counteract systematic trends in the data across multiple blocks. Third-level group analysis was performed for each contrast using FLAME1 (Woolrich et al. 2009). Post-statistical analysis was performed using randomise in FSL to run permutation tests ($n = 50000$) for the GLM and yield in threshold-free cluster enhancement (TFCE) estimates of statistical significance (Freedman and Lane 1983; Kennedy 1995; Bullmore et al. 1999; Anderson and Robinson 2001; Nichols and Holmes
Finally, in order to assess the activation patterns associated with optimal learning, the first-level analysis from the final block was committed to a second-level analysis with two regressors of group average and mean-centered accuracy for the final block.

ROI analysis

Four ROIs, chosen a priori, were defined: (1) left and right DLPFC and (2) left and right putamen. The DLPFC were anatomically defined using the Brodmann Areas 9/46 (Spence et al. 2000; Pochon et al. 2002; Curtis and D'Esposito 2003; Anderson et al. 2004) per the atlas included in the MRIcron package (Rorden 2007). The putamen was anatomically defined using the Harvard-Oxford Subcortical Atlas (Frazier et al. 2005; Desikan et al. 2006; Makris et al. 2006; Goldstein et al. 2007). The masks were linearly registered to the MNI152 space (Grabner et al. 2006) using FLIRT (Jenkinson and Smith 2001; Jenkinson et al. 2002; Figure 5). Percent signal changes in the (correct - incorrect) contrast for feedback processing was calculated by first linearly registering the ROIs to the individual BOLD spaces using FLIRT with the appropriate transformation matrices generated from the first level analysis and nearest neighbor interpolation (Jenkinson and Smith 2001; Jenkinson et al. 2002; Figure 5). Percent signal changes in the (correct - incorrect) contrast for feedback processing was calculated by first linearly registering the ROIs to the individual BOLD spaces using FLIRT with the appropriate transformation matrices generated from the first level analysis and nearest neighbor interpolation (Jenkinson and Smith 2001; Jenkinson et al. 2002; Figure 5). Then, the contrast parameter estimate images were masked for the transformed ROIs, multiplied by height of the double gamma function for the stimulus length of 1 s (0.0288), converted into percent scale, divided by mean functional activation, and averaged within the ROI using fslmaths (Mumford 2007).

Results

Behavioral results

Accuracy

The average performance for the initial block was 23% (SD = 9%; 95% CI [19%, 26%]), close to the chance level of 25%. By the final block, average performance was
54% (SD = 27; 95% CI [42%, 66%]). The performance in the initial and final blocks were positively correlated, r(21) = .432, p = .040, 95% CI [.024, .716]. A mixed effects analysis was conducted to assess the learning progress. The dependent variable was trial-by-trial accuracy (correct vs. incorrect), and the fixed effect was the mean-centered block number. The intercept was not significant, b = -0.16, SE = .23, z = -0.72, p = .47, 95% CI [-0.63, 0.30]. The effect of the mean-centered block number was significant, b = 0.32, SE = 0.70 z = 4.61, p < .0001, 95% CI [0.18, 0.47], indicating an overall learning effect across blocks (Figure 2).

Model-based Analyses

Participants were observed to use various strategies, including all models considered in the process. As described above, for each block a strategy (reflexive, reflective pitch height, reflective pitch direction, or random responder) was assigned according to the best fitting model and several notable patterns could be verified from the mixed effects analysis studying the average block number (mean centered) for each of the assigned strategies. Since the block numbers were mean-centered, positive estimates for each level of strategy would indicate that the given strategy was more likely to be utilized late in learning (block 4, 5, or 6), while negative estimates would indicate that the given strategy was more likely to be utilized early in learning (blocks 1, 2, or 3). The mean block for the reflexive strategy (intercept) was significant, b = 0.79, SE = 0.25, t = 3.10, p = .0024, 95% CI [0.29, 1.28], indicating that a given reflexive strategy was more likely to be utilized later in learning. The random responder model was significant, b = -1.29, SE = 0.36, t = -3.60, p = .00044, 95% CI [-1.98, -0.59], indicating that the random responder strategy was more likely to be utilized in learning earlier than the reflexive strategy. Similar patterns were observed to be statistically significant for unidimensional reflective strategies, which were utilized earlier in learning than the reflexive strategy: pitch direction, b = -1.29, SE = 0.60, t = -2.13, p = .035, 95% CI [-2.46, -0.11]; pitch height: b = -0.94, SE = 0.35, t = -2.66, p = .009, 95% CI [-1.63, -0.25]. Taken together, these results indicate that the slow-learning reflexive strategy was more likely to be utilized late in learning, whereas the fast-learning reflective or random responder strategies where
more likely to be utilized early in learning (Figure 2). In an analysis designed to test whether the reflexive strategies yielded better learning outcomes, a repeated measures logistic regression was conducted with the trial-by-trial accuracy as the dependent variable and the mean-centered block number, block-by-block strategy, and their interaction term as fixed effects. There were two levels in the block-by-block strategy term: reflexive vs. non-reflexive. There was a non-significant interaction between block number and strategy, $b = -0.96$, $SE = 0.84$, $z = -1.15$, $p = .25$. Therefore, we focused on a model that included only main effects. For the average block number (between 3 and 4), the log odds of accurate versus inaccurate for the non-reflexive strategy was negative, $b = -0.37$, $SE = 0.17$, $z = -2.18$, $p = .030$, indicating the probability of an accurate response was significantly below 50%. The block effect was significant, $b = 0.26$, $SE = 0.057$, $z = 4.58$, $p < .0001$, indicating that the odds of producing an accurate response compared to an inaccurate response was higher for later blocks than for earlier blocks. The strategy effect was significant, $b = 0.39$, $SE = 0.19$, $z = 2.07$, $p = .038$, indicating that reflexive strategy use, compared to non-reflexive strategy use was associated with increased odds of producing an accurate response compared to an inaccurate response. These results suggest that learning improves over time, and that reflexive strategy use is associated with better learning than non-reflexive strategies.

Whole brain analysis

Feedback processing

Averaging across correct and incorrect responses (correct + incorrect) did not yield any significant activations associated with feedback processing. Testing whether the activation for correct trials was higher than for incorrect trials (correct - incorrect; Figure 3) yielded areas associated with the corticostriatal loops involved in category learning (Seger 2008; Seger et al. 2010). The ventral striatum including the nucleus accumbens was activated, as well as the anterior cingulate cortex. These two areas form a part of the motivational loop that processes reward value in feedback, which is greater in positive than negative feedback. The left dorsolateral prefrontal cortex and the left head of
caudate were activated, which are parts of the executive loop that form the basic circuitry underlying reflective learning. The bilateral putamen was activated, which are involved in the categorization process via the connection to the motor regions. The left inferior parietal lobule was activated, which functions as the sensorimotor interface that maps sensory speech information onto articulatory gestures (Hickok and Poeppel 2007). Finally, the left middle temporal gyrus / superior temporal sulcus region was activated. During feedback processing, there was no meaningful auditory stimulus to be processed, and the level of auditory sensory input was identical across positive and negative feedback. Therefore, the activation in the superior temporal area as well as the inferior parietal lobule was presumably not driven by the auditory stimulus alone but reflect feedback-driven strengthening of stimulus-to-response/category association (Weil et al. 2010). No brain region showed significantly higher activation for incorrect trials than for correct trials (incorrect - correct).

**Stimulus presentation**

Averaging across the accuracy valence (correct + incorrect), stimulus presentation was found to elicit activation in the bilateral Heschl’s gyri, planum temporales, and the posterior superior temporal gyri concurrent with the auditory nature of the task. Activation for correct trials was higher than for incorrect trials in the right planum temporale and the insular cortex, and the left pre- and post-central cortices (correct - incorrect; Figure 4). Also, the right inferior parietal lobule was shown to be sensitive to accurate categorization, consistent with its proposed role as the sensorimotor interface between auditory processing and articulatory mapping (Hickok and Poeppel 2007). No brain regions showed higher activation for incorrect trials than for correct trials (incorrect - correct).

In order to assess the activation patterns associated with optimal learning, the final block contrast for correct trials relative to incorrect trials (correct - incorrect) during stimulus perception was regressed against the accuracy scores from the final block. Following this analysis, individual accuracy scores were found to positively correlate with increased activation in the speech processing areas of the bilateral Heschl’s gyrus,
right inferior parietal lobule, right inferior frontal gyrus, and the bilateral insula. Additionally, higher accuracy was also associated with increased activation in the bilateral putamen, right caudate nucleus, the motor cortex, and the anterior cingulate cortex, suggesting that better performance by the final block was related to the involvement of the corticolearning systems, and in particular, the motor loop encompassing the motor cortex and the putamen (Figure 5). No brain regions showed negative correlation with the accuracy scores.

Category response

Averaging across correct and incorrect responses (correct + incorrect), the activation associated with category response involved several areas within the extensive cortical networks. The bilateral pre- and post-central areas were activated, reflecting finger movements necessary for making category responses. The decision making network involving the left dorsolateral prefrontal cortex and the anterior cingulate cortex were activated, reflecting the categorization process during response selection. The activation for correct and incorrect trials did not significantly differ (correct - incorrect; correct + incorrect).

ROI Analysis

Reflexive strategy use and increased putamen activation

This analysis tested the hypothesis that the putamen is involved when category learning is mediated by the reflexive processing system. Participants were classified as reflexive versus non-reflexive (reflective or random) strategy users based on the best fitting model in each block. Mixed effects analyses were performed on the putamen and DLPFC on the left and right hemispheres. The dependent measure was the percent signal change (correct - incorrect) value during feedback processing in each block. The fixed effects were the mean-centered block number, and strategy group (reference level: non-reflexive), corrected for random participant intercepts. In the left putamen, the block by
strategy interaction was not significant, $b = -0.15$, SE = 0.82, $t = -1.79$, $p = .076$, 95% CI [-0.31, 0.013]. Therefore, we investigated the model without the interaction. The strategy effect was significant, $b = 0.18$, SE = 0.76, $t = 2.31$, $p = .023$, 95% CI [0.027, 0.324], suggesting that reflexive strategy use was associated with increased activation in the putamen for positive feedback processing relative to negative feedback processing, although Bonferroni correction for the number of ROIs ($n = 4$) renders this effect only marginally significant (corrected $p = .091$). The block effect was not significant, $b = -0.058$, SE = 0.035, $t = -1.65$, $p = .10$, 95% CI [-0.13, 0.011]. The intercept was not significant, $b = 0.054$, SE = 0.041, $t = 1.33$, $p = .19$, 95% CI [-0.025, 0.13]. No effects were significant in other ROIs (Figure 6).

**Discussion**

We examined the neural mechanisms underlying non-native speech category learning in adults. Based on an extensive review of previous behavioral work (Ashby and Maddox 2005; Chandrasekaran et al. 2013; Maddox et al. 2013; Maddox and Chandrasekaran 2014; Maddox et al. 2014), we predicted that speech categories would be optimally learned via corticostriatal circuitry involved in reflexive learning (Seger 2008; Seger and Miller 2010). Computational modeling of behavioral response strategies in this study revealed an increase in the use of reflexive strategies, and a decrease in the use of reflective or random strategies with experience. Reflexive strategy use was associated with increased activation in the putamen during feedback processing. Final block categorization accuracy was associated with increased stimulus-related activation in the auditory areas that have been previously implicated in speech category learning. These include Heschl's gyrus (Wong et al. 2008), inferior parietal lobule (Gandour et al. 2003a, 2003b), and the insular cortex (Wong et al. 2004). Furthermore, individual learning success was associated with activation in the putamen and the motor cortex. These areas have not been directly indicated in speech processing, but they are key components of the corticostriatal motor loop that forms the reflexive category learning system (Seger 2008; Seger and Miller 2010). These behavioral, computational modeling and neuroimaging results help specify the mechanisms underlying feedback-dependent error reduction.
during speech learning. While speech learning has been mostly viewed as a perceptually encapsulated process in previous research (Holt and Lotto 2008, 2010), our findings represent an important conceptual advance in understanding the neurobiological basis of domain-general learning systems during speech processing.

Neural circuitry involved in processing positive feedback

Positive feedback, relative to negative feedback, activated several functional loops within the corticostriatal system. These included the ventral striatum, a part of the motivational loop, which is critical in processing the reward value during corrective feedback (Seger 2008; Seger and Miller 2010). These results are consistent with previous work showing that the ventral striatum was more active during positive than negative feedback (Seger et al. 2010). In addition, the DLPFC, anterior cingulate, and the putamen were more active during positive feedback. The DLPFC and the anterior cingulate are key components of the reflective executive loop, which is involved in the explicit processing of trial feedback (Seger 2008; Seger and Miller 2010). These areas have been found to be more active on correct categorization trials during visual learning (Seger et al. 2010). The DLPFC is hypothesized to generate and store verbalizable rules, which are either retained or discarded by the anterior cingulate cortex depending on the valence of the feedback (Ashby and Alfonso-Reese 1998; Ashby and Ell 2001; Maddox et al. 2003; Ashby and Maddox 2005).

In addition to the DLPFC and the anterior cingulate cortex, which are parts of the reflective learning system, positive feedback also increased the activation in the putamen. The putamen, considered a part of a reflexive, corticostriatal motor loop (Seger 2008; Seger and Miller 2010) is involved in the selection of appropriate motor responses based on prior experience. The putamen is therefore posited to be involved in procedural learning. Studies have shown that changing the button-to-category associations interfere with reflexive learning but not with reflective learning (Ashby et al. 2003; Maddox et al. 2004; Spiering and Ashby 2008; Maddox et al. 2010). Indeed, a recent neuroimaging study suggested that the putamen is integral to reflexive learning of visual categories (Waldschmidt and Ashby 2011). The involvement of the motivational, executive
(reflective), and motor (reflexive) loops is consistent with the predictions from the visual category learning literature. Overall, these results demonstrate a functional role for domain-general corticostriatal category learning systems in speech learning. During feedback processing, the ventral striatum responds to the reward value in positive feedback, the DLPFC and the anterior cingulate cortex generate and select rules based on the content of feedback, and the putamen is activated to transform stimuli representations onto procedural responses.

Outside the corticostriatal category learning areas, particularly noteworthy is the activation of the speech-related auditory areas including the left superior temporal sulcus / middle temporal gyrus. The feedback was presented in the visual modality, and the level of sensory auditory stimulation did not vary across positive and negative feedback. Similar positive feedback-driven activation in sensory regions has been previously reported in the visual domain when the feedback was presented in the auditory domain (Weil et al. 2010). The activation of the visual cortex during positive feedback has been interpreted as evidence for the modulation of early sensory regions by the reward processing network. Indeed, we can interpret our results within this framework. The left STS/MTG regions have been shown to be important for auditory speech processing (Hickok and Poeppel, 2007; Rauscheker and Scott, 2009). Activation of these regions during positive feedback may reflect a strengthening of the sensory representation of the rewarded stimulus, driven by the reward processing network. Future work could need to include several more learning trials and effective connectivity analyses to test the possibility of a causal relationship (i.e., the influence of the reward processing network on sensory regions).

Positive feedback also activated the inferior parietal lobule, which is presumed to be an integral part of the phonological network (Hickok and Poeppel 2007). The IPL has been previously conceptualized as a temporary buffer in phonological working memory (Koelsch et al. 2009), especially regarding comparison and decision making aspects (Strand et al. 2008). The auditory input is only available in the form of sensory memory trace during feedback presentation (Sams et al. 1993; Haenschel et al. 2005). Thus, the IPL activation during positive feedback may reflect the mapping of stored representation of the auditory stimulus onto the phonological categories (Buchsbaum and D'Esposito...
Since negative feedback does not directly provide stimulus-to-category information, we hypothesize that the IPL is not activated in the negative feedback condition. Thus positive feedback engages the reward processing network and may provide the critical learning signal for stimulus-to-category mapping within the IPL.

To conclude, positive feedback activates a large corticostriatal network. The reward value of positive feedback is likely processed in the ventral striatum. Category learning likely occurs within the reflective (dorsolateral prefrontal cortex and the anterior cingulate cortex) and the reflexive (putamen and the motor cortex) networks (Seger 2008; Seger and Miller 2010). Finally, the positive feedback may strengthen the sensory representation of the rewarded stimulus and may promote stimulus-to-category mapping within the phonological network.

Reflexive strategy use associated with increased putamen activation

Individual learners adopt different speech category learning strategies depending on the stage of learning and individual capacities (Maddox and Chandrasekaran 2014). Computational modeling enables direct assessment of this variability in individual response strategies. In this study, response strategies were modeled in each learning block separately for each participant. Multidimensional scaling studies have shown that Mandarin tone categories are most parsimoniously distinguished using two frequency dimensions (height and direction; Chandrasekaran et al. 2010). In the current study, the 40 stimuli were embedded in a two-dimensional space defined by average fundamental frequency and average slope. We hypothesized that the optimal strategy is reflexive and requires a pre-decisional integration of information across dimensions. Non-optimal strategies were also explored that were either reflective, relying on only one of the two dimensions (reflective) or was random. The modeling results revealed that the typical trend was for participants’ early learning to be characterized by the use of reflective (or random responder) strategies and their late learning to be characterized by the use of a reflexive strategy. In addition, the results suggested that reflexive strategy users, as determined on a block-by-block basis, were more accurate in the task. Therefore, learners
initially use reflective strategies, but switch to the more optimal reflexive strategies as they gain expertise. This latter interpretation was supported by the mixed effects modeling result which showed that reflexive strategy use was associated with better learning outcomes.

Reflexive category learning is dependent on the mapping of the perceptual experience of the stimulus onto motor response associated with the appropriate category. The cortical sensory input is relayed to the striatum via many-to-one convergent connections, which give rise to a low-resolution stimulus representation (Wilson 1995; Ashby and Ennis 2006). These striatal units allow association of stimuli to category responses, and these corticostriatal connections form the basis of reflexive category learning. The putamen is a strong candidate in this type of plasticity since it exhibits greater connectivity to the auditory association cortices relative to the caudate nucleus (Di Martino et al. 2008). The putamen is also involved in perceptual processing of auditory stimuli (Geiser et al. 2012), and has been implicated in visual category learning research to be critical to reflexive learning (Waldschmidt and Ashby 2011). Our results showed that reflexive strategy use was associated with increased activation in the left putamen during feedback processing. However, no pattern pertaining to the reflexive strategy use could be found in the DLPFC, suggesting that the optimal strategy use is not the result of increased prefrontal reflective processing. The current study, therefore, supports the prediction that speech category learning is reflexive-optimal, and that reflexive strategies critically involve putamen during feedback processing.

The role of corticostriatal loops in successful speech categorization

During stimulus perception, individual variability in learning performance was associated with the involvement of the corticostriatal motor loop. In the visual category learning literature, the relative dominance of the reflective and reflexive learning systems is dependent on the stage of learning. Early learning is dominated by the executive, reflective learning system (Smith, Berg, et al. 2012; Smith, Crossley, et al. 2012), but later stages of learning are associated with increased automaticity and putamen activation (Haruno and Kawato 2006; Williams and Eskandar 2006; Seger 2009). During reflexive
learning, a single striatal “unit”, presumed to be located within the putamen, implicitly associates an abstract cortical–motor response with a large group of sensory cells within the sensory association cortex (Matelli and Luppino 1996; Seger 2008; Seger et al. 2010; Waldschmidt and Ashby 2011). Synaptic plasticity in the striatal cell is facilitated by a dopamine-mediated reinforcement reward signal from positive feedback, which is processed via the motivational loop that connects the ventral striatum and the anterior cingulate cortex (Seger 2008; Seger et al. 2010). In later stages of learning, the dopamine-mediated reinforcement signal becomes more consistent, allowing a stronger association between the stimulus and an accurate category label. As discussed earlier, optimal speech category learning is thought to be reflexive, given its multidimensionality and high variability. Therefore, optimal speech category learning necessitates a switch to the reflexive strategy (Chandrasekaran et al. 2013), which is likely based on the activity of the loop between the putamen and the motor cortex. This prediction was reflected in the finding that the individual variability in learning performance was associated with increased involvement of the putamen and the motor cortex for correct trials relative to incorrect trials, during stimulus perception.

The putamen receives convergent input (10,000 to 1) from the cortex, as do other parts of the striatum (Wilson 1995). These cortical afferents originate from the prefrontal cortex in the rostral putamen (Selemon and Goldman-Rakic 1985) and the motor and somatosensory areas (Alexander and DeLong 1985) and the superior temporal auditory areas (Yeterian and Pandya 1998) in the caudal putamen. The putamen has been purported to be involved in episodic memory, cognitive control, and category learning, in addition to motor processing. In fact, the putamen has been suggested to be the ideal site of acquisition of stimulus-to-response associations, where sensory stimuli are mapped onto context-specific motor activity that lead to favorable outcomes (Ell et al. 2011). Despite the many functions of the putamen, in the context of the current study, the putamen activation patterns are best interpreted as reflecting reflexive strategy use, as reflexive learning of the speech categories necessitate implicit associations between the speech sounds and behavioral category responses. The findings from this experiment indicated that increased putamen activation was associated with reflexive strategy use, as well as learning success in the final block. However, caution should be taken in inferring
process from the activation of the putamen to a specific task function. Further studies are required to confirm the role of the putamen in reflexive learning of speech categories. The various functions of the putamen relate to different anatomical regions of this structure (Ell et al. 2011). High resolution mapping of the putamen may help clarify the specific role of the putamen in speech learning.

Conclusions

Category learning plays a vital function in human cognition. Speech category learning in adulthood is difficult, but feedback-dependent training can lead to successful speech categorization. In this study we examined the computational and neural mechanics underlying feedback-dependent speech categorization, using a dual-systems approach developed in the visual domain. Considering the complexity of speech categories, it was hypothesized that optimal speech category learning would be associated with the reflexive system. Computational modeling results revealed that the learners were initially biased towards the reflective system, but gradually discarded it in favor of the reflexive system. Throughout learning, reflexive strategy use was associated with better learning performance. Positive feedback was associated with increased activation in reflective and reflexive circuitry. In addition, positive feedback also activated the ventral striatum, a key component of the motivational loop, as well as several regions associated with auditory and speech processing. Furthermore, reflexive strategy use was associated with increased activation in the putamen, which is part of the motor loop that implicitly maps stimuli onto category responses in the motor cortex. Finally, increased activation of this motor loop during stimulus perception was associated with more accurate categorization. The neurocomputational and individual differences approach reveal that successful speech category learning is critically dependent on domain-general corticostriatal learning systems.
Acknowledgements

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Rorden C. 2007. MRICron [Computer software].


Table 1. Whole-brain analysis.

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Regions</th>
<th>Peak MNI coordinates</th>
<th>Voxels</th>
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</thead>
<tbody>
<tr>
<td><strong>Stimulus Perception</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(A) Correct + Incorrect</td>
<td>L HG, L PT, L PSTG</td>
<td>-52, -38, 18</td>
<td>890</td>
</tr>
<tr>
<td></td>
<td>R HG, R PT, R PSTG</td>
<td>60, -24, 0</td>
<td>867</td>
</tr>
<tr>
<td>(B) Correct - Incorrect</td>
<td>L Postcentral gyrus</td>
<td>-30, -28, 70</td>
<td>333</td>
</tr>
<tr>
<td></td>
<td>R Inferior parietal lobule</td>
<td>50, -32, 32</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>R PT</td>
<td>40, -30, 16</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>L Precentral gyrus</td>
<td>-32, -44, 56</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>L SPL</td>
<td>-22, -54, 56</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>R HG</td>
<td>44, -12, 0</td>
<td>18</td>
</tr>
<tr>
<td>(C) Incorrect - Correct</td>
<td>N/A</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Accuracy vs. Stimulus: Correct - Incorrect</strong></td>
<td>R Precentral gyrus, R Inferior frontal gyrus, R putamen, R caudate nucleus, R insula, Anterior cingulate cortex, R HG</td>
<td>38, -12, 34</td>
<td>4638</td>
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<tr>
<td>(A) Positive correlation</td>
<td>L Insula, L HG</td>
<td>-44, 2, 2</td>
<td>149</td>
</tr>
<tr>
<td></td>
<td>R Middle temporal cortex</td>
<td>56, -62, -4</td>
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<td></td>
<td>Anterior cingulate cortex</td>
<td>12, 30, 12</td>
<td>91</td>
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<tr>
<td></td>
<td>L Insula, L Putamen</td>
<td>-38, 6, -4</td>
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<tr>
<td></td>
<td>R Precentral gyrus</td>
<td>48, 0, 38</td>
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<tr>
<td></td>
<td>R Precentral gyrus</td>
<td>22, -16, 60</td>
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<td></td>
<td>Right middle frontal gyrus</td>
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<td></td>
<td>White matter</td>
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<tr>
<td></td>
<td>R Precentral gyrus</td>
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<tr>
<td>Motor Response</td>
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<tr>
<td>(A) Correct + Incorrect</td>
<td>ACC, Paracingulate cortex, Frontal and motor areas</td>
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<tr>
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<td>-2, 22, 38</td>
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<tr>
<td></td>
<td>R Insula</td>
<td>32, 22, 10</td>
<td>229</td>
</tr>
<tr>
<td></td>
<td>R Thalamus</td>
<td>12, -16, 8</td>
<td>25</td>
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<tr>
<td></td>
<td>L Thalamus</td>
<td>-14, -22, 10</td>
<td>11</td>
</tr>
<tr>
<td>(B) Correct - Incorrect</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>(C) Incorrect - Correct</td>
<td>N/A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feedback</td>
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<td></td>
<td></td>
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<td>L Frontal pole</td>
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<tr>
<td></td>
<td>ACC, Paracingulate cortex</td>
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<td></td>
<td>L Caudate, L Putamen</td>
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<td>484</td>
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<td></td>
<td>R Inferior parietal lobule</td>
<td>-60, -52, 38</td>
<td>399</td>
</tr>
<tr>
<td></td>
<td>R Putamen</td>
<td>12, 2, -8</td>
<td>266</td>
</tr>
<tr>
<td></td>
<td>L Superior lateral occipital cortex</td>
<td>-40, -68, 50</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>L Middle temporal gyrus</td>
<td>-70, -22, -10</td>
<td>14</td>
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<tr>
<td></td>
<td>L Frontal pole</td>
<td>-20, 60, 30</td>
<td>12</td>
</tr>
</tbody>
</table>

HG, Heschl's gyrus; PT, planum temporale; PSTG, posterior superior temporal gyrus; SPL, superior parietal lobule; ACC, anterior cingulate cortex. Cluster size restricted to greater than 10 voxels.
Figure 1. (Left) Stimulus space. Two native Mandarin talkers produced four Mandarin lexical tones in five syllable contexts. The x-axis represents normalized average fundamental frequency height of each stimulus. The y-axis represents normalized average fundamental frequency direction of each stimulus. The two dimensions have been found to underlie categorization of Mandarin lexical tones, although multiple other cues are used in real-life speech communication. (Right) Trial design in the learning experiment. In each trial, a stimulus was played for a fixed duration (445 ms). The participants were given a 2 s window to respond. Corrective feedback (750 ms) followed stimulus offset after a jitter of 2 to 4 s. Onset of the next stimulus followed feedback offset by a jitter of 1 to 3 s. A fixation cross was constantly displayed throughout the experiment, except for the feedback phase, in which "RIGHT" or "WRONG" was displayed according to the trial-by-trial response accuracy.
Figure 2. (Left) Individual behavioral learning performance across all blocks, for all participants. Each cell represents the learning profile for individual participants. The x-axis shows the learning blocks. The y-axis shows the average response accuracy per block for each participant. (Right) Response modeling results. Over the course of learning blocks, the number of reflexive strategy users increase.
Figure 3. Activation during feedback processing phase, correct vs. incorrect accuracy valence. Activities in left dorsolateral prefrontal cortex, anterior cingulate cortex, left caudate nucleus, bilateral putamens, ventral striatum, left middle temporal gyrus / superior temporal sulcus and the left inferior parietal lobule are observed. No significant activations were found in the average or in incorrect vs. correct contrasts.
Figure 4. Activation during stimulus presentation phase, correct vs. incorrect accuracy valence. Activities in the left precentral gyrus, postcentral gyrus, superior parietal lobule, right insula, planum temporale and inferior parietal lobule are observed. The cluster size in the left superior temporal cortex was under 10 voxels. The reverse contrast (incorrect vs. correct) did not reveal significant activation.
Figure 5. Correct vs. incorrect activation correlated with individual accuracy scores in the final block, during stimulus presentation phase. Activities in the bilateral Heschl's gyrus, right inferior parietal lobule, right inferior frontal gyrus, bilateral insula, right putamen, right caudate nucleus, the motor cortex, and the anterior cingulate cortex were positively correlated with accuracy scores. No areas were found to negatively correlate with accuracy.
Figure 6. (Left) Dorsolateral prefrontal cortex (DLPFC) defined as Brodmann areas 9/46, and the putamen anatomically defined using the Harvard-Oxford Subcortical Atlas. (Right) Reflexive strategy use associated with increased activation in the left putamen during feedback processing (contrast: correct - incorrect). Outliers are not displayed. No such pattern was observed in the right putamen or the DLPFC, suggesting that the reflexive strategy use is not due to increased prefrontal involvement in reflective category learning, but specifically in the reflexive enhancement of the stimulus-to-category mapping in the putamen.
Supplementary Materials

Results using BIC to determine best fitting models

For each block a strategy (reflexive, reflective pitch height, reflective pitch direction, or random responder) was assigned according to the best fitting model and several notable patterns could be verified from the mixed effects analysis studying the average block number (mean centered) for each of the assigned strategies. Since the block numbers were mean-centered, positive estimates for each level of strategy would indicate that the given strategy was more likely to be utilized late in learning (block 4, 5, or 6), while negative estimates would indicate that the given strategy was more likely to be utilized early in learning (blocks 1, 2, or 3). The mean block for the reflexive strategy (intercept) was significant, \( b = 1.20, \text{SE} = 0.29, t = 4.10, p < .0001, 95\% \text{ CI } [0.0630, 1.770] \), indicating that a given reflexive strategy was more likely to be utilized later in learning. The random responder model was significant, \( b = -1.64, \text{SE} = 0.35, t = -4.68, p < .0001, 95\% \text{ CI } [-2.324, -0.960] \), indicating that the random responder strategy was more likely to be utilized in learning earlier than the reflexive strategy. Similar patterns were observed to be marginally significant for unidimensional reflective strategies, which were utilized earlier in learning than the reflexive strategy: pitch direction, \( b = -1.27, \text{SE} = 0.67, t = -1.89, p = .061, 95\% \text{ CI } [-2.581, 0.038] \); and significant for pitch height: \( b = -1.36, \text{SE} = 0.41, t = -3.33, p = .001, 95\% \text{ CI } [-2.150, -0.563] \).

In an analysis designed to test whether the reflexive strategies yielded better learning outcomes, a repeated measures logistic regression was conducted with the trial-by-trial accuracy as the dependent variable and the mean-centered block number, block-by-block strategy, and their interaction term as fixed effects. There were two levels in the block-by-block strategy term: reflexive vs. non-reflexive. There was a significant interaction between block number and strategy, \( b = 0.28, \text{SE} = 0.13, z = 2.13, p = .03 \), indicating the reflexive strategy use enhanced accurate responses in later trials than in earlier trials. The intercept was not significant, \( b = -0.15, \text{SE} = 0.23, z = -0.65, p = .51 \). The block effect was significant, \( b = 0.29, \text{SE} = 0.06, z = 4.62, p < .0001 \), indicating that the odds of producing an accurate response compared to an inaccurate response was
higher for later blocks than for earlier blocks. The strategy effect was not significant, $b = 0.22$, $SE = 0.15$, $z = 1.43$, $p = .15$.

Finally, we tested the hypothesis that the putamen is involved when category learning is mediated by the reflexive processing system. Participants were classified as reflexive versus non-reflexive (reflective or random) strategy users based on the best fitting model in each block. Mixed effects analyses were performed on the putamen and DLPFC on the left and right hemispheres. The dependent measure was the percent signal change (correct - incorrect) value during feedback processing in each block. The fixed effects were the mean-centered block number, and strategy group (reference level: non-reflexive), corrected for random participant intercepts. In the left putamen, the block by strategy interaction was significant, $b = 0.41$, $SE = 0.17$, $t = 2.43$, $p = .016$, 95% CI [0.082, 0.744], suggesting that the activity in the left putamen increased according to reflexive strategy use in the later blocks. The strategy effect was significant, $b = 0.46$, $SE = 0.15$, $t = 2.98$, $p = .003$, 95% CI [0.159, 0.755], suggesting that reflexive strategy use was associated with increased activation in the left putamen for positive feedback processing relative to negative feedback processing. The block effect was not significant, $b = -0.03$, $SE = 0.036$, $t = -0.85$, $p = .40$, 95% CI [-0.101, 0.039]. The intercept was significant, $b = 0.08$, $SE = 0.036$, $t = 2.24$, $p = .027$, 95% CI [0.011, 0.154]. No effects were significant in other ROIs. Altogether, the analyses using BIC to determine the best fitting models for each block per individual participants yielded in results that directly mirrored those obtained when using AIC to determine model strategy.

Results after the inclusion of the conjunctive model

Behavioral results

Analysis of the behavioral data including the conjunctive model revealed that the conjunctive strategy use did not differ significantly from the reflexive ("SPC") strategy use. Participants were observed to be using various strategies, including all models considered in the process. However, several notable patterns could be verified from the mixed effects analysis with the block number (mean-centered) as the dependent variable.
and the best fitting strategy as the fixed effect (reference level: reflexive strategy). The intercept was marginally significant, $b = 0.5690$, SE = 0.2970, $t = 1.916$, $p = .05756$, 95% CI [-0.00653, 1.1444], indicating a trend of the reflexive strategy having been used at the later stage of learning. The random responder model was significant, $b = -1.2485$, SE = 0.3922, $t = -3.183$, $p = .00181$, 95% CI [-2.00852, -0.48854], indicating that the random responder model was more likely to occur during the early phase of learning. Similar patterns were observed to be statistically significant or marginally significant for unidimensional reflective strategies: pitch height, $b = -0.7899$, SE = 0.3843, $t = -2.055$, $p = .04181$, 95% CI [-1.53460, -0.04521]; pitch direction: $b = -1.4023$, SE = 0.7173, $t = -1.955$, $p = .05270$, 95% CI [-2.79223, -0.01234]. The conjunctive reflective model, however, failed to reach significance, $b = 0.5977$, SE = 0.4583, $t = 1.304$, $p = .19443$, 95% CI [-0.29031, 1.48571], suggesting that a similar level of strategy selection was observed over the course of learning, compared to the reference level of reflexive strategy.

fMRI: ROI results

Also, the putamen ROI results after having grouped the conjunctive as a reflective strategy along with the two unidimensional strategies yielded results with the same interpretation as not having considered the conjunctive model. Participants were classified into reflexive ($N = 6$) versus reflective ($N = 17$) strategy users based on the behavioral response modeling results in the final block. Mixed effects analyses were performed on the putamen and dorsolateral prefrontal cortex on the left and right hemispheres. The dependent measure was the percent signal change (correct - incorrect) value during stimulus presentation, in the first and final blocks. The fixed effects were the block and strategy group (reference level: reflexive strategy), corrected for random participant intercepts. In the left putamen, the block by strategy interaction was marginally significant, $b = 0.87720$, SE = 0.49801, $t = 1.761$, $p = .0827$, 95% CI [-0.09818, 1.85257], suggesting that reflexive strategy users tended to activate the left putamen more during the final block. The intercept was not significant, $b = -0.04379$, SE = 0.20033, $t = -0.219$, $p = .8278$, 95% CI [-0.43031, 0.34272]. The strategy group effect
was not significant, $b = -0.05114$, SE = 0.39221, $t = -0.130$, $p = .8968$, 95% CI [-0.80789, 0.70561]. The block effect was not significant, $b = 0.07617$, SE = 0.25436, $t = 0.299$, $p = .7655$, 95% CI [-0.42200, 0.57435]. In the right putamen, the block by strategy interaction was significant, $b = 1.1664$, SE = 0.4581, $t = 2.546$, $p = .0132$, 95% CI [0.26969, 2.06313], indicating that reflexive strategy users activated the left putamen more during the final block. The intercept was not significant, $b = 0.1040$, SE = 0.1695, $t = 0.614$, $p = .5416$, 95% CI [-0.22283, 1.11087]. The strategy group effect was not significant, $b = -0.3404$, SE = 0.3318, $t = -1.026$, $p = .3090$, 95% CI [-0.98038, 0.29961]. The block effect was not significant, $b = -0.1292$, SE = 0.2340, $t = -0.552$, $p = .5826$, 95% CI [-0.58723, 0.32878].