RESEARCH ARTICLE

The neural basis of implicit learning of task-irrelevant Chinese tonal sequence

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Abstract The present study sought to investigate the neural basis of implicit learning of task-irrelevant perceptual sequence. A novel SRT task, the serial syllable identification task (SSI task), was used in which the participants were asked to recognize which one of two Chinese syllables was presented. The tones of the syllables were irrelevant to the task but followed an underlying structured sequence. Participants were scanned while they performed the SSI task. Results showed that, at the behavioral level, faster RTs for the sequential material indicated that task-irrelevant sequence knowledge could be learned. In the subsequent prediction test of knowledge of the tonal cues using subjective measures, we found that the knowledge was obtained unconsciously. At the neural level, the left caudate, bilateral hippocampus and bilateral superior parietal lobule were engaged during the sequence condition relative to the random condition. Further analyses revealed that greater learning-related activation (relative to random) in the right caudate nucleus, bilateral hippocampus and left superior parietal lobule were found during the second half of the training phase compared with the first half. When people reported that they were guessing, the magnitude of the right hippocampus and left superior parietal lobule activations was positively related to the accuracy of prediction test, which was significantly better than chance. Together, the present results indicated that the caudate, hippocampus and superior parietal lobule played critical roles in the implicit perceptual sequence learning even when the perceptual features were task irrelevant.

Keywords Hippocampus · Caudate · Implicit learning · Task-irrelevant associations

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Introduction

Sequential structures form the basis for efficient and adaptive behaviors (Lashley 1951), which can be noticed in the surrounding perceptual world (e.g., syllables in words) as well as in our daily motor skills (e.g., riding a bike). Previous studies have shown that humans are equipped with powerful learning mechanisms to acquire knowledge of sequential structure without awareness (Stadler and Frensch 1998). This form of learning is known as implicit sequence learning. Implicit sequence learning has been investigated widely using the serial reaction time (SRT) task (Grafton et al. 1998; Nissen and Bullemer 1987; Willingham et al. 1997). In the classical SRT task, participants are required

to respond to sequences of objects by pressing the corresponding buttons. Unbeknownst to the participants, at least one of the dimensions of these objects, such as spatial location, color or shape, follows a specific sequence. Abundant researches have shown that people were able to acquire the underlying structure of these sequences, indicated by shorter reaction times (RTs) for the regular sequences than the random sequences (Brown et al. 2010; Cleeremans and McClelland 1991; Nemeth et al. 2011; Nissen and Bullemer 1987; Rowland and Shanks 2006).

There has been a classical debate on the standard SRT tasks as to what kind of knowledge has been acquired, i.e., motor sequence or perceptual sequence. A growing number of studies have investigated this issue and reported controversial results (Deroost and Soetens 2006; Gheysen et al. 2009; Nattkemper and Prinz 1993, 1997; Remillard 2003, 2009; Stöcker et al. 2003; Willingham 1999; Willingham et al. 2000; Ziessler 1998; Ziessler and Nattkemper 2001). Recently, Rose et al. (2011) developed a novel SRT task which dissociated the different modalities (perceptual and motor) of sequence learning, thus avoiding possible confounding between perceptual sequence learning and motor sequence learning. In their study, six colored squares were presented around the center of the screen, where the target square appeared simultaneously. The locations of these squares corresponded to six different finger buttons. The subjects were asked to press the button corresponding to the square which shared the same color with the target. In each trial, the assignments of the colors to the response locations were randomized. Therefore, the sequence of motor responses was also random. The sequence of the colors for the target square and those for correct responses could thus be independently determined. The results showed that purely perceptual sequences were learned.

In the study by Rose et al., however, the perceptual information was task relevant (also see Gheysen et al. 2009), for one needed to rely on the color of the target to determine the correct motor response. Yet, there were empirical evidences showing that perceptual information which was not primed by the main task nor predicted by the correct motor response, i.e., task irrelevant, could also be learned implicitly (Perlman and Tzelgov 2006; Rowland and Shanks 2006). Recently, using the serial syllable identification task (SSI task), a novel SRT task, Guo et al. (2013) have demonstrated the unconscious learning of the task-irrelevant perceptual stimulus contingencies. This task made use of the fact that Chinese is a tonal language, meaning that each syllable is spoken with one of four "tones." In this task, participants were asked to respond to different syllables (pronounced as 'tsan' or 'yo'; written as 'can' or 'you' in standard transcription) presented randomly. Unbeknownst to participants, however, the tone (1, 2, 3 and 4) of the syllables varied according to a fixed sequence. The

tonal sequence and task requirements were independent of one another. Tones did not indicate which syllables would be displayed and were not primed by task requirements. Therefore, perceptual features were task irrelevant. In addition, tone and syllable were not equally determinative of the meaning of a character; some syllables could still retain their original meanings even when the tones changed, but tones alone did not carry any meaning. People usually paid more attention to the syllable of a character rather than its tone (Dai 1997). This feature of the Chinese language further ensured that the tonal information of the sequences in the SSI task would not be primed by the task, thus confirming the implicit nature of the learning.

However, the neural mechanism underlying the implicit task-irrelevant perceptual sequence learning remained unclear. Neuroimaging studies using the task-relevant SRT tasks have found activation in the striatum (mainly the caudate nucleus) during implicit perceptual sequence learning (e.g., Dennis and Cabeza 2011; Gheysen et al. 2010; Peigneux et al. 2000; Rose et al. 2011; Willingham et al. 2002). Activation has also been found in the MTL (Albouy et al. 2008; Rose et al. 2011; Schendan et al. 2003). It was unclear, though, whether the role of caudate and MTL structures could be generalized to the implicit task-irrelevant perceptual sequence learning or whether their function was restricted to the implicit task-relevant perceptual sequence learning. The present study aimed to investigate the neural basis underlying the implicit task-irrelevant perceptual sequence learning by using the serial syllable identification Task (Guo et al. 2013). Empirical evidences suggested that the caudate played a crucial role in the implicit acquisition and expression of regularities of the environment (Berns et al. 1997; Lieberman et al. 2004). The role of the MTL in implicit sequence learning was now generally accepted, since the MTL had a specific ability of relating or combining information from multiple sources (Squire et al. 2004). Thus, it was predicted that the caudate and MTL would also be involved in the implicit task-irrelevant perceptual sequence learning. Furthermore, previous SRT studies showed that the implicit sequence learning was characterized by the incremental gains of performance rather than an all-or-none phenomenon (unlike learning about facts) (Gheysen et al. 2010) and the activation pattern of the neural regions which were crucial to implicit sequence learning (i.e., caudate and/or hippocampus) matched with the behavioral pattern (Gheysen et al. 2010; Rose et al. 2011). Therefore, we predicted that better behavioral learning performance and greater learning-related activations in hippocampus and caudate would be found in the later stage of the SSI task relative to the early stage.

Additionally, in the SSI task, the task-irrelevant tonal sequences served as contextual information compared
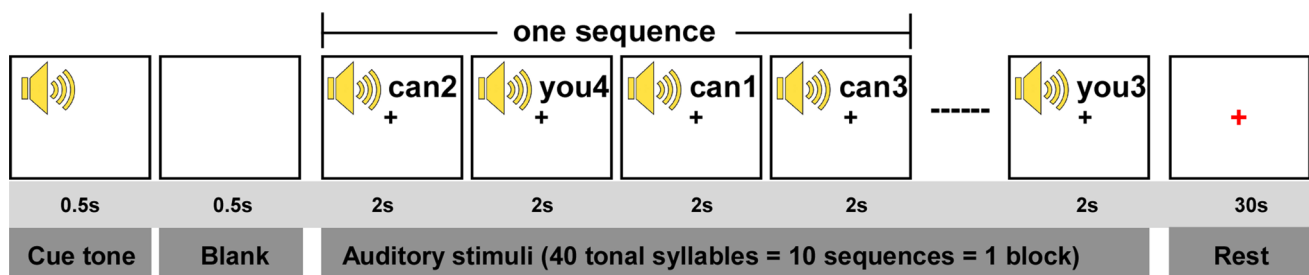
with the task of participants. If the tonal sequences could be implicitly learned, it indicated that contextual information were, to some extent, attended and processed in the absence of awareness. Converging evidence demonstrated that the superior parietal lobe modulated processing of stimuli that automatically captured attention (Mayer et al. 2009) and mediated the automatic shifts of attention (e.g., Kim et al. 1999; Mayer et al. 2009; Salmi et al. 2009; Serences and Yantis 2007). Recent neuroimaging studies demonstrated that superior parietal lobule (SPL) activity was modulated by spatial context; that is, it exhibited more robust responses to targets in repeated contexts relative to novel contexts even though participants were unaware of this contextual manipulation (Giesbrecht et al. 2013). Giesbrecht et al. (2013) argued that automatic attention signaled by the SPL activation contributed to the implicit visual contextual learning. Taken together, we expected that the superior parietal lobule would also be involved in the implicit task-irrelevant perceptual sequence learning.

Further, in order to assess the conscious status of knowledge, we used the method of structural knowledge attributions by Dienes and Scott (2005; as used also by, e.g., Chen et al. 2011; Guo et al. 2011, 2013; Hamrick and Rebuschat 2012; Jiang et al. 2012; Kemeny and Luckacs 2013; Neil and Higham 2012; Norman and Price 2012; Rebuschat and Williams 2009; Scott and Dienes 2010a, b). This method allowed us to systematically establish the conscious status of the acquired knowledge in a sensitive way, where the learning was of genuinely task-irrelevant features. Dienes and Scott distinguished two different types of knowledge: (1) judgment knowledge which was the knowledge about whether a particular test item shared the same structure with the training items and (2) structural knowledge which might include knowledge of particular items, fragments of items or other types of rules that enabled the judgment. Both types of knowledge could be conscious or unconscious. When people said that they were guessing, both types of knowledge were unconscious. When people had confidence in the judgment, judgment knowledge was conscious, but structural knowledge could be unconscious. In this case, people might sense that they were using intuition. To assess the conscious status of structural knowledge, Dienes and Scott (2005) asked the participants to report the basis of their judgments by choosing from four options: guess, intuition, memory and rule. Unconscious structural knowledge was indicated by the attributions of guess and intuition, while conscious structural knowledge by those of memory and rule (see Dienes 2008, 2012, for detailed justification of the methodology).

Materials and methods

Participants

Seventeen right-handed, healthy volunteers from the university community with normal or corrected-to-normal vision (12 females, aged from 18 to 30, $M = 22.06$, $SD = 2.66$) participated in this study. All the participants were native Chinese speakers, and none of them had a history of neurological or psychiatric disorders. Two participants were excluded from further statistical analyses due to an excessively low behavioral response rate (outside of three SD from the mean) and failure to obey instructions, respectively. Each participant was paid RMB100 for participation and given informed consent before scanning. The study was approved by the Ethics Committee of the East China Normal University.

Materials

The Chinese syllables "can" (pronounced as 'tsan') and "you" (pronounced as 'yo') were used as the target stimuli. Each syllable was presented with one of four possible tones (1–4). A total of eight tonal syllables (i.e., can1, can2, can3, can4, you1, you2, you3 and you4) were created using a Chinese pronunciation software (Xunfei interphonic 2.30, sampling rate = 22.05 kHz). Each of these syllables lasted for 0.3 s and was spoken in a female voice.

Procedure

Participants performed the serial syllable identification (SSI) task in an MRI scanner. In the SSI task, 16 experimental blocks were presented including 12 sequence blocks and four random blocks inserted at the 3rd, 7th, 11th and 15th positions. Each block (sequence or random) consisted of 40 tonal syllables which were presented auditorily one by one through headphones. Each tonal syllable lasted for 0.3 s, and inter-stimulus interval (ISI) was 1.7 s. Participants were told to press the corresponding key as quickly and accurately as possible according to which syllable was presented, a "can" or a "you," regardless of its tone. In the sequence blocks, the tones of the syllables followed a structural four-item sequence (2-4-1-3) that repeated ten times consecutively for a total of 40 syllables (e.g., 2-4-1-3-2-4-1-3-2-4-1-3-2-4-1-3…), while the syllables were chosen randomly with the constraint that no syllable repeated itself more than three times (Fig. 1). For the random blocks, both syllables and their tones were presented in random order with the constraint that no syllable repeated itself more than three times and no tone immediately repeated itself. Each

Fig. 1 Time line of a sequence block. In the sequence block, the sequence structure is a four-item deterministic sequence; that is, the tones of the syllables followed a fixed order 2-4-1-3, while the syllables are chosen randomly. Each block consisted of ten consecutive sequences, e.g., 2-4-1-3-2-4-1-3-2-4-1-3… Participants are told to press the corresponding key as quickly and accurately as possible according to what syllable is presented, a ''can'' or a ''you,'' regardless of its tone

block lasted for 80 s. Among blocks was a red fixation cross presented for 30 s. A 0.5-s tonal cue and a 0.5-s blank were displayed before each block to inform the participants of the beginning of a new block. Participants were not told of the existence of the tonal sequence rule, nor were they informed of the fact that there were two different types of blocks.

After being scanned, the participants were tested on their implicit and explicit knowledge of the tonal sequence by doing a prediction task. In this task, participants would listen to a short sequence of tonal syllables and then predict the exact tone of the next syllable by choosing one from the four tones. There were totally 56 short sequences, each of which contained one, two or three syllables (e.g., can1, you2-can4 and you1-can3-can2) and could start at any of the four possible starting points. These sequences were presented sequentially from shortest to longest in order to avoid learning associations of tones from the test phase itself. After each prediction, the participants rated their confidence (as used also by, e.g., Mealor and Dienes 2012; Guo et al. 2013; Li et al. 2013, see discussion concerning confidence ratings, e.g., Dienes et al. 2010; Sandberg et al. 2010; Timmermans et al. 2010) on a 50-point scale (50–100 %), where 50 % indicated pure guess, 100 % indicated absolute certainty and any number in between reflecting gradations of confidence level (e.g., Kuhn and Dienes 2005). Then, the participants gave their structural knowledge attribution (Dienes and Scott 2005): guess, intuition, memory or rule. Participants learned the difference among these structural knowledge attributions through the instruction as follows: ''Guess'' indicated that the judgment was based on nothing at all, which could just as well be based on a toss of a coin; ''Intuition'' indicated that the judgment was based on a hunch or feeling that could not be explicated further; i.e., there was confidence in the judgment, but the person had no idea why the judgment was right; ''Memory'' indicated that the judgment was based on a recollection (or a failure to recollect); ''Rules'' indicated that the judgment was based on a rule that could be stated if asked (Jiang et al. 2012).

fMRI imaging

Scanning was carried out on a 3T Siemens scanner at the Functional MRI Lab (East China Normal University, Shanghai). For functional images, 35 slices were acquired using a gradient-echo echo-planar imaging (EPI) sequence (TR = 2,200 ms, TE = 30 ms, FOV 10 = 220 mm, matrix size = 64 × 64, slice thickness = 3 mm, gap = 0.3 mm). Before the functional run, a high-resolution structural image was acquired using a T1-weighted, multiplanar reconstruction (MPR) sequence (TR = 1,900 ms, TE = 3.42 ms, 192 slices, slice thickness = 1 mm, FOV = 256 mm, matrix size = 256 × 256).

Data preprocessing and statistical analyses were performed with statistical parametric mapping (SPM5, Wellcome Department of Cognitive Neurology, London, UK). During data preprocessing, all volumes were realigned spatially to the first volume of the first time series. None of participants moved more than 3 mm in any direction during the training phases. Then, the resulting images which were resampled to 2 × 2 × 2 mm voxel size were spatially normalized to a standard echo-planar imaging template based on the Montreal Neurological Institute (MNI) reference brain and smoothed with an 8-mm full-width half-maximum (FWHM) isotropic Gaussian kernel.

Statistical analyses were then performed using the general linear model (GLM) implemented in statistical parametric mapping (SPM5, Wellcome Department of Cognitive Neurology, London). The hemodynamic response to each condition (random/sequence in the first and second halves of the training phases) was modeled using a separate block basis function (with block duration set to 80 s), which convolved a canonical hemodynamic response function with a boxcar function. The model additionally included all the cue tones and six movement parameters derived from realignment as covariates of no interest. High-pass temporal filtering with a cutoff of 128 s was also applied in the model. For each subject at the first-level analysis, simple main effects for each of the four event types [sequence 1

(the first half of the scan training phases), random 1 (the first half of the scan training phases), sequence 2 (the second half of the scan training phases) and random 2 (the second half of the scan training phases)] were computed by applying the '1 0' contrasts. The four first-level individual contrast images were then analyzed at the second group level employing a random-effects model (flexible factorial design in SPM5).

Brain activities related to tonal sequence learning were defined by contrasting the sequence condition with the random condition. An interaction defined by the (Sequence2 − Random2) − (Sequence1 − Random1) and reverse contrasts were computed to extract specific regions showing learning-related activations across the training sessions. A voxel-level threshold of $p < 0.001$ (uncorrected) and a spatial extent threshold of $k \geq 35$ were used. Then, a region of interest (ROI) analysis was performed to evaluate the BOLD signal changes in caudate nucleus, hippocampus and superior parietal lobule identified in the interactions. All the significant voxels in the activated clusters within 6-mm spherical regions centered on the peak or local maximum coordinates were included in each ROI. ROIs were defined in the same way throughout the paper. Parameter estimates across ROIs for four events were extracted for further statistics using the MarsBaR toolbox in SPM5. Finally, regions showing significant correlation between brain BOLD signal change in the (sequence vs. random) contrast and the percentage of correct responses by guess attributions at the prediction test with a voxel-level threshold of $p < 0.001$ (uncorrected) and a spatial extent threshold of $k \geq 35$.

Results

Behavioral results

Response times and errors

During the serial syllable identification (SSI) task, the mean error proportions were $M = 0.04$ (SD = 0.05) for the first half and 0.07 (SD = 0.08) for the second half. There was no significant difference between the two halves. The error proportions were calculated for the random and sequence blocks (sequence: $M = 0.05$, SD = 0.06; random: $M = 0.06$, SD = 0.08). No significant difference
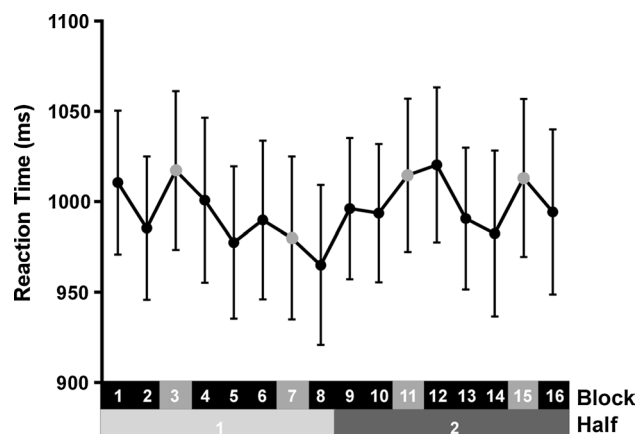
Fig. 2 Mean reaction times in each block. *Error bars* indicated standard error of the mean

between the sequence and the random blocks was detected, $t(14) = 1.19$, $p = 0.26$.

For each subject, incorrect responses or those beyond three standard deviations from the mean RT were excluded from further analyses. Less than 6 % of the data were omitted during this procedure in the experiment. The average RTs of valid trials across all the participants were illustrated in Fig. 2. The learning effect for each half was calculated as the difference between mean RTs of random blocks and sequence blocks. The overall learning effect averaged over two halves (14 ms) was significantly larger than 0, $t(14) = 2.44$, $p = 0.03$, $d = 0.63$. The mean learning effects of the two halves were 10.41 (SD = 31.83) and 17.61 (SD = 25.64). The learning effect was significantly larger than 0 in the second half of the training phases [$t(14) = 2.67$, $p = 0.02$, $d = 0.69$], but not in the first half ($p = 0.23$). However, no difference between these learning effects was detected, $t(14) = 0.80$, $p = 0.44$.

Prediction test and assessment of awareness

The proportion of correct response was calculated by (NC + 0.25)/(N + 1) (NC being the number of correct responses and N being the total number of responses), the correction corresponding to a Bayesian prior of chance performance (25 %) worth just one observation, useful when some participants had low N for some conditions (cf the unit information prior of Kass and Wasserman 1995; also Laplace 1814).

	Implicit attributions		Explicit attributions	
	Guess	Intuition	Memory	Rule
Proportion correct	0.39 ± 0.16	0.54 ± 0.13	0.44 ± 0.14	0.64 ± 0.11
Response proportions	0.38 ± 0.37	0.55 ± 0.35	0.05 ± 0.14	0.01 ± 0.04

Table 1 The proportions of each attribution and their associated proportion correct ($M \pm SD$)

Table 2 Learning-related activations [(Sequence1 + Sequence2) − (Random1 + Random2)]

Brain region	Side	Coordinates			t value	Voxels
		x	y	z		
Caudate nucleus	L	−18	24	8	5.08	1,365
Caudate nucleus	*L*	*−16*	*22*	*2*	*4.19*	
Putamen	*L*	*−32*	*0*	*−4*	*3.91*	
Putamen	R	24	18	−2	4.72	2,145
Middle cingulate cortex	L	−12	−22	40	4.83	1,286
Superior frontal gyrus	*L*	*−26*	*−8*	*54*	*4.04*	
Middle occipital gyrus	L	−38	−70	6	4.14	360
Hippocampus	L	−28	−26	−8	4.73	84
Postcentral gyrus	L	−34	−30	46	3.89	304
Superior parietal lobule	L	−26	−62	66	4.59	320
Precuneus	*L*	*−16*	*−56*	*68*	*4.32*	
Lingual gyrus	L	−10	−88	−14	4.52	345
Middle cingulate cortex	R	12	2	44	4.40	129
Hippocampus	R	36	−20	−14	4.26	42
Hippocampus	*R*	*38*	*−24*	*−12*	*3.88*	
Superior parietal lobule	R	28	−58	62	4.14	368
Precuneus	*R*	*8*	*−46*	*76*	*4.12*	
Inferior temporal gyrus	L	−44	−12	−28	4.13	52
Paracentral lobule	R	14	−34	56	3.94	38

Coordinates (mm) are in MNI space

All the clusters survived a voxel-level threshold of $p < 0.001$ (uncorrected) and a spatial extent threshold of $k \geq 35$. Italic values represent the local maxima within the clusters

L left hemisphere, *R* right hemisphere

The attributions of guess and intuition were combined as indicators of unconscious structural knowledge (implicit attributions) while those of memory and rule, as indicators of conscious structural knowledge (explicit attributions) (see Dienes 2008, 2012, for detailed justification of the methodology). The proportions of each attribution and their associated accuracy were shown in Table 1. Two participants never ascribed their judgments to intuition, and one other participant's judgment accuracy for trials attributed to guess was beyond two standard deviations from the mean. These three participants were excluded from the corresponding analysis.

For implicit attribution, participants' accuracy was significantly higher than chance (0.25), $t(14) = 7.63$, $p < 0.001$, $d = 1.97$, indicating the acquisition of the unconscious structural knowledge of the tonal regularity. Specifically, accuracies for responses based on guess and intuition were both significantly better than chance [guess: $t(13) = 4.19$, $p = 0.001$, $d = 1.12$; intuition: $t(12) = 8.18$, $p < 0.001$, $d = 2.27$]. Further, the accuracies for responses based on intuition was significantly higher than those for guess, $t(11) = 2.60$, p < 0.05. Additional analysis on the confidence levels also revealed a significantly difference between that for guess and intuition [guess: 51.53 ± 2.27; intuition: 61.80 ± 7.70, $t(11) = 4.44$, $p = 0.001$]. Only four participants chose explicit attributions, so nothing further can be concluded about conscious knowledge.

Furthermore, participants were asked to report whether they had detected any kind of regularity in the material. None of the subjects discovered or was able to verbalize any regularity.

fMRI results

Learning-related activations

Brain activities related to the specificity of tonal sequence learning [(Sequence1 + Sequence2) − (Random1 + Random2)] were observed in bilateral hippocampus, left caudate, bilateral putamen and bilateral superior parietal lobule (Table 2; Fig. 3). This finding was similar to previous studies (Albouy et al. 2008; Giesbrecht et al. 2013; Rose et al. 2011; Schendan et al. 2003). The reverse contrast did not detect any suprathreshold activation.
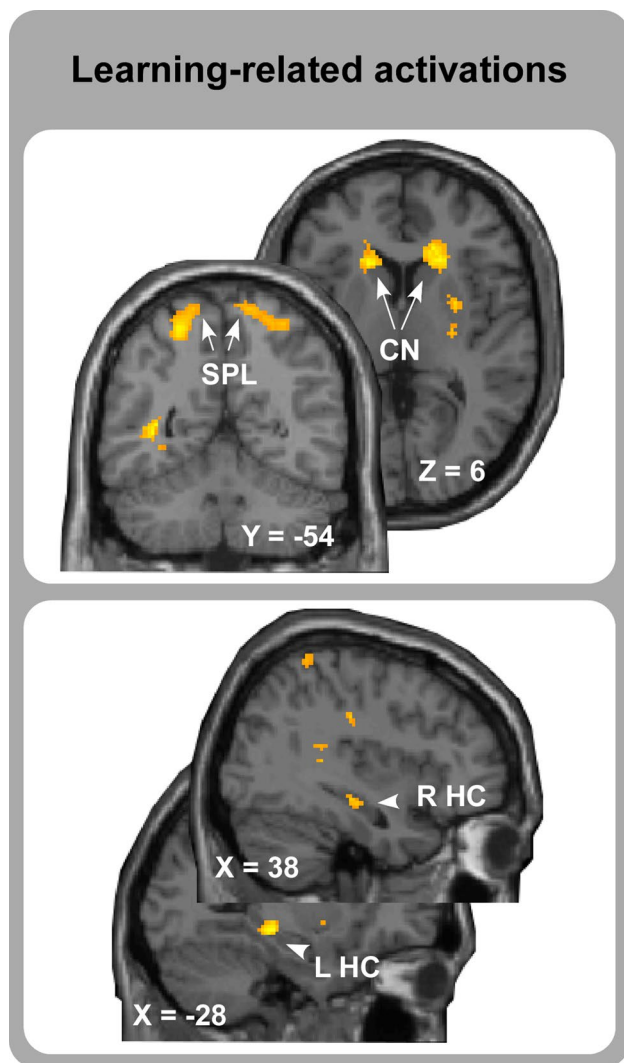
Fig. 3 Learning-related activations [(Sequence1 + Sequence2) − (Random1 + Random2)] are observed in left caudate nucleus, bilateral hippocampus and bilateral superior parietal lobule during training. *CN* caudate nucleus, *L HC* left hippocampus, *R HC* right hippocampus, *SPL* superior parietal lobule

Learning-related changes

To examine the changes related to learning, activation for the sequence rather than random condition was compared across the first and second halves of the training phases [(Sequence2 − Random2) − (Sequence1 − Random1)]. Significant learning-related activity increases were found in bilateral hippocampus, right caudate nucleus and left superior parietal lobule (Table 3; Fig. 4a). The reverse contrast did not reveal any activated regions.

In the first half of the training phases, the contrast (Sequence1 − Random1) revealed activation in left putamen (Table 4). In the second half of the training phases,

data analyses revealed greater activation in regions including bilateral hippocampus, bilateral caudate, right putamen and bilateral superior parietal lobule by contrasting (Sequence2 − Random2) (Table 4).

ROI analysis

To investigate the learning-related activations in caudate, hippocampus and superior parietal lobule across the first and second halves of the scanning phases, an ROI analysis was performed. ROIs in bilateral hippocampus (L HC: −18 −28 −8; R HC: 28 −26 −10), right caudate nucleus (R CN: 16 12 16) and left superior parietal lobule (L SPL: −36 −56 60) were defined by the (Sequence2 − Random2) − (Sequence1 − Random1) contrast. Beta estimates for the sequence and random conditions over the first and second halves of the scanning phases in each ROI were extracted. The results revealed that, for right caudate and bilateral hippocampus, the learning effects computed by the beta estimate difference between the sequence condition and the random condition were significantly higher in the second half of the scanning session than those in the first half ($ts > 2.45$, $ps < 0.05$). Additionally, marginally significant greater learning effect in the second half was observed compared with the first half for left superior parietal lobule [$t(14) = 2.06$, $p = 0.058$] (Fig. 4b).

Correlation analysis

Correlation analyses were performed to determine the regions where BOLD signal change detected from the [(Sequence1 + Sequence2) − (Random1 + Random2)] contrast varied with the average percentage of correct responses under guess attributions in the prediction test, i.e., in the case where both judgment and structural knowledge were unconscious. Interestingly, we again observed that right hippocampus and left superior parietal lobule activation positively correlated with the percentage of correct responses under guess attributions (right hippocampus: $r = 0.86$, $p < 0.001$; left superior parietal lobule: $r = 0.83$, $p < 0.001$, complete list of clusters shown in Table 5). Further, a similar correlation analysis was also performed between the [(Sequence1 + Sequence2) − (Random1 + Random2)] contrast and the accuracy on the intuition responses in the prediction test, i.e., in the case where structural knowledge is unconscious, but judgment knowledge is conscious. No significant correlation was found.

Discussion

We employed a modified version of the SRT (Guo et al. 2013) to explore which brain areas were involved in the

Table 3 Learning-related increases [(Sequence2 − Random2) − (Sequence1 − Random1)]

Brain region	Side	Coordinates			*t* value	Voxels
		x	y	z		
Middle orbital gyrus	R	26	46	−14	4.35	198
Middle frontal gyrus	R	48	26	40	4.84	647
Caudate nucleus	*R*	*16*	*12*	*16*	*4.47*	
Caudate nucleus	*R*	*22*	*4*	*20*	*3.87*	
Parahippocampal gyrus	R	20	−22	−18	4.64	270
Hippocampus	*R*	*34*	*−28*	*−12*	*3.94*	
Hippocampus	*R*	*28*	*−26*	*−10*	*3.67*	
Angular gyrus	R	48	−48	34	4.49	170
Hippocampus	L	−18	−28	−8	3.87	54
Hippocampus	L	−34	−30	−8	3.67	35
Superior parietal lobule	L	−36	−56	60	3.73	84

Coordinates (mm) are in MNI space

All the clusters survived a voxel-level threshold of $p < 0.001$ (uncorrected) and a spatial extent threshold of $k \geq 35$. Italic values represent the local maxima within the clusters

L left hemisphere, *R* right hemisphere

implicit learning based on the task-irrelevant perceptual features. In the present study, the only task of participants was to decide on the identity of a spoken syllable ("can" or "you") which occurred in a random order, whereas the sequential structure was imposed on the successive tones of the syllables which were irrelevant to the task. Consistent with the previous findings (Guo et al. 2013), faster RTs were observed for the sequential material than the random material. Accuracy was significantly higher than chance for implicit attributions in the subsequent prediction test. At the neural level, the left caudate, bilateral hippocampus and bilateral superior parietal lobule were engaged during the sequence condition relative to the random condition. Further analyses revealed that greater learning-related activations (relative to random condition) in the right caudate nucleus, the bilateral hippocampus and left superior parietal lobule were found during the second half of the training phases relative to the first. When focusing on the guess attributions, the magnitude of the right hippocampus and left superior parietal lobule activation was positively related to performance.

Consistent with prior studies (Berns et al. 1997; Grafton et al. 1995; Hazeltine et al. 1997; Peigneux et al. 2000; Rauch et al. 1997; Willingham et al. 2002), the current study showed that the striatum (mainly the caudate nucleus) played a key role in the implicit sequence learning. In the present study, specific learning-related effects were assessed by comparing the sequential condition to the random condition. Greater activation in the left caudate was found in the sequential condition. Furthermore, to examine the changes related to the learning effect, activation for the regular sequence was compared across the first and second halves of training. Significant increases in learning-related activity were found in the right caudate nucleus. Previous results suggested a specific ability of the striatum for chunking elements of the repeated and convergent sequence into functional sub-sequences of movement (Graybiel 1998; Boyd et al. 2009) and storage of learned sequences during implicit motor sequence learning (Doyon et al. 2009; Doyon and Benali 2005; Floyer-Lea and Matthews 2005). Recent fMRI studies have shown that the striatum were also recruited during the implicit pure perceptual-based sequence learning (Rose et al. 2011). Given that the perceptual features are task-irrelevant in the SSI task, the current findings further confirmed the significance of striatum in the unconscious learning of the task-irrelevant perceptual sequences.

Hippocampus was also activated during the implicit learning of tonal associations. When contrasting the sequential with the random condition, task-irrelevant stimulus–stimulus associations during implicit learning activated the hippocampus. Further analyses revealed that greater learning-related activations (relative to the random condition) in bilateral hippocampus were found during the second half of the training phases relative to the first. Taken together, these results indicated that the hippocampus played a critical role in associative learning even when the perceptual features were task irrelevant. The findings were also in accordance with the proposed role of the hippocampus as automatic and obligatory in the binding of perceptually distinct information (e.g., Cohen and Eichenbaum 1993; Ryan et al. 2007). According to this view, the functioning of the hippocampus was to bind together all perceptually distinct information regardless of how it would be involved in the future tasks. So the activation of hippocampus during implicit sequence learning would not be affected by the introduction of a task-irrelevant sequence, though other neural structures (e.g., prefrontal cortices) may be influenced.

We further studied the correlation between brain BOLD signal change in the (sequence − random) contrast and the percentage of correct responses under guess attributions in
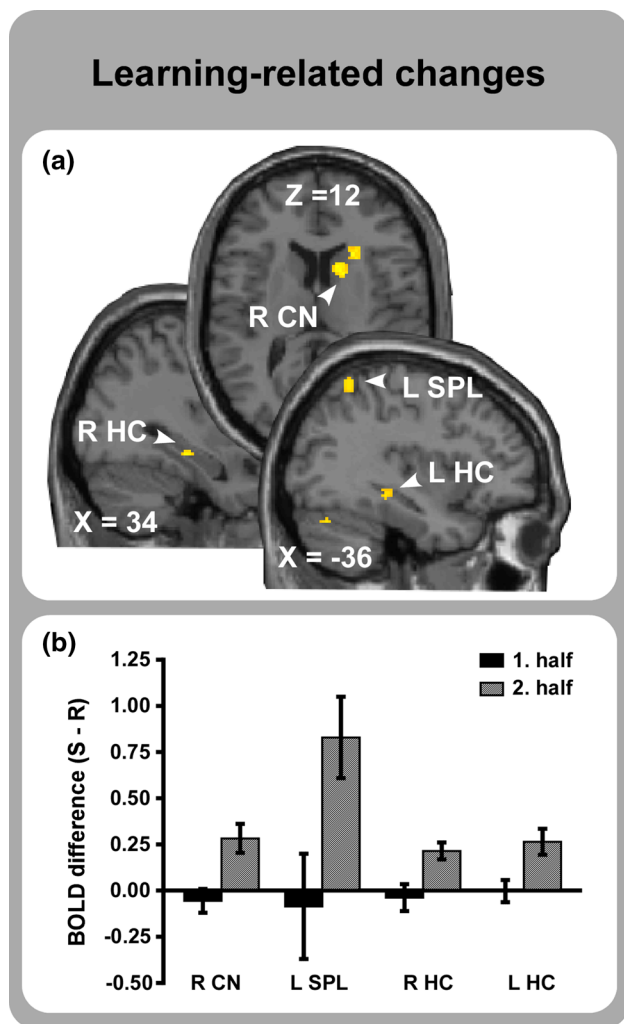
Fig. 4 a Regions of interest [right caudate nucleus (R CN: 16 12 16), bilateral hippocampus (L HC: −18 −28 −8; R HC: 28 −26 −10) and left superior parietal lobule (L SPL: −36 −56 60)] are defined by the (Sequence2 − Random2) − (Sequence1 − Random1) contrast. **b** Differential [(Sequence1 − Random1) and (Sequence2 − Random2)] parameter estimates indicated that learning-related responses in right caudate nucleus and bilateral hippocampus are significantly larger in the second half of the training as compared to the first half. Additionally, a marginal significance is found for left superior parietal lobule when compared learning-related activation observed in the second half with the first half. *Error bars* indicated standard error of the mean

the prediction test. The magnitude of the right hippocampus activation was positively related to performance, confirming its function in implicit associative learning. It has been argued that when both judgment knowledge and structural knowledge distinguished by Dienes and Scott (2005) were unconscious, the phenomenology was mere guessing; no conscious meta-knowledge of what has been learned was expressed (Mealor and Dienes 2012). Thus, the results extended previous findings by showing the role of the

hippocampus in the implicit sequence learning even when both types of knowledge were unconscious. Again, these findings supported the view that the functional role of the hippocampus in learning was to bind distinct information, regardless of whether the learning was explicit or implicit (Rose et al. 2011; Schendan et al. 2003).

Recently, a growing number of neuroimaging studies have also shown that the hippocampus was recruited during implicit learning, indicating that the function of the hippocampus was not necessarily linked to participants' awareness (Degonda et al. 2005; Henke et al. 2003a, b; Rose et al. 2002, 2011; Schendan et al. 2003; Voss et al. 2009; Wang et al. 2010). Chun and Phelps (1999) used a contextual cuing task and found that amnesic patients with MTL lesions were impaired in implicit contextual learning. In other words, repeated visual context relative to new context did not facilitate search performance for amnesic patients. Consistently, Yang et al. (2003) also found that patients with lesions within the MTL were impaired in implicit memory for new associations. The study by Rose et al. (2011) further showed that significant bilateral hippocampus activation was observed in implicit learning of the perceptual sequence, but not of the motor sequence, documenting the functional role of the hippocampus for the extraction the binding of perceptual contingencies during the implicit learning process. The present study extended this finding by the use of the SSI task in which the perceptual features were task irrelevant and further demonstrated that the hippocampus also played a critical role in implicit learning of task-irrelevant perceptual associations.

In addition to the involvement of caudate and hippocampus, we also found that the implicit learning of task-irrelevant tonal sequence entailed superior parietal lobule activation which was not found in the neuroimaging studies using task-relevant SRT tasks (e.g., Dennis and Cabeza 2011; Rose et al. 2011). This was consistent with the findings of the recent studies (e.g., Giesbrecht et al. 2013) that this brain region was specifically involved in the implicit visual contextual learning. The present SPL activity pattern of selective BOLD responses to the sequence condition was probably associated with the bottom-up attentional capture and the automatic shifts of attention during the implicit acquisition of task-irrelevant contextual information (e.g., Kim et al. 1999; Mayer et al. 2009; Salmi et al. 2009; Serences and Yantis 2007).

In the current study, we could clearly claim that the learned perceptual features were not task relevant. Given that tones of Chinese syllables were quite familiar to Chinese participants, the question was raised of whether the linguistic experience played an important role in implicit learning of the task-irrelevant tonal sequence. A recent study of our laboratory further found that non-tonal language speakers could also implicitly learn a Chinese tonal

Table 4 Task-related activation in the first half of training phases (Sequence1 − Random1) and the second half of training phases (Sequence2 − Random2)

Brain region	Side	Coordinates			t value	Voxels
		x	y	z		
Sequence1 −Random1						
Middle cingulate cortex	R	14	−2	42	5.00	163
Supplementary motor area	*R*	*8*	*0*	*46*	*3.75*	
Middle cingulate cortex	L	−12	−24	42	4.72	148
Supplementary motor area	L	−10	−10	64	4.18	46
Putamen	L	−32	0	0	3.92	50
Sequence2 − Random2						
Caudate nucleus	L	−16	22	10	5.68	1,325
Caudate nucleus	*L*	*−16*	*22*	*4*	*4.82*	
Caudate nucleus	R	20	8	22	5.49	4,039
Putamen	*R*	*24*	*18*	*−2*	*4.91*	
Lingual gyrus	L	−10	−88	−14	4.58	1,792
Inferior occipital gyrus	*L*	*−16*	*−92*	*−10*	*4.16*	
Hippocampus	L	−28	−26	−8	5.33	335
Hippocampus	*L*	*−20*	*−30*	*−8*	*4.99*	
Inferior parietal lobule	L	−30	−38	42	3.74	438
Superior parietal lobule	L	−30	−58	56	4.88	594
Hippocampus	R	36	−20	−14	4.73	263
Hippocampus	*R*	*36*	*−24*	*−12*	*4.67*	
Middle frontal gyrus	L	−28	−6	52	4.15	187
Inferior temporal gyrus	L	−44	−10	−26	4.52	40
Superior parietal lobule	R	28	−60	60	3.76	69
Paracentral lobule	R	8	−40	62	3.67	37

Coordinates (mm) are in MNI space

All the clusters survived a voxel-level threshold of $p < 0.001$ (uncorrected) and a spatial extent threshold of $k \geq 35$. Italic values represent the local maxima within the clusters

L left hemisphere, *R* right hemisphere.

Table 5 Regions showing correlation between learning-related activations [(Sequence1 + Sequence2) − (Random1 + Random2)] with the accuracy for guess attributions in the prediction test

Brain region	Side	Coordinates			t value	Voxels
		x	y	z		
Hippocampus	R	32	−10	−26	6.02	98
Parahippocampal gyrus	R	28	−26	−18	5.97	203
Fusiform gyrus	*R*	*38*	*−24*	*−28*	*4.82*	
Superior parietal lobule	L	−18	−70	40	5.16	59
Superior occipital gyrus	*L*	*−20*	*−78*	*34*	*4.91*	
Middle occipital gyrus	R	32	−78	26	4.94	97
Fusiform gyrus	L	−38	−72	−18	4.74	69
Inferior occipital gyrus	L	−24	−96	−4	4.58	61

Coordinates (mm) are in MNI space

All the clusters survived a voxel-level threshold of $p < 0.001$ (uncorrected) and a spatial extent threshold of $k \geq 35$. Italic values represent the local maxima within the clusters

L left hemisphere, *R* right hemisphere

inversion rule (see Jiang et al. 2012, for detailed method), indicating that familiarity may only serve as a soft constraint on the implicit learning of tone sequence. It should be noted that, in the artificial Chinese poetry paradigm by Jiang et al. (2012), the participants were required to listen to and silently repeat the strings which were generated by a Chinese tonal inversion rule. It was hard to conclude that the tones were task-irrelevant features. Therefore, whether

or not task-irrelevant tonal sequence could be learned by speakers of non-tonal languages was still a matter remained for further researches.

In conclusion, the caudate, hippocampus and superior parietal lobule were critically involved in perceptual associative learning even when the perceptual features were task irrelevant.

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