

The role of the striatum in implicit learning: a functional magnetic resonance imaging study

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Previous research has posited striatal involvement in implicit learning. However, imaging studies have not directly compared learners with non-learners. Using functional magnetic resonance imaging with 15 study participants, we used an implicit learning task previously associated with striatal recruitment. Dorsal and ventral striatum activation was observed in the eight participants who demonstrated implicit learning. Ventral striatum activations occurred to a greater extent in implicit learning versus non-implicit learning

participants, and were correlated with the degree of reaction time advantage in implicit learning participants, even after controlling for general decreases in reaction time over time. These findings strengthen the specificity of the striatum in implicit learning and are suggestive of a dissociation of striatal regions relative to elements of implicit learning performance. *NeuroReport* 16:1291–1295
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INTRODUCTION

Implicit learning consists of skill acquisition without awareness through repeated practice and 'appears to be a fundamental and ubiquitous process in cognition' [1]. The striatum and its connections are involved in implicit learning [2]. Individuals with striatal pathology, as in Huntington's [3,4] and Parkinson's disease [5,6], demonstrate impaired implicit learning. The serial reaction time task [7] has been used to assess implicit learning. The development of a reaction time advantage to a repeated implicit sequence versus a random sequence is used as an indicator of implicit learning. Functional imaging studies using a serial reaction time task have reported striatal activation in participants who displayed implicit learning [8–14]. Further, Rauch *et al.* [11] demonstrated a significant positive relationship between the degree of reaction time advantage in implicit learners and functional magnetic resonance imaging (fMRI) signal intensity change within the putamen.

Regarding the association between implicit learning and the striatum, certain caveats should be borne in mind. Most neuroimaging reports involve relatively small group sizes, with 14 participants or less [8–14]. Of greater significance is the fact that no comparisons have been made of participants who demonstrate implicit learning with those who do not. This is important as striatal activations may reflect simple exposure to and execution of an implicit sequence without actual learning taking place. Another consideration is that striatal activation may reflect general visuomotor improve-

ments in performance independent of implicit learning [14].

To investigate the specificity of the striatum in implicit learning, we analyzed a larger sample of healthy participants with the expectation that a modest number of individuals would not demonstrate implicit learning. We hypothesized that differential striatal activation would occur favoring the implicit learning group and that striatal activation in the implicit learning group would be associated with the degree of reaction time advantage after controlling for general changes in visuomotor performance.

MATERIALS AND METHODS

Participants: All 19 healthy participants provided written, informed consent. Two were excluded because of image quality problems and two because of very low task response rates. Of the 15 remaining participants, mean age was 31.2 years (SD=13.3, range 18–59 years), mean education was 14.7 years (SD=2.9, range 11–22 years), five were female, and all were right-handed [15]. Approvals were obtained by the National Research Council of Canada and University of Manitoba Research Ethics Boards.

Task: A serial reaction time task was used (see [9,11,14]). Magnetic resonance imaging (MRI)-compatible eye-pieces (Avotec Silent Vision goggles, Stuart, Florida, USA) displayed an asterisk in one of four horizontally arranged

boxes for 1.0s, followed by a 0.2-s empty-box interval. Participants pressed one of four corresponding keys in response to the asterisk, using separate fingers. A 25-trial practice run was followed by two 312-trial runs each lasting 6.25 min. Each run consisted of alternating blocks of four random and three implicit learning conditions bracketed by a 19.2-s cross-hair fixation block. In the implicit learning condition, the stimuli followed a 12-item sequence repeating six times (72 trials). The random condition entailed 24 pseudo-randomly positioned stimuli. No signs were given to distinguish between random and implicit learning blocks.

Task score: For each participant, an implicit learning reaction time advantage score was estimated using median reaction times [$100 \times (\text{baseline} - \text{implicit}) / \text{baseline}$]. Participants with faster ($p < 0.05$) implicit median reaction times were classified as implicit learners. The covariate for general visuomotor processing changes was estimated using median baseline reaction times [$100 \times (\text{Run 1} - \text{Run 2}) / \text{Run 1}$]. Reaction time scores were compared in implicit learning and nonimplicit learning groups using independent *t*-tests and repeated-measures ANOVA using SPSS 11.0.

Debriefing: Following the two experimental runs, participants were informed that a repeating sequence had been present and were asked to reproduce the sequence by making 15 key presses [9,11,14]. The longest consecutive string that matched the 12-item implicit sequence estimated degree of explicit learning. Scores ≥ 7 were considered evidence that explicit learning had occurred (see [14]).

Magnetic resonance image acquisition: Images were acquired on a General Electric 1.5T MRI system with a clinical transmit/receive head coil. Anatomical scans for each individual used a T1-weighted fast spin-echo sequence (TR/TE=400/8 ms, 2 mm slice thickness) for a $2 \times 1 \times 1$ mm voxel image. fMRI data used a single-shot gradient-recalled echo planar imaging sequence with TR/TE/flip angle=2400/60 ms/45°, respectively. Approximately 80% of the brain was imaged using 23 axial slices and 3.9 mm isometric voxels. The most superior and inferior brain regions were excluded. In each experimental run, 172 volumes were acquired. The first and last eight cross-hair volumes were excluded as unnecessary for the statistical contrasts. Thus, each run was based on 156 volumes (312 volumes in total).

Magnetic resonance imaging individual analyses: Image processing and analyses were performed with Analysis of Functional NeuroImages (AFNI) software [16]. The fMRI data were slice time-corrected. Echo planar images were coregistered to the image that minimized image translation

and rotation relative to all other images. Volumes with visually detectable movements were excluded. The block design time-series was convolved to account for the hemodynamic response function. Multiple regression analysis for each experimental run included six regressors: the convolved experimental condition regressor, three head-motion covariates (i.e. roll, pitch, and yaw), a slope regressor (covariate), and a baseline regressor (control condition). The β -coefficient for the implicit condition was divided by the baseline coefficient to estimate percent blood oxygen-level-dependent (BOLD) signal change to implicit learning relative to the control task. To account for variations in anatomical landmarks, an 8-mm full-width at half-maximum Gaussian filter was applied. Data were transformed into the Talairach and Tournoux coordinate system [17]. The implicit learning neural responses for each run were averaged into a single implicit learning neural response score for each participant [18].

Magnetic resonance imaging group analyses: Three sets of striatum analyses were conducted. A one-sample *t*-test estimated percent signal BOLD change responses among implicit learners. An independent *t*-test compared BOLD scores between the implicit learners and the nonlearners. A multiple regression analysis identified regions that increased in activity as the degree of implicit learning increased, while controlling for general changes in reaction time from Run 1 to Run 2. Monte Carlo simulations determined the voxel-wise probability levels and minimum cluster sizes needed to control Type I error using a connectivity radius of 4 mm [19]. A voxel-wise probability of $p < 0.05$ and a minimum cluster volume size of 512 μl maintained a cluster-wise $p < 0.05$. All areas of activation are reported in Talairach and Tournoux coordinates with positive values as right, anterior, and superior.

RESULTS

Behavioral: Eight of the 15 participants exhibited a significant reaction time advantage, while seven did not. One-sample *t*-tests confirmed that the mean reaction time advantage (range 3.2%–12.7%) was significant for implicit learners, $t(7)=6.1$, $p < 0.0005$, but nonsignificant for non-implicit learners (range -2.4% to 4.0%), $t(6)=1.2$, $p < 0.27$. The group difference in reaction time advantage was not due to a general group difference in mean reaction time in either the random or the implicit learning condition (Table 1). A decrease in reaction time from Run 1 to Run 2 was observed across both conditions and groups, $F(1,13)=37.8$, $p < 0.00005$. Reaction time estimates were based only on correct trial responses. Error rates were less than 10% for all participants (range 0.5%–8.3%), and did not differ between the two groups, $t(13)=1.6$, $p < 0.15$. The mean

Table 1. Reaction time means and differences across design conditions and groups.

Condition	Nonlearners	Learners	Difference	<i>t</i>	<i>p</i>
Baseline ^a	432.9 ± 65.1	420.2 ± 67.9	12.7	0.3	0.77
Implicit ^a	429.2 ± 67.9	388.7 ± 96.8	40.5	0.9	0.37
Reaction time advantage ^b	0.9 ± 2.0	7.8 ± 3.6	-6.9	-4.5	0.001

^aMean of median reaction times ± SD in milliseconds.

^bReaction time advantage=median reaction time [$100 \times (\text{baseline} - \text{implicit}) / \text{baseline}$].

percents correct were 95.6% (SD=2.5) and 97.8% (SD=2.6) for the nonimplicit learners and implicit learners, respectively. None of the participants showed evidence of explicit learning contamination. Nor did the two groups differ in their mean explicit learning scores, $t=-0.6$, $p<0.55$, with means of 4.4 (SD=0.9) and 4.0 (SD=1.4), respectively.

Neural activation: A significant mean implicit learning-related BOLD response was found in the left putamen in the implicit learners (Table 2a and Fig. 1a). The comparison between groups identified a smaller, left putamen cluster (Table 2b and Fig. 1b) that partially overlapped with the

mean implicit learning-related BOLD response. The mean percent BOLD signal change in this cluster was 0.08 (SD=0.08) in the implicit learning group compared with -0.05 (SD=0.09) in the nonimplicit learning group. A multiple regression analysis identified two clusters showing a significant increase in BOLD response as reaction time advantage scores increased while controlling for general decreases in reaction time (Table 2c and Fig. 1c). This latter left putamen cluster is medially contiguous to the group difference cluster and the ventral portion of the implicit learning group mean response cluster.

DISCUSSION

We hypothesized that differential striatal activation (a relative increase in activity during the implicit learning vs. baseline sequence) would occur favoring the implicit learning group and that it would be associated with the degree of reaction time advantage, both of which were confirmed. The implicit learners showed activation in both the dorsal (caudate) and ventral (putamen) striatum, consistent with previous implicit learning studies [8–14]. More interestingly, the implicit learners maintained a greater degree of ventral striatal recruitment than the nonlearners. This novel finding further supports the key role of the striatum in implicit learning.

Another means of examining striatal involvement in implicit learning is by testing whether striatal activation is correlated with the degree of reaction time advantage. Rauch *et al.* [11] reported a correlation between percent reaction time advantage and percent signal intensity in the

Table 2. Neural activations in the striatum associated with implicit learning.

Brain regions	Talairach			Volume (μ l)	t_{\max}
	x	y	z		
<i>(a) Mean BOLD response of the implicit learners (n=8)</i>					
Left putamen and caudate	-18	3	-8	3200	3.8
<i>(b) Mean BOLD difference between learners (n=8) and nonlearners (n=7)</i>					
Left putamen	-22	7	-4	512	3.1
<i>(c) BOLD increase with increase in learning among learners (n=8)</i>					
Left putamen	-22	15	-8	576	90
Right putamen	22	7	-4	640	23.8

Talairach coordinates reflect positive right, anterior, and superior orientations.

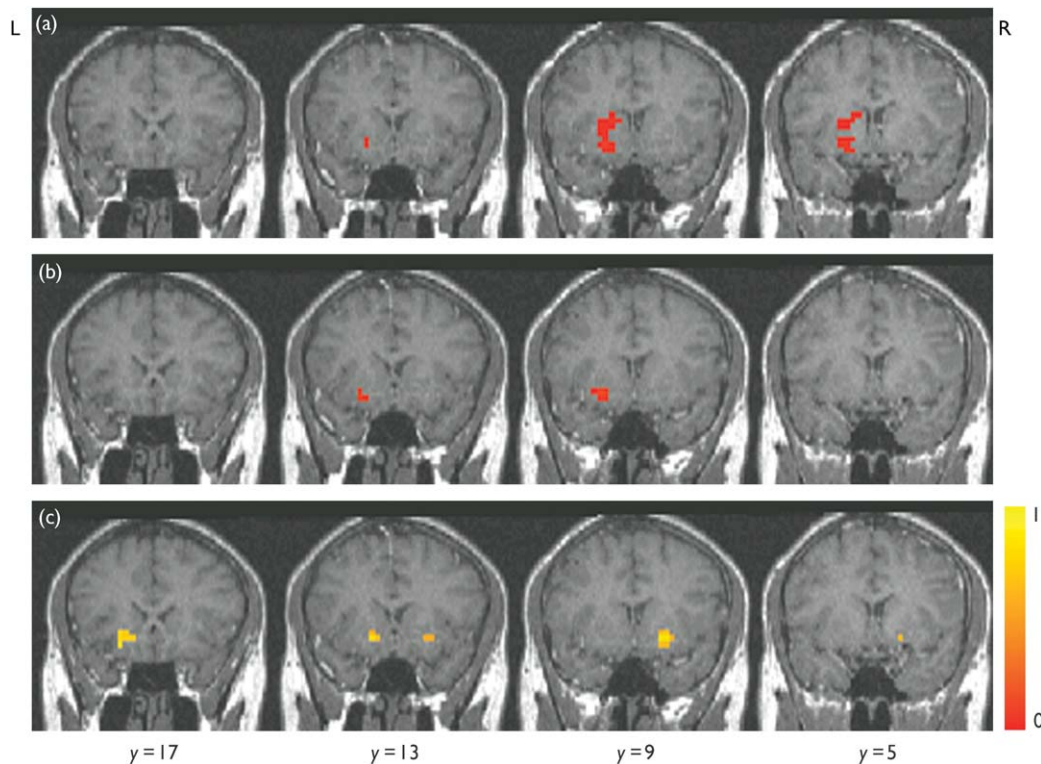


Fig. 1. Implicit learning-related percent blood oxygen-level-dependent (BOLD) signal change in the striatum: (a) mean BOLD response among implicit learners ($n=8$), (b) group difference in BOLD response between the learners ($n=8$) and nonlearners ($n=7$), and (c) relationship between reaction time advantage scores and BOLD response controlling for control task decreases in reaction time ($n=8$).

putamen with implicit learners in the serial reaction time task. Similarly, we found bilateral ventral striatum (putamen) clusters that correlated with reaction time advantage in implicit learners. The left putamen region was contiguous with the areas identified in the group difference and implicit learning group mean analyses. Moreover, we controlled for the general decrease in reaction time, which was anticipated as a general practice effect, to more effectively deconstruct the BOLD signal activations related to implicit learning *per se*. Thus, the results are less likely to be an epiphenomenon related to faster visuomotor processing speed [14].

Implicit learners activated dorsal and ventral striatum more during the implicit learning sequence than during the random baseline sequence. However, only the ventral striatum differed when comparing implicit learners with nonlearners. Conceivably, the dorsal striatum may be related to the basic exposure and execution of an implicit sequence without actual learning taking place, whereas ventral striatal regions may be more directly associated with the processing of motor contingencies to improve motor movement efficacy (i.e. implicit learning). Further, only ventral striatum activation was associated with degree of reaction time advantage, which supports the role of this structure in implicit learning. Similar findings regarding the dissociable roles of ventral versus dorsal striatum have been recently reported in an explicit learning investigation [20]. O'Doherty *et al.* [20] attempted to dissociate stimulus-response learning from value prediction learning using an instrumental conditioning task and a paired Pavlovian conditioning task. The dorsal striatum was recruited exclusively in the former task (a motor response was required to implement a choice), whereas the ventral striatum was activated in both tasks (value predictions occurred in both tasks). In both the study of O'Doherty *et al.* and the current study, the dorsal striatum's role seems tied to motor responses (actor) versus the more cognitive-learning role (critic) of the ventral striatum. In the actor-critic architecture [21], the critic functions to monitor and identify patterns, such as motor contingencies, while the actor functions to alter behaviors so as to improve the synchronization between environmental circumstances and behavioral responses. Functional anatomical distinctions have been drawn with the dorsal striatum consisting predominantly of matrisomes versus striasomes in the ventral striatum [22]. Further, matrisomes have been likened to the actor and striasomes to the critic [23] in the actor-critic architecture [21].

Aside from using larger samples, a future direction would be to alter the implicit sequence in subsequent investigations. Potentially a longer sequence, in conjunction with an event-related design, would yield a finer delineation of the temporal aspects of implicit learning. Similarly, the present sequence used was deterministic rather than probabilistic. An fMRI investigation using a probabilistic sequence would further minimize the risk of explicit learning and thereby accentuate the implicit aspect of learning [13,24].

CONCLUSION

This study investigated the specificity of the striatum in implicit learning using a novel comparator group of participants who did not demonstrate implicit learning on the serial reaction time task. A between-group analysis and correlation analysis with degree of implicit learning both

identified striatal activation, consolidating this relationship. Evidence of dissociation in the role of dorsal versus ventral striatum in implicit learning was observed. These results further validate the fMRI serial reaction time task as a candidate probe for testing hypotheses related to striatal function in the context of implicit learning.

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