Distinct Patterns of Hippocampal Activation in Implicit Versus Explicit Inference

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Introduction

In addition to its well-known importance in semantic and episodic memory, research shows that the hippocampus is involved in context dependent priming tasks as well as relational learning tasks.

A seminal paradigm used to test these relationships is associative inference, which has been shown to be hippocampal dependent in animal models (Bunsey and Eichenbaum, 2006) and in humans when they are informed about the necessary inference and an explicit strategy is used (Preston et al., 2004).

Associative inference differs from the traditional transitive inference paradigm by containing equally weighted stimulus items rather than the differentially weighted items. Associative inference tasks require participants to learn context-dependent relations at study and presents novel configurations of the stimuli at test. During test, the participant is required to infer the correct item based on the relationships learned during study.

Past research has shown the associative inference task may be successfully completed both implicitly and explicitly (Leo & Greene, 2008); further, imaging results from participants whom performed implicitly showed hippocampal activation (Greene et al., 2006). The present study uses fMRI to explore the neural activations during both explicit and implicit associative inference and effectively counters claims that implicit inference is primarily due to the differential stimuli weighting as found in traditional transitive inference (Frank et al., 2006).

Behavioral Results

Participants were broken down into three groups based upon their performance.

Explicit performers:

- Scored above 70% on the inference items at test.
- Scored 3 to 5 on the post-experimental questionnaire.

Implicit performers:

- Scored above 70% on the inference items at test.
- Scored 2 or below on the post-experimental questionnaire.

Nonperformers:

- Scored below 70% on the inference item at test (see Figure 2 to the left).

In regards to accuracy on all pairings, implicit performers, explicit performers, and nonperformers all performed similarly during each of the four study phases. During test, implicit performers and explicit performers tested similarly to training, but nonperformers did significantly worse.

Methods

The task consists of four study phases and one test phase. Four context-dependent relations were learned at study. Participants are presented with two novel inference relations and are asked to solve them at test.

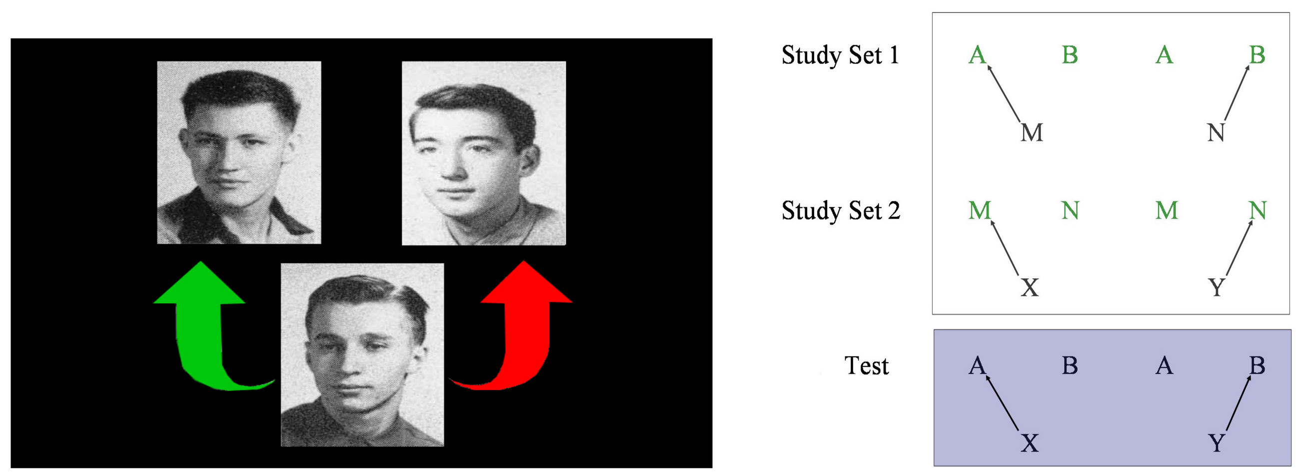

Figure 1: (Left) Face Stimuli and (right) a schematic of Associative inference. The learned relations AM and MX lead to the inference of the AX relation.

During the first study phase, participants were given explicit feedback regarding the correct face associations: A green arrow was used to indicate the correct choice, and a red arrow was used to indicate the incorrect choice (See Figure 1). After each selection, the participant received feedback about the accuracy of their selection. After the first study phase, the arrows were removed. Participants were required to reach a proficiency of 80% correct on each study phase before they were able to move on to the next phase; participants who did not reach criteria were discharged from the study at the end of the phase. Upon completion of the session, participants were given a post-experimental questionnaire to assess their level of awareness, specifically of the relationship between the stimulus items.

Based off of performance and awareness participants were separated into groups (aware performers, unaware performers and nonperformers). Hippocampal activation was compared between explicit performers and nonperformers as well as between implicit performers and nonperformers.

Scanning information: Event-related, whole brain imaging was performed using a research dedicated GE 3 T scanner and analyzed using AFNI software. Whole brain imaging consisted of thirty-five, 4 mm slices (3.75 x 3.75 x 4 mm voxel size). Image resolution was 64 x 64- voxels with a 24 cm FOV. The interscan period (TR) was 2000 msec. Anatomical and functional images were coregistered, converted into Talairach stereotaxic coordinate space, blurred using a 6-mm Gaussain full-width half-maximum filter.

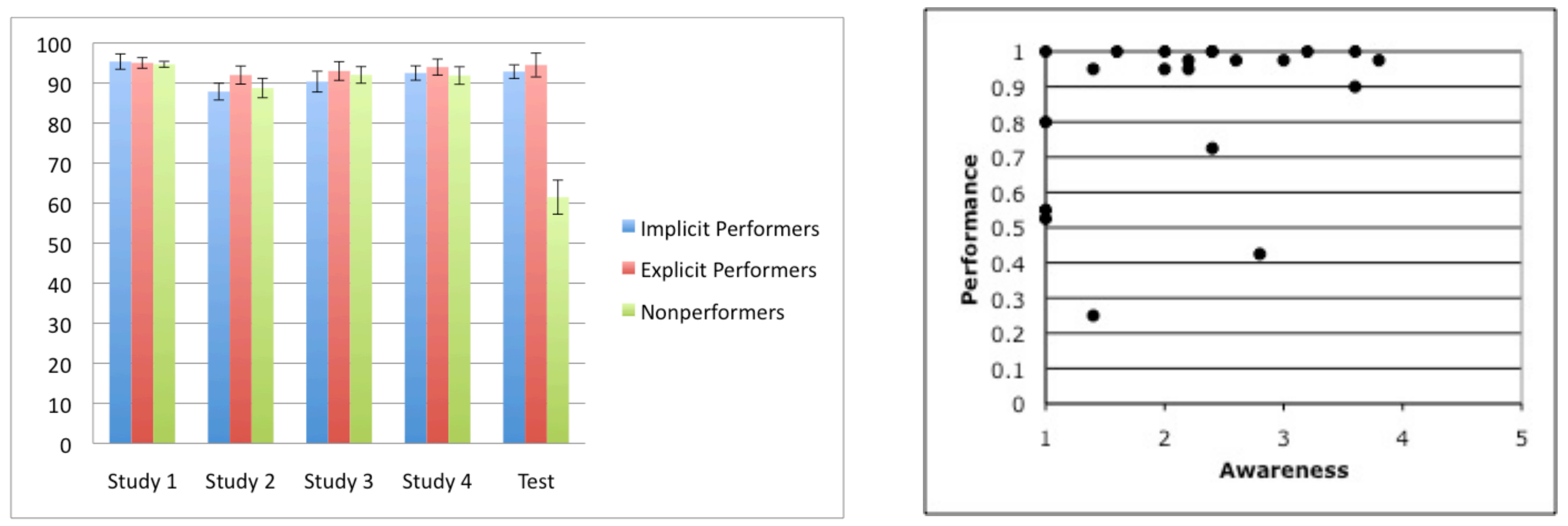

Figure 2: Group Performance and Awareness ratings at test.

Imaging Results

A hippocampal region of interest was used to conduct the group wise imaging analysis. Significance was determined using an AlphaSim cluster correction at a *p*<0.05 level. Differential hippocampal and prefrontal cortex activation was found between explicit performers and implicit performers during test.

Explicit performers:

•Showed increased activation of the left hippocampus during test compared to nonperformers.

•Showed increased activation of the right hippocampus and left prefrontal cortex during test compared to implicit performers.

Implicit performers:

•Showed increased activation of the right hippocampus during test compared to nonperformers (see Figure 3).

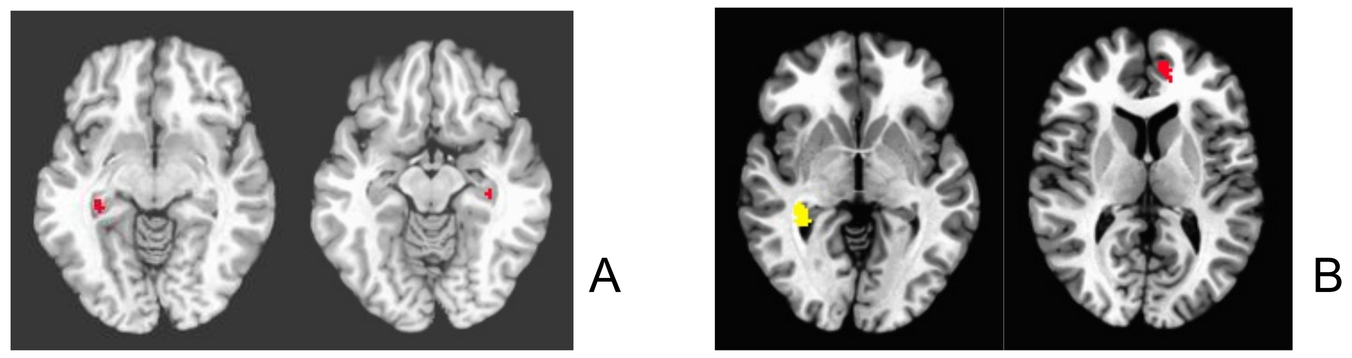

Figure 3: Figure A shows differences between performer and nonperformer groups: explicit performers vs nonperformers (left) and implicit performers vs nonperformers (right). The differential hippocampal activations can be seen between each group. Figure B is a comparison between implicit and explicit performers and highlights the prefrontal cortex and hippocampal activations between differing performer groups. These images are radiologically formatted.

Conclusion

The current experiment examines the role of the hippocampus in an inference task--without endpoints--where context-dependent relations are trained and novel relations must be inferred (c.f., Bunsey & Eichenbaum 1996).

Some models of implicit transitive inference (linear TI) suggest the possibility of a pseudoinference strategy, where each stimulus acquires a differential value according to its proximity to the first and last stimuli in the sequence (Van Elzakker et al. 1997, Frank et al. 2005). However, the design of this task rules out the use of pseudoinference strategies. While this does not rule out the possibility for the usage of pseudoinferential strategies during some linear TI tasks, the present findings do demonstrate that true inference does not require deliberative strategies.

Furthermore, while explicit performers showed greater activation in the left hippocampus at test, implicit performers showed greater activation in the right hippocampus. This suggests that successful inference requires the hippocampus, while implicit and explicit performers vary in which hemisphere of the hippocampus is utilized.