The hippocampus aggregates complex associations to make predictions: Implicit and explicit performers engage the hippocampus in different ways

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SFN 2012: 194.16/XX2

Introduction: The debate surrounding the role of the hippocampus in memory has taken a turn in the last several years. The declarative memory model states that the hippocampus is exclusively involved with explicit (aware) memories (Gabrieli, 1998). In the Relational Memory Model (Konkel and Cohen, 2009), the hippocampus is thought to integrate elements of experiences to create flexible relations that occur with or without awareness. A central question is whether the hippocampus is involved in implicit learning tasks. Our experiment attempts to help resolve this debate by examining the role of the hippocampus along with associated cortical areas in making aware and unaware inferences (Bunsey and Eichenbaum, 1996). In this task, context-dependent relations are trained and novel relations are inferred. This inference task differs from most transitive inference tasks in that there are no "end items" which could allow a pseudo-inference strategy.

Methods: **Behavioral Experiment:** Participants are trained to choose between stimuli A or B, depending upon whether stimuli M or N are present (Fig 2). Two different stimuli groups are taught to the participants. At test, participants must make a transitive association, where they choose A over B in the presence of X and choose B over A in the presence of Y. During the first study phase, participants were given explicit feedback regarding the correct face associations: A green arrow indicated the correct choice, and a red arrow indicated the incorrect choice (Fig 1). The arrows were removed and "correct" and "incorrect" were displayed during the following three study phases. No feedback was given during test. 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. Upon completion of the session, participants were given a post-experimental questionnaire to assess their level of awareness, specifically probing for their awareness of the relationship between the stimulus items.

Methods: MRI processing: 20 subjects underwent MRI scanning. fMRI data was processed using AFNI. Data was volume registered, automasked, normalized, concatenated and deconvolved before an area under the curve analysis was run. The data was warped to tlrc space and blurred using an 8mm blur. A regression was run using 3dregana. A hippocampal ROI was used to conduct the groupwise analysis over the results of the regression. Significance was determined using an uncorrected p value of .001. Cluster size was set to a minimum of 50 voxels with an NN of 2. Masks were produced by ROI cluster analysis, and values were returned using 3dROIstats.

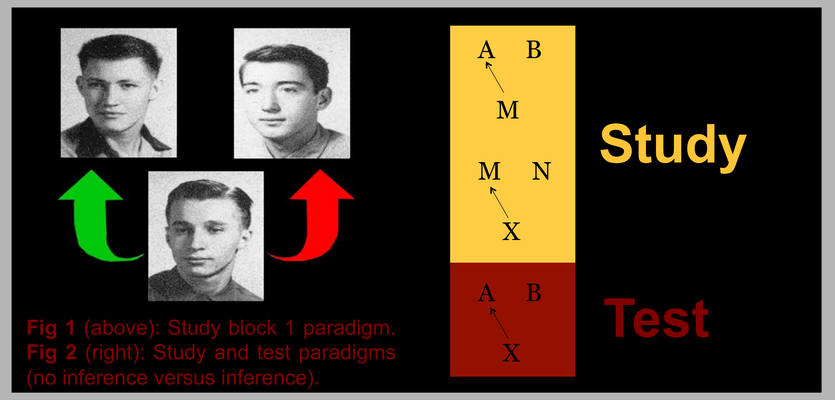


Fig 1 (above): Study block 1 paradigm.
Fig 2 (right): Study and test paradigms (no inference versus inference).

Results: Behavioral: Participants were assessed as either explicit performers, implicit performers, or nonperformers. All three groups performed similarly across training phases. Performers scored above 80% on inference items, while nonperformers scored below 80%. Explicit participants scored 3 to 5 on the questionnaire, while implicit participants scored 2 or below (Figs. 3 and 4).

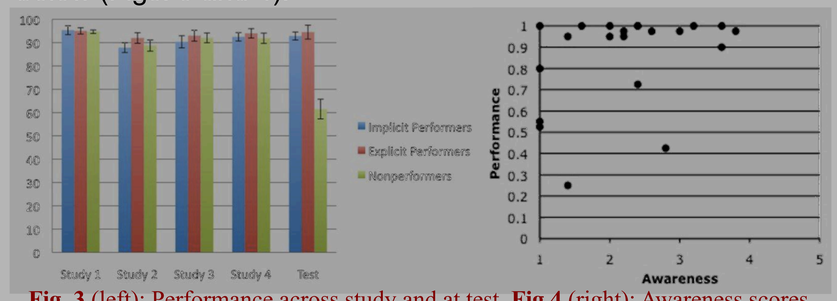
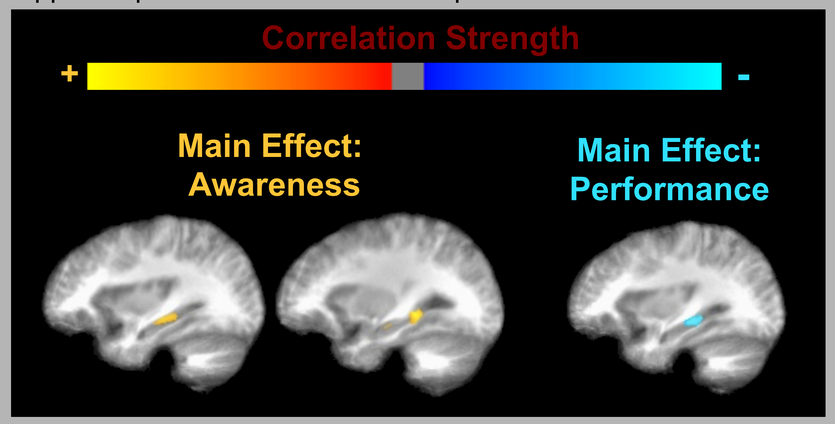
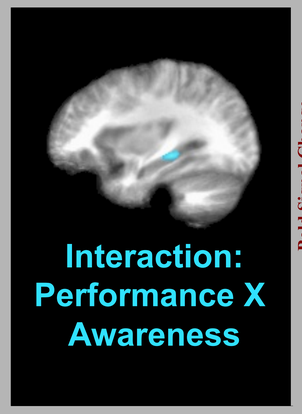
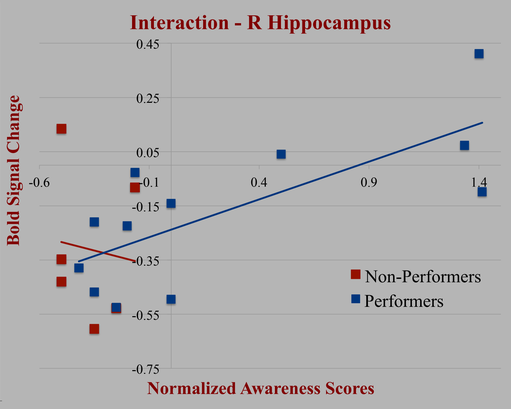


Fig. 3 (left): Performance across study and at test. **Fig 4** (right): Awareness scores versus performance for inference arrays.

Results: Imaging: Main effects were seen for performance (negative correlation in the left hippocampus) and awareness (positive correlations bilaterally in the hippocampus). An interaction exists between performance and awareness in the right hippocampus. Removing aware subjects from the regression showed a negative correlation in the left hippocampus for the main effect of performance.







Conclusion: Our experimental design permits task conditions to be held constant between implicit and explicit participants, allowing inferences about the neuronal structures engaged in each group. We found distinct patterns of hippocampal activation between performers and non-performers, as well as in implicit performers and non-performers. This corroborates with other implicit hippocampal findings (Greene et al. 2006) and suggests, contrary to the Declarative Memory Model and pseudo-inferential models of transitive inference, the hippocampus can be utilized to flexibly retrieve relations between stimuli in the absence of awareness.

Next Steps: The study phases will be analyzed next to gain a better understanding of the differences between groups.

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