

Oscillatory dynamics of active learning in the human brain

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Abstract:

While the benefits of self-directed learning on human memory are well-acknowledged, little is known on its underlying neurophysiological substrate. Here, we investigated the key signatures of volitional learning in the brain as assessed by representational similarity analysis applied to human intracranial EEG (iEEG) data. Epilepsy patients performed an episodic memory task during virtual navigation which tests differences in recognition memory for self-directed versus passive learning. Consistent with previous literature, higher recognition accuracy was observed for items studied in active as opposed to passive movement conditions at the behavioral level. In addition, we demonstrate a critical role of hippocampal low-frequency oscillations for active learning. This is observed in 1) increased hippocampal 2-6Hz power for active versus passive information sampling and 2) significantly greater encoding-retrieval similarity (ERS) for volitional as compared to passive conditions in the first second after cue onset at retrieval. Follow-up analyses will address the contribution of activity at different frequencies for item-specific ERS and volitional versus passive learning. Together, these results offer a first perspective on the key oscillatory mechanisms underlying volitional learning in the human brain.

Keywords: Volitional learning, active navigation, episodic memory, representational similarity analysis

Introduction

The distinction between active and passive learning has been an important research topic in neuroscience, psychology and education. Empirical evidence supports the notion that controlling the flow of information intake during learning enhances subsequent performance in memory tests (Gureckis & Markant, 2012; Kornell & Metcalfe, 2006). However, few studies have looked at the neural correlates of active learning in humans. To our knowledge, only two fMRI studies have explored this problem, showing greater engagement of the hippocampus during volitional as compared to passive learning in a spatial 2D memory task (Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011; Voss, Warren, et al., 2011). However, given the low time-frequency resolution of fMRI, the particular oscillatory dynamics of volitional learning in the human brain are not known.

Studies in the animal literature have pointed to a critical role of hippocampal theta (1-8Hz) oscillations in voluntary movement (Chen, King, Burgess, & O'Keefe, 2013; Terrazas et al., 2005; Vanderwolf, 1969). In humans, intracranial EEG studies have shown hippocampal theta power increases during virtual



movement, although in lower frequencies than the 4-8 Hz band observed in the rat (Ekstrom et al., 2005; Jacobs, 2014). The human literature has also linked hippocampal theta to successful memory encoding of information (Fell et al., 2011; Lega, Jacobs, & Kahana, 2012), which has led to the hypothesis of a critical role of theta in active information sampling (Ekstrom & Watrous, 2014). However, no study has systematically compared differences in oscillatory low-frequency dynamics for active versus passive learning in humans, nor how these relate to the representation of specific contents in the brain.

Methods

Participants. Participants were 13 epilepsy patients (7 male, 21-38 years) who had been surgically implanted with depth electrodes as part of their diagnostic assessment of surgical treatment for medically refractory epilepsy. We also performed the experiment with a group of N=22 healthy controls (students from Universitat Pompeu Fabra). All participants provided written informed consent to participate in the study, which was approved by the local Ethical Committee “Clinical Research Ethical Committee (CEIC) Parc de Salut Mar” (Barcelona, Spain).

Task description. Subjects navigated a squared virtual environment in which discrete visual stimuli, extracted from (Rossion & Pourtois, 2004), were presented at specific locations in a 5x5 grid formed by red “boxes” located on the ground (Fig. 1A, left). An item was presented at each box during navigation through a small inset on the top-right of the screen (Fig. 1A, Middle) which remained present on screen until participants decided to move to another box. Instructions were to visit all boxes and remember all the items for a subsequent recognition memory test.

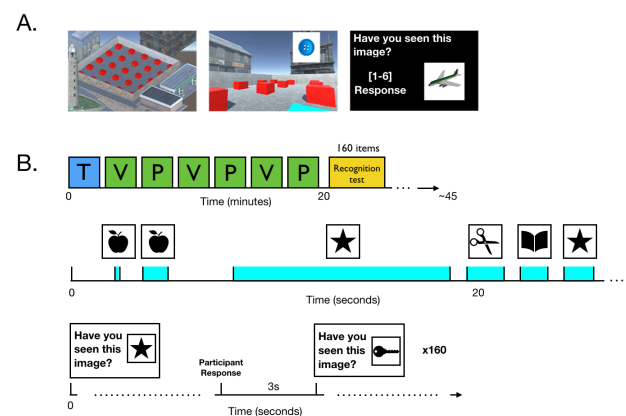


Figure 1: Experimental design. A) Left: top view of the environment. Middle: first person view of item

encoding. Right: screenshot of the memory test. B) Top: Experimental blocks. T = training. V = Volitional. P= Passive. Middle: timeline of 20 s in one block (real data from one participant). Bottom: timeline during the memory test.

Critically, subjects explored the environment under two conditions, one with self-initiated, active control of movement in the VR environment (Volitional) and the other a passive exposure mode with no control over navigation (Passive). Navigation blocks lasted for 3 minutes. Each subject performed three active and three passive blocks (with a 20 s pause after each block, and a training session before conducting the memory test: Fig. 1B top). The sequence of observations of one participant in active mode was presented to a different subject in passive mode, following a “yoked” design (Fig. 1B, middle row). Subjects were tested for their memory for the items with a recognition test (Fig. 1A, right and 1B, bottom). Participants were presented with 160 items, of which 40 were previously shown during active navigation, 40 were presented during passive navigation and 80 were new. During the test, an image was displayed on the screen and subjects were asked to indicate whether they had seen it before using a confidence scale — from 1 (sure old) to 6 (sure new, Fig. 1A, right). Patients could control navigation in the active condition with a joystick while sitting in the hospital bed, interacting with a 17” inch portable computer installed on a mobile table.

Results

Behavioral results

Both patients and healthy controls exhibited greater memory for items learned in volitional as compared to passive modes. Healthy subjects showed differences both in terms of percentage of correctly recognized old items ($p = 0.036$) and percentage of high confidence correctly recognized old items ($p = 0.028$). Patients showed differences in terms of percentage of high confidence correct ($p = 0.048$).

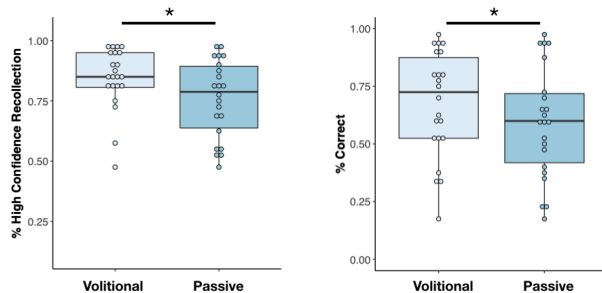
iEEG Results

We quantified hippocampal low-frequency power during the encoding phase of our experiment, including all navigation time points during active and passive navigation. Using the FieldTrip toolbox, we decomposed the signal using complex Morlet wavelets with a variable number of cycles, i.e., linearly increasing between 3 cycles (at 1 Hz) and 6 cycles (at 29 Hz) in 29 steps for the low-frequency range, and from 6 cycles (at 30 Hz) to 12 cycles (at 150 Hz) in 25 steps. We then z-

scored all power values by taking the mean and standard deviation of all navigation blocks for each frequency independently.

In our representational similarity analysis (RSA), we calculated encoding-retrieval similarity (ERS) for all items presented in active and passive conditions based on time-frequency resolved, broadband oscillatory power distributions captured at all available contacts.

Behavioral results: healthy controls (N=22)



Behavioral Results: patients (N=13)

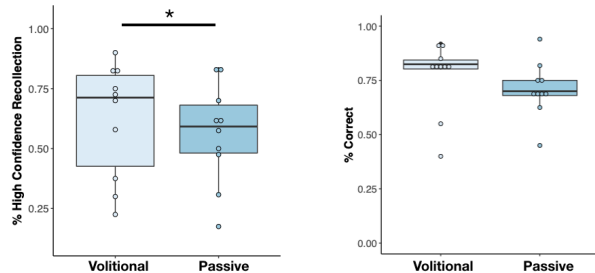


Figure 2: Behavioral performance for A) healthy controls and B) patients. Left column in A) and B) shows percentage of old items correctly identified as old with high confidence for volitional and passive conditions. Right column in A and B shows percentage of old items correctly identified as old for the same conditions

Specifically, feature vectors were constructed by concatenating z-transformed power values between 1 and 150 Hz from all channels, in 500ms time windows with 80% overlap. Fisher-Z transformed Spearman's correlations were calculated at every encoding retrieval time-pair and paired *t*-tests were performed at each time bin across different contrasts. We corrected for multiple comparisons using cluster-based permutation statistics (number of permutations in all analyses = 1000; Maris & Oostenveld, 2007). Analysis was time-locked to onset at encoding and retrieval.

Increased 2-6Hz oscillations in the hippocampus for active learning. We found that irrespective of performance in the memory test, there was a significant

effect of encoding condition in the observed hippocampal z-scored power in a cluster of 5 frequencies from 2-6Hz, with a peak at 3Hz (cluster corrected, $p = 0.01$, Figure 3 left). Mean power within this cluster was significantly higher for volitional as compared to passive trials ($t(8) = 2.96$, $p = 0.018$; Fig 3B).

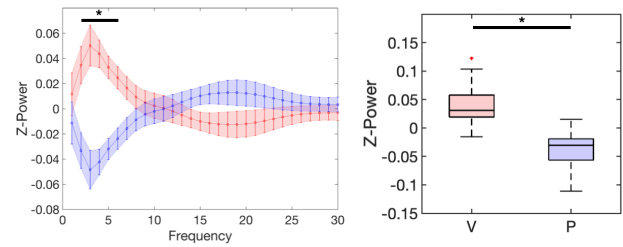


Figure 3: Differences in oscillatory power for active versus passive conditions in the anterior hippocampus. Left: individual frequency analysis. Right mean power in the cluster of frequencies identified in A) (2-6Hz).

Behaviorally relevant ERS. In our first RSA approach, we compared encoding retrieval similarity (ERS) between high confidence hit trials (putatively linked to hippocampus and context dependent memory) with aggregated data from all other types of trials (i.e. combining incorrect with low confidence correct responses). Our preliminary results showed a cluster of significant differences between conditions which notably overlapped with the numerical increases observed in the high confidence condition between 0 and 1s after cue onset ($p=0.01$, Fig. 4).

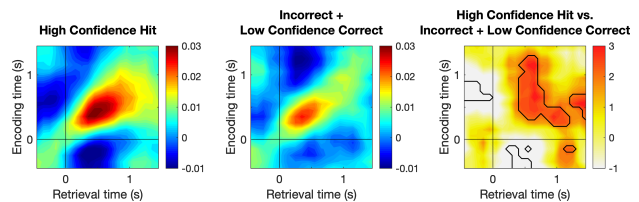


Figure 4: Increased ERS for high confidence hits versus low confidence hits and incorrect trials.

Higher reinstatement for volitional as opposed to passive trials. Critically, we found a clear modulation of ERS values by volition. Indeed, a significant cluster was observed from 300ms after cue onset until 1.1s in the active versus passive contrast ($p = 0.034$; note that here we compared all trials from each condition irrespective of memory performance, Fig. 5). Taken together, these results demonstrate the behavioral

relevance of reinstatement and a significant modulation of ERS values by volition during encoding.

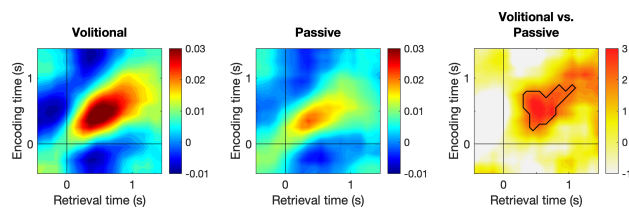


Figure 5: Increased ERS for volitional as opposed to passive trials.

Discussion

We reveal the key neurophysiological signatures of volitional learning in the human brain and its relationship with episodic memory. Our results suggest a critical role of hippocampal low-frequency oscillations in coordinating representational content during active learning, as observed in

- (I) Increased hippocampal low-frequency power (2-6Hz) for active versus passive information sampling and
- (II) Significantly greater ERS for active versus passive information encoding in the first second after cue onset during retrieval, i.e., at the time of behaviorally relevant ERS.

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