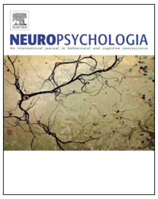
Neuropsychologia 90 (2016) 200–209

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia



Responses of neurons in the medial temporal lobe during encoding and recognition of face-scene pairs

Indre V. Viskontas [a,*], Barbara J. Knowlton [a], Itzhak Fried [b]

[a] *Department of Psychology, UCLA, Los Angeles, CA 90095, United States*
[b] *Department of Neurosurgery, UCLA, Los Angeles, CA 90095, United States*

ARTICLE INFO

Article history:
Received 15 March 2016
Received in revised form
9 July 2016
Accepted 12 July 2016
Available online 14 July 2016

Keywords:
Episodic memory
Hippocampus
Entorhinal cortex
Epilepsy
Electrophysiology

ABSTRACT

Associations between co-occurring stimuli are formed in the medial temporal lobe (MTL). Here, we recorded from 508 single and multi-units in the MTL while participants learned and retrieved associations between unfamiliar faces and unfamiliar scenes. Participant's memories for the face-scene pairs were later tested using cued recall and recognition tests. The results show that neurons in the parahippocampal cortex are most likely to respond with changes from baseline firing to these stimuli during both encoding and recognition, and this region showed the greatest proportion of cells showing differential responses depending on the phase of the task. Furthermore, we found that cells in the parahippocampal cortex that responded during both encoding and recognition were more likely to show decreases from baseline firing than cells that were only recruited during recognition, which were more likely to show increases in firing. Since all stimuli shown during recognition were familiar to the patients, these findings suggest that with familiarity, cell responses become more sharply tuned. No neurons in this region, however, were found to be affected by recombining face/scene pairs. Neurons in other MTL regions, particularly the hippocampus, were sensitive to stimulus configurations. Thus, the results support the idea that neurons in the parahippocampal cortex code for features of stimuli and neurons in the hippocampus are more likely to represent their specific configurations.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

To gain a complete understanding of memory representations in the brain, we need to understand the cellular basis of memory, in addition to the relationship between neural activity and memory function at the population level. Neuropsychological (e.g., Scoville and Milner, 1957; Reed and Squire, 1998) and neuroimaging (e.g. Wagner et al., 1998; Nyberg et al., 1996) studies can inform us as to the roles of different brain regions with respect to memory, but the level of resolution using these techniques does not go beyond relatively large ensembles of neurons. Many models of memory, however, make predictions at the level of single neurons (e.g. Norman and O'Reilly, 2003). Therefore, data concerning firing patterns of individual neurons are necessary to evaluate the appropriateness of current memory models.

Here, we survey the activity of individual neurons in the medial temporal lobe (MTL) over the course of memory encoding and retrieval. By observing the changes in particular neurons as memories are formed and retrieved, we may be able to infer the mechanisms that support memory processes at the neural circuit level. Previous work has shown that the hippocampus and surrounding cortical areas show changes in neural firing to items that are repeated in a continuous recognition procedure (Viskontas et al., 2006). In the parahippocampal region, many neurons responded to the novel stimuli, with firing returning to baseline for repeated presentations. These findings are consistent with findings of repetition suppression in the medial temporal lobe, and a novelty preference in these neurons. In the hippocampus, many units that did not respond to the initial presentation of a stimulus decreased firing below baseline during repeated presentations. This pattern may indicate that with repetition, activity is inhibited in neurons that do not respond to the stimulus, which may be a mechanism for enhancing the signal-to-noise ratio for recognizing sparsely coded items.

Rutishauser et al. (2006) also found neurons in the hippocampus and the amygdala that decreased firing with repetition, along with another population that increased firing with repetition, consistent with the idea that repetition involves tuning of activity in MTL. Pedreira et al. (2010) examined neurons that were selective for specific stimuli and found that these neurons generally reduce their responses when a preferred stimulus is repeated. Unlike neurons in other MTL regions examined, however, neurons in the parahippocampal cortex that were selective for

---

[*] Corresponding author.

http://dx.doi.org/10.1016/j.neuropsychologia.2016.07.014
0028-3932/© 2016 Elsevier Ltd. All rights reserved.

Please cite this article as: Viskontas, I.V., et al., Responses of neurons in the medial temporal lobe during encoding and recognition of face-scene pairs. Neuropsychologia (2016), http://dx.doi.org/10.1016/j.neuropsychologia.2016.07.014

specific stimuli actually increased activity with repetition. In the Pedreira et al. (2010) study, subjects were not performing an overt memory task, which may have contributed to the results. It is also likely that selective neurons and those neurons that were responsive to a large number of stimuli respond differently to repetition.

Previous recordings of MTL single neuron activity in humans have also shown that firing patterns of hippocampal cells during encoding predict subsequent memory, while firing patterns in the entorhinal cortex during retrieval reflected whether or not items were successfully recalled (Cameron et al., 2001). Furthermore, recordings from the human MTL have demonstrated that individual neurons can be highly selective in terms of the stimuli to which they respond (Quan-Quiroga et al., 2005). Out of a set of 100 visual images across several categories such as faces, animals and landmarks, some cells may show robust responses to only a handful of pictures, sometimes even pertaining to a single conceptual category, such a particular famous person. In addition, the more personally-relevant the stimulus, the more likely it is that selective neurons will be observed (Viskontas et al., 2009).

Selectivity of neuronal responses in humans has been found for stimulus categories such as faces or places (Kreiman et al., 2000), as well as for specific visual features (Fried et al., 1997) and even to individual words and faces (Heit et al., 1988). This selectivity may provide an important clue as to the mechanism by which the brain represents information currently in awareness. In fact, the idea that the MTL represents information using a sparse code is one of the basic tenets of most contemporary memory models (Norman and O'Reilly, 2003; Bogacz and Brown, 2003; Meterage et al., 2005).

In animals, sparse coding has also been observed in recordings from the MTL (Jung and McNaughton, 2003; Treves and Rolls, 1992). As mentioned above, neural responses showing increases from baseline firing that are selective to specific concepts (such as a particular famous individual or place) have also been well-documented in the human MTL (Quian-Quiroga et al., 2005) and these selective responses are most likely to be observed when the stimuli are personally-relevant and familiar (Viskontas et al., 2009). Recently, selective neurons that track the formation of associations between unfamiliar faces and places in the human MTL have also been reported (Ison et al., 2015). In this current study, we were interested in characterizing responses that were less selective in terms of individual stimuli but may also be involved in mnemonic processes.

Given that the hippocampus assigns only a very small number of neurons to a given stimulus, how does the MTL use this code to perform the memory processes that it supports? Previously, we have shown that many cells in the hippocampus proper have a tendency to reduce firing when a previously-seen stimulus comes into view, providing one mechanism by which the signal-to-noise ratio may be increased, allowing those few cells that represent that particular stimulus to be heard by downstream cortices (Viskontas et al., 2006). In the present study, we will examine differences in firing of neurons during encoding and recognition of the same stimuli. We hypothesize that different MTL regions may show different patterns of changes across encoding and recognition, with a majority of responsive hippocampal neurons showing a reduction in firing during the recognition phase based on the sparse coding of specific memories. In contrast, recognition may be accompanied by increases in firing in parahippocampal cortex that are associated with a familiarity signal.

While several studies have examined changes in firing patterns during repetition, subjects in these studies were performing tasks that were not highly dependent on the hippocampus. According to several current views, the hippocampus plays a role in associating items in context (Eichenbaum et al., 1994). Patients with selective damage to the hippocampus have particular difficulty with the rapid formation of arbitrary associations between stimuli and the context in which they occur (Yonelinas et al., 2002). It may be that when subjects are forming item in context associations, neural activity even at the single-cell level may reflect these associations. Our task is designed to mimic a real-life situation in which individuals must associate an item with its context. The premise is a situation in which the patient is meeting a new person. Patients are asked to ‘remember where they met a particular person’ and are shown non-famous faces superimposed on pictures of places. Their ability to remember the face/place conjunction is then assessed using recognition and cued recall tests. Using a similar task, Hannula and Ranganath (2008) demonstrated that hippocampal activity during the presentation of a scene cue was associated with correct memory responses when target and foil faces were presented. Based on the hippocampal dependence of this task, we hypothesize that cells in the hippocampus will be more sensitive to face/place conjunctions than neurons in the parahippocampal cortex given the purported role of the hippocampus in the formation of binding items to context.

2. Methods

2.1. Patients

Participants were five patients with pharmacologically-resistant epilepsy for whom extensive non-invasive evaluation failed to yield a single epileptogenic focus. All five patients were right-handed and three were male. Each patient participated in the experiment at least two and up to four times, for a total of twelve sessions. For further monitoring, patients were stereotactically-implanted with 6–14 electrodes from a lateral orthogonal approach based on clinical criteria (surgeries were performed by I.F.) for one to two weeks. Patients had a mean age of 26.0 (±8.4, range:17–39) years and a mean education of 13.4 (±1.9, range: 11–16) years. All patients provided informed consent and every session conformed with the guidelines of the Medical Institutional Review Board at UCLA.

2.2. Experimental protocol

2.2.1. Encoding phase

Patients were shown 10 black and white images of a non-famous face from the Stirling Psychological Image Collection (PICS) database (http://pics.psych.stir.ac.uk/) superimposed onto an unfamiliar indoor or outdoor scene (with the exception of one session, in which we used 15 images for a patient with a particularly good memory). Patients were tested 2–4 times, with each session including unique images. Each stimulus was presented for 2 s and 6 times per encoding session (with the exception of one session in which the pairs were presented 8 times each to generate more trials for that particular patient). Patients were told that they were ‘meeting these people for the first time’, and need to remember where they met each person. They were also asked to judge whether the face was ‘indoors’ or ‘outdoors’ by button press. Patients were instructed to make a response only after the stimulus disappeared. The next trial began after the response. The distances between repeated stimuli varied randomly with the constraint that no more than two minutes elapsed between repetitions. The procedure is shown in Fig. 1a–c.

2.2.2. Recall phase

Immediately following the encoding phase, patients were cued with one member of the face-place pair and asked to indicate whether they remembered the paired item by pressing a button.

Please cite this article as: Viskontas, I.V., et al., Responses of neurons in the medial temporal lobe during encoding and recognition of face-scene pairs. Neuropsychologia (2016), http://dx.doi.org/10.1016/j.neuropsychologia.2016.07.014

Download English Version:

https://daneshyari.com/en/article/5045380

Download Persian Version:

https://daneshyari.com/article/5045380

Daneshyari.com