

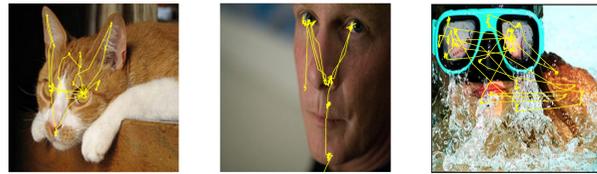
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## Introduction

The perception and encoding of faces are of critical importance for the recognition of individuals and social signals conveyed through their facial expressions. Humans with autism spectrum disorders frequently show impairments in these processes (Joseph & Tanaka, 2002), but the neurophysiological mechanisms are currently poorly understood. Selective responses of single neurons to faces have been recorded from rhesus macaques in the inferior temporal cortex, (Bruce, Desimone and Gross, 1981); amygdala (Rolls, 1984; Gothard, 2007), orbitofrontal cortex (Rolls et al., 2006) and prefrontal cortex (O'Scalaidhe, 1999), suggesting a network of neuronal ensembles that selectively encode faces. Face-selective neurons have also been recorded in the human hippocampus, and may play a role in the formation of memory traces (Fried, 1997). However, face-selective neurons have previously not been described in the macaque hippocampus.

Figure 3: Stimuli coded as faces based on scan path.



Stimuli were coded as faces if the subject fixated on at least one facial feature. On average, there were 30 (± 9) images coded as faces in each set of 200.

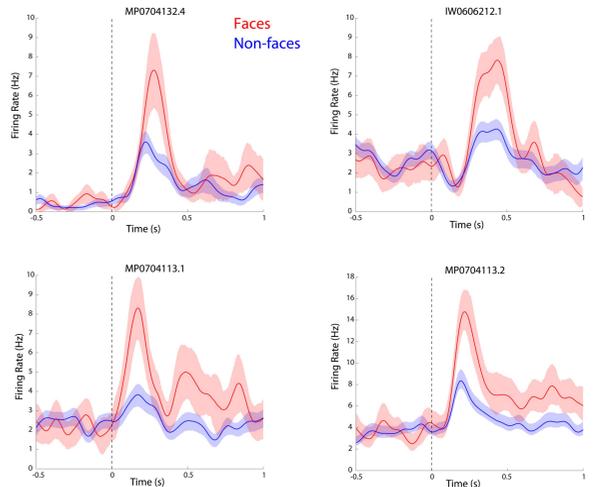
Figure 4: Examples of non-face stimuli.



All other stimuli were coded as non-faces. This included faces that were not fixated upon, animals, flowers, landscapes and man-made objects.

## Results

Figure 5: Examples of face-selective neurons.



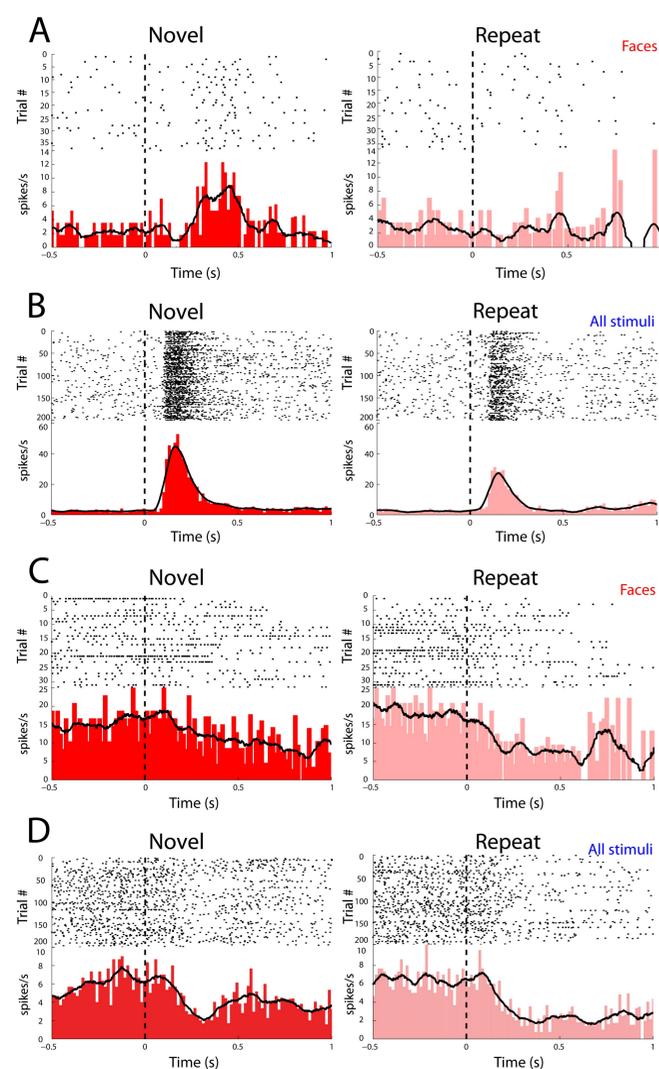
Example neurons whose average firing rate from 100 to 600 msec after stimulus onset (vertical dashed line) in response to novel faces (red) was significantly different ( $p < .05$ ) from that of novel non-face images (blue). Face-selective neurons whose firing rate increased after stimulus onset gave an average firing rate that was 50% greater in response to faces compared to non-faces.

Table 1: Visual responsiveness and selectivity.

Total hippocampal single-units recorded: 126				
	Novel only	Repeat only	Both	Total
Face responsive single-units	20 (24%)	15 (18%)	29 (35%)	64 (51%)
Increase in firing rate	5 (25%)	2 (13%)	14 (48%)	21 (33%)
Decrease in firing rate	15 (75%)	13 (87%)	15 (52%)	43 (67%)
Face selective single-units	6 (30%)	8 (53%)	3 (10%)	17 (27%)
Increase in firing rate	3 (50%)	7 (88%)	1 (33%)	11 (65%)
Decrease in firing rate	3 (50%)	1 (12%)	2 (67%)	6 (35%)

Stimulus response properties of all single-units showing significant differences in firing rate between baseline and the 100-600 msec period after onset of face images ( $p < .05$ ). Bolded percentages for face responsive units are based on the total number of visually responsive neurons; Bolded, italicized percentages are based on the total number of face responsive neurons; all other percentages are calculated from the total number of single-units in the response category: Encoding only, Recognition only, Both or Total.

Figure 6: Firing rate modulated by memory



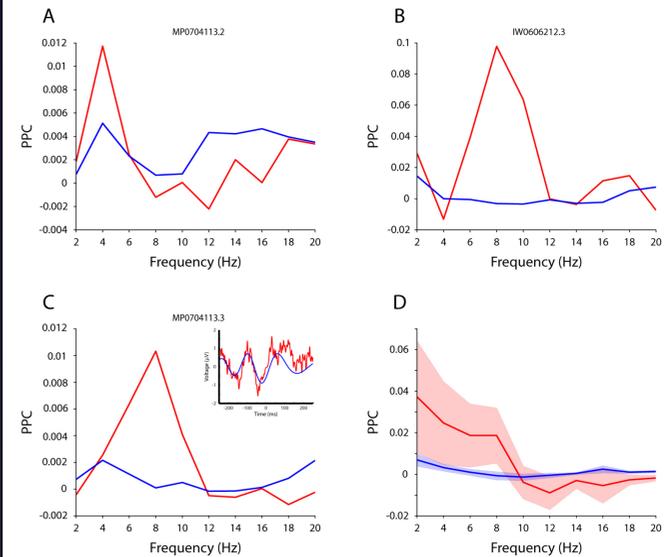
Modulation of firing rate across stimulus presentation in example face-selective (A, C) and non-selective (B, D) neurons. For face-selective neurons, (A & C), only responses to face trials are shown, and for non-face-selective neurons (B & D), responses to all trials are shown. Previous analysis disregarding stimulus category (B, D) found a strong positive correlation between the magnitude of firing rate modulation and recognition memory performance ( $r = .71$ ,  $p < .01$ ) across all differentially responsive neurons<sup>6</sup>.

Table 2: Modulation of firing rate by stimulus novelty in face responsive and face-selective cells.

Total hippocampal single-units recorded: 126			
	Total	Novel > Repeat	Repeat > Novel
Face Responsive	64 (51%)	14 (82%)	3 (18%)
Modulated by Novelty	17 (27%)	6 (86%)	1 (14%)
Face Selective	17 (27%)	6 (86%)	1 (14%)
Modulated by Novelty	7 (41%)	6 (86%)	1 (14%)

Summary of firing rate modulation for all neurons that were visually responsive to faces and all cells that were selective for faces. Previous analysis of these data disregarding stimulus category found that 30 of 84 (38%) visually responsive cells were modulated by novelty. Of these 30, 57% decreased their firing rate upon repeated presentation. Data from Fried et al., 2002 are given for comparison.

Figure 8: Theta-band phase synchrony for faces and non-faces



Plots of pairwise phase consistency (PPC), a measure of the consistency of spike-LFP phase relationships<sup>10</sup>, in three example face-selective neurons (A-C) and across all face-selective neurons (D). Phase synchrony was assessed for both face (red) and non-face (blue) trials. Of the 17 face-selective neurons, 9 (53%) were significantly phase locked to theta-band frequencies in the LFP, while 52 (40%) of the total population were theta phase locked.

## Conclusions

Here we provide evidence for face selectivity in single neurons in the monkey hippocampus, consistent with single-unit recordings in humans<sup>2,3</sup>. Furthermore, these face-selective neurons demonstrate recognition memory signals through firing rate modulation that are similar to those seen in non-face-selective hippocampal neurons. Finally, face-selective neurons in the hippocampus show evidence of phase synchrony in the theta-band and some show enhanced phase synchrony for faces relative to non-faces. These data suggest that face-selective neurons in the hippocampus utilize similar neural mechanisms for recognition memory as other hippocampal neurons, but are category-selective.

## References

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## Acknowledgments

Work supported by funding from the Yerkes National Primate Research Center, Emory Alzheimer's Disease Research Center, and a National Institute of Health grant MH080007. We thank Megan Tompkins and Kiril Staikov for assistance with the testing of monkeys.

## Methods

Figure 1: The Visual Preferential Looking Task.

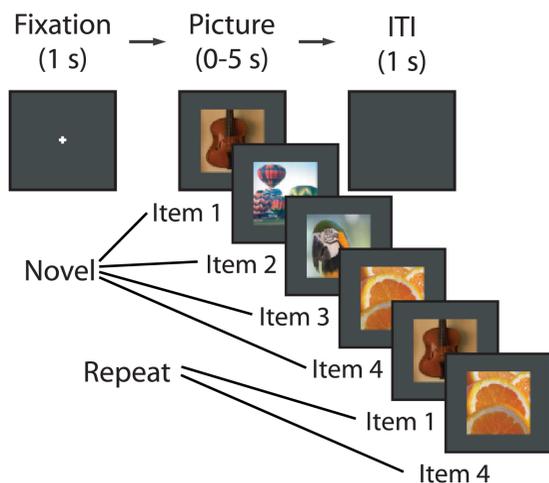
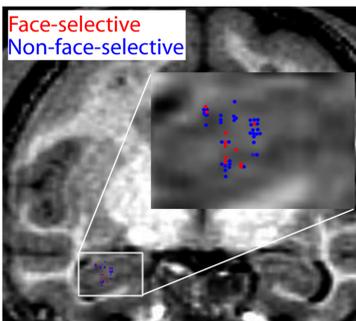


Figure 2: Locations of face-selective neurons.



200 unique stimuli were presented in each test session and each stimulus was presented twice during the session, with up to 10 trials intervening between novel and repeat presentations. 126 single-units were recorded in the hippocampus of two rhesus monkeys. Red and blue dots indicate locations where face-selective and non-face-selective neurons were recorded, respectively.