Different Levels of Category Abstraction by Different Dynamics in Different Prefrontal Areas

Highlights

- Category abstraction was organized by oscillatory dynamics and PFC subregion
- Gamma oscillations in the ventrolateral PFC signaled low-level category abstraction
- Beta oscillations in the dorsolateral PFC signaled high-level category abstraction

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In Brief

Wutz et al. show that different levels of category abstraction engage different oscillatory dynamics in different prefrontal cortex (PFC) areas. This suggests a functional specialization within PFC for low-level, stimulus-based categories (e.g., cats) and high-level, rule-based categories (e.g., animals).
Different Levels of Category Abstraction by Different Dynamics in Different Prefrontal Areas

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SUMMARY
Categories can be grouped by shared sensory attributes (i.e., cats) or a more abstract rule (i.e., animals). We explored the neural basis of abstraction by recording from multi-electrode arrays in prefrontal cortex (PFC) while monkeys performed a dot-pattern categorization task. Category abstraction was varied by the degree of exemplar distortion from the prototype pattern. Different dynamics in different PFC regions processed different levels of category abstraction. Bottom-up dynamics (stimulus-locked gamma power and spiking) in the ventral PFC processed more low-level abstractions, whereas top-down dynamics (beta power and beta spike-LFP coherence) in the dorsal PFC processed more high-level abstractions. Our results suggest a two-stage, rhythm-based model for abstracting categories.

INTRODUCTION
Categorization is the capacity to organize items based on shared characteristics. Those characteristics can vary by level of abstraction. Sometimes they are more feature-based, with members looking physically similar (e.g., housecats). Other times they are more conceptual (e.g., animal), with members looking different (e.g., cats and elephants). There is little known about how the brain achieves different levels of abstraction. Does higher-level abstraction simply engage more of the same mechanisms and networks as lower-level, feature-based categorization? Or do they engage different mechanisms and/or areas?

We used a dot-pattern categorization task (Posner and Keele, 1968; Knowlton and Squire, 1993; Vogels et al., 2002) that varied abstraction by the degree of spatial distortion of each exemplar from its category prototype. Low-distortion exemplars look alike. High-distortion exemplars require greater abstraction of the category’s “essence” (Figures 1A and 1B). Monkeys learned two new categories in each session. Local field potentials and multi-unit spiking activity were recorded in the dorsolateral prefrontal cortex (dPFC) and ventrolateral prefrontal cortex (vPFC) (Figure 1C).

Neural correlates of categorization have been reported in many cortical and subcortical brain areas (Merchant et al., 1997; Kreiman et al., 2000; Sigala and Logothetis, 2002; Hampson et al., 2004; Ashby and O’Brien, 2005; Seger, 2008; Poldrack and Foerde, 2008). For high-level abstraction, however, the prefrontal cortex (PFC) may play a central role (Wallis et al., 2001; Fabre-Thorpe, 2003; Freedman et al., 2003; Badre and D’Esposito, 2009; Christoff et al., 2009; Cromer et al., 2010; Goodwin et al., 2012). Likewise, different oscillatory dynamics may subserve different functions for category processing. There is growing evidence that beta (~20 Hz) versus gamma (~40 Hz) oscillations are involved in top-down versus bottom-up cortical processing, respectively (Jensen et al., 2007; Buschman and Miller, 2007; Engel and Fries, 2010). Thus, different oscillatory dynamics might reflect different functional roles for categorization based on bottom-up features or more abstract concepts (top-down). We found abstraction organized by PFC area and oscillatory rhythm. vPFC-gamma oscillations were more engaged for lower-level abstraction and dPFC-beta oscillations for higher abstraction.

RESULTS
Two monkeys were trained in a delayed-match-to-category task (Figure 1D). First, a sample exemplar from one of the two categories appeared for 1 s. After a memory delay period (0.85 s plus a jitter of 0.4 s maximum), two test exemplars appeared on the right and left. One of the exemplars was the same category as the sample (match); the other was from the other category (non-match). The monkeys free-viewed the test exemplars and were rewarded for maintaining fixation (0.7 s) on the match. Each session was organized into a set of training blocks, each of which contained an increasing number of category exemplars. To move on to the next block, animals had to perform at or above 70% correct. We used correct trials from training blocks five and above (minimum of 64 exemplars per category). Level of abstraction was varied by the degree of exemplar distortion from the category prototype (summed Euclidean distance median ± interquartile range [IQR] = 0.95 ± 0.2 degrees visual angle [DVA]; Figure 1B). A complete description of the methods and analyses can be found in STAR Methods.

PFC Was Organized into Beta and Gamma Regions
Local field potentials (LFPs) were recorded from chronic multi-electrode arrays in the dlPFC and vlPFC (Figure 1C). There was a task-related increase in LFP oscillatory power in different

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