

## On Neural Correlates of Categorical Perception

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## Summary

The neural substrates of visual categories have been the subject of an increasing number of neurophysiological studies. Categorization tasks are often used as a tool, in these studies, to induce well-defined categories via behavioral training. Here, we highlight the important difference between the neuronal substrates underlying *perceptual* versus *behavioral* categories. To illustrate this distinction, we examine a recently reported study of the neural representation of motion categories. Using a simple model of categorical perception, we identify potential neural signatures of perceptual motion categories. Our exercise indicates that the neural correlates of categorical motion perception can be subtler than the binary response profile that is often treated as the litmus test of visual categorization.

## **Introduction**

The influences of categories on perception have been the subject of extensive psychophysical investigations (e.g., Goldstone et al., 2001; Livingston et al., 1998; Notman et al., 2005; Yokoi and Uchikawa, 2005; for a collection of categorical perception literature see Harnad, 1987a). Recently, a number of researchers have trained monkeys to classify visual stimuli into arbitrary categories and then examined the neural correlates of this categorization (e.g., Freedman et al., 2001; Jiang et al., 2007; Sigala and Logothetis, 2002; Suzuki et al., 2006; Vogels, 1999). Freedman and Assad have extended this approach to the domain of visual motion (Freedman and Assad, 2006). The authors report a neural representation of motion categories induced by behavioral training. These findings, as exciting as they are, fall short of identifying the neural imprints of perceptual motion categories.

Following a brief summary of Freedman and Assad's findings, we bring out the distinction between perceptual and behavioral categories. Without a perceptual assay, we argue, it is not clear whether their neurophysiological findings reflect perceptual or behavioral categories. Next, we model the modulation of motion perception by perceptual motion categories. Using this model, we characterize the expected neuronal correlates of categorical motion perception.

## **Categorizing Motion Directions**

Using a delayed match-to-category (DMC) task, Freedman and Assad trained monkeys to categorize 12 motion directions into two categories: Category 1 with  $-30^\circ$ ,  $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ ,  $90^\circ$ , and  $120^\circ$  motion stimuli as members, and Category 2 with  $150^\circ$ ,  $180^\circ$ ,  $210^\circ$ ,  $240^\circ$ ,

270°, and 300° as members (Figure 1A). Once the monkeys learned to categorize motion directions, the authors recorded from neurons in the lateral intraparietal (LIP) area, and found that responses exhibited binary response profiles, reflecting the two motion categories (Figure 1B). The monkeys were subsequently retrained to categorize the same motion directions into two new categories. After the monkeys learned these two new motion categories, LIP neural response profiles switched to reflect the new category membership of motion directions. These data clearly attest to the plasticity of the neural representation of motion categories in LIP.

Freedman and Assad also recorded from neurons in the middle temporal (MT) area. MT neurons, unlike LIP neurons, did not exhibit binary response profiles. Although these findings clearly reveal that MT does not play the same role as LIP in categorical representation, there are two fundamental limitations to what can be concluded about the role of MT from the Freedman and Assad study. First, unlike behavioral categorization, perceptual categorization is not typically binary. The binary response profile is thus not an appropriate criterion for identifying neural correlates of *perceptual* categorization. Second, the Freedman and Assad study provides no evidence that perceptual (as opposed to behavioral) categories were actually created by the learning regime. We take these issues up in greater detail in the following section.

### **Behavioral Categories and Perceptual Categories**

Categorization can be perceptual or merely behavioral: one can respond similarly to two stimuli even though the two stimuli are perceived differently. A slice of pizza, for example, does not look like a hamburger, and yet both are categorized as FOOD and in

turn elicit the same behavioral response i.e., EAT. Nevertheless, it seems unlikely that pizza and hamburger will look visually similar however many times we eat them. It is important to distinguish between behavioral categories and perceptual categories.

Freedman and Assad clearly induced behavioral categories via their DMC task as testified by the performance of the monkeys in the task, but it is unclear whether training on this task induced perceptual categories. A hallmark of categorical perception is better discrimination between stimuli of different categories than between stimuli that are equally (physically) dissimilar but belonging to a single category (Harnad, 1987b). If the behavioral categorization observed by Freedman and Assad reflects perceptual categorization, then one would expect to see increased perceptual sensitivity for directional differences across the category boundary and decreased sensitivity within categories (Figure 1C). In the absence of a perceptual assay of directional discrimination, it seems prudent to conclude that their data clearly establish the plasticity of parietal cortical representation of behavioral categories, but are agnostic as to whether these categories were also perceptual.

### **Neural Correlates of Categorical Motion Perception**

The observation that members of a category look similar to one another and distinct from non-members can be accounted for by assuming a categorization-training induced stimulus-perception remapping, or warping of perceptual space (Livingston et al., 1998). As a result of the categorization training, perceived motion direction is assumed to move away from the “veridical” stimulus motion direction towards that of the prototype (Figure 1D). If we further assume that the responses of area MT neurons co-vary with perceived

motion direction (Albright and Stoner, 2000; Cohen and Newsome, 2004), then this remapping predicts that MT neurons will exhibit a variety of neural tuning changes including broadening, narrowing, and peak shifts. The exact nature of the tuning changes depends on the direction tuning of individual MT neurons.

To illustrate the predictions that can be drawn from the hypothesized remapping, we consider MT neurons tuned to 3 motion directions: prototype of Category 1 (i.e.,  $45^\circ$ ), boundary between the two categories (i.e.,  $135^\circ$ ), and a member of Category 1 (e.g.,  $90^\circ$ ). Let us first consider an MT neuron tuned to  $45^\circ$ . According to the model, a  $60^\circ$  (a member of Category 1) motion stimulus will be perceived as moving in a direction little less than  $60^\circ$  and will thus elicit a larger response in a neuron tuned to  $45^\circ$ . Reflecting the attraction of category members towards the category prototype in perceptual space, the tuning of an MT neuron with a peak at the category prototype broadens (Figure 2A). The binary response profile that Freedman and Assad looked for in MT is an extreme scenario likely to be found only if all motion directions belonging to a motion category elicit identical motion direction percepts.

As a result of categorization training, due to the remapping that we postulate, motion directions in the vicinity of category boundary ( $135^\circ$ ) tend to be biased away from the boundary in perceptual space. In line with these predictions, perceptual biases away from a discriminating boundary have recently been documented (Jazayeri and Movshon, 2007). The categorization-training induced stimulus-perception remapping in the vicinity of category boundary predicts sharpening of the tuning of a neuron with a peak at the boundary (Figure 2B). Lastly, let us consider an MT neuron with peak at  $90^\circ$  (a member of Category 1). Paralleling the perceptual changes in the neighborhood of a category

member motion direction, direction tuning of MT neurons with a peak at a category member is predicted to undergo peak shift as illustrated in Figure 2C. All these changes in the directional tuning of MT neurons are correlates of the changes in motion perception resulting from the categorization training.

The stimulus-perception remapping presented here is intended to illustrate the point that unless categorical perception is itself binary, the underlying neural correlates are likely to be more diverse than the binary response profiles Freedman and Assad observed for LIP neurons but did not find for area MT.

### **Concluding Remarks**

Our everyday visual perceptual experience –e.g., familiar faces in the hallways, dark chocolate chip cookies on the lunch table, and speeding cars on the freeways– owes more to the neural interpretation of retinal images than to the precise physical measures of the images. Visual perception can indeed be identified with the neural interpretation of retinal images. Visual categories facilitate the neural interpretation of measured image intensities as visual objects out in the world. Neurophysiological investigations of these interactions between categories and vision need to be cognizant of the distinction between behavioral and perceptual categories.

Freedman and Assad's report does not include an assessment of perceptual changes expected from learning novel motion categories. Because of this shortcoming, the category selectivity that they found in LIP need not necessarily be that of visual categories. Neurophysiological recordings paired with assays of categorical perception are needed to further our understanding of how the brain reads meaning—the constellation

of visual objects populating our perceptual universe—into the spatio-temporal variations of wavelength and intensity of light. It is also important to recognize that the binary response profile that is usually taken as the defining attribute of categories is but a special case of categorical perception. Once we recognize this, Freedman and Assad's data, i.e., MT neurons do not exhibit binary responses, is not very telling. Therefore, the role of MT in categorical motion perception remains an open question.



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## Figure Legends

Figure 1. Motion Categories and Categorical Motion Perception. (A) Categorization of motion directions. The 12 motion directions used in the study of Freedman and Assad (2006) are depicted as arrows. Monkeys were trained to categorize the 12 motion directions into two categories. Red arrows indicate motion directions ( $-30^\circ$ ,  $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ ,  $90^\circ$ , and  $120^\circ$ ) belonging to Category 1, while green arrows indicate motion directions ( $150^\circ$ ,  $180^\circ$ ,  $210^\circ$ ,  $240^\circ$ ,  $270^\circ$ , and  $300^\circ$ ) belonging to Category 2. The black dotted line denotes the boundary between the two motion categories. (B) Neural representation of motion categories in LIP. The figure shows a cartoon rendering of an LIP neuron's responses to the 12 motion directions. Red and green filled circles represent the neural activity elicited by motion directions belonging to Category 1 and Category 2, respectively. Adapted from Freedman and Assad, 2006. (C) Defining characteristic of categorical motion perception. To ease the exposition, prior to any motion categorization training, motion direction discrimination sensitivity is assumed to be isotropic (violet circle). In the polar graph, radial axis represents a measure of sensitivity such as  $d'$  and the polar axis represents stimulus motion direction. Following the categorization training, perceptual sensitivity across the category boundary (black dotted line) increases, while sensitivity within categories decreases (blue ellipse). For example, the pair of  $120^\circ$  and  $150^\circ$  motion direction stimuli will be more easily discriminated compared to the pair of  $30^\circ$  and  $60^\circ$ , even though both pairs are separated by same angular difference. (D) Stimulus-perception remapping. As a result of categorization training, stimulus motion directions belonging to a category tend to move closer to their corresponding category prototype in the perceived motion direction space. The four filled circles on the middle

horizontal line denote stimulus motion directions:  $0^\circ$  and  $90^\circ$  of Category 1, and  $180^\circ$  and  $270^\circ$  of Category 2. Violet arrows indicate stimulus-perception mapping prior to categorization training. A  $0^\circ$  motion stimulus, for example, is perceived as moving in the direction of  $0^\circ$ . Following categorization training, there is a remapping of stimulus motion directions to perceived motion directions as indicated by the blue arrows. The four blue arrows indicate the perceptual bias of  $0^\circ$  and  $90^\circ$  towards  $45^\circ$ , and  $180^\circ$  and  $270^\circ$  towards  $225^\circ$ .  $45^\circ$  and  $225^\circ$  are the prototypes of Category 1 and Category 2, respectively.

Figure 2. Predicted Changes in the Direction Tuning of MT Neurons. (A) Prototype neuron tuning broadens. Following categorization training, the direction tuning of an MT neuron coding for perceived motion with peak at a category prototype (e.g.,  $45^\circ$ ) broadens (blue curve) with respect to the tuning prior to training (violet curve). Blue arrows on x-axis indicate the stimulus-perception remapping induced by categorization training. Motion stimuli that appeared, prior to categorization training, to move in the directions indicated by the tails of blue arrows will look, after training, as if moving in directions indicated by the arrowheads. Paralleling these changes in perceived motion directions, motion stimuli belonging to a category will elicit, after categorization training, larger responses (compared to the responses elicited prior to training) in MT neurons tuned to the direction of the corresponding category prototype. (B) Boundary neuron tuning narrows. Consider an MT neuron whose direction tuning curve peaks at the category boundary ( $135^\circ$ ). After categorization training, stimulus motion directions nearby  $135^\circ$  will move away, in perceived motion direction space, from  $135^\circ$  (as

indicated by the blue arrows). Thus motion direction stimuli in the neighborhood of category boundary will elicit smaller responses (compared to the responses elicited prior to training) in the MT neuron tuned to the category boundary. The sharpening of the boundary neuron tuning (blue curve compared to violet curve) mirrors the changes in perceived motion directions. (C) Category member neuron tuning shifts. Calculations of the stimulus-perception remapping in the vicinity of a category member motion direction indicate that the tuning of a neuron with peak at a category member (e.g.,  $90^\circ$ ) will undergo a peak shift. Directional tuning after categorization training is shown in blue. Tuning curves prior to categorization training are colored violet in all three panels. Black dotted lines mark, in all three panels, the category boundary.

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Figure 1

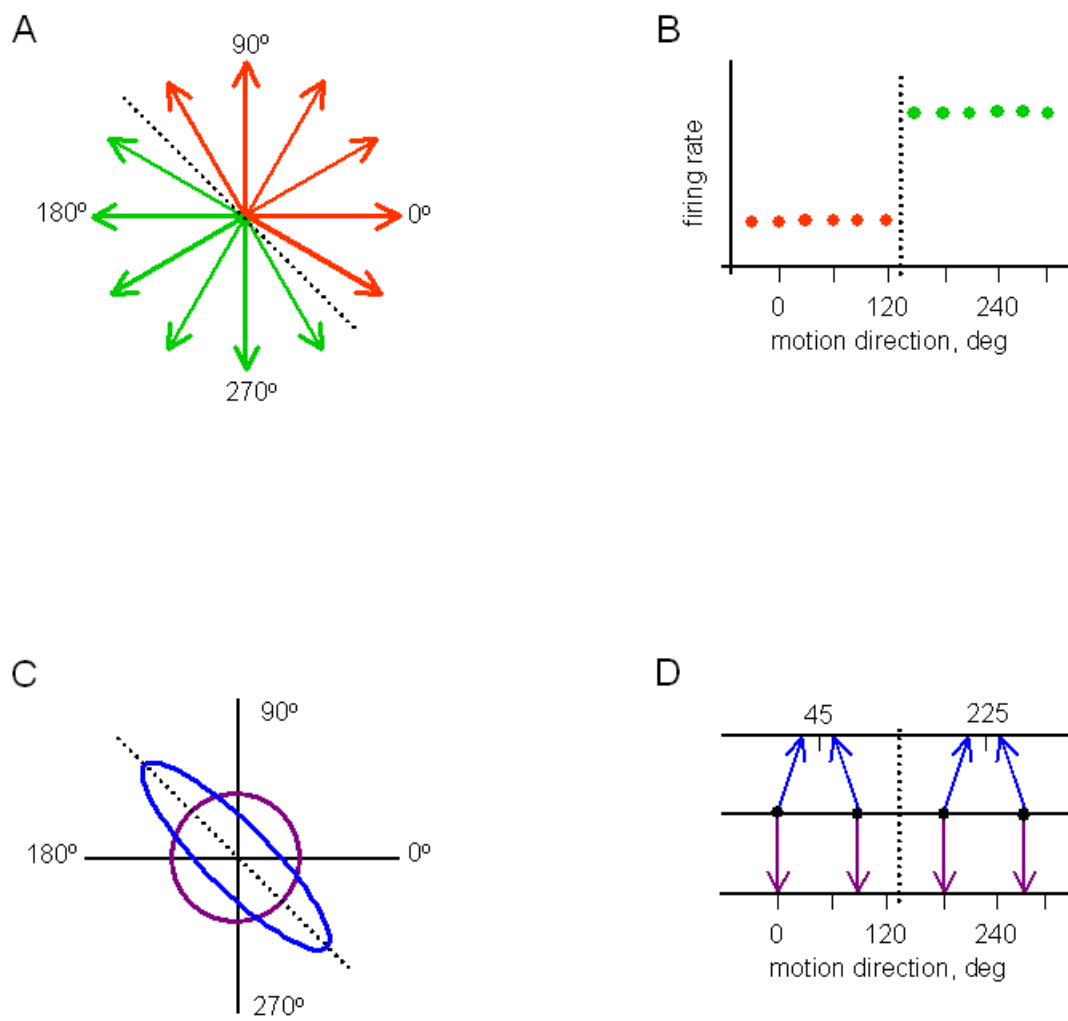


Figure 2

