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The crowded window of object recognition revealed by cortical population codes

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When a target is surrounded by nearby flankers, it becomes difficult to identify or discriminate its feature. This phenomenon is known as visual crowding (Pelli and Tillman, 2008). It is ubiquitous in peripheral vision and occurs in everyday activities such as reading and visual search. As a major bottleneck in conscious perception and object recognition, crowding has been explained by a lack of sufficient resolution in the visual system (He et al., 1996; Liu et al., 2009). Due to this limit, the target-flanker distance needs to exceed a critical spacing. In other words, target identification would not be affected unless the distractors are placed outside the "crowded window", termed as the crowding zone (Toet and Levi, 1992).

So far, the neural substrate of the spatial extent of crowding has not been directly measured in the visual cortex. It is naturally believed that the crowding zone has a close link with the neural receptive field. The development of population receptive field (pRF) mapping enables us to estimate a voxel's preferred spatial location based on the aggregate activation from neural populations (Dumoulin and Wandell, 2008). Using this method, a recent fMRI study addressed the 'resolution' issue of crowding in human visual cortex (He et al., 2019).

Firstly, He and colleagues computed individual correlations between the average pRF size in multiple visual areas and the crowding strength (Figure 1A). They observed a significant positive correlation in area V2. Next, they used crowded orientations in the pRF mapping protocol to measure the task-relevant pRF. In V2, a crowding-dependent modulation of pRF size was observed: a stronger crowding effect was associated with a larger population receptive field (Figure 1B). Further, they trained subjects to discriminate the target orientation over a week. They found that perceptual learning induced a significant reduction in the crowding effect, as well as the size of V2 pRF (Figure 1C). The reduction in pRF size occurred only when the target was presented with flankers during training.

The above findings are of unique significance both technically and conceptually. First, the study addressed a longstanding issue—the "bottleneck" question. Using a computational neuroscience method, it investigated how perceptual resolution constraint resides in the visual cortex. Second, the results showed that pRF size predicts the individual difference in the objective discrimination ability with the crowded stimulus, adding important evidence for the key roles of pRF properties in visual perception at the individual level. Third, unlike traditional studies that measured pRF properties with task-irrelevant stimuli, the pRF properties were also estimated with task-relevant stimuli to reveal the dynamic nature of pRF. Finally, the pRF is plastic. A recent study found reorganization in the visual cortex underlying a training-induced shrinkage of the crowding zone (Chen et al., 2019). Consistently, He and colleagues demonstrate that perceptual learning alleviates crowding and shrinks the pRF. These re-

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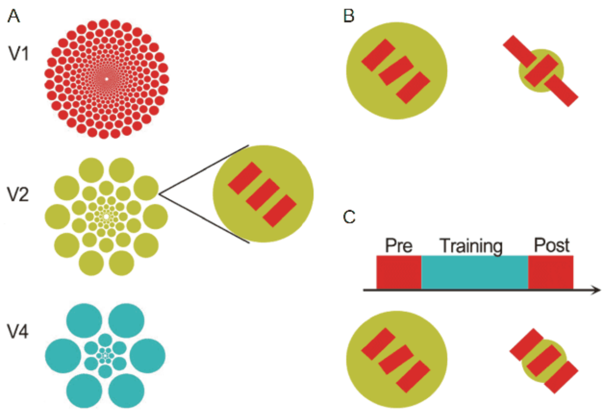

Figure 1 (Color online) Illustration of the critical role of V2 pRF size in crowding. A, A link between V2 pRF size and crowding effect. Each circle denotes a pRF estimated at the corresponding location in the visual field. The size of pRF scales with the eccentricity as well as the cortical processing hierarchy (Freeman and Simoncelli, 2011, reproduced with permission from Winawer and Horiguchi, http://hdl.handle.net/2451/33887). B, Task-relevant modulation of the pRF size in V2. A larger pRF size was estimated in a stronger crowding condition induced by parallel flankers; a smaller pRF size was estimated in a weaker crowding condition induced by perpendicular flankers. C, Perceptual learning reduces the pRF size in V2.

sults lend strong support to the critical role of V2 population receptive field in crowding.

The pRF mapping provides a quantitative way to measure the "resolution" in the visual cortex. On the other hand, the development of the inverted encoding model offers a possibility to transform the aggregate population activation into feature-specific response profiles (Serences and Saproo, 2012). In crowding research, an intriguing question is how features in clutter are pooled and encoded—if an item cannot be identified clearly, is the information lost in the visual cortex? Using the inverted encoding model, a recent study reconstructed the orientation tuning at a population level along the visual hierarchy. Target-specific tunings were observed in the early visual areas, and did not diminish until V4 (Chen et al., 2018). These findings demonstrate that while crowding limits the conscious access to the individual items, the information can be preserved in the early processing stages, indicating a dissociation between consciousness and neural representation in the early visual cortex.

Here we report advances on using computational models in fMRI measurement to investigate the cortical population codes underlying crowding. There remain many open questions about crowding. It is known that the crowding zone scales with eccentricity, has inner-outer asymmetry and radial-tangential anisotropy (Whitney and Levi, 2011). Could we map point-to-point crowding zones in the visual cortex with these spatial features? Regarding the pooling model of crowding, if many details are lost in the periphery, what do we see? Texture? Floating features or their fruitless combination? The development of encoding models enables researchers to explore the information embedded in the neural population activation. Future fMRI studies need to incorporate new computational approaches to unveil the full picture of the bottleneck in object recognition and conscious perception.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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