Position coding in the visual word form area

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How does our brain achieve its impressive expertise to effortlessly read written words? It has been proposed that a key element of the capability to recognize visually presented words (as well as other objects) is a normalization process that is assumed to operate along the visual hierarchy. This normalization process would remove varying aspects of presented words from the evoked retinal representations in the eye and early visual cortex, including spatial position, size, and rotation, resulting in standardized (invariant) representations in higher-level visual areas (Fig. 1 A and B). Numerous studies (1–5) have identified a region in a small strip of the fusiform gyrus in the left hemisphere that seems to be specialized for orthographic processing of words called the visual word form area (VWFA). Because this area is at a rather high level within the visual hierarchy and in close proximity to areas specialized for object recognition (e.g., faces), dominant reading theories assume that the representations within the VWFA contain invariant representations of words (5).

The study by Rauschecker et al. (6) challenges this traditional view, showing, with a series of elegant experiments, that the representations in VWFA are actually position-dependent (i.e., they reflect the original position of words at the retina) (Fig. 1 C and D), despite the rather high-level location of this area in the visual hierarchy.

How does the study by Rauschecker et al. (6) reveal position-dependent representations in VWFA? Previous brain imaging studies using centrally presented word stimuli reported only one VWFA in the left hemisphere (1–5). This finding had been used as additional evidence that this area contains invariant word representations, because it is generally assumed that, at a level of invariance across the whole visual field, a single specialized brain area in only one hemisphere would be sufficient. This reasoning parallels findings for the fusiform face area, a specialized area for face processing (7) that is located in close proximity to the VWFA and reported to exist (mainly) in the right hemisphere. The study by Rauschecker et al. (6) investigates this assumption systematically by measuring brain activity with functional MRI while words are presented at different positions in the visual field (Fig. 1). When words are presented at the right side of the point of gaze (marked by the blue fixation cross in Fig. 1), activation is observed primarily in the VWFA of the left hemisphere (Fig. 1C), whereas words presented at the left side result in activity primarily in the right hemisphere in a region at a corresponding hierarchical level (Fig. 1D). This observation not only shows position dependence, but it also reveals that the area specialized for visual word form is located in both hemispheres. Because the traditional view locates this area only in the left hemisphere, the study by Rauschecker et al. (6) labels the VWFA in the right hemisphere as rVWFA.

Although a hemispheric bias of activity for words presented in the left vs. right visual field is sufficient to show position-dependent coding in VWFA, the study by Rauschecker et al. (6) also reveals that words displaced vertically with respect to the point of gaze evoke different activity patterns in VWFA. Because the presentation of words at different vertical positions in the visual field leads to strongly overlapping responses in VWFA in both hemispheres, the study by Rauschecker et al. (6) relies on the results of multivariate pattern classification to infer position-sensitive coding. By analyzing differences in distributed spatial patterns, such multivariate classifiers are often able to separate activation from different experimental conditions, even if they evoke similar levels of activity in the same brain region. To show that they are able to separate conditions from each other, classifiers first learn to distinguish condition effects based on one part of the data.

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(training), and then prove their ability to classify activity patterns using a separate part of the data (testing). The classifiers trained in the study by Rauschecker et al. (6) are, indeed, able to correctly predict at which vertical position a word had been presented based on the evoked activity patterns in a combined left–right VWFA. Additional evidence for position-dependent coding is obtained from electrophysiological recordings in a human subject with intracranial electrodes implanted for clinical purposes.

What does position-dependent coding in VWFA mean for our understanding of word recognition? Although the study by Rauschecker et al. (6) convincingly shows that the (combined) VWFA contains position-dependent representations, the question about the mechanisms used by the brain to recognize letter strings as words so effortlessly remains unanswered. At first sight, the study by Rauschecker et al. (6) moves us a step back by telling us that the problem of invariance is not solved at a rather high level in the visual hierarchy. The study, thus, forces us to rethink how invariant representations are achieved or whether they are needed for successful reading. It is difficult to completely abandon the concept of position invariance; it is evident from considerations based on neural network models that a level of invariant representations facilitates learning, because different retinal representations of the same word would activate the same (or at least very similar) representation at the normalized processing level. This representation would provide access to associated knowledge in subsequent areas such as word meaning. There is also recent evidence that the VWFA at least exhibits modest levels of location invariance (8). It could, thus, well be that the VWFA is an intermediate area with partial position invariance in a larger processing stream and that a subsequent brain area contains more complete position-invariant word representations. Along this line, a recent electrode recording study in the macaque (9) investigated the related face-processing network and observed that only the area at the highest level of six interconnected face-selective regions reached a rather complete level of view invariance. In the domain of word recognition, there are, however, no higher-level areas described in the ventral visual cortex of the human brain, and it is generally assumed that the VWFA transfers information about words directly to language-related areas. It might, thus, be a possibility that a visual area with completely invariant word representations does not exist or that VWFA contains both position-dependent and -invariant representations.

It should be noted that position invariance is only one aspect of the general problem of recognizing varying word representations. Besides position, size, and rotation, the largest challenge lies in achieving invariance for the letters that make up words (10). The same letter “a”, for example, can appear in many different shapes depending on the font used to print the letter. It is far more economical to reach invariance for 26 letters than for tens of thousands of different words. Reading, however, does not only involve invariance to isolated letter shapes but requires the analysis of the order in which letters appear within a word. It would be interesting to learn whether the VWFA, although not (fully) invariant to position, contributes to solve these more difficult letter shape and letter string invariance problems. Note that position-dependent coding in VWFA might provide the basis for parallel letter recognition operations that would process letters within letter strings at the same time as opposed to a sequential letter-by-letter recognition process. The view that letter strings are processed in parallel as single (sublexical) units has been proposed in connectionist word recognition models, and it is also in line with the large psychophysical literature on word recognition and reading. Recent brain imaging results at least support the view that VWFA is sensitive to orthographic information (5, 8, 11).

Although the study of Rauschecker et al. (6) provides constraints for our thinking about how the brain recognizes words, it also clearly reveals how little we know about representations used in different areas of the visual system, especially in those regions unique to the human brain such as the VWFA, which develops its expertise during a complex learning process without a specific genetic disposition (12). As long as functional brain imaging does not provide the possibility to resolve fine-grained representations within specialized visual areas, we may continue to struggle with indirect speculations about how the brain codes letters, sublexical letter strings, and words. Fortunately, the latest developments in ultrahigh-field functional MRI (13) seem to provide the possibility to measure brain function at a level that is detailed enough to reveal the features coded in cortical columns within specialized brain areas (14, 15). If this technology is applied to specialized regions such as the VWFA, we might be able to more directly test our hypotheses about letter and word representations used by the brain at different levels of the visual system.

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