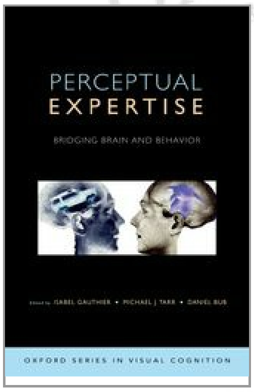

Perceptual Expertise: Bridging Brain and Behavior

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The Case for Letter Expertise

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[–] Abstract and Keywords

The perception of single letters is a critical component of reading, as evidenced by deficits in letter perception in individuals with dyslexia. Thus, visual letter recognition is a type of perceptual expertise, but it differs from face-like perceptual expertise in several important ways based on different perceptual and task demands. For example, relative to faces, letters are less visually complex and are recognized at the basic rather than subordinate level. However, as with face-like perceptual expertise, our extensive experience with letters leads to behavioral effects not observed for other objects (e.g. orientation priming) and neural specificity. Letter perception and word perception each recruit selective neural substrates that are left-lateralized, perhaps because of the relationship between letters, words, and language. Letter perception can also recruit motor cortices, depending on writing experience.

Keywords: letter perception, word perception, perceptual expertise, font tuning, vWFA, dyslexia

Visual letter recognition is a type of perceptual expertise resulting from our extensive experience with printed material. We perceive letters at an amazing speed during reading, and efficient letter perception has been shown to be the basis for successful reading performance in psychophysical and neuropsychological studies (Arguin, Fiset, & Bub, 2002; Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1999; Legge et al., 2007; McClelland, 1976; Nazir, Jacobs, & O'Regan, 1998; Pelli, Farell, & Moore, 2003; Pelli et al., 2007; Saffran & Coslett, 1998). Letter perception can also be distinguished from perception of other shapes and objects, as indicated by the recruitment of selective neural substrates (Cohen et al., 2000; Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; James & Gauthier, 2006; Longcamp, Anton, Roth, & Velay, 2003; Peterson, Fox, Snyder, & Raichle, 1990; Polk & Farah, 1998; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Pugh et al., 1996; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Jobard, James, James, & Gauthier, 2009) and association with specific behavioral phenomena (e.g. Gauthier & Tarr, 2002; Sanocki, 1987, 1988, 1991a,b,c; Wong & Gauthier, 2007).

What makes letter processing different from that of other objects, and what factors contribute to the specialized mechanisms underlying letter perception? Certainly, language forms a large part of what makes letter perception different from the perception of other objects. After all, we learn letters for the purpose of reading and only for that purpose. It is not surprising, therefore, that the majority of research on letter perception has been performed in the context of word recognition and reading, focusing on different linguistic processes (e.g. Johnson & Pugh, 1994; McClelland, 1976; Perfetti, Liu, & Tan, 2005; Reicher, 1969) or on the perceptual units used to recognize words (Carreiras, Alvarez, & De Vega, 1993; Healy, 1994; Prinzmetal, Treiman, & Rho, 1986; Rey, Ziegler, & Jacobs, 2000; Spoehr & Smith, 1973). Nevertheless, as will be discussed in this chapter, a substantial part of the unique nature of letter perception can also be explained in a framework of visual object recognition.

Recently, the object recognition field has witnessed an increasing interest in the topic of perceptual expertise with a variety of objects such as faces, cars, birds, dogs, fingerprints, novel objects, and so forth (Busey & Vanderkolk, 2005; Gauthier, Curran, Curby, & Collins, 2003; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, et al., 2000; Tanaka & Curran, 2001). Although considerable progress has been made to understand the **(p.306)** nature of perceptual expertise, much less is known about how expert letter perception compares with other types of perceptual expertise and object perception in general. To better understand these relationships, it may be fruitful to consider different aspects of visual letter recognition, including the stimulus properties, task demands, and so forth, involved in letter recognition in daily reading experiences. In this chapter we will begin by describing how letter perception relates to reading before outlining the evidence supporting neural selectivity for letter processing. We will then discuss potential reasons for the specialized neural mechanisms devoted to letters, in terms of both the interaction between letter processing and other modalities, and, in greater detail, the specific perceptual nature of letter perception.

Letter Perception and Word Reading

Learning to recognize individual letters is the very first ability that children are trained to acquire when learning to read, and it is crucial for successful reading. A seemingly simple activity such as reading these introductory lines already required the reader to perceive and recognize several hundreds of letters in a matter of just a few seconds. In natural situations such as this, however, letters are not perceived in isolation because they do not convey meaning on their own; rather, they are combined to be recognized as words. The idea that word recognition is the goal of reading has led some researchers to consider that letters may not be the perceptual unit that is used for reading. Instead of recognizing each letter individually, embedded within a letter string, some researchers have argued that we may rely on the identification of perceptual units formed of several letters.

Supraletter Perceptual Units

In a seminal experiment, Reicher and Wheeler demonstrated an experimental effect known as the “Word Superiority Effect” (WSE) (Reicher, 1969; Wheeler, 1970). In this experiment, stimuli were briefly exposed, followed by a visual mask, and subjects had then to perform a forced choice task pertaining to the identity of a letter present at a certain place in the target letter string (e.g. WORK tested at the fourth position for K/D). The choice between two letters that formed candidates similar in nature (words or nonwords) ensured that the lexical status could not interfere with subject's accuracy. Reicher thus showed that although the subject’s decisions concerned the identity of a single letter, performance was facilitated when the target letter was perceived in the context of a word rather than in the context of a nonword or in isolation. By demonstrating that knowledge about a perceived word could be better than that of its constituent letters, these results suggest that in the context of reading, the perceptual unit most available to the reader may not be individual letters. One may question the perceptual origin of the WSE and argue that it could be the mere consequence of a top-down influence of either lexical semantic or phonological **(p.307)** processing. Such an interpretation is, however, challenged by work that has replicated this WSE with words, pseudowords (e.g. “thap”) and nonwords (e.g. “yibv”), showing increasing context facilitation for letters in nonwords, followed by pseudowords and finally words (Adams, 1979). The fact that a “WSE” can be obtained in the context of letter strings devoid of meaning indicates that its origin cannot be semantic, while the phonological hypothesis is brought into question by the effect showing with unpronounceable stimuli such as the nonwords. The WSE would therefore be related to a perceptual stage of word reading, in which orthographic units of various natures could help the recognition of single letters. The gradual growth of facilitation from nonwords to words observed by Adams confirms this because these stimuli present increasingly more familiar letter combinations. In fact, several reading experiments advocated the role of prelexical units composed of several letters but that were smaller than words. For example, graphemes have an effect on letter processing: letters are harder to detect when they are embedded in complex rather than simple graphemes (e.g. is there “an ‘o’ in boat?” vs. “is there an ‘o’ in rope?”) (Rey et al., 2000; see also Drewnowski & Healy, 1977, and Healy, 1994). This result indicates that after being exposed to words, graphemes are easier to access than letters because subjects exhibit more difficulties when they have to segment the stimuli to accurately detect the presence of a target letter. Similar results with different paradigms have also shown a role in reading of different orthographic units such as open bigrams[1] (Whitney & Berndt 1999), syllables (Carreiras et al., 1993; Mewhort & Beal, 1977; Prinzmetal et al., 1986; Rapp, 1992; Spoehr & Smith, 1973), or onsets and rimes (Treiman, 1994; Treiman and Chafetz, 1987).

Although these results all demonstrate that perceptual units relying on several letters (from bigrams to whole words) do play a role in reading and seem to be more readily available to the reader than letters, they do not necessarily imply that letter identification is not critical to reading. In fact, systems that can lead to the recognition of supraletter units are more or less explicitly described as intervening after the identification of single letters.

The Contribution of Individual Letters to Reading

The two main families of reading models (dual route and connectionist models) rely on a perceptual, orthographic stage in which words would be represented as an ordered sequence of abstract identities of letters constituting an “abstracted word shape” (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Paap, Newsome, McDonald, & Schvaneveldt, 1982; Rumelhart & McClelland, 1982; Seidenberg & McClelland, 1989). An interesting aspect of the conceptualization adopted by most recent reading models **(p.308)** is that individual letter recognition is the starting point of correct lexical access. The central role of letters during reading has been recently demonstrated by Pelli and colleagues by presenting letters and words embedded in noise, and estimating performance as a function of word length (Pelli et al., 2003). They found that in these degraded conditions, the effect of word length was much larger than WSE. While human recognition performance suffered a five-fold decrease with a five-letter word compared with a letter, WSE only improved performance by a factor of 1.3. This suggests that even if the word context is useful, its effect on letter perception may be rather small compared with factors such as the length of the word that all fell into fovea during a fixation. Concordant reports have been recently published that demonstrated that the number of letters that can be correctly identified within a single fixation is a critical factor that determines the reading speed of subjects (Legge et al., 2007; Pelli et al., 2007).

Another interesting line of research to study the contribution of letters to reading has been the use of letter confusability, defined as the extent to which a letter can be confused with another. A measure of this confusability is obtained by presenting letters in degraded presentation conditions and by collecting subject’s answers concerning the identity of the stimulus exposed (Bouma, 1971; Gilmore, Hersh, Caramazza, & Griffin, 1979; Loomis, 1982; Townsend, 1971; Van Der Heijden, Malhas, & Van Der Roovart, 1984). These studies result in confusability matrices that show what letters are harder to be uniquely identified, and with which letters they are more susceptible to be confused. Not surprisingly, results demonstrate that letters sharing visual features (such as curves, or vertical or horizontal lines) are much more likely to be confused with one another. Similarly, presenting a visually similar prime results in greater letter naming times than presenting visually dissimilar primes (Arguin and Bub, 1995). While these studies indicate that some letters are easier to perceive in isolation than others, some researchers sought to evaluate whether letter confusability had an impact on word recognition. Using words constructed with low- and high-confusability letters, several studies showed that letter confusability had no effect during word reading (Arguin et al., 2002; Cosky, 1976).

The lack of letter confusability effects in word reading may seem in contradiction with the above results showing that the best predictor of correct word identification is the ease with which we can recognize the individual letters. We believe these two results are actually complementary and illustrate the direction of the dependence between words and letters. The experiments of Pelli et al. (2003) degrade the perception of letters themselves in a quite drastic way and therefore target the initial perceptive stages of reading, leaving few chances for activation to propagate to higher levels of perception (that of supraletter units). In that sense, these results demonstrate quite convincingly how critical the perception of letters is to reading. The manipulation of letter confusability however, renders the perception of letters more difficult without introducing any perceptual degradation. In other words, in a situation where visually similar stimuli can be activated with some degrees of imprecision, supraletter units may intervene to help disambiguating the letters perceived.

(p.309) Behavioral patterns exhibited by individuals with dyslexia prove to be quite informative concerning the role of letters in reading. For example, the hallmark feature of letter-by-letter reading (LBL) in dyslexia is an abnormal increase of reading times as a function of word length—this increase is not as extreme in the typical reader. Although individuals that are LBL readers adopt a strategy that relies on the identification of single letters in a sequential fashion, it has been shown that a deficit in letter perception is very likely to be the cause of LBL reading in dyslexia (Behrmann & Shallice, 1995). According to these authors, skillful word reading would depend in the first place on the efficiency of the processes involved in letter identification. A compatible conclusion has been obtained by Fiset that proposed that letter processing deficits would have an impact particularly on the parallel letter identification that takes place during word reading and that requires perception of several letters simultaneously without fixating on them individually (Fiset, Arguin, Bub, Humphreys, & Riddoch, 2005). Complementary experiments showed that when individuals with dyslexia were required to process single letters in the context of a word (that is, in a way that is compatible with a sequential processing of individual letters) the effect of word length was not modulated by the confusability of letters. When these same individuals processed words shown in a horizontal format, the word length effect could be eliminated by using gradually less confusable letters as their number in the word increased. These last results would therefore lend further support to the fact that the most critical deficit affecting LBL readers would be the parallel identification of letters, a process that would be more difficult when more confusable letters are present. Such a process would be instantiated during word reading.

While it does seem to rely on individual letter recognition, reading is a complex activity: high-level processes related to linguistics and supraletter orthographical processing modulate the coarse identification of letters. Although issues concerning letter recognition have often been debated in the larger framework of reading, the studies above argue for processing that differs substantially between the perception of letters embedded in words and in isolation. Such a distinction has to be kept in mind for the researcher interested in discovering the specificity of letter recognition as a visual object because it may require studying letter processing outside the activity of recognizing words. As we will now see, the distinction outlined above between isolated letters and letters strings finds its counterpart at the cerebral level when we consider the specificity of letter processing.

Cerebral Selectivity for the Visual Perception of Letters

Selectivity for Letter Strings or Word Forms

About a century ago a case study was reported of a patient who suffered from a left inferior occipitotemporal lesion and lost the ability to recognize letters and words, while having no trouble speaking, writing, or recognizing other **(p.310)** visual material (Dejerine, 1892, as cited in Bub et al., 1993). Although Dejerine interpreted this pure alexia as a specific blindness to the visually presented letters, later works focused on the visual processes involved in reading through the recognition of word forms. Word forms have been regarded as perceptual units with distinct representations, and a visual word form system has been proposed for the parsing of letter strings into familiar units for further analyses (Carr & Pollatsek, 1985; Warrington & Shallice, 1980). Recent neuroimaging studies have identified a visual word form area (VWFA) in the left inferior occipitotemporal region, including parts of the left fusiform gyrus, which may be responsible for such processes (Cohen et al., 2000). This region has been shown to play a critical role in reading and responds more to various strings of letters, such as words, pseudowords, and consonant strings than to other shapes (Cohen et al., 2003; Joubert et al., 2004; Tagamets, Novick, Chalmers, & Friedman, 2000; Vigneau, Jobard, Mazoyer, & Tzourio-Mazoyer, 2005). Importantly, the neural response in this region is invariant to changes in location, case, and font (Cohen & Dehaene, 2004; Cohen et al., 2000; McCandliss, Cohen, & Dehaene, 2003), indicating some level of abstraction needed to recognize letter strings despite perceptual variations.

The nature of selectivity of the VWFA has generated much discussion. Some studies showed that perceiving words and consonant strings activated the VWFA more than perceiving checkerboards (Cohen et al., 2003), geometric symbols (Tagamets et al., 2000), textures and faces (Puce et al., 1996), faces and buildings (Hasson, Levy, Behrmann, Hendler, & Malach, 2002), and digit strings (Polk et al., 2002). Consistent with this, intracranial recordings in the bilateral posterior fusiform gyrus have found a larger N200 component for letter strings (in the form of words, pronounceable pseudowords, or consonant strings) than for cars and butterflies (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Nobre, Allison, & McCarthy, 1994). Other studies, however, failed to show a greater engagement of the VWFA during the perception or naming of objects than of words (Moore & Price, 1999; Price & Devlin, 2003).

Selectivity for Single Letters

Relatively few studies have directly tackled the question of selectivity for individual letters. The question of how letters are processed used to be addressed through the generalization of results obtained using letter strings, and some researchers suggested that the region responsible for the recognition of letters may actually be a subregion of the visual word form area (Dehaene et al., 2004).

Recently, some studies using isolated letters have shown a degree of cerebral selectivity for these simple stimuli. At an electrophysiological level, an EEG study showed that an early negative component occurring at about 170 ms after stimulus onset was enhanced with single, familiar characters compared with unknown characters or pseudoletters at posterior channels **(p.311)**

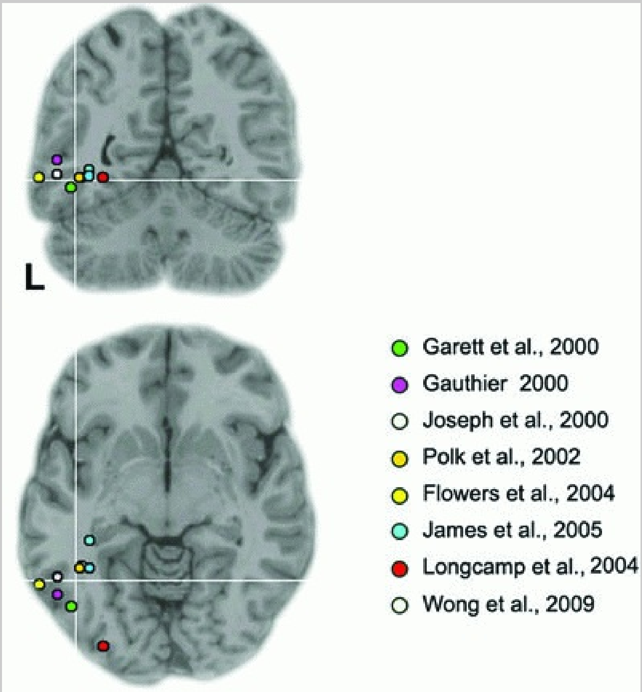

Figure 10.1 Schematic of approximate peak % BOLD signal change activation for letters recorded across several experiments. For coronal section, Talairach Y = (-50); for transverse section, Talairach Z = (-4). Note that activation peaks are quite variable but are all left lateralized and fall either on the fusiform gyrus or middle temporal gyrus.

(Wong et al., 2005). Concordant with this result, an MEG study has also shown an early component at about 150–200 ms that is larger for single letters than geometric shapes (Tarkiainen et al., 1999). In functional imaging studies (see Figure 10.1), isolated letters elicited higher activation in the left fusiform gyrus than oblique lines (Longcamp et al., 2003), faces (Gauthier, Tarr, et al., 2000), Chinese characters (James et al., 2005), and simple objects (James & Gauthier, 2006). Further, the left occipitotemporal region was recruited more when attention was paid to letters compared with colors and symbols

(Flowers et al., 2004), and a correlation could be observed between the activity level of this region and the performance of discrimination between letters and symbols (Garrett et al., 2000).

Although varying to some extent from one study to another, the localizations of the identified “letter sensitive area” are all situated in the occipitotemporal junction that also hosts the VWFA, and the question remains as to how these two regions relate. A recent study that addressed the selectivity for words together with isolated letters indicated, however, that these stimuli may recruit separate neural substrates (James et al., 2005). We found that the **(p.312)** region showing selectivity for single letters but not letter strings was situated in a fusiform region anterior to the VWFA, while the region showing selectivity for strings but not single letters overlapped with the VWFA.

Interaction with Other Cognitive Systems

Neuroimaging results have shown that our perceptual expertise with letters is subtended by a cerebral region located in the visual processing stream. Letters are a special kind of visual object whose identification may trigger activation in systems devoted to other modalities than vision, and we will now consider the possible impact of this interaction on the letter area.

Interactions with the Linguistic System

Writing systems are all designed to enable the translation of what are initially auditorily encoded items to be transferred into the visual modality. As such, letters are meant to cooperate with other cognitive systems pertaining to phonology or semantics, to activate words. In most models of reading, two ways of accessing words are usually implemented. The letter-to-sound is referred to as the grapho-phonological route, also called “indirect” because words meanings are mediated by their pronunciation. The word–meaning association (also called lexico-semantic route) is called “direct” since an orthographic representation of the word is directly mapped onto its signification. A meta-analysis of 35 neuroimaging studies of word and nonword reading suggested that these two possible ways to access words have a common starting point in the left ventral occipitotemporal region for the direct (lexico-semantic) and indirect (grapho-phonological) routes of reading (Jobard, Crivello, & Tzourio-Mazoyer, 2003). The meta-analysis identified activation peaks for direct route contrasts (words > pseudowords, Kanji[2] words > Kana words and Kanji words > fixation, lexical or semantic decision > phonological decision, irregular words > regular words) and indirect route contrasts (the opposite of the direct route contrasts). It was indeed found that the left ventral occipitotemporal region contained peaks for both routes. Hence, it seems that all the stages subsequent to the visual analysis of letter strings rely on left-lateralized networks, independently of the two possible routes used to process them. Other studies have also shown that characters in alphabetic and nonalphabetic writing systems recruit highly overlapping regions in the left occipitotemporal cortex (Bolger, Perfetti, & Schneider, 2005; Wong et al., 2009) and cause enhancement of the same early electrophysiological component (Wong et al., 2005), despite the greater reliance on the indirect route for alphabetic languages for their regular grapheme-to-phoneme correspondence. The need to communicate with regions involved in various components of the **(p.313)** linguistic system may therefore constitute a constraint related to the hemisphere in which the letter-selective area can establish.

Sensorimotor Interactions

Recent research has suggested that visual perception of objects may access stored information that is multimodal, depending upon how we learn and experience the given object. For example, visual identification of objects that we interact with motorically not only involves visual processing but also automatically activates motor areas of the brain (Bartolomeo et al., 2002; Boronat et al., 2004; Buccino et al., 2005; Chao & Martin, 2000; Grezes & Decety, 2002; James et al., 2006; Kato et al., 1999; Longcamp et al., 2005; Mecklinger et al., 2002; James & Atwood, 2008). Presumably this activation is due to our sensorimotor experience with the objects, as the motor cortices are not engaged when we perceive objects with which we do not usually interact motorically, such as faces, animals, and buildings (Grezes & Decety, 2002).

We not only learn letters visually, but we also learn to write them, which may establish letter-specific motor programs. We have recently found that simply perceiving letters activates motor regions of the brain, and writing letters (without seeing them) activates visual areas of the brain (James & Gauthier, 2006; see also Longcamp et al., 2005), resulting in a letter processing "network" (Figure 10.2). Recent work has shown that handwriting perception activates motor cortices more than print perception (Longcamp et al., 2006). The neural activation to individual letters that we do not see to

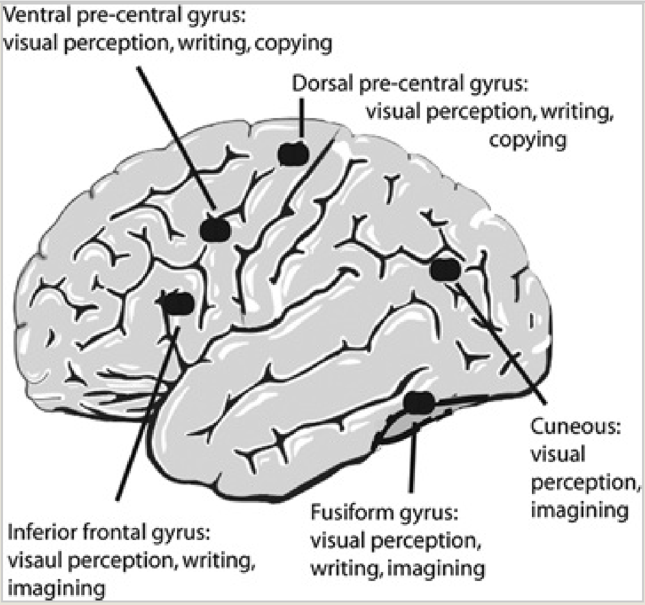

Figure 10.2 Schematic of a sensorimotor network of neural activation patterns found to letters but not to other, similar shapes (used with permission from K. H. James and I. Gauthier, 2006, "Letter processing automatically recruits a sensory-motor brain network," *Neuropsychologia* (4), with permission of Elsevier).

(p.314) letter strings (James et al, 2005) can be explained in terms of motor efferents.

That is, we write words letter-by-letter, and therefore, we may have a motor program associated with individual letters but not with words per se (independently of the constituant letters). Furthermore, we have also shown that other forms such as pseudoletters (letter-like symbols) activate letter-selective areas of the brain only after writing training (James & Atwood, 2009, see also Longcamp et al., 2008). That is, practice writing pseudoletters results in left fusiform gyrus and left precentral gyrus activation that is not apparent after typing training or visual-only training on the same pseudoletters. The selective processing that we, and others, have observed for letter perception may be due partly to the involvement of the motor system in processing these stimuli. In fact, we have recently seen the emergence of a letter-selective area in the left fusiform gyrus in preliterate children as they learn how to print letters that is not present if children are exposed to letters with visual only practice (James, in press). These results suggest that the development of the ventral "letter area" may be reliant upon, at least partially, our writing experience (James & Gauthier, 2006).

The Perceptual Specificities of Letters

Apart from the fact that letter identification uniquely necessitates the cooperation of visual with linguistic and sensorimotor processes, letters are also unique as visual objects in regard to their perceptual characteristics. Three aspects of perceptual processing could contribute to the special nature of letters: spatiotemporal properties, task demand, and geometry of individual letters.

Spatiotemporal Properties

Co-occurrence

The fact that letters tend to occur together in space and time has been suggested as a reason why letters form a special category of objects. Polk and colleagues (Polk & Farah, 1998; Polk et al., 2002) offered a co-occurrence hypothesis to account for neural selectivity for letters. According to this account, letter selectivity is a result of the close occurrence of letters in terms of time and spatial location (with themselves but not with other object types) in the environment, captured by correlation-based mechanisms of neural learning. Their network model makes some natural predictions about letter representations in the brain. First, segregated cortical areas for letters should be more common and robust than other object categories, like digits, because letters appear more frequently with each other than digits occur with each other. Also, separate neural substrates should be recruited by different object categories because co-occurrence occurs much more frequently within, than between categories (Polk & Farah, 1995).

Nonetheless, some fMRI results are hard to reconcile with the idea that co-occurrence alone can account for neural selectivity for letters. First, with **(p.315)** fixation as a baseline, Polk and colleagues observed a high degree of overlap between letter- and digit-selective areas, despite the low co-occurrence of letters and digits for most people. Similarly, using unfamiliar characters as baseline, our recent fMRI work used unfamiliar characters as control and found an overlap of activations not only between letters and digits (James et al., 2005), but also between Roman and Chinese characters in bilinguals (Wong et al., 2009). Such findings seem to contradict the co-occurrence model's predictions and suggest that co-occurrence is not likely the only cause for the neural selectivity for letter perception, at least not at the coarse scale in the order of millimeters. However, other properties accompanying the spatiotemporal co-occurrence of letters may play a role, as discussed below.

Regularity in Orientation

Letters tend to appear not only in clusters close in space and time but also with a coherent style (as in words and passages). Given that reading requires fast letter perception, it would be advantageous to utilize such regularity to help meet the high demand on speed. Behavioral studies have shown that regularity of, for example, orientation, across different letter instances is extracted, leading to more efficient letter and word perception (e.g. Jolicoeur, 1990). Triplets of uppercase letters were presented, and participants named the letters with a higher accuracy when the orientation was regular for the three letters (e.g. all rotated for 60° clockwise, i.e., 60°) than when the orientation changed. Orientation change was less detrimental when it was gradual and along a fixed direction than when it was random, even with the average disorientation of the letters controlled for the two conditions. These results suggest that identification of a letter is sensitive to the relative orientation of other neighboring letters.

Sensitivity to the regularity in orientation has also been shown for novel characters (Gauthier & Tarr, 1997), though only among structurally similar ones that presumably belong to the same “basic-level” (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976) category. In that study, participants first learned to name two-dimensional line shapes in a canonical orientation. Later, they were asked to name the same shapes presented one by one in several different orientations presented in random order. A typical view sensitivity pattern was found, with performance the best at the canonical view and deteriorating more with larger view difference from the canonical view. The viewpoint cost was greatly reduced when orientations were blocked, suggesting the use of orientation information of an object to facilitate subsequent identification. This orientation priming effect, however, only eliminated the viewpoint cost for similar shapes (e.g.  and ) but not between less similar shapes (e.g.  and ), which indicates that orientation tuning may occur only for objects within the same basic-level category. Another study also found that orientation priming did not occur between objects from different basic-level categories; for example, a 60° horse does not facilitate subsequent recognition of a 60° chair (McKone & Grenfell, 1999).

(p.316) Here we see one important difference between the orientation priming patterns for letters and common objects. Whereas orientation priming does not occur across basic levels for objects, it exists for letters that differ greatly in shape and thus constitute different basic-level categories (e.g. B, V, C). One likely reason involves our differential experience with letters and objects. The prolonged experience of perceiving clusters of letters in the same orientation may result in the formation of transletter features, or strengthening of connections between units representing different letters in the same orientation, both of which would lead to orientation priming.

Regularity in Font

Apart from orientation, font also occurs with a high regularity in texts. It has been demonstrated that letters are identified faster within a string with the same font compared with a string with mixed fonts (Sanocki, 1987, 1988, 1991b, 1992). A recent study suggested that such font tuning effects may occur only for certain type of font changes (aspect ratio) and may depend on expertise (Gauthier et al., 2006). That is, font tuning effects were found only with familiar characters (e.g. Roman letters for English readers, Roman letters or Chinese characters for Chinese readers) but not novel ones (e.g. Chinese characters for English readers).

It is a reasonable postulate that the use of regularity in font or style for letters in text can be one of those characteristics that make letter perception different from the perception of other objects. Although there are also cases where objects appear in a coherent style (e.g. different types of furniture in a particular designing style), such regularity may not be used as extensively as for letters for several reasons. First, regularity in style occurs more frequently for letters (almost every time one sees a text) than for other objects. More importantly, there is a higher demand for speed on letter perception (as a result of a large number of letters to be processed during reading) than on object perception, resulting in a larger driving force for the visual system to utilize whatever is useful in the stimuli (such as font regularity) to increase efficiency in letter perception.

Different mechanisms underlying font tuning have been suggested. One involves the explicit, separate representation of information about letter identity and style. According to some accounts, a letter contains both a letter concept and font parameters (Hofstadter & McGraw, 1995; Sanocki, 1988). A letter concept is an abstract description of the parts of a letter and how they are connected (e.g. a “p” has a post and a loop attached to its upper right). Font parameters describe the variations in the parts (e.g. length of the post and curvature of the loop in “p”). During reading, to recover the letter concepts and thus efficiently recognize the letters, one has to also establish the parameter values for the styles and factor them out from the letter description. Such parameter value establishments cost time, and it would help to have a regular font and style since no new parameters need to be determined. In other words, with font regularity in a text, one would be able **(p.317)** to utilize the font information of the current letter to facilitate abstraction of letter concept information of subsequent letters. Computational studies in the field of optical character recognition (OCR) have also suggested that performance of OCR programs deteriorates with font variations, and that explicit extraction of font information improves recognition accuracy (Baird & Nagy, 1994; Chaudhuri & Garain, 2001). This is analogous to some studies suggesting that extraction of certain speaker characteristics (e.g. pitch) facilitates speech recognition (e.g. Hariharan & Viikki, 2002).

Contrary to the abstractionist view mentioned above, one can also explain font tuning in terms of retrieval of exemplars or instances in memory (Logan, 1988). It was suggested that the same letter in different fonts is represented and stored as different instances (Sanocki, 1992). Texts with regular fonts will improve letter recognition because the greater similarities of same-font letters (as opposed to different-font letters) result in the currently perceived letter activating representations of other letters of the same font to a greater extent. A similar nonabstractionist, instance-based account has also been suggested for handling speaker variability in speech recognition (Goldinger, 1998; Pisoni, 1993).

The instance-based account is more consistent with behavioral and neural findings. In an identification task with backward-masked strings, it was found that accuracy was lowered when a change in size or style occurred. Importantly, the reduction in performance was the same whether the size, the style, or both size and style changed (Sanocki, 1991c). In another study where participants judged if a string contained all letters or one nonletter, one subset of letters was first presented and later a new subset was used without any warning. Performance was lowered when a new set of letters in the same font was used, to a similar extent as when a new set of letters in a new font or the same set of letters in a new font was used (Sanocki, 1992). In other words, keeping the font unchanged did not reduce the costs of switching to a new set of letters. These findings suggest that font-specific letter instances are represented as separate entities. Neuroimaging work also supports the possibility of exemplar representations for letters. The letter-selective areas in the ventral occipitotemporal cortex showed more adaptation to the same letter presented repeatedly in the same font compared with the same letter presented consecutively in different fonts (Gauthier, Tarr, et al., 2000). These studies provide support for the storage of exemplars instead of the separated representations of letter concepts and font parameters.

Task Demand

Generalization across Cases

Different cases exist in certain writing systems (e.g. Latin, Greek, Cyrillic, and Armenian alphabets) but not others (e.g. Arabic, Hebrew, and Georgian alphabets, Kanji, and Kana). Case generalization, the ability to name or perceive two examples of a letter presented in a different case at the same **(p.318)** efficiency as two different letters presented in the same case, has been demonstrated repeatedly in priming experiments (e.g. Bowers et al., 1991; Bowers, Vigliocco, & Haan, 1998; Evett & Humphreys, 1981). However, in naming tasks, letters of different case are named more slowly than two identical letters presented in the same case (e.g. Posner, Boies, Eichelman, & Taylor, 1969, Posner & Boies, 1971), indicating imperfect generalization. This being said, the demand for case generalization has historically been thought to be somewhat unique to letter perception.

Two lines of research have addressed the representations for letters in different cases (e.g. Coltheart, 1981; Posner, 1978; Posner & Boies, 1971; Posner et al., 1969; Rynard & Besner, 1987). Posner and colleagues postulated two types of codes, visual codes and phonetic (name) codes, for the representation of letters. For instance, while “A” and “a” are represented by two different visual codes, they share the same phonetic codes (Posner, 1978; Posner & Boies, 1971; Posner & Mitchell, 1967; Posner et al., 1969). Based on the results that response time in a name match task was faster for physically identical (e.g. AA) pairs than pairs with the same name but differing visually (e.g. Aa), Posner and colleagues postulate that the visual code is computed followed by the phonetic code, which allows for generalization of letter recognition across cases. Follow-up studies by other labs have also offered support for a level of phonetic letter representation, in that naming performance was worse for phonologically similar letter pairs like “D” and “p” than phonological dissimilar pairs like “F” and “h” (Dainoff & Haber, 1970; Ellis, 1981; Marmurek, 1985).

The idea of the phonetic nature of the name code has been challenged by researchers arguing instead that an abstract letter identity is the representation for the same letter across cases. Besner and colleagues asked participants to perform speeded classification on two simultaneously presented letter strings based on physical matches (i.e., respond “same” only to the same strings in the same case but not in different cases) (Besner & Coldheart et al., 1984). In different trials, it was harder to say “different” when the strings shared the same abstract letter identities (e.g. HILE/hile) and differed in case, compared with the condition when the strings shared the same phonological code but differed in spelling (e.g. HILE/hyle). In other studies, no phonological effect has been found (Arguin and Bub 1995; Boles and Eveland, 1983). In a letter-matching task, response time was similar in the different conditions with either phonologically similar (e.g. “A” and “j”) or dissimilar pairs (e.g. “A” and “z”). It has also been suggested that the phonological effects found in some earlier studies (Dainoff and Haber, 1970; Ellis, 1981) were purely a result of the use of reversible letters (e.g. “p,” the mirror image of which is another letter, “q”) in the phonologically confusable condition (Bigsby, 1988). This provides support for the notion that letter abstraction does not require an intermediary based on phonology.

Neuropsychological studies have also identified patients who failed to name letters but could match the upper and lower cases of the same letter **(p.319)** (Bigsby, 1990; Coltheart, 1981; Mycroft, Hanley, & Kay, 2002; Rynard & Besner, 1987). Recently, an fMRI study revealed that a posterior portion of the fusiform area showed masked priming of letters across cases, suggesting that the area may be responsible for representing abstract letter identities (Dehaene et al., 2004).

Contrary to what has been suggested above, one could argue that the demand for case generalization may not play a large role in the recruitment of specialized mechanisms for letter perception. The rationale is that the mechanisms underlying case generalization may not be distinct from similar processes that occur for object recognition in general. Imaging studies have located common areas in the occipitotemporal cortex not only for Roman letters but also for characters that do not involve case, such as Chinese and Japanese characters (Bolger et al., 2005; Wong et al., in press). In addition, in most cases of reading, letters appear in the same case (except for the initial letter of a proper noun or the initial word of a sentence). The demand for treating the upper- and lowercase versions of letters as the same may not be that high. In fact, case can provide important information about syntax (e.g. capital letters at the beginning of a statement) and meanings (e.g. to indicate an emphasis), and sensitivity to case changes within a word is often found (Mayall, Humphrey, & Olson, 1997). Also, the underlying mechanisms for case generalization may not be any different from other processes related to object perception, such as 3-D viewpoint generalization. Different views of an object have been shown to vary to a greater degree than similar views of different objects. For example, image analyses have shown a larger difference between different views of a face than the same view of different faces (Ullman, 1989). One way to recognize different views of an object is to arbitrarily assign the different view-specific representations of an object to the same category in memory. Generalization of object recognition to familiar and novel views could be achieved by a system with object units receiving a weighted sum of inputs from a few view-specific units (Bülthoff & Edelman, 1992; Poggio, 1990; Wong & Hayward, 2005). Neurons in the inferotemporal cortex are also able to associate pairs of visually distinct patterns (Sakai & Miyashita, 1991). Research is needed to determine whether similar mechanisms are used for assigning the same letter in different cases to the same category.

Resolution Demand

There are two different views concerning the resolution demand required for letter perception. Some suggest that letter perception is an extreme case of object perception requiring a high resolution. Others regard letter perception as not particularly demanding in terms of analyses of detail.

The idea of letter perception requiring a high resolution comes from studies of eccentricity biases associated with different object categories (Hasson et al., 2002; Hasson, Harel, Levy, & Malach, 2003; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Levy, Hasson, Harel, & Malach 2004; Malach, Levy, & Hasson, 2002). Accordingly, a continuum exists such that **(p.320)** at one extreme there are substrates with a foveal bias and thus the capacity for object analyses at high resolutions, while at the other extreme substrates manifest a peripheral bias and low spatial resolutions. Evidence comes from studies showing that areas selective for different object categories seem to follow the distribution of the areas showing preference for foveal or peripheral presentation, with letter- and face-selective areas overlapping with the fovea-bias regions whereas building-selective areas with the periphery-biased regions (more details discussed in the next section). Words and letters represent the extreme case of object perception requiring high resolution and foveation, even more so than face recognition. Therefore, letters engage regions that are even more fovea-biased than faces.

In contrast with the view described above, one can regard letter perception as a less demanding task than face perception in terms of analysis of detail (Wong & Gauthier, 2007). We learn the optimum procedure for letter recognition with repeated experience at an early age. The recognition demands that are placed on the visual system for letter recognition are quite different than those for other types of objects. For instance, our usual task during object recognition is to simply recognize that a chair is a chair so that we may sit down. Recognizing that a chair is a chair requires that we realize that it is not a bed, or a table—a decision that requires distinguishing objects that are very different in their overall shape. This type of decision has been called one of "basic-level discrimination" (Rosch et al., 1976). We can also distinguish one chair from another—which may require a finer-grained analysis of features, rather than distinguishing overall shape. This is often called “subordinate-level” categorization and is based more on second-order relations among parts, such as distances from one part to another as well as size and shape of individual parts. While basic-level categorization is the default task demand during recognition of the majority of common objects, subordinate-level categorization is thought to underlie most face recognition tasks (Gauthier, Tarr, et al., 2000). Letter recognition, though also a type of perceptual expertise, requires decisions to be made at the basic level. That is, many letters are of very different overall shapes, requiring one to disregard slight variations in second-order similarities (e.g. individual differences in how the lower case “b” is written). Extensive experience with characters in a particular writing system results in a greater ability to discriminate and use basic-level differences in images while efficiently filtering out subordinate-level noise like font and handwriting (Gauthier et al., 2006). Such difference in recognition demand leads to opposite phenomena associated with letter and face perception: whereas expertise with a character set is associated with a larger basic-level advantage (better performance for basic- than subordinate-level recognition), expertise with faces is typically linked to a shrink in this advantage (Wong & Gauthier, 2007). Similarly, Zhang and Cottrell have shown that a network trained for discriminating among letters was not as good as a face discrimination network in performing a fine-grained discrimination task on blob patterns (each with four blobs forming a Y-shape-like configuration) that differ in small shifts in the blob locations **(p.321)** (Zhang & Cottrell, 2004). These suggest that letter perception requires a lower resolution than face perception.

The basic-/subordinate-level account and the eccentricity bias theory characterize letter and face perception differently because they focus on different aspects of object perception. According to the eccentricity bias theory, the conclusion that letter perception requires a higher resolution than face perception is based on these premises and findings: (1) The changes in the ventral occipitotemporal region have to be continuous from low resolution in the medial portion to high resolution in the lateral portion; (2) letter-selective areas are more lateral than face-selective areas; and (3) letters appear smaller than faces in general, and their perception thus requires a higher resolution. The levels-of-categorization account, however, stresses the difference in within-category homogeneity between letters, other objects, and faces. It does not consider the size differences between letters and faces as they appear in daily-life situations. Nor does it assume continuous biases for processes along the ventral occipitotemporal region. Further work could help resolve the differences by teasing apart the effects of different factors like size and within-category homogeneity.

Constraints from a Fixed Letter Set

Another unique aspect of letter processing concerns the limited number of instances and features involved in perception and recognition. Letters or characters in a particular writing system consist of a limited number of features combined in different ways. An expert system can possibly utilize this characteristic to limit the features to be considered during letter perception. A study by Rouder suggested such possibility (Rouder, 2001). He examined the effect of the number of alternatives on the efficiency of line length identification and letter identification. Results demonstrated that having fewer alternatives to choose from facilitated line length identification but not letter identification. While Rouder (2001) gives no account for this difference, one explanation lies in our expertise with letters. For identification of unfamiliar stimuli like lines of different lengths, having fewer alternatives may increase efficiency by drawing attention to certain length values. For letters, however, we are used to identifying one letter out of the 26 alternatives in real-life contexts. The prolonged experience of considering all features or letters useful for this task may render us less flexible. So even when there are fewer alternatives and fewer features can be considered, we cannot take advantage of this, and identification thus does not benefit from fewer alternatives.

That letter perception involves a limited set of items differentiates it from the perception of other objects, where the set is open. As described above, such a set property provides various constraints to facilitate letter perception. Various types of connections between different features' nodes are likely to capture such information. The word-to-letter-level and the letter-to-feature-level constraints are achieved by the feedback connections, while the Rouder results are likely contributed by lateral connections among features and **(p.322)** obligatory use of stored exemplars (Logan, 1988). The rich connectivity between and within levels may be a reason for the segregation of neural substrates for letter perception.

Conclusion

Letter perception has been heavily studied in the context of reading, and relatively less emphasis has been placed on the underlying visual mechanisms in letter processing. This chapter is aimed at discussing the mechanisms involved in visual letter perception that may distinguish it from processing of other objects and other types of perceptual expertise. The selectivity of certain neural substrates for letter perception may be explained by a comprehensive consideration of the stimulus characteristics, and experience associated with letter perception. Letter perception requires putting perceptually dissimilar instances such as the same letter in different fonts and cases into the same category, in contrast with face perception requiring discrimination among highly similar instances. In addition, the emphasis on speed for letter perception may have urged an experienced reader to utilize the regularities (e.g. in terms of font type) available in texts. Our motor and linguistic experiences with letters also may require neural processing that is different from that of some other objects and faces. One postulate is that the high-level visual system, as reflected in ventral occipitotemporal processing, contains different units with different pre-existing biases. Some parts of the high-level visual system are associated with certain objects because of the representations and processes suitable for the stimulus characteristics and perceptual demands for those objects. Experience plays a role in forming such associations between certain objects and neural substrates. In the end, a good theory of perceptual expertise with objects should not only explain the computational and implementation similarities and differences among expertise with different objects, but also predict what behavioral and neural markers are associated with object expertise.

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Notes:

(1) Defined as ordered pairs of letters coding for a given word: “take” would be coded by the units TA, TK, TE, AK, AE, and KE.

(2) Kanji and Kana refer to two different writing systems used in Japan. Kanji are ideograms that are sometimes arbitrarily associated to a meaning, while Kana refer to syllables of the Japanese language.