A TALE OF TWO RECOGNITION SYSTEMS: IMPLICATIONS OF THE FUSIFORM FACE AREA AND THE VISUAL WORD FORM AREA FOR LATERALIZED OBJECT RECOGNITION MODELS

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ABSTRACT

Two areas of current intense interest in the neuroimaging literature are that of the visual word form area (VWFA) and of the fusiform face area (FFA) and their roles in word and face perception respectively. These two areas are of particular relevance to laterality research because visual word identification and face identification have long been shown to be especially lateralized to the left hemisphere and the right hemisphere respectively. This review therefore seeks to evaluate their significance for the broader understanding of lateralization of object recognition. A multi-level model of lateralized object recognition is proposed based on a combination of behavioral and neuroimaging findings. Rather than seek to characterize hemispheric asymmetries according to a single principle (e.g., serial-parallel), it is suggested that current observations can be understood in terms of three asymmetric levels of processing, using the framework of the Janus model of hemispheric function. It is suggested that the left hemisphere represents features using an abstract-category code whereas the RH utilizes a specific-exemplar code. The relationships between these features are also coded asymmetrically, with the LH relying on associative co-occurrence values and the RH relying on spatial metrics. Finally, the LH controlled selection system focuses on isolating features and the RH focuses on conjoining features. It is suggested that each hemisphere utilizes efficient (apparently parallel) processing when stimuli are congruent with its preferred processing style and inefficient (apparently serial) processing when they are not, resulting in the typical left-lateralization for orthographic analysis and right-lateralization for face analysis.

Key Words

Laterality, Faces, Words, Visual Word Form Area, Fusiform Face Area, Object Recognition

INTRODUCTION

A long-standing unresolved topic in cognitive neuroscience is the nature of hemispheric asymmetries in cognitive function. While many observations have contributed to the various models (for a review, see Dien, 2008), one of the most important is that the left hemisphere (LH) is generally better at identifying Roman letters/Arabic numbers/English words and the right hemisphere (RH) is generally better at identifying faces (Geffen, Bradshaw, & Wallace, 1971; Hilliard, 1973; Klein, Moscovitch, & Vigna, 1976; Marcel & Rajan, 1975; Mishkin & Forgays, 1952; Pirozzolo & Rayner, 1977; Rizzolatti, Umilta, & Berlucchi, 1971), although laterality patterns seem to depend on a number of parameters (White, 1969). In the laterality literature, there are three primary accounts for this particular observation but each has encountered difficulties that have raised doubts about their applicability. Recent neuroimaging findings provide new insights into this issue. These two literatures are complementary in that the behavioral literature has given rise to most of the theoretical treatments of lateralized object recognition whereas the neuroimaging literature has provided a rich trove of new information that nonetheless has thus far largely not been applied to issues of laterality. This review will therefore seek to utilize these new findings to generate an updated model of lateralized object recognition. But first, a brief review of visual half-field and neuroimaging methodologies since this review is directed at readers from both areas of research, who may therefore not be familiar with both approaches.

VISUAL HALF-FIELD STUDIES

The majority of laterality research has been conducted using the visual half-field technique (Banich, 2003; Bourne, 2006) in which a lateral presentation of stimuli causes initial processing to occur in only one hemisphere (Franz, 1933). Lateral presentations have this effect because the visual system is organized so that peripherally presented visual information is directed to the contralateral hemisphere. Although both hemispheres eventually have access to the information, studies demonstrate differences in both accuracy and latency of responses depending on the field of presentation for many tasks. To facilitate discussion, stimuli presented to the right visual field (RVF) will be described as LH presentations and left visual field (LVF) presentations will be termed RH presentation, with the understanding that the information is in fact eventually shared bilaterally.

There are two main accounts for these visual half-field effects. The callosal relay model holds that laterality effects reflect an inability by one hemisphere to carry out a task, such that when stimuli are presented to it there is a need to relay it to the competent hemisphere, resulting in increased reaction time (Geffen et al., 1971; Moscovitch, 1970; Rizzolatti et al., 1971). In addition, there may be both reaction time delays and decreased accuracy if the relayed percept is degraded in the process. The direct access model (Geffen et al., 1971) holds that laterality effects reflect a tendency for the initial hemisphere to take control of the processing and that differences in performance reflect differential proficiencies of the two hemispheres (for an in depth consideration of the implications of these two accounts for visual asymmetry measures, see Moscovitch, 1986).

Neuroimaging and lesion studies provide support for both models. Evidence for the callosal relay model is provided by a functional magnetic resonance imaging (fMRI) study (Cohen et al., 2002) reporting that the VWFA (which they implicitly defined as a mid-fusiform activation responsive to alphabetic stimuli) is left-lateralized regardless of in which visual field the stimulus appears. If the left-lateralization had been due to hemispheric efficiency, then they would have obtained activations contralateral to the side of presentation (albeit stronger for right visual field presentations). Evidence for the direct access model is provided by an fMRI study (Hemond, Kanwisher, & Op de Beeck, 2007) of object and face processing that was preferentially contralateral in visual cortex selective for these stimuli including the FFA, although less so for the fusiform region, and another study that reported widespread activations contralateral to picture presentation (Schiffer et al., 2004). A lesion study (Buchtel, 2001) using the visual half-field method reported evidence for both positions in that face recognition in both visual fields was impaired by RH lesions whereas simple letter judgments were impaired only by lesions contralateral to the visual field of presentation.

NEUROIMAGING STUDIES

Neuroimaging methods, defined in this case as fMRI and positron emission tomography (PET), have the potential to provide important information for laterality studies. Unlike visual half-field methods, it is possible to present stimuli at foveation, a more common circumstance. They also allow for direct measures of which hemisphere is mediating a computation. Furthermore, it is possible to be more specific about the neural basis of a computation than simply which hemisphere is involved. A particularly powerful method is repetition priming (Henson & Rugg, 2003), which capitalizes on the tendency for neuronal populations to habituate to repetitions of identical stimuli. This effect makes it possible to determine what stimulus variations are considered to be equivalent by a neuronal area.

On the other hand, neuroimaging methods also have a number of limitations. Most importantly, not all neural effects are expected to register in such a measure. For example, it has been noted (Kanwisher, Tong, & Nakayama, 1998) that an effect of face inversion seen in event-related potential (ERP) studies is a small delay in the N170 neural response (Jeffreys, 1989; Perrett et al., 1988; Rossion et al., 2000b); such a delay would not be visible in the blood oxygenation level dependent (BOLD) response used by most PET and fMRI studies since it has poor temporal resolution. Also, neuroimaging measures are correlates and therefore cannot by themselves be used to infer causality.

Nonetheless, PET and fMRI methods have a clear potential to contribute to laterality research. It is therefore somewhat surprising how limited such efforts have actually been. For example, although all neuroimaging studies necessarily produce data that can be assessed for lateralized effects, very few apply the necessary statistical tests to do so. The absence of such testing makes it difficult to draw inferences about lateralized activity. There are a number of reasons for why such testing has been limited. Many studies use a type of exploratory statistic that identifies clusters of significant voxels. While this method includes corrections for multiple comparisons, taking an additional step of contrasting effects with that of the homologous region in the other hemisphere would risk bias towards the original hemisphere. Another issue is that the hemispheres are physically not entirely symmetrical (Mechelli, Friston, Frackowiak, & Price, 2005; Watkins et al., 2001) and so it might not be appropriate to use the same coordinates in the other hemisphere, even if a normalization procedure is used to constrain both hemispheres to having the same morphology (see Stevens, Calhoun, & Kiehl, 2005). Finally, assessing laterality of effects adds an additional factor of complication that is often irrelevant to the goals of a research report. Thus, although this review will highlight points of correspondence between the behavioral and neuroimaging findings, it would be best to keep in mind these caveats. There is especially a need to conduct more visual half-field experiments using neuroimaging methods in order to better bridge the two literatures.

Finally, it may be helpful to define two terms more precisely than has been the practice. In the neuroimaging literature on orthographic and face processing, the term “area” has been central to certain core debates but not directly defined. The implicit definition appears to be that “area” refers to a circumscribed neural territory whose cortical columns share a common functionality, such that at the spatial resolution of fMRI technology they appear to be activating in concert in experiments. For the purposes of the following definition, the term “region” will be defined as a larger circumscribed neural territory containing multiple areas, as just defined, that can be usefully described as sharing some functionality in common.

GENERAL MODELS OF LATERALIZED OBJECT RECOGNITION

The LH-Verbal/RH-Visuospatial Model

The oldest of the three traditional laterality models, the LH-verbal/RH-visuospatial model, starts with the early observations (e.g., Broca, 1865) that language disorders such as aphasias generally arise from left hemisphere lesions. In contrast, it was observed that neglect cases typically arise from right hemisphere lesions (Brain, 1941; Vallar, 2001). Neglect patients tend to ignore the left side of space in spite of demonstrating intact vision. The spatial nature of this and other disorders linked to the right hemisphere led to the formulation that the right hemisphere mediates “visuospatial” processing, in contrast to the verbal functions of the left hemisphere (Milner, 1958; Kimura, 1973; Milner, 1971). Thus, orthographic analysis would be left-lateralized and face analysis (which involves spatial processing) would be right-lateralized.

While the LH-verbal/RH-visuospatial model continues to be a useful guideline, visual half-field studies suggest that not only can both hemispheres make judgments in both the verbal and spatial domains, they both display superiority in some aspects of each domain. For example, Kosslyn and colleagues (1989) reported that the LH is especially capable at judging categorical spatial relations (such as “in” or “out”). Conversely, RH language skills have their own points of strength (Lindell, 2006; Zaidel, 2001), such as for metaphorical phrases (Bottini et al., 1994; Giora, 2002).

With respect to orthography, while studies of (apparently) monolingual English-speakers (Bouma, 1987; Dimond, 1971; Gross, 1972; Marcel & Rajan, 1975; Miller & Turner, 1973; Mishkin & Forgays, 1952; Neill, Sampson, & Gribben, 1971; Pirozzolo & Rayner, 1977; Terrace, 1959; Turner & Miller, 1975), Dutch speakers (Bouma, 1973), and Hebrew-speakers (Babkoff & Ben-Uriah, 1983; Eviatar & Ibrahim, 2007; Faust, Kravetz, & Babkoff, 1993; Koriat, 1985; Lavidor, Ellis, & Pansky, 2002) have reported that word and consonant-string recognition shows a LH advantage, using lexical decision, forced choice, stimulus report, and semantic categorization tasks, RH dominance has been found under conditions of perceptual degradation (Sergent & Hellige, 1986; Sergent, 1983). Furthermore, lateral masks (Polich, 1978) and visual distractors (Marsolek, Schacter, & Nicholas, 1996) can increase RH advantage, as well as short stimulus durations (Ellis, Ansorge, & Lavidor, 2007; Marsolek & Hudson, 1999; Pring, 1981) and difficult to read word sizes (Pring, 1981). These latter observations are not consistent with a pure LH-verbal/RH-visuospatial view that language should be entirely left-lateralized as one would expect that difficult viewing conditions should instead accentuate the advantage of the left hemisphere.

Finally, although one could argue that face recognition findings are genetically determined in a domain-specific fashion given the strong association of such stimuli with the FFA, the even stronger association of the VWFA with words (a stimulus type too recent for the VWFA to be credibly attributed to a genetic basis) suggests that genetically determined domain-specific mechanisms need not be involved (Kleinschmidt & Cohen, 2006; Reddy & Kanwisher, 2006). It therefore seems reasonable to seek general organizational principles that could give rise to such asymmetry patterns in object recognition.

The LH-Analytic/RH-Configural Model

The second of the three laterality models is that the LH is characterized by analytic processing and the RH is characterized by configural processing (Bradshaw & Nettleton, 1981)[1]. This distinction has in turn usually been operationalized as a LH orientation towards serial analysis of stimuli (as each individual feature is examined in turn) and a RH orientation towards parallel analysis of stimuli (with configural analysis being applied holistically). In this view, LH analytic/serial analysis is especially suited for the sequential nature of words and RH configural/ parallel analysis being especially suited for the simultaneous analysis of multiple facial features.

The LH-analytic/RH-configural distinction has generally been supported for studies of face recognition. The starting place of this research is the postulate that the RH might be defined as "configural," meaning that it utilizes parallel information about spatial relations, in contrast to a LH system that serially focuses on components (Carey & Diamond, 1977). It was further proposed that inverting faces disrupts this configural analysis (face inversion studies reviewed in Rossion & Gauthier, 2002; Valentine, 1988). In support of this hypothesis, they (Carey & Diamond, 1977) presented evidence for two face recognition systems (with the configural one not developing till about ten years of age) by demonstrating that children below this age were not impaired by face inversion but were easily confused by simple disguises (such as a hat or glasses) while older children showed the reverse pattern. The interpretation of these results is that younger children focus on individual components and hence are confused by simple changes even when they do not obscure the face; in contrast, older children focus on the overall configuration, making them resistant to the effects of simple changes but making them vulnerable to manipulations that interfere with analysis of the overall face, such as face inversion. The hypothesis that these two systems might be lateralized was not tested in this study. Subsequent studies have supported this general account while establishing a more gradual developmental time course (Flin, 1985).

Further studies helped confirm that the process affected by inversion is indeed spatial in nature (Leder, Candrian, Huber, & Bruce, 2001; Rhodes, Brake, & Atkinson, 1993) and that inversion produces a shift to a serial component search strategy (Barton, Keenan, & Bass, 2001; Searcy & Bartlett, 1996). It has also been demonstrated that this face inversion effect is perceptual in nature and not due to effects of encoding in long-term memory (Freire, Lee, & Symons, 2000).

Finally, studies have indicated that these two perceptual systems are lateralized by showing that the inversion effect preferentially affects RH processing. An early study found that patients with right posterior lesions were impaired in recognizing upright faces but not reliably different from controls for inverted faces (Yin, 1970). Also, a RH superiority occurs for making judgments for upright but not inverted faces (Leehey, Carey, Diamond, & Cahn, 1978).

Face inversion studies overall suggest that "configural" in this context comprises at the least four types of information (Searcy & Bartlett, 1996). The first has been termed first-order spatial information (Diamond & Carey, 1986), which is the general visual schema that allows a face to be recognized as such (e.g., location of eyes, nose, and mouth). The second has to do with deviations from a norm for this schema and has been termed second-order spatial information (Diamond & Carey, 1986). The third is holistic information or the extent to which the features have been represented as a single indivisible whole, just as the eyes can be represented as a whole rather than as a set of separate features like the iris and the eye lashes (Tanaka & Farah, 1993). The fourth is the particular combination of features that characterize a specific face, where spatial information is either not relevant or is at most treated as an additional feature without special status (Sergent, 1984).

Although the last is not always included due to its apparently non-spatial nature (see Maurer, Grand, & Mondloch, 2002), the ability to detect simultaneous changes in multiple features as opposed to an isolated feature has been shown to be specially affected by inversion (Hillger & Koenig, 1991; Sergent, 1984) and to be right-lateralized (Hillger & Koenig, 1991; Patterson & Bradshaw, 1975). Apparently the use of multiple simultaneous feature changes encourages the use of a RH strategy as opposed to a LH serial top-down scan (Sergent, 1982a) even though in principle the participant could just focus on a single feature. All four meanings of "configural" have been reported to be affected similarly by laterality and inversion manipulations so this paper will treat all four meanings as sub-types of "configural."

Overall, these face studies reveal LH serial search of features and RH parallel configural analysis. For example, visual half-field studies have demonstrated a LH superiority for detecting changes in a single feature but a RH superiority for configural (multiple) changes (Hillger & Koenig, 1991; Patterson & Bradshaw, 1975). Evidence suggests that the LH strategy is to conduct a serial top-down search for feature changes (Sergent, 1982a) but no such pattern is seen in the RH data. Furthermore, the RH advantage for configural changes is cancelled by inverted presentations (Hillger & Koenig, 1991).

However, if anything, evidence seems to indicate that orthographic processing actually reverses the pattern with LH being parallel and RH being serial. As one might expect from a serial analysis wherein each letter is analyzed one at a time, the RH, but not the LH, has a longer reaction time for longer words (Bouma, 1973; Bub & Lewine, 1988; Ellis, Young, & Anderson, 1988; Gill & McKeever, 1974; Iacoboni & Zaidel, 1996; Lavidor et al., 2002; Lavidor, 2005; Melville, 1957; Young & Ellis, 1985 for a nice review, see Ellis, 2004). Additional support for this observation comes from the study of a split-brain patient who displayed similarly divergent effects for words presented to the two hemispheres (Reuter-Lorenz & Baynes, 1992). Furthermore, length-independent reading is disrupted by posterior LH, but not RH, disruption by repetitive transmagnetic stimulation or rTMS (Skarratt & Lavidor, 2006). According to the modes of processing model (Young & Ellis, 1985; Ellis et al., 1988; Ellis, 2004), there are two modes of lexical processing, Mode A and Mode B (Young & Ellis, 1985; Ellis et al., 1988; Ellis, 2004). Mode A is only available in the LH and involves efficient, parallel analysis of the word forms. Mode B is available in both hemispheres and involves translation of the letters into abstracted letter-level graphemes (resulting in length effects due to the need to process each of the letters) that can then access the LH lexicon (Ellis, 2004).

A possible solution for this puzzle (of serial LH for faces but serial RH for orthography) is to suggest that serial versus parallel is not a valid operational definition for LH-analytic/RH-configural. Although serial has usually been associated with analytic and parallel with configural, this need not be the case. It will therefore be argued that the LH is indeed analytic at some levels and the RH is indeed configural at some levels but that this does not in turn result in the LH being reliably serial in its operations and the RH being reliably parallel in its operations. Instead, it is argued it is better to conceptualize “parallel” results as being indicative of processing that is so efficient that the added time accruing from additional features is not detectable (see Wolfe, 1998). In such a view, “serial” results reflect a mismatch between the stimulus and the hemisphere’s preferred mode of processing, resulting in inefficient processing. Thus, the RH analyzes words inefficiently because its preferred approach (of which configural analysis is a part) is not applicable and the LH analyzes faces inefficiently because its preferred approach (of which analytic analysis is a part) is generally not applicable. Finally, it is argued that the difficulties in mapping serial versus parallel onto the LH-analytic/RH-configural model is a sign that it is an incomplete description of the hemispheric asymmetries.

The LH-High Frequency/RH-Low Frequency Model

The third and most recent model is the LH-high frequency/RH-low frequency model. In this laterality account, the left hemisphere is specialized for high frequency information and the right hemisphere is specialized for low frequency information (Sergent, 1982b; Sergent, 1983). Such a difference is explained as being due to asymmetries in the size of the receptive fields used to analyze the sensory information, with (for example) larger fields resulting in lower spatial frequencies for visual information. The most recent iteration of this model is the double filtering by frequency theory or DFF (Ivry & Robertson, 1998), which postulates a relative difference between the hemispheres, centered on initial attentionally selected frequencies. By this account, words are especially suited for the LH capacity to tell apart the fine differences in letter shapes whereas faces are especially suited for the RH capacity to discern broad differences in facial configuration.

This model is applied in essentially three forms. The first is the simple observation of differences in sensory acuity between the hemispheres. The second is to explain other hemispheric dichotomies in terms of underlying confounds with frequency (see Sergent, 1982b). The third is to invoke the underlying mechanism of receptive field differences to explain how other types of asymmetries might arise (see Kosslyn, Chabris, Marsolek, & Koenig, 1992).

While this model is currently the most influential laterality model of perceptual processing, there have been a series of conflicting studies that suggest the need for further elaboration of this model (for a brief review, see Dien, 2008). Nonetheless, the frequency model may very well be correct. However, it is argued that in order to develop a more complete understanding of these asymmetries, it is helpful to adopt a componential approach to the cognitive processes involved (see Moscovitch, 1979). Even if asymmetries in frequency analysis lie at the base of the lateralized differences at each level of processing, the effects of these asymmetries seem to manifest in different ways at each level and need to be characterized accordingly. As will be seen, a number of asymmetries are not directly predictable by the frequency model. In order to carry out this componential approach, the present review will focus solely on visual object recognition and the stages involved in this process.

THE VISUAL WORD FORM AREA AND THE FUSIFORM FACE AREA

New insights for updating laterality models are provided by two neural regions (the visual word form area, VWFA, and the fusiform face area, FFA) that reliably correlate with word and face recognition respectively. Not only are the two areas both lateralized into opposite hemispheres, they are located in very similar positions, namely the left (VWFA: [-44 -68 -4] Cohen, Jobert, Le Bihan, & Dehaene, 2004) and right (FFA: [38 -50 -7] Gauthier, Skudlarski, Gore, & Anderson, 2000a) fusiform gyri, although the FFA is anterior to the VWFA. It therefore seems reasonable to suggest that these findings might shed light on lateralized object recognition.

The VWFA is a region in the left fusiform region that seems to be responsive to orthographically regular letter strings (Petersen, Fox, Posner, Mintun, & Raichle, 1988), although the localization of the original VWFA varied somewhat from later reports (Cohen et al., 2000). This responsiveness to even nonsense words, as long as they are spelled according to the conventions of the reader’s native tongue, was interpreted as evidence that it reflects a lexical level word form representation, independent of semantic meaning. It is thought that such a lexical representation serves as an intermediate step in the translation of written words into semantic meaning (Reicher, 1969; Wheeler, 1970). Also, the VWFA is not sensitive to side of visual field presentation, indicating that it represents a functionally lateralized process (Cohen et al., 2002).

Although there has been a vigorous debate regarding whether the VWFA is indeed specialized for visual word form analysis or has a more general role (Cohen & Dehaene, 2004; Price & Devlin, 2003; Reinke, Fernandes, Schwindt, O'Craven, & Grady, 2008; Starrfelt & Gerlach, 2007), for the purposes of the present review this issue is not important. The inferences drawn from the VWFA studies would be equally applicable to a general model of lateralized object recognition regardless of whether the VWFA is dedicated solely to visual word analysis (with neighboring areas responsible for other types of stimuli) or whether it processes many types of stimuli.

The most relevant data on lateralized face recognition processing is provided by neuroimaging studies of the fusiform face area (FFA). The FFA has been the subject of a particularly spirited and productive debate amongst proponents of three hypotheses. The expertise hypothesis proposes that the FFA embodies an expertise system for faces and other stimuli that require a "holistic" representation (Bukach, Gauthier, & Tarr, 2006; Gauthier & Palmeri, 2002; Palmeri & Gauthier, 2004; Tarr & Gauthier, 2000), based on the LH-analytic/RH-configural view. The domain-specificity position is that the FFA is specifically devoted to analysis of faces (Kanwisher, 2000), based on the LH-verbal/RH-visuospatial view. The object form topography position (Haxby et al., 2001) takes the view that the FFA essentially does not exist as a discrete area (Hanson, Matsuka, & Haxby, 2004); instead, it views object representations as involving distributed activation patterns that overlap widely without any areas having any special properties.

As with the VWFA, the question of whether the FFA is a generalized configural module or is just one of many domain-specific configural modules is not pertinent to the present review as long as it can be used to infer some general principles of RH object recognition. There does appear to be a strengthening consensus of a RH configural analysis role at what could be termed the regional level. For example, it has been suggested by the side arguing for face-specificity of the FFA that although the FFA may be specialized for faces, it may have differentiated from the local neuronal pool due to intense practice (Reddy & Kanwisher, 2006), consistent with single-unit observations of cat and dog stimuli (Freedman, Riesenhuber, Poggio, & Miller, 2006) and configural fish and face stimuli (Sigala & Logothetis, 2002). Thus, regardless of the final disposition of the FFA debate, there appears to be a growing consensus on the configural capabilities of the RH fusiform region.

A more critical concern is to address the view implicit in the object form topography position that the FFA may not be right-lateralized, given that it holds the FFA does not even exist.

Indeed, a prominent review (Haxby, Hoffman, & Gobbini, 2000) of the literature by this camp did not even discuss laterality, aside from a sample figure where it was noted that the activations were bilateral. Although reviews of the neuroimaging literature have noted a general tendency for FFA activations to be right-lateralized (Cabeza & Nyberg, 1997; Cabeza & Nyberg, 2000), there has been no systematic effort to evaluate this issue.

A review of the literature uncovered only seven studies where an explicit statistical test was conducted on FFA lateralization. Of these, four reported RH lateralization (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Haxby et al., 1999; Ishai, Schmidt, & Boesiger, 2005; Rhodes, Byatt, Michie, & Puce, 2004), two reported a non-significant trend towards RH lateralization (Gilaie-Dotan & Malach, 2007; Puce, Allison, Gore, & McCarthy, 1995), and two reported bilateral activity (Haxby et al., 1991; Ishai, Haxby, & Ungerleider, 2002). This sampling suggests a general tendency for right-lateralization but is too limited to make broad statements, especially since the decision to test lateralization could be biased by the observed results. The limited number of studies explicitly testing laterality further underscores the need for a stronger consideration of the laterality perspective in this literature, a goal of this present review.

Given this rather inconclusive set of reports, a broad, but by no means comprehensive, sample of 116 published reports was evaluated to determine overall trends (selected blind to the laterality patterns). Studies were included in the sample if they utilized either PET or fMRI methodologies, either described face vs. non-face results or face localizer results, used a young adult healthy sample, reported results from static neutral faces (since motion or emotional expressions could potentially introduce unrelated RH activity), and did not reanalyze a study already in the sample. Only studies reporting peak voxels or centroids within 12 mm of the FFA X- and Y- coordinates reported in a study chosen as the reference point ([38 -50 -7] Gauthier et al., 2000a) were included (the z-axis coordinates ranged as far down as -24). When bilateral activations were reported, lateralization was based on reported peak amplitudes or statistical scores (studies providing only measures of cluster size, figures that could not be unambiguously categorized, or only single subject-level results were excluded). Of this sample, 57 did not meet criteria, 51 reported greater RH activation and 8 reported greater LH activation[2]. According to a chi-square test (Likelihood Ratio), this ratio is significantly different from being equally distributed between LH and RH: 34.96, $p < .0001$.

Thus, this rough analysis supports the characterization of the FFA as being generally right-lateralized (in a relative rather than absolute sense), consistent with the overall behavioral evidence. Since reports do not consistently distinguish between the LH and RH FFA, the following discussion will describe the responses of the bilateral FFA except where noted (keeping in mind that it tends to be relatively right-lateralized).

Although this meta-analysis demonstrates a reliable tendency for the RH to be strongly activated by faces, the degree of lateralization is clearly variable with occasional reversals to LH lateralization. It is likely that various experiment parameters contribute to the overall lateralization pattern. For example, it has been suggested (Kanwisher, McDermott, & Chun, 1997) that contrasting faces against objects may enhance the right-lateralization by subtracting out more general object recognition processes. Indeed, amongst the studies explicitly testing for laterality, three of the four reporting RH lateralization used artificial objects called greebles (Gauthier et al., 1999), houses (Haxby et al., 1999), or a combination of insects and objects (Rhodes et al., 2004) as the comparison conditions (each using a fixation subtraction) while the four reporting no significant difference used fixation (Gilaie-Dotan & Malach, 2007), dot matching (Haxby et al., 1991), or scrambled faces (Ishai et al., 2002; Puce et al., 1995). On the other hand, one of the significantly RH lateralized studies (Ishai et al., 2005) also used scrambled faces, so other factors seem to be at work as well. There is a need for a study to examine this issue more explicitly. In general, though, it would seem that, as with the behavioral literature, the view that face recognition is solely right-lateralized is not supported.

MULTI-LEVEL MODEL OF OBJECT RECOGNITION

As has been seen, these three generalized laterality models not been successful at accounting for asymmetries in word and face processing. It may be that any effort to find a single differentiating principle (e.g., serial-parallel) for the entire object recognition system might be an ill-posed question. For now, at least, it may be more fruitful to focus on a single level of mental functions at a time. Thus, rather than make a single generalization across levels of cognitive processing, one might characterize the nature of laterality differences separately at each level. The reasoning behind this approach is that the differences only need to work adaptively together without having to derive from the same asymmetry principles at each level (Dien, 2008). While this adaptive approach is inspired by the Janus model (Dien, 2008) and is consistent with its overall framework, this multi-level lateralized object recognition model can stand on its own and will be presented as such.

It will be argued that one can understand these findings in terms of asymmetries at three separate levels of processing: feature representation, feature relations, and controlled selection, consistent with the hierarchical nature of current neural models of object recognition (Haxby et al., 2000; Riesenhuber & Poggio, 1999; Ullman, Vidal-Naquet, & Sali, 2002; Ullman, 2007) and the participation of top-down influences (Fenske, Aminoff, Gronau, & Bar, 2006; Freedman, Riesenhuber, Poggio, & Miller, 2001; Freedman, Riesenhuber, Poggio, & Miller, 2002). It is the combined effects of these asymmetries that result in the overall left-lateralization for orthogaphic analysis and the right-lateralization for face recognition, even though both hemispheres can be dominant for aspects of both types of stimuli (contrary to the LH-verbal/RH-visuospatial model).

FEATURE REPRESENTATION

It is argued that at the level of representing features, the two hemispheres use qualitatively different codes. This position is best embodied in the neural subsystems model (Marsolek, Kosslyn, & Squire, 1992; Marsolek et al., 1996; Marsolek, 2004; Marsolek & Andresen, 2005) which argues that object recognition, of which orthographic analysis is treated as a special case, relies on two subsystems, one specialized for abstract-category codes and one specialized for specific-exemplar codes. The abstract-category subsystem is said to use feature-based analysis whereas the specific-exemplar subsystem is said to use whole-based analysis (Marsolek et al., 1996; Marsolek & Andresen, 2005). For example, the specific-exemplar system would be sensitive to the holistic form differentiating between different cases or fonts whereas the abstract-category subsystem would be oriented towards generalizing between such variant forms by focusing on relatively invariant features. With respect to laterality, while both systems are proposed to exist in both hemispheres, the abstract-category subsystem is stronger in the LH and the specific-exemplar subsystem is stronger in the RH, hence the LH should be better at generalizing across case variations.

Some of the best evidence for the view that the LH can utilize an abstract-category representation comes from studies of the VWFA. The VWFA is case-insensitive in repetition priming (Dehaene et al., 2001; Dehaene et al., 2004), whereas a case-dependent priming effect was observed in the RH in the lateral occipital area (Dehaene et al., 2001). These observations are consistent with proposals that these priming effects reflect a left-lateralized abstract lexical representation and a right-lateralized perceptually specific representation. The VWFA also shows evidence of an abstracted representation in that it is not affected by a shift in the retinal position between repetitions but it is still sensitive to changes in the ordering of the letters, as in anagrams (Dehaene et al., 2004) and in that it responds to mixed case words more than pure case consonant strings (Polk & Farah, 2002).

Conversely, reports of novelty effects in the FFA provide suggest that facial features themselves are being represented in the RH using specific-exemplar codes. Detection of novelty requires coding stimuli in a specific-exemplar fashion in order to detect novelty at the individual (rather than categorical) level. Several studies (Eger, Schyns, & Kleinschmidt, 2004; Eger, Schweinberger, Dolan, & Henson, 2005; Gauthier et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005c; Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007c) have noted that face repetition effects emerge most strongly in the RH FFA, producing a progressive diminution of response as the repeated stimuli become increasingly less novel.

A particularly interesting study (Rotshtein, Henson, Treves, Driver, & Dolan, 2005) used faces that were morphed along a continuum between two famous faces (so a 70% face was a mix of 70% of the first face and 30% of the other face). Using a repetition priming design, it was reported that the RH FFA responded more strongly to the second face when the pairs consisted of 70% and 40% (which were perceived as being different people) than when the pairs consisted of 100% and 70% (which were perceived as being the same people). In contrast, the RH OFA was more responsive to the physical differences in 100% and 70% pairs. This observation suggests that the RH FFA is responsive not just to repetition of physical identity *per se* but to whatever aspects of a face subjectively distinguish it from other faces.

This right-lateralized novelty effect can also be seen in the effect of prolonged familiarization with photos prior to the scanning session (Rossion, Schiltz, & Crommelinck, 2003; Rossion, Schiltz, Robaye, Pirenne, & Crommelinck, 2001). An exception to this right-lateralized pattern (Gobbini & Haxby, 2006) used a familiarization task consisting of learning individual features, a process that has been shown to be left-lateralized (e.g., Hillger & Koenig, 1991) and which neuroimaging data (Rossion et al., 2000a) indicates is associated with the LH FFA.

While the classic view is that face recognition is right-lateralized and that one would therefore expect only to see right-lateralized activity that would habituate with repeated exposures, other findings suggest an increase in LH activity as well. Such an observation would be consistent with the account that the left hemisphere has an increasing role in face recognition over repeated exposures as an abstract-category code develops. For example, compared to a gender judgment task, photos briefly studied a minute before the scanning session evoked a RH FFA activation but photos thoroughly studied a week before the session evoked a LH FFA activation (Wiser et al., 2000). If the gender judgment task is taken as an estimate of the baseline, an increase in LH FFA activity is being seen in addition to the reduction in RH FFA activity. Such an interpretation of a left hemisphere role in face recognition would also account for the repeated findings of LH FFA (and no RH FFA) activity to presentations of one's own photograph (Sugiura et al., 2000; Sugiura et al., 2005).

FEATURE RELATIONS

In addition to representing features, it is also necessary to represent the relationship between these features. A particularly dramatic example of a dissociation between feature representations and feature relations was provided by a patient with object agnosia, but not prosopagnosia, who could recognize faces but not the component features, even when the face was made of objects such as fruits (Moscovitch, Winocur, & Behrmann, 1997). Another supporting example is a patient with integrative agnosia, who appears to have a selective impairment of representation of spatial arrangement but with intact representation of parts (Behrmann, Peterson, Moscovitch, & Suzuki, 2006).

According to the leading model (Kosslyn, 1987; Kosslyn, 1994), the core distinction is between qualitative differences (LH-categorical) and quantitative differences (RH-coordinate). For example, it has been demonstrated that participants are quicker to judge categorical relations (e.g., above versus below) with LH presentations and are quicker to judge coordinate relations (e.g., 3 millimeter distance versus more) with RH presentations (Hellige & Michimata, 1989; Kosslyn et al., 1989). It has been proposed on the basis of computer simulations (Kosslyn et al., 1992) that this distinction emerges from the differential receptive fields that are thought to underly the LH-high frequency/RH-low frequency asymmetry.

It is proposed herein that it might be helpful to conceptualize LH relational codes as being not just categorical but also associative. The LH superiority for categorical relations could in principle be mediated by a coding system for association values that ignored metric distances, at least to a point. Thus, all values of "outside" would count as "not associated" and all values of "inside" would count as "associated". The strength of the association would be determined by frequency of co-occurrence (e.g., rarely appearing "inside" would be "low association" and frequently appearing "inside" would be "high association"). Thus, rather than being a hemispheric distinction between qualitative (LH) and quantitative (RH) information, it would be between two different types of quantitative information.

VWFA studies provide the strongest evidence that the LH focuses on these sorts of associative relationships. Evidence suggests that this ventral temporal region conducts an ongoing Hebbian analysis of associations between letters (Polk & Farah, 1995; Polk & Farah, 1997). Such an analysis would focus on local co-occurrences of the letters, such as that "q" and "u" tend to appear together in the English language, making it possible to quickly analyze orthographic regularities. Such a process would also help explain why two such arbitrarily categorized stimuli as letters and numbers seem to be represented in different cortical regions (Polk & Farah, 1998). In this view, the VWFA mediates analysis of visual word forms into bigrams (letter pairs) as part of a series of steps forming representations of increasingly larger fragments of words (Dehaene, Cohen, Sigman, & Vinckier, 2005), a hypothesis that is supported by the observation (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006) that VWFA activity is correlated with the frequency of bigrams in non-orthographic non-words, not just words. This observation could also account for a report that the VWFA correlates with word frequency (Kronbichler et al., 2004), insofar as word frequency and token-based bigram parameters are related (Novick & Sherman, 2004); note also a failure to replicate the fusiform word frequency effect (Carreiras, Mechelli, & Price, 2006).

Conversely, the FFA literature on face recognition provides some of the best evidence for RH configural coding. If one accepts the general consensus that prosopagnosia is produced by right-lateralized injuries, sometimes exacerbated by additional LH damage (Ettlin et al., 1992; Farah, 1990), then support for an explicit distance representation in the RH process is provided by the observation that prosopagnosics are impaired at within-object distances for both faces and dot pairs (Barton & Cherkasova, 2005); furthermore, the distance judgment deficit was observed only for within-face distances, not between-face distances, suggesting that it represented a deficit in configural processing rather than a more general deficit in processing spatial information. This study provides an interesting suggestion for why some RH lesion patients might display difficulty with configural judgments for stimuli such as faces while not showing impairment on other types of spatial judgments. Thus overall, hemispheric superiority for face judgments seems to depend on whether the task requires analytic or configural processing (Sergent & Bindra, 1981).

Further support for the configural aspect of face recognition and the RH can be found in developmental studies. It has been found that cataracts in the first few months of infancy result in permanent inability to make configural judgments on faces, defined as feature spacing (Le Grand, Mondloch, Maurer, & Brent, 2001). A further study (Le Grand, Mondloch, Maurer, & Brent, 2003) capitalized on the observation that for the first 24 months of infancy information from one eye is conveyed almost entirely to just the contralateral hemisphere. They showed that unilateral cataracts in infancy that block RH, but not LH, vision result in permanent loss of configural (feature spacing) processing of faces.

The increasing left-lateralization with increasing face familiarity could be understood as reflecting the strengthening associative relationships between the facial features. Based on this reasoning, it would be reasonable to predict that the LH representation is relatively insensitive to metric information, thus allowing it to recognize a wide array of stimuli as being members of the same face or word class based on the co-occurrence of the constituent abstracted features. It would be interesting to examine the effect of configural manipulations on the LH FFA self-face effect. In doing so, it would be necessary to keep in mind the possibility that certain feature combinations (such as a pair of eyes or even the entire face) have been learned by the LH as a single unit, much as repeated practice judging a specific distance can change the right-lateralization of this metric task into a left-lateralization (Banich & Federmeier, 1999; Kosslyn et al., 1989). It appears that the LH is indeed capable of representing metric distances, but requires repeated exposures to a specific unvarying stimulus, and it is suggested that this takes place by learning the pair of features as a single integrated feature whereas the ability to represent metric distances between separately learned features is right-lateralized.

An emphasis on pairwise associations, as in the bigrams proposed for the VWFA (Dehaene et al., 2005), would result in a particular strength for representing chains of stimuli, such as linear arrays (as well, in principle, as closed figures and branched figures). It would be especially interesting to determine if a monkey is capable of developing a left hemisphere VWFA equivalent with sufficient exposure to orthographically regular stimuli during development just as they already seem to have a right hemisphere FFA (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003; Tsao, Freiwald, Tootell, & Livingstone, 2006) because it would help confirm that orthography developed to take advantage of pre-existing, genetically determined properties of the VWFA rather than the other way around, in contrast to the currently dominant view that the evolutionary development of language resulted in the left-lateralization of related cognitive functions (see Corballis, Funnell, & Gazzaniga, 2000). It should be noted that the proposal that the LH object recognition system is especially facile at linear arrays is distinct from the proposition that it is serial in nature (Bradshaw & Nettleton, 1981; Cohen, 1973) as the latter is defined as a consecutive analysis of the individual items whereas expertise at linear sets of stimuli does not rule out parallel analysis (see also Polich, 1982).

CONTROLLED SELECTION

At the level of controlled selection, it is hypothesized that the LH has a superiority for isolating out a single feature and the RH has a superiority for conjoining multiple features. Some of the best evidence for this distinction come from studies of configural processing of faces. As noted earlier, one of the sub-types of RH configural analysis is the monitoring of a combination of features without regard to their spatial positioning.

This proposal is especially well supported by a PET investigation (Rossion et al., 2000a) of the FFA activity while processing faces or houses. Participants were presented with pairs of either houses or faces in sequential order. In the configural condition they were asked to match them based on the entire form and in the analytical condition they were asked to match them based on a single feature. The second stimulus could differ on one or all of the relevant features. In this case, “configural” was therefore operationalized as a change in multiple features. In the contrast between the analytical and configural face conditions, the RH FFA activity was significantly increased by the configural condition and the LH FFA activity was significantly increased by the analytical condition. No effect was seen in the OFA. The effects were sizeable with percentage changes of 1.56% and 1.51% respectively, compared to the face-house difference of 1.67% in the LH FFA and 2.85% in the RH FFA.

This proposal of a separate asymmetry at the controlled selection level addresses the theoretically anomalous evidence (Hillger & Koenig, 1991; Patterson & Bradshaw, 1975) that configural processing of faces, defined as being disrupted by inversion and being right-lateralized, includes making judgments about simultaneous changes in multiple features (Sergent, 1984). Such a definition raises conceptual questions about how “configural” information is instantiated at the neural level, given the non-spatial nature of this type of “configural” manipulation. It is possible that this aspect of “configural” involves the additional modulation of the FFA by other RH regions, such as the parietal cortex (for an example involving the LH parietal in reading, see Vinckier et al., 2006). A divided-visual field behavioral study (Smith et al., 2005) that indicates the potential of such an approach reported that when participants were trained to identify artificial four-legged animals defined as having a combination of certain features, they initially showed a LH advantage for distinguishing them from animals that did not have the appropriate combination of features that shifted to a RH advantage after extensive training; a critical question is whether the FFA would mirror this behavioral effect.

It is suggested that this combinatorial aspect of “configural” information reflects a RH process different in kind from that of the other “configural” information. It may instead reflect a process at the level of controlled selection. From this point of view, the face studies suggest that the LH mediates isolating a feature from surrounding features for further analysis whereas the RH mediates conjoining features for further analysis. Thus, tasks with either verbal (Hardyck, Tzeng, & Wang, 1977; Miller & Butler, 1980) or face (Hillger & Koenig, 1991; Rossion et al., 2000a) stimuli were left-lateralized when they involved remembering a limited set and comparing them to a target stimulus. Since monitoring a single facial feature is left-lateralized, it would appear that this effect is not domain-specific. Conversely, remembering changes in a set of facial features appears to be right-lateralized (Hillger & Koenig, 1991; Sergent, 1984). It may be that some kind of spatial working memory is being used to conjoin the features into a temporary configural representation. Support for this view comes from neuroimaging studies (not using verbal stimuli) reporting lateralized prefrontal activations for shape versus location cues (Ventre-Dominey et al., 2005) and categorical versus coordinate relations (Slotnick & Moo, 2006).

Making this distinction between the act of attentionally conjoining features (as in monitoring changes in a set of different features) and detecting changes in the metric distances between features would address the conceptually awkward proposition that there is a single RH "configural" specialization that is able to mediate both types of tasks; instead, they would be reflections of two entirely different RH capabilities that are nonetheless complementary. Some evidence supporting this distinction is the report (Rotshtein, Geng, Driver, & Dolan, 2007a) that changes in multiple features activated the RH FFA but changes in second-order information significantly activated only the RH intraparietal sulcus, with additional activation in other areas including the RH FFA only when individual differences in using spatial information was factored in.

ISSUES TO BE RESOLVED

The Face Inversion Effect

An issue that needs further discussion is that of the face inversion effect. Many of the present arguments are based on the effects of face inversion on "configural" analysis and yet the results of testing the inversion effect on the FFA have been mixed. Positive reports have found that the FFA displayed diminished activation for inverted faces (Kanwisher et al., 1998) that, unlike the STS, which also evidenced an inversion effect, correlated with the behavioral inversion effect (Yovel & Kanwisher, 2005). It was further observed in a third study (Mazard, Schiltz, & Rossion, 2006) that this inversion effect appears to occur because the FFA initially responds to both orientations but, when differing faces are used, there is recovery from the repetition priming for the upright faces but not the inverted faces, consistent with the inverted faces "all looking the same," resulting in smaller responses to the inverted faces. Given the strength of these results and their clear correspondence to behavioral studies, it is an unresolved question why other studies have yielded a bewildering mix of results including inversion effects in the OFA but not the FFA (Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006), enhanced RH FFA activation and LH OFA for inverted faces (Joseph et al., 2006), enhanced activation to inverted faces in fusiform object areas but not FFA (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999), and finally diminished activation only in the STS and not the FFA (Leube et al., 2003). There are also questions about the laterality of the FFA effect, with two of the three positive studies not reporting laterality (Kanwisher et al., 1998; Yovel & Kanwisher, 2005) and the third (Mazard et al., 2006) apparently finding the inversion effect to be larger in the LH FFA, although laterality was not explicitly tested.

The most direct challenge to the inversion effect in the FFA being an indicator of configural processing is posed by an fMRI study (Yovel & Kanwisher, 2004) that examined faces and houses, manipulating inversion, and type of change (features or second-order spatial information). Participants judged whether two successive presentations of faces were the same or different and instructions were given before every block as to whether there would be feature or spatial changes during that block. Feature changes could be both the eyes and the mouth and spatial changes could be both the lip-nose and the inter-eye distances. The paper reported that while an inversion effect was seen for faces and not houses, the inversion manipulation did not interact with the spatial manipulations, either in the behavioral or fMRI data (for additional reports in behavioral studies, see Rhodes, Hayward, & Winkler, 2006; Riesenhuber, Jarudi, Gilad, & Sinha, 2004). This is a critical finding since the effect of inversion on making second-order spatial judgments is at the center of the argument that inversion impairs configural processing rather than face-specific processing.

The authors (Yovel & Kanwisher, 2004) suggested that the reason no inversion effect was seen in the spatial judgments is that prior studies were flawed because, unlike in their own study,: 1) they manipulated colors as a feature change (which could be mediated by very low-level perceptual processes and therefore would not be an appropriate comparison), 2) the feature task was easier than the spatial task and therefore inversion had an enhanced effect on it, or 3) difficulty levels were not set at a moderate level resulting in floor/ceiling effects. While this was certainly a well-constructed study, it might be somewhat premature to dismiss such a large body of studies. For example, a visual half-field experiment (Hillger & Koenig, 1991) that reported a face inversion effect on configuration judgments for the RH: 1) did not use color changes, 2) did have a feature task that was harder, not easier, than the configural task, and 3) had moderate difficulty levels.

They (Yovel & Kanwisher, 2004) also reported no task effect in the FFA activation levels, further arguing against a special role of the right FFA in the analysis of inter-feature distances. However, this null effect conflicts with that of an earlier study (Rossion et al., 2000a) that did find an FFA effect such that the left FFA was more active when matching faces based on a single feature and the right FFA was more active when matching faces based on configural changes, meaning that all three features changed. Yovel and Kanwisher (2004) argued that this discrepancy was not an issue since in their own study the participants focused on the whole face whereas in the prior fMRI study participants focused only on one feature in the feature change condition (p. 891). This observation may hold the key to resolving these divergent findings. As noted earlier, detecting multiple feature changes apparently invokes the same RH configural mechanisms invoked by other configural manipulations (Hillger & Koenig, 1991; Patterson & Bradshaw, 1975; Sergent, 1984). It is therefore likely that the reason for the null result, both behavioral and fMRI, in the Yovel and Kanwisher (2004) experiment is that the experiment inadvertently invoked the RH configural mechanism in both conditions. This reasoning predicts that if stimuli had differed only in one feature, regardless of whether the participants were informed regarding which would be changing, they would have also found a smaller inversion effect for the feature condition than for the spatial manipulation condition. This parameter is apparently critical because it seems to induce participants to adopt a LH top-down serial scan strategy (Sergent, 1982a) rather than a parallel monitoring of all the features. The same applies to behavioral studies (Rhodes et al., 2006; Riesenhuber et al., 2004) and neuroimaging studies (Rotshtein et al., 2007a) that also changed multiple features. In sum, evidence does support the contention that the RH FFA activity reflects configural analysis and that this therefore suggests that the RH utilizes spatial metrics for coding featural interrelationships.

Similarly, it is suggested that other face inversion studies have not been sufficiently controlling the cognitive processes to obtain replicable results. It is now known that the FFA is quite responsive to strategic influences such as imagery (Ishai, Ungerleider, & Haxby, 2000), task set (Rossion et al., 2000a), and selective attention (Wojciulik, Kanwisher, & Driver, 1998). While theoretically face inversion is thought to minimize configural analysis, upright faces can be perceived either analytically or configurally. If the subject strategy is neither constrained nor monitored then it becomes unpredictable and potentially influenced by subtle experimental design variations. If the subjects are, for example, adopting a putatively LH analytical strategy then one would predict left-lateralized FFA activity (see Rossion et al., 2000a) with levels that could very well be comparable for both upright and inverted faces, leading to non-significant effects of inversion. As an example, in one such study (Haxby et al., 1999) the task was to detect scrambled faces amongst upright and inverted faces. If the subjects adopted a strategy of detecting when pairs of eyes did not appear in the middle of the face then they could execute the task successfully with a minimum of configural face processing.

It is therefore suggested that future studies explicitly control subject strategy, using designs already developed in the behavioral literature (cf. Rossion et al., 2000a). It would also be helpful to follow the suggestions (Mazard et al., 2006) to use differing faces and long epochs to maximize the inversion effect in repetition designs by increasing the opportunity for differential repetition recovery to develop. It has also been demonstrated (Moscovitch, Scullion, & Christie, 1976; Moscovitch, 1979) that lateralized face effects are strongest when stimulus conditions prevent a reliance on lower-level perceptual traces, as with inter-stimulus pattern masks or inter-stimulus periods of over 100 ms. Thus, it is likely that a study using simultaneous stimulus presentation (e.g., Joseph et al., 2006) may not show the normal inversion effect.

As an example, an fMRI study (Schiltz & Rossion, 2006) study that did control such strategic factors, linked the RH FFA to both the inversion effect and configural processing (in the holistic sense) by focusing on the composite face effect (Young, Hellawell, & Hay, 1987). The participants were presented with composite faces made of top and bottom halves separated by a white line and their task was to respond to rare top-halves colored red. In a given block, the top half was always the same and the bottom half was either unchanging or changing. Repetition priming was used to provide a covert measure of whether changes in the bottom half affected perception of the top half of the faces. Although overall responses to faces were quite comparable in the two FFAs, there was a marked right-lateralized holistic effect, with a much greater difference between the same and different blocks. Most importantly, this distinction between same and different blocks was largely eliminated by both inversion and misalignment of the two face halves, thus ruling out a direct effect of the bottom half on the neuronal response and supporting the configural interpretation of the effects.

The Mixed Case Effect

Another issue that needs further discussion is the mixed case effect. The contention that features are represented in the LH in an abstract-category form is based to a large extent on the reports (Dehaene et al., 2001; Dehaene et al., 2004) that the VWFA exhibits case-independent priming. However, a recent report (Kronbichler et al., in press) has found that mixed case (e.g., MiXeD) stimuli produce more VWFA activation than normally capitalized stimuli. This observation is echoed in ERP data currently being prepared for publication in my lab. These authors note that this finding seems to suggest that the VWFA is not in fact case-independent. There is insufficient data at this point to resolve these contradictory observations. One possibility is that the reports of case-independent priming (Dehaene et al., 2001; Dehaene et al., 2004) utilized subliminal primes whereas the mixed case study (Kronbichler et al., in press) did not, thereby resulting in contamination by top-down influences (as in extra attention being directed at the harder to read mixed case stimuli, resulting in increased activation even at the VWFA level of processing).

IMPLICATIONS FOR GENERAL MODELS OF LATERALITY

The reviewed literature further reinforced the conclusion that the LH-verbal/RH-visuospatial model is inadequate to accurately portray the observed patterns of asymmetries. For example, while face recognition is usually right-lateralized, factors such as familiarity were seen to reverse the pattern to left-lateralization. It also did not account for observations such as the RH sensitivity to novel faces.

The LH-analytic/RH-configural model fared better in this review but was seen to be too imprecise. Different types of asymmetries, notably at the feature relations level and the controlled selection level, are conflated together in the term “configural.” Furthermore, since serial analysis was seen not to be necessarily indicative of LH processing it is become unclear what “analytic” means. The present review shows that feature-by-feature analysis can be conducted in either hemisphere, left for faces and right for orthography. It is suggested by the present multi-level model that at the controlled selection level the LH is indeed analytic with a focus on isolating features from distractors. The term “analytic” is not, however, a useful descriptor of LH processing at the feature representation or feature relations levels. As for the serial vs. parallel distinction (in terms of the nature of cognitive processing rather than the operational definition of whether reaction time increases with number of features), it seems to only apply meaningfully to the level of controlled selection.

The LH-high frequency/RH-low frequency model was not directly addressed in this review. As noted earlier, this model is applied in three forms. It may very well play a role in the form of sensory acuity and to therefore contribute to the observed behavioral asymmetries in object recognition. In the form of confounds, frequency asymmetries could not be solely responsible for the observations reviewed in this paper. For example, the case-independent repetition priming in the VWFA seems inconsistent with such an account. High spatial frequencies should be more, not less, sensitive to the often subtle distinctions between upper and lower case letters. In the form of asymmetric receptive field sizes, it may very well be the underlying neural mechanism at every level of processing but it would still be necessary to characterize the asymmetries at each level of processing, much as studies of the underlying genetics do not obviate the need to study human behavior (in other words, one must avoid the error of reductionism). It may therefore be appropriate to treat feature perception as a fourth level of analysis (prior to feature representation), with spatial frequency asymmetries being its characteristic lateralized property. Whether receptive field asymmetries ultimately lie at the base of these different lateralized processes will require further study.

Although eschewing simple global dichotomies avoids the effort to oversimplify hemispheric asymmetries by attributing all observations to a single principle, such an approach has the opposite problem of potentially developing laundry lists of asymmetries without making sense of them in a manner that would further conceptual understanding or prediction of new findings. It is argued elsewhere (Dien, 2008) that although asymmetries may differ for each cognitive function, they may be understood in terms of their adaptive value for overall hemispheric roles. These three proposed hemispheric asymmetries are collectively consistent with the Janus model of laterality, which argues that the LH is adapted to respond to predictable events and the RH is adapted to respond to unpredictable events. Thus, the LH specializations could help it recognize a member of a predicted stimulus class (abstract-category) to trigger a planned action based on observed regularities (associative relations) in the environment and to focus attention on the stimulus predicted to be of importance (isolating selection). Conversely, the RH specializations would be especially helpful for identifying novel stimuli (specific-exemplar), or novel arrangements of stimuli (metric relations), that might signal an unexpected event that would require some kind of rapid response and to monitor multiple such stimuli (conjoining selection).

Some additional points need to be clarified with respect to the argument for the Janus model. It is not argued that one never needs to predict, for example, a specific exemplar (LH role but RH specialty). Darwinian selection is based on what is overall most adaptive and so any such mismatches would merely be a cost to what is an overall benefit. It is also not being argued that the LH cannot form expectations using RH specialties such as specific-exemplars. Hemispheric asymmetries are best thought of as being relative strengths, not absolute differences (Bradshaw & Nettleton, 1981). Finally, it should be said that while the Janus model provides a useful heuristic framework for understanding the pattern of asymmetries across the levels of processing, not all such asymmetries can be directly predicted from the model. Only functions that can relate directly to the LH role of acting on predicted events and the RH role of reacting to unexpected events serve as critical tests of the theory. Thus, asymmetries relating to detection of novelty, such as the representation of specific exemplars, should definitely be right-lateralized. In contrast, the asymmetries relating to controlled selection can arguably be said to be consistent with the Janus model but do not serve as critical tests since they do not relate as directly to the hypothesized hemispheric roles.

A final implication of this laterality review is the potential contribution of neuroimaging studies to the interpretation and understanding of visual half-field asymmetry findings. It has been argued (Moscovitch, 1986) that a visual half-field asymmetry due to direct access to the more efficient hemisphere should respond to manipulations at all processing stages whereas an asymmetry due to callosal relay delays should only respond only to manipulations of levels at, or prior to, the stage at which the first such interhemispheric transfer occurs. Evidence (Cohen et al., 2002) indicates that the VWFA is a case of callosal relay whereas it is unclear at present whether the FFA asymmetries reflects direct access or interhemispheric transfer. Further studies combining visual half-field techniques with neuroimaging measures are needed. If, for example, FFA response to one's own face continued to be left-lateralized even when presented to the left visual field whereas novel faces continued to be right-lateralized even when presented to the right visual field, then it would be an example of callosal relay.

CONCLUSION

Thus, it is argued that recognition of orthography and of faces shed light on more general lateralized object recognition processes. By synthesizing the behavioral and the neuroimaging literatures on these topics, it is proposed that these hemispheric asymmetries can be understood as being due to lateralized differences at the three levels of feature representation (LH abstract-category/RH specific-exemplar), feature relations (LH associative/RH metric), and controlled selection (LH isolating/RH conjoining).

This simple model builds on three existing models of object recognition. The neural subsystems model (Marsolek et al., 1992; Marsolek et al., 1996; Marsolek, 2004; Marsolek & Andresen, 2005), as described earlier, focuses on whether the objects are encoded in an abstract form or a specific-exemplar form. As such, it addresses the feature level but not the manner in which they are parsed and grouped and so this present model accepts and builds on this model by adding this new element. The categorical-coordinate model (Brooks & Cooper, 2006; Cooper & Wojan, 2000; Laeng, Shah, & Kosslyn, 1999; Laeng, Zarrinpar, & Kosslyn, 2003) differs from the neural subsystems model in that it focuses on the relationships between the features rather than the nature of the features themselves. Like the present model, it is based on the proposition that one should identify the different component cognitive subprocesses and characterize asymmetries for each one (Kosslyn, 1994). The categorical-coordinate model differs in that it characterizes inter-feature relations in terms of categorical versus metric relationships (Kosslyn et al., 1989; Kosslyn et al., 1992) rather than associative versus spatial relationships, although it is possible that associative relationships are simply the mechanism by which categorical spatial relationships are formed. The present model combines the two approaches in a fashion consistent with the fragment-based hierarchy model (Ullman, 2007; Ullman et al., 2002) that proposes that the visual system focuses on features of intermediate complexity and groups them hierarchically to form object representations. The present model builds on this approach by adding a laterality component and a deeper consideration of the nature of the featural interrelationships.

In summary, studies of the FFA and the VWFA have yielded new insights that necessitate a renewed appraisal of lateralized object recognition processes. The present manuscript demonstrates, in the context of visual object recognition, how a deeper application of neuroimaging findings to laterality theories may help advance them by switching to a more focused effort to determine the nature of lateralized differences at specific levels of processing (see Moscovitch, 1979).

FOOTNOTES

1) A seeming alternative to the LH-analytic/RH-configural model is the LH-analytic/RH-Gestalt Levy-Agresti and Sperry (1968) or LH-analytic/RH-holistic model (Nebes, 1978). In this view (at least the holistic version whereas the Gestalt version is not fully specified), the RH represents objects like faces not as a configural array of component features but rather as a single integrated representation. For the purposes of this paper the distinction between the LH-analytic/RH-configural and LH-analytic/RH-holistic models is not pertinent. Whether or not the memory representation is in the form of a configural array or a holistic representation that can be decomposed after retrieval is beyond the scope of this discussion. Indeed, it has been noted that "if by a configurational representation we mean one in which the spatial relations among the parts of a face are as important as the shapes of the individual parts themselves (Haig, 1984; Hosie, Ellis, & Haig, 1988), then we would suggest that the concepts of configurational representation and holistic representation are highly similar, and possibly identical" (Tanaka & Farah, 1993, p. 242). The key theoretical point at the heart of their argument is whether the features of an overall representation, be it a configural array or a holistic unity, are encoded in a manner that makes them independent of changes in the other elements of the representation; this paper takes no position on this question. This paper will therefore include this view within the LH-analytic/RH-configural approach.

2) Of these studies (Table 1), 23 reported only RH activations, 26 with bilateral activations greater in the RH, 1 indicating that the greatest activation was in the RH but with no information about the LH, 4 with bilateral activations greater in the LH, and 4 with only LH activations. There were also 9 reports where there were no peak activations within the prescribed region, although it is certainly possible that part of a cluster did include the FFA, 25 reports where the

group-level amplitude results were not available, 18 where the needed group-level coordinates were not available, two reports where only a RH activation was reported but did not indicate if the LH FFA was an ROI or just not analyzed, and three reports which were reanalyses of studies already in the sample.

TABLES

RH activations only
(Campanella et al., 2001; Clark et al., 1996; Clark, Maisog, & Haxby, 1998; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Eger et al., 2004; Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Gorno-Tempini & Price, 2001; Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Hofer et al., 2007; Joseph et al., 2006; Kim et al., 1999; Kuskowski & Pardo, 1999; Leube et al., 2003; Leveroni et al., 2000; Morris, Pelphrey, & McCarthy, 2007; Nakamura et al., 2000; Passarotti et al., 2003; Pourtois et al., 2005a; Rotshtein et al., 2007c; Sergent, MacDonald, & Zuck, 1994; Simons, Graham, Owen, Patterson, & Hodges, 2001; Sung, Kamba, & Ogawa, 2007; Wiser et al., 2000)
Bilateral activations greater in the RH
(Bokde et al., 2005; Caldara et al., 2006; Dubois et al., 1999; Eger et al., 2005; Epstein et al., 2006; Gauthier et al., 1999; Gilaie-Dotan & Malach, 2007; Golarai et al., 2007; Golby, Gabrieli, Chiao, & Eberhardt, 2001; Gorno-Tempini et al., 1998; Grill-Spector, Knouf, & Kanwisher, 2004; Haxby et al., 1994; Haxby et al., 1999; Henson, Shallice, & Dolan, 2000; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Ishai et al., 2000; Ishai et al., 2005; Kanwisher et al., 1997; Kelley et al., 1998; Kesler-West et al., 2001; Maurer et al., 2007; Puce et al., 1995; Reinholz & Pollmann, 2005; Rhodes et al., 2004; Rossion et al., 2000a; Shah et al., 2001; Sugiura et al., 2001)
Greatest activation was in the RH but no information about the LH
(Paller et al., 2003)
Bilateral activations greater in the LH
(Gobbini & Haxby, 2006; Lee, Scahill, & Graham, 2008; Mazard et al., 2006; Pourtois et al., 2005c)
LH activations only

(Iidaka, Matsumoto, Haneda, Okada, & Sadato, 2006; Katanoda, Yoshikawa, & Sugishita, 2000; Sugiura et al., 2000; Sugiura et al., 2005)
No activations
(Andreasen et al., 1996; Courtney, Ungerleider, Keil, & Haxby, 1996; George et al., 1999; Grady et al., 1996; Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Kim et al., 1999; Platek et al., 2006; Rossion et al., 2001; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005)
Group-level amplitude results were not available
(Aguirre et al., 1999; Alexander et al., 1999; Bernstein, Beig, Siegenthaler, & Grady, 2002; Chao, Martin, & Haxby, 1999; Gauthier et al., 2000c; Grady, McIntosh, Horwitz, & Rapoport, 2000; Grill-Spector, Sayres, & Ress, 2006; Halgren et al., 1999; Haxby et al., 2001; Hemond et al., 2007; Henson et al., 2003; Hoffman & Haxby, 2000; Horovitz, Rossion, Skudlarski, & Gore, 2004; Ishai et al., 2002; Joseph & Gathers, 2002; Kanwisher, Stanley, & Harris, 1999; Leinsinger et al., 2007; McCarthy, Puce, Gore, & Allison, 1997; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; McKeeff, Remus, & Tong, 2007; O'Craven & Kanwisher, 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Schiltz & Rossion, 2006; Spiridon, Fischl, & Kanwisher, 2006; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000)
Group-level coordinates were not available
(Clark et al., 1997; Druzgal & D'Esposito, 2001; Furey et al., 2006; Grady et al., 1992; Haxby et al., 1991; Horwitz et al., 1992; Huettel & McCarthy, 2001; Kanwisher et al., 1998; Mechelli, Price, Friston, & Ishai, 2004; Pierce, Muller, Ambrose, Allen, & Courchesne, 2001; Ranganath, DeGutis, & D'Esposito, 2004; Rotshtein et al., 2007a; Schwarzlose, Baker, & Kanwisher, 2005; Sergent & Signoret, 1992; Spiridon & Kanwisher, 2002; Wojciulik et al., 1998; Yovel & Kanwisher, 2004; Yovel & Kanwisher, 2005)
RH activation was reported but no information about LH
(Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein et al., 2005)

Reanalyses
(Ishai, Ungerleider, Martin, & Haxby, 2000b; Mechelli, Price, Noppeney, & Friston, 2003; Rossion et al., 2003)

Table 1. Summary of Meta-Analysis of Fusiform Face Area Lateralization.

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