LOOKING BOTH WAYS THROUGH TIME: THE JANUS MODEL OF LATERALIZED COGNITION

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ABSTRACT

Existing models of laterality, while often successful at describing circumscribed domains, have not been successful as explanations of the overall patterns of hemispheric asymmetries. It is therefore suggested that a new approach is needed based on shared contributions to adaptive hemispheric roles rather than functional and structural intrahemispheric similarities. This paper proposes a model of laterality, the Janus model, based on evolutionary considerations of complementary hemispheric roles. It is proposed that the left hemisphere has the role of anticipating future scenarios and choosing between them while the right hemisphere has the role of integrating ongoing information into a unitary view of the past in order to immediately detect and respond to novel and unexpected events. Evidence for these complementary roles is provided in research on motor control and semantic priming. Finally, the Janus model is contrasted with efforts to cast the frequency model as a general model of laterality.

Key Words

Attention, Event-Related Potentials, Laterality, Motor, Semantic Priming, Animal Cognition

1. INTRODUCTION

One of the fundamental mysteries of the human brain is the functional nature of the division of the human brain into the left hemisphere (LH) and the right hemisphere (RH). Very few cognitive functions are not touched by lateralized differences at least in some respect. Despite the ubiquity of lateralized activity, the underlying organizational principle for these findings remains obscure. It will be argued that efforts to formulate generalized dichotomies have proven inconclusive, resulting in a diverse but disorganized body of observations. A past effort to develop an integrative model of brain lateralization (Bradshaw & Nettleton, 1981) served as an opportunity for laterality researchers of the time to have a conversation about the state of the field. It is suggested that it would be useful to mark the twenty-fifth anniversary of this landmark discussion by reviewing the current state of the laterality field and making an updated effort to form an integrative framework. Furthermore, recent developments documenting pervasive patterns of lateralization in animals (Rogers, & Andrew, 2002) have profound implications for laterality theory that also need to be addressed.

This paper will be divided into three major sections: 1) a broad overview of five major lines of laterality theory (Table 1), with a special focus on frequency theory and its Coarse Coding extension to the semantic domain. 2) a proposal for the Janus model of laterality, and 3) a comparison of contrasting predictions by the Janus model and the Coarse Coding model. Given the impossibility of addressing the full scope of laterality findings in a single journal article, the goals of this manuscript are limited to making the case that the Janus model is a viable alternative to current cross-domain laterality frameworks and that it may apply to at least two domains, that of motor control and that of semantic priming. No claim will be made that it applies to all aspects of laterality.

1.1 Review of Five Laterality Models

It is a reflection of the fragmented state of the laterality field that there is no review available at present that summarizes and contrasts the main laterality theories (for some earlier reviews, see Allen, 1983; Bradshaw & Nettleton, 1981; Moscovitch, 1979; Segalowitz, 1983). Because of this fragmentation, laterality papers usually cite only one theoretical view, leading to further balkanization. This fragmentation is largely a reflection of dissatisfaction with efforts to forge broad dichotomies to account for hemispheric asymmetries (clearly evident in the commentaries on perhaps the last major such effort: Bradshaw & Nettleton, 1981). Efforts have therefore largely turned to single-process models. A thoughtful argument for such an approach (Allen, 1983) held that it might be more fruitful to approach laterality findings from the standpoint of subprocessors scattered throughout the two hemispheres and to decompose tasks accordingly rather than to posit hemispheric level generalities (see also Moscovitch, 1979). The potential problem with pursuing this approach is that it can result in the present state of affairs, which is largely that of a laundry list of hemispheric differences without broad principles with which to organize them. While it may indeed be the true state of affairs, it seems worthwhile to try to reverse the theoretical pendulum somewhat and seek a more moderate position between the extremes of simplistic dichtomania and fatalistic anarchy. The present treatise will seek to propose a model posed in terms of subprocessors rather than broad hemispheric asymmetries, consistent with current approaches, but to also argue that the distribution of the subprocessors into the two hemispheres can nonetheless be understood as following meaningful principles of adaptiveness.

In order to further the goal of providing an integrative perspective, this paper will first review the five primary lines of laterality theory. In doing so, it is important to note that the boundaries for each of these theories are largely unspecified. That is, each has been proposed as an explanation for observations in a limited range of laterality studies, followed by ongoing efforts to apply them more widely. Thus, no claims will be made that a laterality model must account for all laterality findings to be valid. Likewise, it should be understood that the researchers who have developed these theories have not made broad claims about their domain, leaving it to individual researchers to investigate broader applications. Rather, this review should be understood as being a survey of how these models have fared in these ongoing incremental efforts to extend them and to what extent they can currently be used as broader explanatory frameworks for laterality findings. The critical test, then, will be whether a model can be applied outside of its core domain of cognitive processes.

In making this point, it may be helpful to utilize a distinction between proximal and distal (or ultimate) causes made by comparative psychologists (Alcock, 1993). A proximal cause is the immediate mechanism for an event, such as wings and a loud noise for the event of a bird flying. A distal cause is the circumstances that led the mechanism to be developed in the first place, as in the need to avoid predation. The following models concern the proximal causes of laterality observations within a domain of research and, as such, take a structural approach to explaining the differences between hemispheres. As has been argued at various times (Bogen & Bogen, 1969; Federmeier, 2007; Hutsler & Galuske, 2003; Ivry, & Robertson, 1998; Kosslyn, Chabris, Marsolek, & Koenig, 1992; Levy, 1977; Sergent, 1982; Vallortigara, Rogers, & Bisazza, 1999), they have the potential to be extended to the distal level by making the argument that when there are two approaches to a computation, one can optimize them by differentially instantiating them in the two hemispheres, in what might be termed the architectural efficiency framework. Such a distal cause suggests the potential for these structural differences to extend to other domains than the one directly addressed by a laterality model.

1.1.1) The LH-Verbal/RH-Visuospatial Model

The LH-verbal/RH-visuospatial model characterizes lateralized functions according to discrete domains of information. Neuropsychologists noted early on (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). Visuospatial has generally been understood as including pictorial representations, not just spatial judgments. Of course, this dichotomy is meant to describe the general case as it pertains to right-handers, where estimates suggest (Knecht et al., 2000) suggest that roughly 8% of the right-handed population has RH dominance for language.

Much of this research has been conducted using the visual half-field technique (Banich, 2003; Bourne, 2006) in which a lateral presentation of stimuli isolates initial processing of the stimuli to one or the other hemisphere (Franz, 1933). The organization of the visual system is such that stimuli seen in the left visual field are projected first to the right hemisphere and vice versa. Although the information is clearly shared at some point with the other hemisphere, it appears that presenting stimuli to the more appropriate hemisphere results in superior performance either because otherwise it is transferred to it in degraded form and/or the wrong hemisphere takes primary responsibility for processing (Kimura, 1973; Marsolek, Nicholas, & Andresen, 2002; Zaidel, 1983a). Neuroimaging studies have provided examples of both hemispheric transfer (Cohen et al., 2002) and contralateral dominance (Hemond, Kanwisher, & Op de Beeck, 2007; Schiffer et al., 2004). To facilitate discussion, stimuli presented to the right visual field will be described as a LH presentation and vice versa, with the understanding that the information is in fact eventually shared bilaterally. Although visual half-field studies have been criticized on occasion with reminders of task factors (Hellige & Sergent, 1986) and perceptual factors (Sergent & Hellige, 1986) that need to be considered, the results of such studies have generally been in accord with that of other methods.

The LH-verbal/RH-visuospatial model gained theoretical weight with the extension of dual coding theory (Paivio, 1971) to laterality research, proposing that the hemispheres use different codes (linguistic codes in the left hemisphere, visuospatial codes in the right) to arrive at meaning (Paivio & te Linde, 1982; Paivio, 1991). Efforts to test the resulting hypothesis that the RH should be more sensitive to high-imageability, that is, concrete words, than to low-imageability, or abstract, words, using the visual half-field technique have been mixed with many negative results (Boles, 1983b; Howell & Bryden, 1987; Lambert & Beaumont, 1983; Shanon, 1979) although some positive (Day, 1977; Ellis & Shepherd, 1974; Young & Ellis, 1985). Findings from functional magnetic resonance imaging (fMRI) data have also failed to support a connection between this distinction and laterality (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Giesbrecht, Camblin, & Swaab, 2004). In general, it appears that although there is some evidence that the RH may indeed be better at concrete than abstract words, the evidence is weak; furthermore, it is unclear that such an effect, even if it exists, reflects the dual-coding distinction.

The LH-verbal/RH-visuospatial distinction has fared better in visual half-field studies when English words and numbers are directly contrasted with non-verbal stimuli such as dot enumeration (Sheehan & Smith, 1986), faces (Geffen, Bradshaw, & Wallace, 1971; Marcel & Rajan, 1975; Mishkin & Forgays, 1952; Pirozzolo & Rayner, 1977; Rizzolatti, Umilta, & Berlucchi, 1971), and geometric figures (Fontenot, 1973; Gross, 1972; Hatta & Dimond, 1980; Hellige, 1978; Simion, Bagnara, Bisiacchi, Roncato, & Umilta, 1980). Furthermore, a lesion study using the visual half-field technique (Shai, Goodglass, & Barton, 1972) has helped confirm that these visual field effects do reflect hemispheric differences in the ability to process these two types of stimuli. Thus, there is some support for the laterality extension to the Dual Coding model, but only if one abandons imageability/concreteness ratings as an approach to operationalizing this distinction.

Even this generalization must be tempered. For example, even with nonverbal stimuli, the RH advantage for figures seems to only apply to complex forms and not to simple forms (Bryden & Rainey, 1963; Fontenot, 1973). It has been suggested that the critical variable is whether the stimuli can be verbally coded (Fontenot, 1973; Polich, 1978). This seems to be true in that when subject strategy is more tightly controlled, lateralization tends to depend on the task. For example, with drawings of familiar objects, naming advantage is LH (Bryden & Rainey, 1963; Wyke & Ettlinger, 1961) but visual comparison of sequentially presented pairs is RH (Tomlinson-Keasey, Kelly, & Burton, 1978). Multiple-choice recognition of simple shapes like hearts and squares, which could be done either verbally or visually, results in no net lateralization (Heron, 1957). However, there have been reports of RH advantage for semantically identifying and categorizing familiar objects (Hass & Whipple, 1985; McAuliffe & Knowlton, 2001), contrary to this view. An alternative possibility is suggested by one study in which the RH advantage for complex forms only emerged in a comparison task after a delay of at least five seconds, implicating working memory rather than perception (Dee & Fontenot, 1973); it may be that it is the mediation of working memory that is the critical variable but most experiments did not isolate this process. Thus, the literature on the laterality of nonverbal form processing is somewhat inconclusive.

Careful studies of callosotomy patients have raised further questions about this approach. Callosotomy patients typically suffer from poorly controlled epilepsy whose attacks have become life threatening; in an effort to reduce the effects of the attacks, the primary connection between the two hemispheres is cut, preventing the epileptic activity from spreading to the opposite hemisphere (Bogen, 1969; Sperry, 1982). Since each hemisphere receives information about the contralateral side of space, it is possible to communicate separately with each hemisphere simply by presenting information to one side of the patient's visual field (Gazzaniga, Bogen, & Sperry, 1965). Studies of such patients suggest that although the left hemisphere primarily mediates verbal processes, the right hemisphere also has some degree of language skills (Baynes, & Eliassen, 1998; Nebes, 1974; Searleman, 1977; Sidtis, Volpe, Wilson, Rayport, & Gazzaniga, 1981; Zaidel, 1976). Conclusions in this respect must be taken cautiously as it is unclear to what extent callosotomy patients suffer from neurological abnormalities due to their preoperational epilepsy and associated neurological abnormalities (Whitacker & Ojemann, 1977), although it has been suggested that, if anything, they underestimate the language competence of the intact brain (Zaidel, 1983b).

Visual half-field studies suggest that both hemispheres are capable of making different kinds of judgments in both the verbal and spatial domains. Kosslyn and colleagues (1989) provided evidence that the left hemisphere is superior for categorical spatial relations (such as "in" or "out") whereas the right hemisphere is superior for coordinate spatial relations (such as distance). Conversely, RH language skills are not just a degraded version of LH abilities but rather have their own points of strength (Lindell, 2006; Zaidel, 2001). Furthermore, there are many findings, to be reviewed, that do not correspond to this distinction. Thus, although the LH-verbal/RH-visuospatial model is a useful heuristic (most verbal processes are LH and most spatial processes are RH), it appears to be an incomplete account even within this restricted domain.

Some of the power of the LH-verbal/RH-visuospatial derived from observations that lateralization of function seemed to be limited to humans. It was therefore hypothesized that laterality might therefore arise from adaptations to abilities limited to humans, especially language. For example, one theory (Corballis, Funnell, & Gazzaniga, 2000) was that language might have developed as a specialization in the left hemisphere for reasons of efficiency and that this development came at the expense of the left hemisphere's spatial abilities, resulting in right-lateralization of spatial processing. This line of thought provided support at the distal level for this model. As noted later in this review, recent findings that lateralization of function is widespread through the animal kingdom has largely disproven this hypothesis and has in turn weakened this model.

1.1.2) The LH-Categorical/RH-Coordinate Model

These findings of spatial abilities in both hemispheres have led to the second of the major laterality models, the LH-categorical/RH-coordinate model (Kosslyn, 1987; Kosslyn, 1994). This line of thinking has described how both hemispheres might code the same types of information but in different, complementary ways. 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, Koenig, Cave, Tang, & Gabrieli, 1989). Despite some negative reports (e.g., Sergent, 1991a; Sergent, 1991b) various factors have been identified that could account for the mixed results. For example, a metric judgment can become categorical if a specific distance is highly practiced (Banich & Federmeier, 1999; Kosslyn, Koenig, Cave, Tang, & Gabrieli, 1989). The categorical/coordinate distinction has also been supported in a study where patients had a hemisphere temporarily anesthetized by sodium amytal (Slotnick, Moo, Tesoro, & Hart, 2001); as long as the task was difficult, deactivation of a hemisphere caused deficits in the corresponding spatial task. Likewise, in a positron emission tomography (PET) study (Kosslyn, Thompson, Gitelman, & Alpert, 1998) it was reported that categorical and coordinate spatial tasks most activated the appropriate hemisphere and an fMRI study of working memory reported appropriate prefrontal activations (Slotnick & Moo, 2006).

There has been two efforts to generalize the model to object recognition. First, there has been the demonstration, using a visual half-field technique, that participants are more efficient at labeling pictures at the basic-level (e.g., "bird") when presented to the LH and are more efficient at the subordinate level (e.g., "penguin") when presented to the RH (Laeng, Zarrinpar, & Kosslyn, 2003). The authors of this research suggest that the LH utilizes prototypes whereas the RH utilizes exemplars (Laeng, Shah, & Kosslyn, 1999; Laeng, Zarrinpar, & Kosslyn, 2003). These conclusions echo findings by other researchers regarding lateralization of category levels (Gauthier, Behrmann, & Tarr, 1999; Gauthier et al., 2000) and exemplars (Marsolek, 2004). They related this inference to the LH-categorical/RH-coordinate model by reasoning that categorical judgments involve discarding some aspects of the information (distance in the case of spatial judgments, individuating details in the case of object recognition) whereas coordinate judgments focus on just these details. This reasoning, if supported, also has the potential to be applied to other domains such as semantic representations. However, another study (Smith et al., 2005) reported that judgments of category membership of artificial objects (based on combinations of features) shift from LH to RH, suggesting that some other principle may account for these observations.

Another effort (Brooks & Cooper, 2006; Cooper & Wojan, 2000) has more literally applied the LH-categorical/RH-coordinate model to object recognition by specifying that it applies to the spatial aspects of the object representations. This approach is more tightly linked to the existing spatial findings but does not generalize this model past spatial representations but rather just applies it to a new arena (faces and animals). Thus, the LH-categorical/RH-coordinate model has been quite successful at accounting for a range of observations but it is as yet unclear if it can be extended to address phenomena outside its core domain.

1.1.3) The LH-Analytic/RH-Configural Model

A third class of laterality models, which this paper will term LH-analytic/RH-configural (a more detailed treatment is the subject of a separate manuscript in submission), has shifted to a focus on how the representations are internally organized. It differs from the LH-categorical/RH-coordinate model in that it focuses on internal organization of a representation rather than the nature of the relations between different representations. The core of this approach is the suggestion that the RH might be better defined as "configural," meaning that it utilizes information about spatial relations, in contrast to a LH system that focuses on components (Carey & Diamond, 1977). For example, inversion of faces affects spatial analysis (Leder, Candrian, Huber, & Bruce, 2001; Rhodes, Brake, & Atkinson, 1993) leading 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). Furthermore, it has been shown 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). Furthermore, a RH superiority occurs for making judgments for upright but not inverted faces (Leehey, Carey, Diamond, & Cahn, 1978).

A related version of this laterality family is the LH-analytic/RH-Gestalt (Levy-Agresti & Sperry, 1968) or 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. Evidence in support of this position is that after faces are memorized, isolated facial features (like a nose) are recognized better when presented in the context of the original face, but more so when the face is upright compared to when it is inverted or scrambled (Tanaka & Farah, 1993). This effect is abolished by instructions to attend to the features (Farah, Tanaka, & Drain, 1995) and also applies to working memory tasks (Farah, Wilson, Drain, & Tanaka, 1998). These authors argued that if the features were memorized as a set of separate elements, then memory for them should not be affected by the presence or absence of the other features. To the extent that "holistic" means a representation that includes spatial information, configural and holistic can be considered to be equivalent terms (Tanaka & Farah, 1993, p. 242).

In contrast to the focus on the RH, the nature of the LH processes has not been examined as thoroughly. Although the original view was that the "analytic" approach would therefore result in a serial approach to evaluating stimuli (Cohen, 1973), succeeding studies (Fairweather, Brizzolara, Tabossi, & Umilta, 1982; Magaro & Moss, 1989; Polich, 1980; White & White, 1975) did not reliably find lateralized serial RT effects (see Moscovitch, 1979). Indeed, later studies found that serial visual search for dot targets can be right-lateralized (Polich, 1982; Umilta, Salmaso, Bagnara, & Simion, 1979) and serial letter reading can be right-lateralized (Bub & Lewine, 1988; Young & Ellis, 1985). In any case, it has been noted that an analytic approach (parsing stimuli into discrete units) does not preclude the ability to process the consequent units in parallel (Polich, 1982).

Although this model has from the beginning been conceptualized quite broadly (consider Bradshaw & Nettleton, 1981), the core of this line of research has been with face stimuli and, as such, is currently embroiled in basic questions about the nature of face perception and whether such findings are illustrative of more general object recognition processes (Bukach, Gauthier, & Tarr, 2006) or whether faces are a special case (McKone, Kanwisher, & Duchaine, 2007). For this reason, there have been few current efforts to broaden this model beyond its base in face perception.

1.1.4) The LH-Routinization/RH-Novelty Model

The fourth laterality model, LH-routinization/RH-novelty (Goldberg & Costa, 1981), focuses on learning processes. In this model, the RH is specialized for handling novel situations where new descriptive systems (e.g., skills or knowledge) are needed and the LH is specialized for situations where well-routinized descriptive systems are already available. Furthermore, the RH mediates responsiveness to external cues (as in novel situations where one may not be sure what to do) whereas the LH mediates behavior based on internally directed processes, as in situations where one has extensive experience to draw upon to identify the best response (Goldberg, Podell, & Lovell, 1994; Goldberg & Podell, 1995). Thus, an initial RH dominance in a newly encountered situation will gradually shift to a LH dominance. It has been proposed (Goldberg, 1995) that underlying this shift is differential hemispheric organization such that the RH is amodular whereas the LH has the capacity to develop specialized modules. Thus, the left-lateralization of language is understood to be the result of extensive practice in this skill.

A variety of evidence supports this model. For example, these authors cite dichotic listening studies reporting that recognition of simple melodies is RH in non-musicians but LH in musicians (Bever & Chiarello, 1974; Johnson, 1977). Shifts have also been demonstrated with practice for verbal naming of unfamiliar visual symbols (Gordon & Carmon, 1976) and developmentally in young children for face recognition (Reynolds & Jeeves, 1978), using a visual half-field technique. Similar results have been reported in more recent studies, such as a fMRI study where participants learned to tell apart two sets of visual patterns and shifted from RH activity to bilateral activity (Seger et al., 2000). The finding (Banich & Federmeier, 1999; Kosslyn, Koenig, Cave, Tang, & Gabrieli, 1989) that a coordinate judgment can become left-lateralized with practice is also consistent with this view. An indication that this account may not provide a full account even within its core domain is provided by studies of face recognition, which is generally considered to be a case of visual expertise (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Tarr & Gauthier, 2000) or at least tuned by experience (Kanwisher & Yovel, 2006) and yet is lateralized to the RH. This model does appear to account for at least some observations but more research is needed to better delimit these boundary conditions.

1.1.5) The LH-High Frequency/RH-Low Frequency Model

The fifth, and arguably the leading candidate for a broad laterality framework, is the LH-high frequency/RH-low frequency model. This paper will argue that although it does seem to work well for at least some findings within its core domain of perceptual phenomena, evidence does not support its application as an integrative framework. This conclusion will in turn provide a justification for proposing a new addition to this list of laterality theories and one that is argued to have more promise as an integrative framework for laterality findings (i.e., one that can be applied across multiple domains, although not necessarily all domains).

Much of the initial impetus for this work on lateralized frequency processing arose from the local-global effect described earlier under the LH-verbal/RH-visuospatial model. This observation has been interpreted according to findings that vision can be described as decomposing scenes into different spatial frequencies, such that closely spaced sharply delimited patterns are high frequency and diffuse blurred patterns are low frequency (Blakemore & Campbell, 1969; De Valois, & De Valois, 1988). Although it may seem counterintuitive that vision is analyzed with frequency gratings rather than with edge detectors, the evidence in support of this model is quite extensive and is quite effective for explaining texture processing. In the laterality account, the left hemisphere is specialized for high frequency information and the right hemisphere is specialized for low frequency information (Sergent, 1982; Sergent, 1983); this is a descendant of an earlier focal-diffuse distinction made by an earlier paper (Semmes, 1968).

An extension of this model, the double filtering by frequency theory or DFF (Ivry, & Robertson, 1998), adds a consideration of attention in this process, postulating an initial symmetrical attentional frequency filtering of sensory information followed by an asymmetric filtering in the two hemispheres (resulting in a relative difference between the hemispheres, centered on the initial selected frequencies). Visual half-field studies have reported the presence of a hemispheric asymmetry in discrimination, but not detection, judgments of spatial frequency gratings (Christman, Kitterle, & Hellige, 1991; Kitterle, Christman, & Hellige, 1990; Kitterle & Selig, 1991). Also, fMRI results (Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Peyrin, Baciu, Segebarth, & Marendaz, 2004) have also been consistent with this model, although they have been more complex, with differing regions showing effects and sometimes mixed patterns of lateralization within different regions. One behavioral report (Peyrin, Mermillod, Chokron, & Marendaz, 2005) suggests that stimulus duration time may play a role. This laterality effect has also been extended to the auditory modality (Ivry & Lebby, 1993), suggesting that this distinction reflects a broader perceptual principle.

A LH-local/RH-global distinction in object recognition has become closely associated with this model. For example, studies of figures constructed from a smaller figure, such as a T shape constructed from small E's (Kinchla, 1974; Navon, 1977), suggest that attention to the smaller local features is left-lateralized and attention to the larger global shape is right-lateralized. This pattern can be understood as being due to local information being smaller and hence represented more by high frequency features while global information is larger and hence is represented more by low frequency features (Sergent, 1982). Including studies with trends in the predicted direction, the local-global effect has been demonstrated with visual half-field data (Hubner & Malinowski, 2002; Hubner & Volberg, 2005; Kimchi & Merhav, 1991; Sergent, 1982; Yovel, Levy, & Yovel, 2001), lesion data (Robertson, Lamb, & Knight, 1988), event-related potential data (Heinze, Hinrichs, Scholz, & Mangun, 1998; Volberg & Hubner, 2004; Yamaguchi, Yamagata, & Kobayashi, 2000), positron emission tomography data (Fink et al., 1996; Fink et al., 1997a), functional magnetic resonance imaging data (Han et al., 2002; Lux et al., 2004; Martinez et al., 1997), and callosotomy data (Robertson, Lamb, & Zaidel, 1993).

The LH-high frequency/RH-low frequency model can be argued to be the leading model because all of the other laterality models have at times been characterized in terms of this model. The LH-verbal/RH-visuospatial model can be understood on the basis that letters (verbal) require high-frequency analysis to be recognized whereas most spatial judgments require the broad distinctions of low frequency information (Sergent, 1982). As for the LH-categorical/RH-coordinate model, it has been suggested that differential spatial frequency differences could underlie this distinction (Jacobs & Kosslyn, 1994; Kosslyn, Chabris, Marsolek, & Koenig, 1992) and visual half-field data support this proposition (Okubo & Michimata, 2004). Likewise, LH-analytic/RH-configural could be understood as involving a focus on high-frequency details versus a focus on low-frequency contour (Grabowska & Nowicka, 1996; Sergent, 1982) or spatial (Goffaux, Hault, Michel, Vuong, & Rossion, 2005) information. Finally, the LH-routinization/RH-novelty model can be understood as resulting from a greater utility of RH low-frequency information for initial analysis of novel stimuli and LH high-frequency information for further analysis of familiar stimuli (Sergent, 1982). However, the report (Banich & Federmeier, 1999; Kosslyn, Koenig, Cave, Tang, & Gabrieli, 1989) that coordinate judgments can become left-lateralized with practice seems inconsistent with this view since practice should be irrelevant to the lateralization of spatial frequency processing.

A particular strength of this model is that it provides plausible neural mechanisms by which it might be implemented. There are two such possible mechanisms and they are not incompatible with each other. The first is the proposal that these hemispheric differences could be mediated by differences in the size of the "receptive fields" of the appropriate neurons in the two hemispheres. Computer simulations have provided evidence that this argument is plausible (Baker, Chabris, & Kosslyn, 1999; Kosslyn, Chabris, Marsolek, & Koenig, 1992), although these simulations were originally specified with respect to the LH-categorical/RH-coordinate model. A second formulation is the Neural Control Systems model (Tucker, 1981; Tucker & Williamson, 1984) which suggests that the LH has a redundancy bias, a tendency towards maintaining patterns of neural activation, while the RH orientation is mediated by a habituation bias, a tendency towards changing patterns of neural activation. The LH bias could lead it to keep a steady and unchanging attentional focus and hence be able to maintain sharp distinctions whereas the RH bias could lead it to keep changing attentional focus, resulting in broad diffuse activations. These differences were proposed to be mediated by asymmetrical arousal systems. This model also makes a number of intriguing proposals on motivational issues that are not pertinent to the present discussion.

Despite the interest in this model, it needs to be said that the empirical data are mixed. A review (Grabowska & Nowicka, 1996) of this literature concluded that evidence points towards RH superiority for early sensory processing of both high and low frequency stimuli (see also Boeschoten, Kemner, Kenemans, & van Engeland, 2005). It went on to suggest that consistent lateralization is only found when higher cognitive capacities are involved, as in discrimination judgments and local-global judgments (see also Moscovitch, 1979). Visual half-field discrimination judgments of frequency gratings do seem to yield reliable results (Christman, Kitterle, & Hellige, 1991;

Kitterle, Christman, & Hellige, 1990; Kitterle & Selig, 1991) although negative results have been reported (Niemeier, Stojanoski, & Greco, 2007; Okubo & Nicholls, 2005). Also, studies with higher-level stimuli have been more mixed (Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007).

Also, local-global judgments have yielded mixed results. In the visual half-field data, there have been many negative results (Boles & Karner, 1996; Polich & Aguilar, 1990; Van Kleeck, 1989), although a meta-analysis did report that published studies have a trend in the predicted direction (Van Kleeck, 1989). Likewise, null reports (i.e., those without at least a notable trend in either direction) have been made with ERP (event-related potential) data (Boeschoten, Kemner, Kenemans, & Engeland, 2005; Han, Liu, Yund, & Woods, 2000; Han, He, Yund, & Woods, 2001; Han, Yund, & Woods, 2003; Jiang & Han, 2005; Malinowski, Hubner, Keil, & Gruber, 2002), PET data (Heinze, Hinrichs, Scholz, & Mangun, 1998) and fMRI data (Sasaki et al., 2001; Weissman & Woldorff, 2005). On the other hand, lesions studies (Robertson & Lamb, 1991; Robertson, Lamb, & Knight, 1988) and callosotomy patients (Robertson, Lamb, & Zaidel, 1993) have provided dramatic examples of asymmetries

There have been efforts to explain these mixed results on the basis of experimental design variations. One report (Han et al., 2002) has indicated that lateralized activations may be weaker with lateralized stimulus presentations, echoing visual half-field reports of stronger effects with bilateral displays in which a central cue indicates which stimulus is to be attended (Boles, 1983a; Boles, 1994); on the other hand, an fMRI study did find effects with lateralized presentations (Lux et al., 2004) and an ERP study did not find effects with bilateral presentations (Jiang & Han, 2005). The visual half-field meta-analysis paper (Van Kleeck, 1989) suggested that effects might only be seen with short stimulus durations, few experimental trials, and/or small stimulus eccentricities. A follow-up visual half-field study (Boles & Karner, 1996) that tested this suggestion, along with bilateral displays, not only did not find the laterality effect, but it found a RH superiority for local features at a short stimulus duration. On the other hand, another visual half-field study (Yovel, Levy, & Yovel, 2001) reported that equalizing the saliency of the local and global levels and having participants monitor both levels for targets produced the laterality effect. The effect of equalizing saliencies would also be consistent with the report that lateralized effects are seen most strongly when the two levels signal incongruent responses (Hubner & Malinowski, 2002; Volberg & Hubner, 2004). Even if such optimizations are required to produce effects, it still does not explain why one PET study (Fink et al., 1997b) reported a reversed laterality pattern, attributing the reversal to the use of nonverbal stimuli, although a different study that also used nonverbal stimuli (Martinez et al., 1997) did not report this reversed pattern (Mangun, Heinze, Scholz, & Hinrichs, 2000). Furthermore, an fMRI study using normal verbal stimuli also reported reversed laterality effects (Weissman, Mangun, & Woldorff, 2002).

Finally, although current local-global papers are usually framed within the context of the LH-high frequency/RH-low frequency model, there are reasons to question whether spatial frequency analysis is in fact the mediating process. For example, one model suggests that extraction of local and global features is bilateral and hemispheric asymmetries arise at the level of integrating the features with the level of representation (Hubner & Malinowski, 2002; Hubner & Volberg, 2005); the bilateral availability of the features is consistent with a review (Grabowska & Nowicka, 1996) that concluded that spatial frequency analysis is not lateralized at the lower sensory levels. Indeed, evidence has been presented that attention to local versus global levels at the least need not be based on attention to a spatial frequency (Lamb, Yund, & Pond, 1999; Robertson, 1999).

Other alternatives have been proposed. Two recent reports have argued for a salience confound in that for typical stimulus arrays the global level is more salient ("global precedence"); when salience was manipulated using both left parietal lesion patients (Mevorach, Humphreys, & Shalev, 2006a) and repetitive transcortical magnetic stimulation or rTMS (Mevorach, Humphreys, & Shalev, 2006b) it was found that the left posterior parietal mediates attention away from the salient level and the right posterior parietal towards the salient level, regardless of which was local and which was global. This is consistent with the finding that local-global effects are stronger in visual half-field studies when saliency of the levels is equalized (Yovel, Levy, & Yovel, 2001). Another alternative that has been proposed is that the LH is specialized for consecutive analysis of fine then coarse features (high then low frequency) and the RH has the complementary specialization (Peyrin et al., 2005); fMRI data supported this in a task in which participants compared two consecutive pictures, one filtered for low spatial frequencies and the other filtered for high spatial frequencies. More research will be required to settle these issues.

In any case, the LH-high frequency/RH-low frequency model remains the leading laterality formulation despite these questions, at least within the perceptual domain. Overall, it does appear to provide a satisfactory account for a wide range of observations but it is also appears that these effects are mediated via attentional mechanisms that may be limited to spatial frequency analysis of textures (e.g., Ivry, & Robertson, 1998). There is evidence that even local-global effects are not necessarily due to spatial frequency asymmetries but rather may reflect a different lateralized process. These limitations weigh against the frequency model being applicable as a broad cross-domain description of hemispheric differences, although it remains enormously useful as a description of certain perceptual-level asymmetries.

In any case, in order for this frequency model to be considered a general integrative model for lateralized functions, it would need to explain observations outside the domain of perception. Recent studies have sought to extend this formulation to the domain of semantics and it is here that this paper will make the case that a new model based on hemispheric roles provides a more effective general account. This paper will first briefly review the background literature on semantic priming, then describe how the frequency theory has been applied to semantics, and then make the case that it does not satisfactorily account for the empirical data. This paper will then propose a new approach to providing an integrative cross-domain framework for laterality findings.

1.2 Semantic Priming Review

Since this treatment is directed at a broader audience than cognitive psychologists, some review of semantic priming is necessary. Priming is said to have occurred when a stimulus is recognized more quickly or accurately because of exposure to another related stimulus (Meyer & Schvaneveldt, 1971). A common priming paradigm is a lexical decision task in which the participant decides whether a letter string is a word. If the target is a word, it will be recognized more quickly if it is preceded by a related word (e.g., nurse-doctor) than if it is preceded by an unrelated word (e.g., flag-doctor).

For the purposes of this review, this paper will follow the hybrid model of semantic priming (Neely, 1991; Neely, & Keefe, 1989), as illustrated in Figure 1. Automatic spreading activation or ASA (Collins & Loftus, 1975) is the fast automatic activation of neighboring nodes in the semantic network (e.g., "bird" will activate "wing"). It is generally thought that this type of priming fades away between 400 and 700 ms (Anderson, 1983; McNamara, 2005) although this view is not universal (Deacon, Uhm, Ritter, Hewitt, & Dynowska, 1999). ASA is thought to be independent of strategic processing and hence provides a relatively pure reflection of the structure of the semantic network, although the exact nature of the network remains controversial (Hutchison, 2003; Lucas, 2000). It appears to produce only facilitation, not inhibition.

The two other types of priming are controlled processes. Expectancy priming (Posner, & Snyder, 1975) is produced by a conscious effort to activate semantic nodes in advance of the target presentation. It appears to require more time to engage than ASA (Neely, 1977), although the exact timing is unclear with at least one study suggesting that even a 300 ms stimulus onset asynchrony (SOA) is sufficient (Hutchison, Neely, & Johnson, 2001). Some of the chief evidence for the strategic nature of expectancy priming is that the nature of the stimulus list influences whether it takes place. The presence of expectancy-priming seems to depend on the relatedness proportion (RP), the extent to which a target word can be predicted from the prime (Tweedy, Lapinski, & Schvaneveldt, 1977). In other words, subjects appear to only utilize this mechanism under conditions where it will be useful. ASA, in contrast, is unaffected by this parameter (den Heyer, Briand, & Dannenbring, 1983) and will operate even when it is counter-productive (Neely, 1977).

Semantic matching (Neely, & Keefe, 1989), the third type of priming, is a controlled strategy in which the initial recognition that there is no relationship between the target and the prime can be used as a shortcut to determine that the target is likely to be a non-word. The resulting bias towards the non-word response results in non-word reaction times (RTs) being facilitated and unrelated word RTs being slowed. This slowing increases the difference between related and unrelated RTs and hence the size of the priming effect. Semantic matching therefore differs from the other two processes in that it occurs after the target is presented, but before the response is made. The chief evidence for its strategic nature is that its use is influenced by the stimulus list parameter of non-word ratio (NWR), essentially the ratio of non-words to word targets for trials in which the target has no relation to the prime (Neely, & Keefe, 1989). In other words, the utility of this strategy (measured by the NWR) is again predictive of the extent to which it is deployed, consistent with it being deployed in a volitional manner. ASA, in contrast, is not affected by this ratio. Semantic matching can produce both facilitation and inhibition. One way to minimize semantic matching effects is to use a naming task as the simple recognition of a relation between the prime and the target does not suffice to facilitate a verbal response, unlike the binary lexical decision choice (Seidenberg, Waters, Sanders, & Langer, 1984).

For settings where verbal naming is not practical for methodological reasons (such as ERP or fMRI experiments where there is concern about motor artifact), expectancy priming and semantic matching can be most easily distinguished from each other via forward and backward priming. For a conventional prime, the target can be predicted from the prime. Such a prime is a "forward prime" if the relationship between the two words is asymmetrical, such that the prime reminds one of the target but not vice versa (e.g., stork-baby). At an SOA too long for ASA, a forward prime should be most readily mediated by expectancy. In contrast, a "backward prime" (e.g., baby-stork) is one where the target reminds one of the prime but not vice versa (Koriat, 1981). In such a case, neither expectancy nor ASA can mediate priming since the target will not be spontaneously activated in advance and yet priming is observed in the reaction time measures; it is thought that backward priming must therefore be mediated by semantic matching since the relationship between the prime and the target can only be recognized once the target has been presented. Thus the direction of relationship between the prime and target can be used to distinguish semantic matching from expectancy, and SOA can be used to distinguish between automatic and controlled priming processes.

Although not formally part of the Hybrid model, a fourth process, semantic feedback, has been accepted by Neely (Stolz & Neely, 1995). This paper demonstrated that the non-additive interaction between stimulus degradation and semantic priming is not due to semantic expectancy by showing that the interaction occurs to the same degree at a short SOA when expectancy was not operating, as indicated by the absence of an RP effect on priming, and a long SOA, when expectancy was operating, as indicated by the presence of an RP effect. However, it also found that changes in NWR (confounded with RP) did not affect this process, thereby also ruling out semantic matching as being necessary for the overadditive interaction. Those authors go on to suggest that the effect represents something else entirely, a semantic feedback (Besner & Smith, 1992; Borowsky & Besner, 1993) from the semantic level to the lexical level, providing top-down enhancement of lexical and pre-lexical processing. The most parsimonious account of their results is that semantic feedback operates at both short and long SOAs and expectancy only at the long SOA.

Although this hybrid model of priming was given only a brief treatment in a recent review (McNamara, 2005), it did not criticize the hybrid model's ability to account for the broad scope of the priming literature and the conditions under which different mechanisms are activated. Indeed, McNamara credits the hybrid model by saying that "the important contribution of this model is that it combines a model of automatic, attention-free priming with strategic, attention-laden processes" (p. 45). While McNamara (2005) makes the somewhat dismissive comment that "not surprisingly, Neely and Keefe's (1989) model can account for a greater variety of findings than any one mechanism alone can (see Neely, 1991)" (p. 45), the key point is that this model was able to account for a systematic and comprehensive range of semantic priming findings with a parsimonious set of just three (four including semantic feedback) mechanisms. An equivalent effort has not been made with the alternative models. Further, most of the "alternatives" to the Hybrid model, like the Verification Model (Becker, 1980; Becker, 1985), are not actually alternatives but rather specifications of how components of it, in this case expectancy, operate.

The hybrid model accounts for hundreds of semantic priming studies, although a review of this vast literature would lie outside the scope of this manuscript and so interested readers are encouraged to consult existing treatments (McNamara, 2005; Neely, 1991). For the purposes of the present manuscript, understanding of these processes is needed to evaluate the evidence regarding lateralization of semantic processes.

1.3 Lateralized Semantic Coding

The reason why the frequency model is a candidate for being an integrative cross-domain framework for laterality findings is that it has been suggested that it may apply to semantics as well as perception. It has been suggested that there are lateralized differences in the frequency and depth of semantic coding (Beeman, 1998; Jung-Beeman, 2005). As noted in the discussion of the LH-high frequency/RH-low frequency model, studies of lateralized visual cognition suggest that the left hemisphere is specialized for processing high frequency, fine differences whereas the right hemisphere is specialized for low frequency, broad distinctions (Sergent, 1982; Sergent, 1983). In this view, a similar distinction is present in the semantic domain: The right hemisphere engages in "coarse semantic coding" in which a word prime activates a very large and diffuse field of semantic concepts when presented to the right hemisphere. The RH SOA results could be understood as the result of slow spread of activation (first to close associates and then only later to distant associates). The left hemisphere engages in "fine semantic coding" or the activation of just a few very closely related concepts (Beeman, 1993).

A critical test of the Coarse Coding account was provided by an examination of summation priming in which three primes were presented simultaneously, followed by lateralized presentation of the target at a long SOA (Beeman et al., 1994). According to this model, a target that is only distantly related to its prime should show more facilitation when presented to the RH than when presented to the LH, because in the RH the target will have activated a large set of semantic concepts only loosely related to the word prime. However, the opposite should be so if the prime and target are very closely related, because in the LH the target will have activated a smaller set of semantic concepts more closely related to the prime. Indeed, targets presented to the RH gained the most benefit when the three primes were weak associates of the target. This experiment was done under conditions favoring controlled processes (long SOA and a high proportion of related trials). In a second experiment the authors (Beeman et al., 1994) replicated their experiment but with a low proportion of related trials. It is also worth noting that both experiments used a naming task, which minimizes semantic matching (Seidenberg, Waters, Sanders, & Langer, 1984). They also added a priming type with one strongly associated prime and two neutral primes that they termed a Direct Prime. Consistent with the Coarse Coding account, targets presented to the LH gained more benefit from the Direct Primes than did targets in the RH.

These conclusions were further reinforced with a succeeding divided-field study (Faust & Kahana, 2002) using homographs, building on prior laterality studies (Burgess & Simpson, 1988; Nakagawa, 1991; Titone, 1998). The prime triplets (centrally presented) consisted of zero to three primes related to the dominant meaning (e.g., although the study was conducted in Hebrew, an English equivalent would be Money-

Bank), with the remaining primes related to the subordinate meaning (e.g., River-Bank). Thus, rather than manipulating association strength, the experiment manipulated to what extent the primes converged onto the same meaning versus diverged onto different meanings. The target was then presented laterally after 800 and 2500 ms SOA (thus favoring controlled priming) and the participants made a lexical decision. In accordance with their interpretation of the Coarse Coding account, they reported that the RH showed more benefit from divergent primes at 800 ms SOA and all types of primes at 2500 ms whereas the LH showed the most benefit from primes that converged on the dominant meaning at both SOAs, suggesting that the LH was focused on the dominant meaning whereas the RH had a more diffuse activation that included both meanings. Similar findings were found in a replication (Faust & Lavidor, 2003).

While the Coarse Coding model is a widely cited model of lateralized semantics (the 1994 paper having 172 citations as of September 2007), close examination of their empirical data (Beeman et al., 1994) does not support their conclusions. For example, in contrast to weak associations showing more priming in the RH under controlled priming conditions, summation priming was equivalent for both hemispheres under automatic conditions. The authors therefore concluded that under controlled priming conditions either the LH was suppressing peripheral activations or the RH was facilitating summation priming: "It is possible that the RH semantic field is larger or somehow summates more easily when controlled processing is possible. It is also possible that the LH narrows its semantic field more when controlled processing is possible than when limited to automatic processing. The latter possibility seems more likely..." (p. 36). One problem then is that although the model is posed in terms (i.e., fields of activation of semantic fields) that the major cognitive models would consider to be automatic spreading activation (Anderson, 1983; Collins & Loftus, 1975), there is no evidence of lateralized differences in automatic priming in this study (Beeman et al., 1994).

Furthermore, as reasoned in a recent paper (Coulson & Wu, 2005), one example of a summation prime in that study was "cry," "foot," and "glass" for the target CUT; although the Coarse Coding account is that the three activation fields of the features for the three terms summated in the RH, "foot" and "glass" do not have intersecting features. Coulson and Wu go on to suggest that the combined primes might have retrieved incidents where the three co-occurred, resulting in priming for CUT, suggesting a predisposition by the RH to activate such information. This insightful critique, then, provides yet another argument against the Coarse Coding model. As noted by another group (Sundermeier, Virtue, Marsolek, & van den Broek, 2005), this example can also be understood as the result of a RH bias towards summing weak associations rather than in terms of the semantic similarity relations suggested by Beeman. While this is a plausible mechanism, it does undercut the theoretical basis for the model, which is posed in terms of semantic feature fields and would require a reconsideration of the basic mechanisms and whether it is truly an extension of the frequency model.

Likewise, the results of the follow-up experiments (Faust & Kahana, 2002; Faust & Lavidor, 2003) have been questioned in a recent report (Kandhadai & Federmeier, 2007). In this divided field experiment, pairs of primes were presented at fixation, followed by the lateralized target. The key differences were that the primes were presented sequentially (with a 200 ms SOA between primes and an 800 ms SOA between the second prime and the target) and the primes were always unrelated to each other. For convergent primes, they represented different associations (e.g., Lion-Stripes-Tiger) and for divergent primes, the target was a homograph and they were associated to different meanings (e.g., Kidney-Piano-Organ). No lateralized differences were found, contrary to what Coarse Coding should predict. A number of potential alternative interpretations were offered.

Thus, although the Coarse Coding formulation is intriguing and has generated some interesting results, it is not clear that it can actually be characterized as a generalization of the LH-high frequency/RH-low frequency model to semantics. Furthermore, this paper has argued that even within the perceptual domain, evidence indicates that the LH-high frequency/RH-low frequency distinction applies to a limited range of processes. We will argue that a new view of lateralized cognition grounded in an adaptive perspective might be more promising for organizing multiple domains of the laterality literature. This paper takes as a starting point the finding that the two hemispheres constitute independent resource pools that can cooperate (Banich, 1998) and that they are both capable of cognitive processes (Bogen, 1997) and presents a model for how they might cooperate by adopting different roles in everyday life. This paper will then review evidence supporting these two general hemispheric roles.

2 PROPOSING A NEW APPROACH

2.1 Taking an Adaptive Viewpoint

Thus, it is argued that the existing models have not proven able to provide a general explanation for laterality findings via the architectural efficiency framework, whatever their success within their core domains. Indeed, one review has concluded that one must instead focus on domain-specific laterality principles (Brown & Kosslyn, 1993). This conclusion is endorsed in part by the present author. It seems likely that many of the existing disputes regarding lateralized differences will prove to be similar to that of the great debate between the Young-Helmholtz trichromatic theory of color and the Hering opponent-process theory of color; the current consensus is that they are both correct and that the former accounts for color as implemented in the photoreceptors and the latter accounts for color as implemented in higher levels of the perceptual systems (Solomon & Lennie, 2007).

On the other hand, while it seems likely that different principles will be found to underlie lateralized differences at different levels in the system, this position does not rule out efforts at establishing a general framework within which to understand hemispheric differences. Theories can be said to have two major aspects. The first aspect is the specification of the parameters of interest. A theory that fails at this aspect will lack predictive power, an important test of theoretical models (Popper, 1959). The second aspect is the provision of a context (a paradigm) that allows for findings to be incorporated into the wider understanding of how things work, including the scientific literature (Kuhn, 1962). A theory that fails at this level will lack face validity in that it will not make sense or will seem lacking in relevancy. While it is suggested that more studies are needed to form a full account for the first aspect, there may be sufficient evidence accumulated at this time to begin forming a framework for the second aspect. Such a framework can be helpful as a heuristic, to inspire new hypotheses, and as a paradigm, helping guide experimenters as to what questions are important and to formulate what tests are needed to advance the field. A framework that inspires successful hypotheses and accounts for more observations can be said to be more successful than alternatives; it is not necessary to explain everything, merely more than the current alternatives. While the current framework, the architectural efficiency framework, provides a rationale for the observation of hemispheric differences, it has provided very few benefits at the level of the second aspect.

One of the best-known frameworks is Darwin's theory of evolution by natural selection (for an accessible review, see Patterson, 1999). In its basic form, it lacks the detail (as in the specification of genetics) to provide predictive power (as in determining the future form of humans) and it cannot be disproven with regards to events in the distant past and yet it has tremendous power as a heuristic and a paradigm, making sense of a wide range of observations and successfully inspiring a wide range of experiments that have advanced scientific knowledge. This paper suggests that the evolutionary perspective may also be helpful in developing a new framework for laterality findings based on principles of adaptiveness. By "adaptive" this paper means taking an evolutionary approach to understanding lateralized functions by consideration of their contribution to overall functioning in the environment. The measure of success in such an endeavor is the plausibility of the interpretations and the relative simplicity of the proposed principles.

In making this argument, this author is making a distinction between what one might call local versus global predictions. For example, evolution predicts that overall one should expect that species should be related at the genetic and biochemical levels in ways consistent with speciation over time (Eldridge, Way, Sonleitner, & Gross, 1981). Furthermore, at the level of an individual experiment regarding whether species A is related to species B, it provides the hypothesis that two similar appearing species should have similar genetics due to sharing a common ancestor; however, if the hypothesis is disproven it would not disprove evolution. One would instead posit that one had encountered an example of convergent evolution from two originally disparate species (for an example of convergent evolution, see Mares, 1976). It is only if the accumulated bulk of such experiments resulted in such "exceptions" that one would begin to question the theory itself. Similarly, the Janus model is posed at the global level. Unlike existing laterality models, one cannot unfortunately seek to disprove it at the level of a single experiment (in contrast to the frequency model where a negative result would have to be attributed to the experimental design or methods). However, the Janus model can be disproven if repeated experiments showed that the predicted pattern was not supported over a broad range of tasks. In this sense it is a weaker theory than the frequency model. Darwinian evolution shows that such a global theory can still be quite useful and that such a model is still scientific since it is ultimately also falsifiable. Although one might wish for a stronger type of theory, it would appear that in the case of laterality such a strong model might simply not be an appropriate description of reality.

As this author has found in the past that the term "adaptive" is not necessarily self-explanatory for those not having a background in biology, it may be helpful to refer to a concrete example. An example of the adaptive approach can be found in contrasting the features of a tiger and a hippo. One might say that three functions they have in common are hiding, moving, and eating. Thus, a tiger has stripes, fast legs, and sharp teeth whereas a hippo has gray skin, stumpy legs, and blunt teeth. The physical parameters of the features in one of these domains could not be used to predict the nature of the features in the other three features (the tiger features are not physically more similar to each other than the hippo features). At the purely structural level sharp teeth have nothing in common with muscular legs. In contrast, knowledge of the ecological roles that the two animals are adapted for could enable one to predict the nature of the features in the other two domains. A tiger is adapted to its role as a predator of large game animals. For such a role, stripes are useful for camouflage while stalking prey, fast legs are useful for chasing prey, and sharp teeth are useful for bringing the prey down. In contrast, a hippo is an amphibious herbivore so a hide that blends into muddy water is more useful than stripes, stumpy legs are more useful for traversing both land and water, and blunt teeth are more useful for grinding vegetation. Similarly, one might seek an account of left and right brain differences by identifying their respective adaptive roles and how their differences might serve a common purpose, rather than seeking to explain all differences according to a single structural feature, like frequency (for a different view of evolutionary considerations, see Bertelson, 1981).

Further insight into this line of argument may be found with respect to analytic studies of human lateralized differences. A number of studies have examined the question of whether laterality patterns across different tasks might covary across individuals (and thus mediate a broad personality trait of hemisphericity, either individually or linked to group differences such as gender or handedness). From a biological point of view, one can envision three major mechanisms in which this could prove to be the case. First of all, if lateralized asymmetries arise from structural differences between the two hemispheres then one would expect that individual differences in this structural characteristic would affect broad domains of hemispheric functioning. An example of such a characteristic is the size of the "receptive fields" posited by some accounts (e.g., Baker, Chabris, & Kosslyn, 1999; Jung-Beeman, 2005). Another example is the neuroregulatory arousal systems in which a small brainstem nucleus could modify the functioning of broad expanses of a hemisphere (Tucker & Williamson, 1984). The second potential mechanism would be if broad aspects of cognition share a reliance on a common lateralized cognitive resource, such as working memory. In such a case, individual differences in genetic coding of the resource would manifest as correlated asymmetries in all the cognitive operations relying on this resource. The third potential mechanism would be if the neural systems underlying a broad array of hemispheric cognitive functions were genetically linked (for an accessible review of genetics, see Klug, & Cummings, 2005). Such linkages can occur due to underlying genes that are located on the same segment of a chromosome such that they tend to be co-inherited even in the case of cross-over events or other genetic reshuffling processes. A linkage could also occur if a single master regulatory gene affects the development of broad aspects of cortical development that otherwise, in the adult, share no apparent commonalities (for further consideration of potential mechanisms of covariation, see Klingberg, 2005).

Studies of individual differences have generally not shown any evidence of such broad hemispheric covariations (Boles, 1992; Boles, 1998b; Boles, 2002; Hellige, Bloch, & Taylor, 1988; Hellige et al., 1994). The absence of such covariations is an important argument against accounts that rely on structural asymmetries such as asymmetric arousal (Boles, 1998a) and is a further obstacle for utilizing the five models as global accounts of laterality (although one could posit versions of the five models that do not rely on such global structural asymmetries). It is not, however, an obstacle to an account based on adaptive roles. In such an account, it would not be problematic for cognitive functions to be specified by separate genes and therefore vary independently across individuals. There is no requirement for there to be a coherent personality trait of hemisphericity. The appropriate level for a quantitative analysis would not be across individuals of a species, it would be across norms for different species (for a review of quantitative comparative methods, see Gittleman & Luh, 1992). If, for example, one conducted a factor analysis of measurements of species norms that included such parameters as teeth sharpness and types of digestive enzymes, one might very well find patterns of covariation with carnivores having sharp teeth and the ability to digest meat and herbivores having flat teeth and the ability to digest plants, as well as omnivores who are intermediate in both respects (for an example of this type of analysis, see Gittleman, 1986). Despite common characteristics that derive from the common selective pressures for animals inhabiting the same ecological niche (Futuyma & Moreno, 1988), at the individual level one would not necessarily expect covariations for the individual traits. Thus, one might find that in humans teeth sharpness and digestive enzymes vary independently even though the intermediate population norm for these two parameters reflect the omnivorous nature of our species. Indeed, Darwinian selection is predicated on the presence of individual variation in each characteristic.

In the domain of laterality, an adaptive account would make the argument that in normal functioning each hemisphere has developed different roles (to be proposed at a later point). Over the course of evolutionary history, variations in asymmetry that are consistent with these roles have enhanced survivability and have been selected for and variations that are not consistent have not. This selective pressure would result in asymmetry patterns that complement each other even though they may result from independent structural characteristics, cognitive processes, and genetic codes. Factor analyses of individuals would not detect any relationship because they rely on covariation. The relationships would be present in the population means, which are not analyzed by factor analysis of individual members of a population. One could perhaps perform a factor analysis across the population means of different species if one could identify comparable cross-species traits.

Recent findings from comparative studies of animals have provided a basis for proposing such an adaptive basis for laterality. The animal literature has become a rich venue for laterality findings in recent years and a complete review would require a full article in its own right. To give a representative sampling of reports, studies have documented pervasive lateralization of function across a wide array of species including lower vertebrates such as lizards and fish (Bisazza, Rogers, & Vallortigara, 1998; Halpern, Gunturkun, Hopkins, & Rogers, 2005; Vallortigara, Rogers, & Bisazza, 1999). These studies suggest that hemispheric lateralization may provide benefits at the individual level above and beyond potential benefits at the species level (see Vallortigara & Rogers, 2005).

Some provocative data (Yamazaki, Aust, Huber, Hausmann, & Gunturkun, 2007) were recently summarized as thus "A detailed analysis of pigeons learning to categorize hundreds of pictures with everyday scenes into those that contain a human figure or not shows that left and right hemispheres use complementary strategies... The LH concentrates on local features and is able to generate categorical distinctions based on the invariant properties of the target stimulus. The RH, however, relies on the configuration and possibly the global cues of the stimuli and seems to base its decisions on a memory-based exemplar strategy" (Halpern, Gunturkun, Hopkins, & Rogers, 2005 p. 10353).

Some especially illuminating data on the complementarity of the hemispheres have arisen from studies of chickens. Chickens are especially suitable for laterality studies because: 1) they have an almost complete decussation of the optic nerves such that each eye projects almost entirely to the contralateral hemisphere and 2) the direction of laterality is controlled by which eye is exposed to light during incubation (normally the right eye), such that laterality can be abolished simply by incubating the egg in darkness (Rogers, 1990).

Studies of chicks have reported results consistent with four of the five laterality models. In a finding that particularly seems to echo LH-verbal/RH-visuospatial findings in humans, in chicks the RH is biased towards spatial cues whereas the LH gives greater weight to object cues (Regolin, Garzotto, Rugani, Pagni, & Vallortigara, 2005) when the cues conflict and chicks show a relative neglect of the left visual hemi-field (Diekamp, Regolin, Gunturkun, & Vallortigara, 2005). A finding that seems to echo the

LH-categorical/RH-coordinate findings is that chicks have been reported to rely more on absolute distances with the LH and on relative distances with the RH (Tommasi & Vallortigara, 2001), a finding that either contradicts the LH-categorical/RH-coordinate model if absolute distance representation is held to be a coordinate representation (Vauclair, Yamazaki, & Gunturkun, 2006) or is consistent with it if practiced absolute distances are considered to be an example of LH categorical representations (Banich & Federmeier, 1999; Kosslyn, Koenig, Cave, Tang, & Gabrieli, 1989). Consistent with the LH-analytic/RH-configural model, it has been reported that the RH of chicks are more capable of recognizing partially occluded objects (Regolin, Marconato, & Vallortigara, 2004). A finding that echoes the LH-routinization/RH-novelty distinction is that chicks initially show a preference to respond to novel objects with their RH (Regolin & Vallortigara, 1996). While the frequency model does not seem to have been evaluated in chicks, an effort to detect asymmetries in spatial-frequency acuity in pigeons failed to observe any such differences (Gunturkun & Hahmann, 1994) consistent with human studies of low-level sensory asymmetry (Grabowska & Nowicka, 1996); studies examining higher-level perceptual analysis that take attention into account (cf. Ivry, & Robertson, 1998) have yet to be conducted.

More importantly for the present line of reasoning, a series of studies have found that lateralized chicks have a LH that is more efficient at finding grains amongst pebbles and a RH that is more efficient at detecting predators (Rogers, 2000; Rogers, Zucca, & Vallortigara, 2004). The right-lateralization for responding to predators has also been observed in toads (Lippolis, Bisazza, Rogers, & Vallortigara, 2002) and marsupials (Lippolis, Westman, McAllan, & Rogers, 2005). Critically, it has been reported that this lateralization may be adaptive because such chicks are more efficient at simultaneously finding food and detecting predators, as if each hemisphere is independently maintaining a separate watch (Dharmaretnam & Rogers, 2005).

This independence of cognition is consistent with observations of callosotomy patients. For example, in one report (LeDoux, Wilson, & Gazzaniga, 1977) when a boy was asked questions about his name and friends and so forth, both hemispheres were able to make appropriate responses via spelling with scrabble pieces (each hemisphere has primary control over the contralateral hand), although the right hemisphere was limited to simple one or two word responses. When asked what he would like to do for a living, the LH spelled "draftsman" whereas the RH spelled out "automobile race." A systematic study of the hemispheric opinions of two callosotomy patients found them mostly in accordance but with some interesting differences in attitude and self-image (Schiffer, Zaidel, Bogen, & Chasan-Taber, 1998). Roger Sperry, who co-won the Nobel Prize for his work on callosotomy patients, has expressed the opinion that the two hemispheres are indeed separate selves, although their shared existence for the most part constrains divergence (Sperry, 1968). While the indications of independence of the hemispheres is intriguing, it is important not to overinterpret them; even in a callosotomy patient the overall behavior is quite unified and casual observation will not discern any signs of the operation (Beaumont, 1997).

More important for the present proposal, regardless of whether the hemispheres can constitute distinct selves, evidence suggests that they can serve as separate self-contained information processors. In a finding seeming to echo the chick studies, callosotomy patients are able to scan visual arrays for targets separately, thus being twice as efficient as normal subjects (Luck, Hillyard, Mangun, & Gazzaniga, 1989), indicating the ability to process information independently in each hemisphere. Likewise, they can perform visual discriminations simultaneously with each hemisphere without penalty, unlike controls (Gazzaniga & Sperry, 1966). Although such independent processing is apparently not normal in this task, studies suggest that even intact brains can operate semi-independently in other tasks (Banich, 1998; Dimond & Beaumont, 1971a; Friedman & Polson, 1981; Hellige, Cox, & Litvac, 1979; Hines, 1975), especially when operating on information appropriate to the two hemisphere's domains of specialization (Moscovitch & Klein, 1980). These findings thus suggest that while the two hemispheres act like two specialized parts of one mind, they have the capacity to make independent judgments. Research on human laterality therefore suggests that human hemispheres may be able to operate cooperatively with complementary roles as seen in chicks.

2.2 The Janus Model

The guiding principle of this paper is that the hemispheres might have developed lateralized specializations in each cognitive domain to support the overall differing roles of the two hemispheres. This paper will start by presenting a general framework of what these roles might be, the Janus model. Findings in motor control will be used to clarify the general nature of these two roles. They will then be further developed in the cognitive realm by focusing on the quintessentially human area of semantic processing. This model differs from the existing five models in that it starts with the distal level and then uses it to direct the specifications of the proximal level mechanisms rather than vice versa.

Given the observed ability of the two hemispheres to operate semi-independently, albeit collaboratively, it is proposed that the hemispheres operate in this fashion in normal unified brains as well. This paper proposes that the left hemisphere is generally specialized to anticipate multiple possible futures while the right hemisphere is generally specialized to integrate ongoing strands of information into a single unitary view of the past that it can then use to respond to events as they occur (see Figure 2). Many hemispheric specializations can then be understood as helping facilitate these two contrasting roles. In this sense, this model is posed in terms of subprocessors but is also a type of hemispheric parallel processing model (see Allen, 1983). This proposal is named the Janus model, after the Roman god of beginnings and endings who had two faces, one facing forward looking into the future and one facing backward into the past. This paper suggests that metaphorically all humans are like Janus and that this duality enables us to navigate the river of time, choosing our future course while responding to unexpected events as they occur.

This paper will characterize the left hemisphere future orientation by the term "proactive" and the right hemisphere past orientation by the term "reactive." In general, this paper suggests that the LH is characterized by planning and the RH by improvisation; the LH by envisioning the future and the RH by hindsight; the LH by hypothesis-testing and the RH by trial-and-error learning; the LH guided by internal predictions and goals, the RH guided by external unforeseen events. Given a mystery novel, the LH will try to guess who is the murderer and foresee the twists and turns of the plot while the RH will enjoy the story as it unfolds and try to understand how each event makes sense as it happens (see Calvo, Castillo, & Schmalhofer, 2006; Fincher-Kiefer, 1995). To put it in terms familiar to scientists, according to the Janus model, the two roles of theories posed earlier (forming predictions and providing an explanatory context) correspond to these two hemispheric specializations; thus, one might say that Popper emphasized LH thinking to Kuhn's RH thinking, providing an illustrative contrast to the unfortunately common lay view that LH thinking is scientific and RH thinking is artistic.

It is important to note that the Janus model does not propose that learning and memory are solely characteristics of the RH. The "future" orientation of the LH and the "past" orientation of the RH is meant to denote their respective specializations for forming LH representations of events that have not occurred yet and acting upon them and comparing a RH representation of the context to events that have just occurred and reacting to them; the LH proactive focus does not preclude an ability to learn from experiences to improve its predictions while the RH reactive focus does not denote a focus on memory per se but rather on using the past to detect novel events and responding to them. In some sense, both hemispheric representations involve a type of expectation but those of the LH take the form of discrete predictions whereas those of the RH take the form of a baseline summary of past experiences against which deviations, anomalies, and novelties can be detected.

Thus, the finding in chicks that the LH, but not the RH, updates food preferences for remembered food caches when one type of food is devalued (Cozzutti & Vallortigara, 2001) is consistent with the Janus model in that this represents modification of preferences in representations of potential choices in the context of planned seeking behavior (proactive) rather than an improvisational response to a sudden unexpected event (reactive). Conversely, the finding that the RH in chicks is more responsive to the detection of novelty whereas the LH is more competent for choosing responses to familiar stimuli (McKenzie, Andrew, & Jones, 1998) is quite compatible with the Janus model; the RH sensitivity to novelty is past-oriented in the sense that it requires a comparison with past experiences to recognize that a stimulus is novel. Long-term memory is certainly consulted by the LH as it forms expectations for the future. Thus, long-term memory is not the sole domain of the RH according to the Janus model; rather, they differ in the manner in which memories are used. The key difference is that the LH is forming working memory representations of future potential choices and contingencies whereas the RH is maintaining an ongoing working memory representation of the context in order to detect novel and unexpected events and to quickly respond to them.

Nonetheless, there have been some findings suggestive of lateralized long-term memory processes. The two major categories of declarative memory are semantic memory, which stores explicit world knowledge, and episodic memory, which stores memories of specific personal experiences (Tulving, 1972; Tulving, 1989). According to the hemispheric encoding/retrieval asymmetry or HERA model (Nyberg et al., 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994), the frontal LH is involved in semantic memories and in episodic encoding whereas the RH is involved in episodic retrieval. Evidence for this position has been provided by analyses of a number of brain imaging studies (LePage, Ghaffar, Nyberg, & Tulving, 1999). Further support has been provided by repetitive transcortical magnetic stimulation (rTMS) data in which it has been shown that temporarily inactivating these regions does affect these memory functions (Rossi et al., 2001; Sandrini, Cappa, Rossi, Rossini, & Miniussi, 2003). Although the HERA model has been criticized on a number of grounds regarding laterality of episodic encoding (Miller, Kingstone, & Gazzaniga, 2002), there does seem to be agreement even by these critics that at least some aspects of semantic memory are left-lateralized and some aspects of episodic retrieval are right-lateralized (see Gazzaniga, 2000).

Although it is tempting to suggest that these findings may be consistent with the Janus model (i.e., episodic memory encoding could be associated with LH forward planning and episodic memory retrieval could be associated with the RH's reactive past orientation), the past orientation of the RH in the Janus model refers to ongoing active comparisons of present events to the baseline provided by the past (and continuing updating of that baseline), not long-term memory retrieval in general. Furthermore, there is not, at present, evidence that memory itself is lateralized in callosotomy patients (in the sense of the right-hemisphere having no long-term memory). It may be that the HERA findings reflect the use of lateralized abilities for helping encode and retrieve long-term memories but that the memories are not otherwise differentially lateralized. Some anecdotal evidence that these lateralized specializations affect long-term memory abilities is the observation that the verbal LH of a number of callosotomy patients has "very poor episodic memory for the timing, both absolute and relative, of recent events" (Zaidel, 2001, p. 397). Formal assessments of memory (without any effort to restrict testing to a single hemisphere) have revealed widespread memory deficits on neuropsychological tests (Huppert, 1981; Phelps, Hirst, & Gazzaniga, 1991; Zaidel & Sperry, 1974). It would be interesting to determine if there is any lateralized differentiation between semantic and episodic memory deficits. In any case, although it is possible that the HERA findings could be understood in the context of the Janus model, there is no evidence at this point that this is necessarily the case and more data are needed.

This paper will make the argument more rigorously for the Janus model by making the case that it applies to the widely disparate systems for motor control and semantics. While it might seem desirable to provide a full review of every relevant laterality domain, this article will focus only on these two areas due to insufficient space to do justice to all such related topics. Motor control and semantics are two especially suitable topics because language has played a central role in laterality theories whereas motor control is a rich line of research that has nonetheless largely been ignored by mainstream laterality theorizing, mostly because it has not been readily accommodated by the five primary lines of laterality theories; the ability of the Janus model to find a place for this intriguing line of research helps illustrate how it can contribute a perspective that addresses issues not currently being fully considered or cited by the wider laterality community. A detailed consideration of lateralized object recognition processes from the standpoint of the Janus model is the subject of another review (Dien, submitted), as is a comprehensive consideration of lateralized working memory contexts (Dien, in preparation).

2.3 The Proactive Versus Reactive Distinction

2.3.1 Motor Control

In the domain of motor control, a relevant distinction is that between "feedforward" and "feedback" motor control (Goldberg, 1985; Goldberg, 1987). Feedforward control is characterized by the execution of advanced planning and feedback control is characterized by responsiveness to outside events. Although Goldberg proposed this distinction in regards to the functions of the supplementary motor area and the lateral premotor area respectively, recent research suggests that this distinction may apply at least as well to hemispheric motor control. It has long been observed that apraxias, difficulties with controlling motor movements, are most associated with LH lesions (Liepmann, 1913; Kimura & Archibald, 1974). Further investigations found evidence that the RH also has a different role, as will be discussed, in motor control (Serrien, Ivry, & Swinnen, 2006). Such a distinction is consistent with the Janus model's proposed LH-proactive/RH-reactive distinction. This paper will review findings in motor programming (the generation of internal representations of motor actions), motor selection (the choice of which motor program to execute), and motor execution (the translation of motor programs into actions). This section will finish with consideration of the related issues of cognitive selection and vigilance.

2.3.1.1 Motor Execution

This paper will begin with the last of the three motor stages, motor execution, as the most clearly motoric aspect of motor control. A leading formulation for motor execution was that the LH mediates open loop movements (as in programmed ballistic movements) and the RH mediates closed loop movements (movements that are modified in an online fashion by feedback). This view originated in observations that reaching motions tend to have two phases, an initial ballistic movement that puts the hand in the vicinity of the target and a second more controlled movement to actually reach the target (Flowers, 1975; Flowers, 1976). The suggestion was that the first phase is under LH control and the second phase is under RH control (Haaland & Harrington, 1989; Winstein & Pohl, 1995). Findings that both hemispheres do appear to make use of proprioceptive feedback have proven problematical for this model (Haaland, Prestopnik, Knight, & Lee, 2004).

In the newer dynamic dominance hypothesis (Sainburg, 2002), the hemisphere controlling the dominant hand (usually the left hemisphere and right hand) uses the ability to predict the dynamics of the limb segments and their interactions to increase efficiency of movements. In contrast, the right hemisphere/non-dominant hand is better when lifting a weight that proves to be different from the expectation and correcting for it (Bagesteiro & Sainburg, 2003). Thus, the left hemisphere is better for feedforward movements and the right hemisphere is better at feedback movements based on unexpected somatosensory information (Sainburg, 2005).

2.3.1.2 Motor Programming

Studies also suggest hemispheric differences in motor programming. Support for a feedforward view of the LH in motor programming comes from demonstrations that the

LH is especially important for programmed series of actions such as finger movements (Haaland, Elsinger, Mayer, Durgerian, & Rao, 2004) and redirecting motor attention from one action to another (Rushworth, Johansen-Berg, Gobel, & Devlin, 2003). Another recent study (Elsinger, Harrington, & Rao, 2006) cued sequences of finger movements using a set of digits (e.g., "13213") either in advance of the actual movement cue or at the time of the movement. The former yielded greater activation in the left parietal whereas the latter yielded greater activation in the right fronto-parietal regions, consistent with a LH-proactive/RH-reactive distinction.

2.3.1.3 Motor Selection

Studies of the kinematics of motor control also provide insight into motor selection, as opposed to execution or programming. For example, findings suggest the LH is dominant for making choices about motor actions when those choices have been defined in advance. Left hemisphere lesions are more disruptive for accuracy in a four-choice task where the button press is dictated by which of four colored rectangles appears (Tartaglione et al., 1991). When subjects are instructed to make one of two finger presses based on which of four symbols appear, disruption of the left, but not the right, lateral premotor cortex with rTMS impaired the ability to do the task, but not clearly so for a simple reaction time task where there was no choice of finger response (Schluter, Rushworth, Passingham, & Mills, 1998). Additionally, rTMS of the left anterior parietal, which is proposed to mediate motor attention, disrupted the ability to disengage from an invalidly cued motor action (Rushworth, Ellison, & Walsh, 2001). Also, LH damage seems to specifically impair ability to select responses, including but not limited to sequences (Godefroy & Rousseaux, 1996; Rushworth, Nixon, Wade, Renowden, & Passingham, 1998). Furthermore, a PET study revealed that motor action selection increased activation in the LH regardless of hand of response, compared to simple reaction time responses (Schluter, Krams, Rushworth, & Passingham, 2001). An ERP study reports that motor preparation is greater over the LH regardless of hand of response when a warning signal provides advance information about which finger to use compared to uninformative warning signals (Hammond & Fox, 2005). Likewise, a PET study of motor attention in which participants were scanned while preparing to move a finger of the left hand generated mostly LH activations despite the fact that movements are primarily controlled by the opposite hemisphere (Rushworth, Krams, & Passingham, 2001).

In contrast, a RH advantage is seen in a pointing task where the target location is not known in advance (Barthelemy & Boulinguez, 2002; Carson, Chua, Goodman, Byblow, & Elliott, 1995; Velay, Daffaure, Raphael, & Benoit-Dubrocard, 2001). This observation is consistent with the postulate that the RH is specialized for responding to unexpected events. Furthermore, a simple target detection task, which does not involve significant motor planning, also revealed the same RH advantage (Barthelemy & Boulinguez, 2001). Finally, when a target shifts midway through pointing, a RH advantage is seen for targets that shift to the left visual field (Elliott, Lyons, Chua, Goodman, & Carson, 1995); although a LH advantage was also reported for the right visual field, reports of this nature have been inconsistent (Sainburg, 2005).

2.3.1.4 Cognitive Selection

These lateralized differences in motor planning seem to include more cognitive aspects of the process. One way to examine this issue is to use signal detection analysis (Green, & Swets, 1966), which can determine in binary decision tasks whether misses (false negatives) represent difficulty in discriminating the targets or whether they represent a shift in decision criteria (i.e., one's relative willingness to make false positives versus false negatives). Signal detection analysis in another study (Riege, Klane, Metter, & Hanson, 1982) revealed that whereas RH strokes impair ability to recognize nonverbal stimuli, LH strokes result in normal recognition but a heightened bias against reporting them (making false negatives). Similarly, a study (Stuss, Binns, Murphy, & Alexander, 2002) where dorsolateral frontal patients made judgments about simple colored shapes reported that LH lesions had a heightened bias, this time towards false positives, whereas RH lesions produced, again, high error rates. Thus, LH lesions seem to produce impairments in decision criteria but not necessarily accuracy. This finding implies that it is the LH that mediates the choice process (the decision of what response to make in the presence of some level of uncertainty) once object recognition processes have been completed. Apparently the patients are coping with their damaged LH decision mechanism by opting to treat all uncertain trials in the same manner (as non-targets in the first study and targets in the second).

The conclusion that it is the LH that mediates the choice process for expected events is consistent with the observation in a PET experiment that a choice (signaling which of four shapes appeared) versus a simple response task was associated with greater LH activations regardless of response hand (Schluter, Krams, Rushworth, & Passingham, 2001). The Janus model suggests that a go-no go task (respond to one stimulus, do not respond if a different stimulus) should be LH since both the timing of the events and the two choice options are known in advance. Indeed, behavioral data in a visual half-field experiment (Bisiach, Mini, Sterzi, & Vallar, 1982) was consistent with LH mediation of a go-no go task. Furthermore, concurrent backward counting, which normally interferes with the LH in visual half-field experiments using a simple response task (Rizzolatti, Bertoloni, & Buchtel, 1979; Rizzolatti, Bertoloni, & De Bastiani, 1982), affected responses to both fields, as if even presentations to the RH had to be relayed to the distracted LH for decision-making (Vallar, Bisiach, Cerizza, & Rusconi, 1988).

In an especially relevant study (Rausch, 1977), left and right temporal lobectomy patients were compared on a decision task. On each trial the patient was given a pair of cards that varied along four different dimensions (each binary, such as "X" vs. "T" or small vs. large) and was told that one value (e.g., "X") would be present on every trial (16 total trials). The task was to deduce the secret value by choosing a card and getting feedback (correct or incorrect). It was found that LH patients (intact RH) tended to generate fewer hypotheses and tended to shift even when the current hypothesis was receiving support from the feedback. In contrast, the RH patients (intact LH) tended to retain a hypothesis even in the face of negative feedback. These findings are consistent with a LH that generates multiple hypotheses and chooses one (proactive) and a RH that learns from disconfirming feedback (reactive).

2.3.1.5 RH Vigilance

An alternative account to some of these latter results is that they are due to a RH role in generalized alerting, insofar as responding to unpredictable events tends to require being alert for longer periods. It is well established that the RH has a special role in vigilance over extended periods of time (Posner & Petersen, 1990), meaning that the RH is better at vigilance rather than that the LH is incapable of vigilance. In callosotomy patients it has been reported that the RH is much better at sustained attention tasks (Dimond, 1979b) whereas the LH has a tendency to "space out" for seconds (sometimes fifteen or more) at a time (Dimond, 1976; Dimond, 1979a). In a variety of imaging studies it has been reported that the need for sustained attention or vigilance produces right fronto-parietal activations (Deutsch, Papanicolaou, Bourbon, & Eisenberg, 1987;

Pardo, Fox, & Raichle, 1991; Sturm et al., 1999; Sturm et al., 2004). Lesions to the frontal RH especially produced slowed RTs in simple reaction time tasks (Tartaglione, Oneto, Manzino, & Favale, 1987) and impaired performance in a counting task for a 1/s rate but not a 7/s rate (Wilkins, Shallice, & McCarthy, 1987).

Divided visual field studies initially did not show behavioral differences in vigilance (Andreassi, Rebert, & Larsen, 1983; Dimond & Beaumont, 1971b); in a later experiment it was reported that at a long delay period of 12 seconds between trials a reliable RH superiority was observed while at 3 seconds there was a trend towards LH superiority (Whitehead, 1991). One difference between the early experiments and the latter experiment is that in the former experiments the inter-trial period was long (averaging 100 and 30 seconds respectively) and highly variable; perhaps there are limits to how long the RH can maintain vigilance as well, although longer than the LH. In any case, it has also been reported that performance on visual half-field tasks is improved when a pre-target alerting stimulus (Heilman & Van Den Abell, 1979), or the target on the previous trial (Cherry & Hellige, 1999; Levy, Wagner, & Luh, 1990), is in the left visual field and thus seen first by the RH, compared to the right visual field (LH). One hypothesis is that the LH is able to perform at a higher level but only for a limited time whereas the RH performs less well but more consistently (Dimond & Beaumont, 1973).

A direct test of the vigilance hypothesis for explaining lateralization of aiming movements found that the RH superiority seems to be due to motor planning rather than vigilance since it only applies to targets in the left side of space and not for simple unaimed movements (Mieschke, Elliott, Helsen, Carson, & Coull, 2001). In any case, RH vigilance is also consistent with a RH role in responding to unexpected events.

2.3.1.6 Conclusion

In summary, in this context proactive/feedforward refers to the ability to generate motor plans in advance, select an appropriate plan, and then use predictions to guide the motor execution of the chosen plan. Reactive/feedback, on the other hand, refers to actions that are responsive to external events, programming and modifying actions as they occur, especially when they are unexpected.

2.3.2 Semantic Priming

Semantic priming paradigms provide a well-characterized and constrained situation. In the context of the Janus model, semantic expectancy would correspond to proactive expectancy insofar as it involves constructing a representation of a specific word(s) in advance of the target presentation. Semantic matching, on the other hand, would correspond to a reactive process insofar as it represents an effort to make sense of a non-predicted target after it has already appeared. The Janus model therefore predicts that semantic expectancy should be left-lateralized and semantic matching should be right-lateralized.

2.3.2.1 Behavioral Data

Evidence has indeed been reported that expectancy and semantic matching are differentially lateralized. In an initial lexical decision study (Koivisto, 1998) asymmetric associative pairs (e.g., STREET-LAMP) were presented in either a forward or backward direction. The primes were presented either laterally or centrally and the targets laterally with an SOA of 550 ms and an RP of .50 and an NWR of .67. They observed backward priming only with central and RH presentations and forward priming only with central and LH presentations.

In a follow-up study (Koivisto, 1999), again using a visual half-field technique with a 750 ms SOA, a LH advantage for forward priming was found which was attributed to expectancy on the grounds that it only occurred with a high RP (which favors expectancy). Conversely, they reported a RH advantage for backward priming under conditions of a high NWR (which favors semantic matching); although the RP was high as well, the use of backward primes rules out expectancy. Furthermore, these effects only occurred when the participants were specifically instructed to make use of the primes which was used to further support the argument that the effects were controlled rather than automatic in nature; however, since the primes were laterally presented and hence hard to read it is likely that the effect of the manipulation was due to the controlled deployment of spatial attention (which could just as easily facilitate ASA) rather than controlled priming per se (see Neely, & Kahan, 2001).

In a succeeding visual half-field experiment with categorical non-associates and a centrally presented prime (Koivisto & Laine, 2000), it was again reported that a high NWR, which promotes semantic matching, produced RH priming. Under a low NWR, priming was found in the LH instead. The authors argued that the LH priming represented ASA on the basis that expectancy was ruled out by a low relatedness proportion; however, if it was ASA then it should have been present in the high NWR condition as well since an automatic response is not controllable by definition (Chiarello, 2000). Although it is true that a low relatedness proportion discourages the use of expectancy by reducing its effectiveness as a strategy, a recent study has presented evidence that expectancy can occur even with a low RP of .25 and a short SOA of 300 ms (Hutchison, Neely, & Johnson, 2001). Also, the SOA used in both cases (500 ms and 750 ms respectively) are on the long side for ASA to be remaining in effect (Anderson, 1983; McNamara, 2005), but see (Deacon, Uhm, Ritter, Hewitt, & Dynowska, 1999). For these reasons it seems likely that the LH effect was in fact an expectancy effect.

This LH-expectancy/RH-semantic matching hypothesis conflicts with a study (Chiarello, Richards, & Pollock, 1992) that made the opposite conclusion, namely that semantic matching occurs in the LH. This study made the intriguing observation that when comparing priming for word pairs that share an association (DOG-BONE), non-associated category membership (DOG-GOAT), or both (DOG-CAT), only some studies show what they called semantic additivity, where the effect of an associative categorical pair was the sum of the two types alone. They went on to propose that semantic additivity reflects semantic matching and that it is only seen for LH processing. In the first of three experiments they used lexical decision and a high RP and NWR in a divided visual field design and reported semantic additivity in the LH only. In order to determine whether the effect was due to expectancy or semantic matching, the experiment was repeated with a naming task, which should preclude semantic matching (Seidenberg, Waters, Sanders, & Langer, 1984). Although they did find semantic additivity, they argued that semantic matching can be present even with a naming measure if the stimulus is degraded (in this case by lateralized presentation) and bolstered this argument by demonstrating in a third experiment that the semantic additivity was eliminated when the experiment was replicated with central presentation. They therefore concluded that semantic matching is a LH process.

Although these findings are of interest, this author suggests a different interpretation. A chief reservation is that this author could find no support for the contention that semantic matching can influence naming measures whereas there is a substantial consensus that it does not (Neely, 1991; Seidenberg, Waters, Sanders, & Langer, 1984), although Chiarello and colleagues (1992) do cite a paper (Durgunoglu, 1988) demonstrating that perceptual degradation (masking) changes the pattern of priming effects. This paper suggests instead an alternative presented by a more recent paper (Stolz & Neely, 1995) that was not available when Chiarello and colleagues interpreted their effects. As described earlier, this more recent paper demonstrated that the interaction between stimulus degradation and semantic priming is not due to either expectancy or semantic matching. Thus, these results may be understood as reflecting semantic feedback to the lexical level and back to the letter level (Besner & Smith, 1992; Borowsky & Besner, 1993). It is not particularly clear at this point whether semantic feedback is prospective in nature although the Janus model would predict it is if it is LH. Thus, this paper agrees that the semantic additivity effect reflects a process other than expectancy but that it represents the presence of semantic feedback rather than semantic matching. It is therefore not incompatible with the broader proposal that expectancy-priming mechanisms are LH and semantic matching mechanisms are RH.

2.3.2.2 Neural Data

Some further evidence for RH semantic matching comes from this author's own laboratory. This author has reported a putative semantic matching component, the N400RP (for right parietal), which seems to be different from the more midline N400 component, which this author has also observed (Figure 3). Note that this paper terms the latter the N400 since it is the form this author has observed in his sentence studies both published (Dien, Frishkoff, Cerbone, & Tucker, 2003) and otherwise, the experimental design in which the N400 was first reported (Kutas & Hillyard, 1980), although the original reports did not have sufficient electrodes to provide a full scalp topography. In an initial experiment (Dien, Franklin, & May, 2006) participants performed a lexical decision task with an SOA of 1000 ms between the prime and the target. The stimulus list, from a previously published study (Thompson-Schill, Kurtz, &

Gabrieli, 1998), contained asymmetric associative pairs (half semantically related and half not) as well as standard symmetric pairs sharing both associative and semantic aspects, such as NURSE-DOCTOR. The RP was .33 and the NWR was .6, thus favoring semantic matching. A statistically significant N400RP effect was observed to unrelated pairs compared to asymmetrically associated pairs regardless of direction (e.g., FRUIT-FLY or FLY-FRUIT) but not to symmetrically associated word pairs; the presence of a semantic relationship had no effect.

In a second experiment (Franklin, Dien, Neely, Waterson, & Huber, 2007), lexical decision was performed with a 500 ms SOA. This stimulus set, consisting largely of word pairs from a different published study (Kahan, Neely, & Forsythe, 1999), contained forward and backward associated pairs and standard symmetric pairs. The RP was .6 and the NWR was .78, thus favoring expectancy in addition to semantic matching. This time the N400RP effect was evoked only by the backward priming pairs, which are thought to be mediated only by semantic matching. This paper interprets these results as indicating that in the second experiment the participants focused on expectancy but were able to employ semantic matching when it failed to be of use; such a pattern is consistent with the two hemispheres operating in parallel and the RH assisting when the LH was unable to apply expectancy. Note that hemispheric lateralization cannot be directly inferred from the scalp topography since a source in the LH could produce a right-lateralized scalp topography if appropriately angled, so further study is needed, but the topography does strongly suggest a RH source, consistent with the behavioral studies. Furthermore, a follow-up fMRI study (Dien, O'Hare, Waterson, and Savage, in preparation) found that the activations for backward priming pairs were almost entirely right-lateralized.

Conversely, evidence suggests that the N400 reflects controlled (Silva-Pereyra et al., 1999) post-lexical updating of semantic expectancies in situations where ASA or expectancy priming has occurred (Franklin, Dien, Neely, Waterson, & Huber, 2007), and is left-lateralized. An N400 study of callosotomy patients in which sentences were presented to either the left or right hemisphere found that a larger N400 was consistently elicited by incongruent endings in the LH but only two of the five patients in the RH, implicating the LH as the primary source. Furthermore, source localization efforts and intracranial recordings have also primarily indicated LH generators, although there has been some dispute over the exact locations (Frishkoff, Tucker, Davey, & Scherg, 2004; Johnson & Hamm, 2000; McCarthy, Nobre, Bentin, & Spencer, 1995; Meyer et al., 2005; Nenov et al., 1991; Nobre, Allison, & McCarthy, 1994; Nobre & McCarthy, 1995; Van Petten & Luka, 2006).

In the fMRI and PET literature, thus far, no explicit effort has been made to distinguish expectancy from semantic matching. Only one study seems to have any grounds at all for making conclusions in this respect. This PET study (Mummery, Shallice, & Price, 1999) sought to identify strategic aspects of semantic priming in a lexical decision task by systematically varying the RP from 0 to 1.00. Brain regions that responded to this manipulation could be understood as reflecting controlled processing since automatic processes should be insensitive to such strategic considerations. The authors were careful to avoid interpreting the results as being expectancy versus semantic matching since they presumably understood that NWR was confounded with RP, as it usually is (Neely, Keefe, & Ross, 1989). Thus, their results likely reflected both types of processes. The regions that responded to the manipulation were left anterior temporal (BA38), left anterior cingulate, right parietal (BA7), and right premotor (BA6). This paper therefore can hypothesize that the LH effects reflect expectancy and the RH effects reflect semantic matching (although laterality was not statistically evaluated). Certainly a right parietal source would be consistent with the scalp topography of the N400RP effect that has been suggested to index semantic matching.

2.3.2.3 Sentence Priming

That these lateralized differences in semantic priming might extend to more general language processing can be seen where sentence stems are the prime. The initial findings were seen in studies of humor, such as what makes a joke funny, as in the Robin Williams definition: “Politics: 'Poli' a Latin word meaning 'many'; and 'tics' meaning 'bloodsucking creatures'.” An influential cognitive model of humor (Suls, 1972) proposes that humor appreciation requires a two-step process: 1) The listener recognizes that the punch line is unexpected and 2) the listener recognizes that the punch line nonetheless makes sense. The first step is a violation of proactive expectancy and the second meaningfulness step could be understood as the unexpected retrospective recognition that the punch line can nonetheless make sense. Humor studies of brain lesion patients suggest that the ability to make the expectancy judgment is left-lateralized whereas the ability to make the meaningfulness judgment is right-lateralized (Bihrle, Brownell, Powelson, & Gardner, 1986; Brownell, Michel, Powelson, & Gardner, 1983).

A recent ERP study has found a similar pattern in normal participants reading normal sentences (Dien, Frishkoff, Cerbone, & Tucker, 2003). In this study, participants read sentences one word at a time for comprehension, half of which ended with a semantically congruent ending and half of which ended with an incongruent ending. Using a novel item averaging procedure, ERP averages were computed for each individual sentence. The sentences were then normed by a separate group according to how expected the endings were and how meaningful the full sentences were. It was found that a left-lateralized N2 (Recognition Potential) was highly correlated with the expectancy ratings, whereas a right-lateralized N2 (Meaningfulness Recognition Potential) was highly correlated with the meaningfulness ratings. These findings suggest that not only are these two judgments lateralized in accordance with the studies of lesion patients but that they also appear to be occurring in parallel in the two hemispheres.

Further support for this hemispheric distinction, but in different ERP components, is provided by an ERP experiment that presented sentence endings to the visual half-fields (Federmeier & Kutas, 1999) and was replicated using pictures instead of the final word (Federmeier & Kutas, 2002). An initial sentence established the semantic context and then a second sentence that was equally congruent with all three possible endings was presented. The first sentence was presented as a whole and the second sentence was presented one word at a time at fixation, except for the ending, which was presented to one side. An example sentence pair is "Justin put a second house on Park Place. He and his sister often spent hours playing..." The sentence endings were either expected ("monopoly"), unexpected but from the same category ("chess"), or wholly unexpected ("baseball"). The task was to read for comprehension with a recognition task at the end of each block. For LH presentations, the first two categories produced smaller N400s than for the unexpected endings, suggesting a general expectancy set for items from that category (e.g., all board game words). The N400 from RH presentations of unexpected endings, on the other hand, were equally large regardless of whether they were from the expected category or not (e.g., only "monopoly" okay). The authors suggest that the LH generates a prediction (i.e., "monopoly") and the N400 reflects the ending's discrepancy from this prediction whereas the RH directly matches the ending word to the context once it has both available, hence the greater specificity in the N400 response. In this sense then, the LH is predictive and the RH is retrospectively integrative, although Federmeier characterizes the RH role as being more veridically descriptive than integrative (Federmeier, 2007).

2.3.2.4 Conclusion

To sum up, this paper finds that in the area of semantic priming, as in the area of motor control, there is evidence of a distinction between LH proactive processes and RH reactive processes. Although both lateralized effects are consistent with common adaptive roles, neither effects are currently construed as being due to a single functional difference between the two hemispheres, such as high versus low frequency analysis, and seem unlikely to lend themselves to such a formulation.

3 COMPARISON WITH COARSE CODING MODEL

An example of how the Janus model can provide the basis for alternative predications to existing models concerns the Coarse Coding Model (Beeman, 1993; Beeman et al., 1994) and the distinction between predictive and coherence inferences. When reading, a good comprehender must make inferences in order to make sense of the passages. As the passage unfolds, s/he may try to anticipate the next development in order to better build the meta-structure of the discourse, which is termed a predictive inference (McKoon & Ratcliff, 1986). Conversely, it may be necessary to infer an event that is only implied, which is termed a bridging or coherence inference (Haviland & Clark, 1974).

The Janus model would clearly indicate that predictive inferences should be LH and coherence inferences should be RH. Instead, a study (Beeman, Bowden, & Gernsbacher, 2000) reported that the reverse was true. Recordings of passages were played to the participants, which they were told to listen to for comprehension. They were further instructed to perform a secondary task, consisting of a naming task on words laterally presented on the monitor. These words were intended to be probes tapping the inferences made by the participants during the comprehension process. In the example passage: "The shuttle sat on the ground in the distance (1), waiting for the signal to be given (2). After a huge roar (3) and a bright flash, the shuttle disappeared into space (4)..." probes were given at each of the numbered points. LAUNCH might be presented at points 1 and 2 in order to probe for a predictive inference (that a launch would be occurring shortly) or at points 3 and 4 to probe for a coherence inference (that a launch had occurred, although not explicitly stated). The priming effect for the probes evidenced as shorter naming latencies for predictive inferences for the RH and for coherence inferences for the LH. A subsequent fMRI experiment (Virtue, Haberman, Clancy, Parrish, & Jung Beeman, 2006) supported these findings, with LH superior temporal sulcus activity at coherence breaks and RH superior temporal sulcus activity at a point that should generate predictive inferences.

It was argued that these findings supported the Coarse Coding model (Beeman, Bowden, & Gernsbacher, 2000). "Because large semantic fields tend to overlap, activation capable of supporting predictive inferences is more likely to occur in the RH than in the LH" (p. 328). "When activation of a potentially connective concept is found, the concept is selected by enhancing its activation. This is more likely to occur in the LH, due to its tendency to strongly activate small semantic fields" (p. 328). It seems to the present author, however, that the opposite case is a stronger argument. One would expect that highly predictable occurrences, such as a launch, would be a strong associate for "shuttle" in the LH and that this hemisphere would therefore dominate the predictive inference process. Conversely, a coherence inference might require the RH summation priming of several clues (such as "roar", "flash", and "shuttle") to activate the concept of a shuttle launch. This paper therefore suggests that this very interesting empirical finding does not support the Coarse Coding model any more than it supports the Janus model.

Furthermore, these findings also do not seem to be consistent with other existing studies. A study of RH lesion patients reported that they were largely unimpaired in their ability to generate predictive inferences, as measured by slowed reading of disconfirming final sentences (Lehman-Blake & Tompkins, 2001). Another interesting fMRI study (St George, Kutas, Martinez, & Sereno, 1999) compared the results when participants read an ambiguous passage with an explanatory title and without (but see Maguire, Frith, & Morris, 1999), following a classic cognitive experiment (Bransford, Barclay, & Franks, 1972). In the example, the passage started with: "This is very rewarding but tends to be quite expensive even if you own all that you need. The outfit does not really matter. One can get seriously injured without proper instructions even if it comes more naturally to some people than others" (p. 1318). When reading with the title "Horse-back riding," the left middle temporal sulcus was active but when reading without it, the right middle temporal sulcus was active. Without the title predictive inferencing is largely impossible and one would expect heavy reliance on coherence inferencing efforts (which the shuttle study says is LH), and yet activity was right-lateralized as both the Janus model and, this author argues, the Coarse Coding theory, as well, should predict.

This paper suggests that the key to this conundrum is a consideration of the cognitive processes involved in these two inferences. This paper suggests that, at least in the examples provided in the two papers (Beeman, Bowden, & Gernsbacher, 2000; Virtue, Haberman, Clancy, Parrish, & Jung Beeman, 2006), the passages corresponded to very predictable scenarios. For example, from the very first mention of the word "shuttle" the sequence of events could easily be foreseen as forming a script. This LH could therefore predictively bridge coherence breaks, such as the shuttle launch, without need for complex retrospective inferences.

Some evidence that "predictive" inferences are not necessarily proactive is a study (Calvo, Meseguer, & Carreiras, 2001) using eye movement measures that reported predictive inferences that were post-lexical in nature. Unlike the effects from an unexpected word, which affect the initial pass (Ehrlich & Rayner, 1981), predictive inferences affected the second-pass reading, which occurs after the reader has already read through the sentence. This was interpreted as showing that predictive inferences were affecting text integration rather than facilitating lexical analysis. This finding is therefore consistent with the proposition that such predictive inferences represent a retrospective process. One possible objection is that naming measures should have precluded post-lexical processes (Potts, Keenan, & Golding, 1988; Seidenberg, Waters, Sanders, & Langer, 1984). On the other hand, while it is thought that naming precludes semantic matching, it does not necessarily preclude all types of post-lexical processes, such as semantic integration.

4 CONCLUSION

This paper has sought to argue for a more integrative approach to laterality research. It has begun by providing a systematic summary of the major lines (defined as potentially being applied to multiple domains) of laterality theory, something that has not been recently made available for the current literature. It has then gone on to argue that the current leading approach to integrating large aspects of laterality (from perception to semantics), is the frequency model, via the architectural efficiency framework. It has then summarized evidence that although the frequency model may be viable for certain domains of cognition (notably perceptual), support for applying it more widely to areas such as semantics is questionable.

Rather than conclude that it is not possible to integrate across laterality domains, this paper then argues that it may be possible to find a broad approach to understanding many (although probably not all) laterality findings by using a different adaptive framework and the Janus model is offered as such an approach. It has been argued that because the Janus model is constructed with a focus on the distal level, the Janus theory provides a framework that can incorporate aspects of laterality findings, such as the RH role in vigilance, that are not accounted for under current instantiations of the architectural efficiency approach. At the same time, it has been demonstrated that the Janus model is nonetheless sufficiently specified as to enable falsifiable predictions, as illustrated in the comparison with the Coarse Coding model, although clearly more studies are needed to test these competing accounts.

Given the space limitations of this publication venue, an effort has been made to illustrate the potential application of the Janus model to only two topics, motor control and semantic priming. The question of whether and how it could be applied to other domains will therefore have to be left for future efforts. At this point, the goal is only to make the argument that the Janus model is a viable contender as an integrative framework for at least some domains of laterality findings. Indeed, there is no reason to claim that the Janus model should be able to account for every instance of lateralized asymmetries, merely that it may usefully account for some of them. Potential topics to be addressed in the future include the role of long-term memory (see Tulving, Kapur, Craik, Moscovitch, & Houle, 1994), mental time travel (Suddendorf & Corballis, in press), motivated behaviors (see Harmon-Jones, 2003), and coordination between the hemispheres (see Levy & Trevarthen, 1976).

Although the specific mechanisms at each level of the cognitive machinery need to be specified, the Janus proposal suggests how many of these diverse observations might be organized along evolutionary grounds, with multiple dichotomies reflecting the needs of the two roles. As an example of what shape such an effort could assume, in a separate manuscript (Dien, submitted) it is proposed that observations in orthographic analysis and face recognition could be accounted for by asymmetries in three separate levels of cognitive operations. The proposal is that the left hemisphere represents features using an abstract-category code whereas the RH utilizes a specific-exemplar code. Furthermore, the LH codes feature relationships using associative co-occurrence values whereas the RH relies on spatial metrics. Finally, it is suggested that the LH attentional system is biased towards isolating features and the RH is biased towards conjoining features. In this account, each hemisphere utilizes parallel processing when stimuli are congruent with its processing characteristics and serial when they are not, resulting in left-lateralization for orthographic analysis and right-lateralization for face recognition.

This proposal is consistent with the Janus model in that characteristics that facilitate detection of novel stimuli would help the RH to carry out its function of reacting to unexpected events. Specific-exemplar codes (e.g., the face of a specific person) and spatial metrics (which are helpful for differentiating specific faces) would be especially helpful for detecting novel stimuli (e.g., a stranger). In contrast, characteristics that facilitate making explicit predictions would help the LH to carry out its function of forming action plans for future events. Abstract-category codes would be helpful for making generic predictions (e.g., how to act if a predator of some kind emerges from a cave) and associative co-occurence values (e.g., bones on the ground tend to be associated with the presence of a predator). In this view, the left-lateralization of orthographic analysis and the right-lateralization of face recognition are the by-products of these role-based specializations and indeed the literature reveals that these lateralization patterns can be reversed under certain conditions. Finally, the Janus model suggests the likelihood that the asymmetries at these different levels are independently implemented and hence have nothing in common other than that they have been subject to common selective pressures.

With respect to what has been argued to be the leading laterality model, the frequency model, it is argued that the Janus model is posed in contention with it at the distal level (via the architectural efficiency framework) rather than the proximal level, although it does lead to some competing predictions in the area of semantics. That is, only mechanisms that directly involve the core features of predicting the past or responding to unexpected events can be said to be necessarily incompatible with the Janus model as currently formulated. The core features of the frequency model, such as those involved in perception, could potentially be accommodated by the Janus model and therefore are not necessarily contradictory. This is not to say that the Janus model is irrelevant to other issues, however; if this were the case, then it too would be a domain-specific model.

The strength of the Janus model is its potential as a heuristic, generating proximal-level hypotheses in other domains. This can be done by taking the proposed adaptive roles of the two hemispheres as a starting place and then extrapolating what characteristics might facilitate these roles. To the extent that proximal-level mechanisms can be framed in this manner, the Janus model can be said to have succeeded at the level of being a cross-domain framework and therefore successfully functioning as a

Kuhnian paradigm. An example of how the Janus model could serve as a paradigm is how it highlights how studies of motor control might be relevant to other areas of laterality research. The Janus model also potentially has the heuristic value of a paradigm. Efforts in this direction are outside the scope of the present journal article due to space considerations and are being made elsewhere (Dien, in preparation). In general, any task that involves making plans and acting upon those plans should be left-lateralized and any task that involves detecting unexpected events and reacting to them should be right-lateralized. While there have been some cases of using the architectural efficiency framework as a cross-domain heuristic, making the suggestion that principles seen in one domain might apply to another (Beeman, 1993; Laeng, Zarrinpar, & Kosslyn, 2003), for the most part it has not been very fruitful, focused as it is on justifying observations at the proximal level rather than on forming a generalized account at the distal level.

Application of an organizational framework such as this one could be helpful in organizing the massive accumulation of data that is currently impeding further theoretical progress. Efforts such as this are also potentially helpful in facilitating cross-disciplinary communication. As the current manuscript illustrates, relevant data has been accumulated by such diverse researchers as cognitive psychologists, comparative psychologists, neuropsychologists, and neuroimagers. This rich diversity of laterality findings can either result in cross-fertilization or it can result in balkanization. This manuscript is therefore intended to serve as an effort to help spark communications between these diverse lines of research, to identify areas where more research is needed, and to serve as an invitation to skeptics to generate alternatives.

Figure Captions

Figure 1. The Time Course of Semantic Priming in Lexical Decision According to the Hybrid Model. The key feature of this illustration is that whereas ASA, Expectancy, and Semantic Feedback are all put into operation before the target, Semantic Matching has its effect after the target presentation and is therefore a retrospective process.

Figure 2. The Janus Model. This figure illustrates the proposed temporal orientations of the two hemispheres. The left hemisphere looks to the future and generates multiple potential scenarios that it will then prepare for and/or choose between; meanwhile, the right hemisphere integrates the ongoing events into a single gestalt by which to understand events that have occurred in hindsight and to detect anomalies that require further consideration or swift response.

Figure 3. Contrasting the P300, N400, and N400RP. Figures provide scalp topography and time course of the ERP components. The white dot indicates the location corresponding to the waveform. The arrow indicates the time point corresponding to the scalp topography. a) P300 difference map from Spencer, Dien, and Donchin (1999). The waveforms are the grand average data. b) N400 factor difference map from Dien, Franklin, and May (2006). c) N400RP difference map from Dien, Franklin, and May (2006). The waveforms are the grand average data.

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