Hemispheric Asymmetry in Prefrontal Cortex for Complex Cognition

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Abstract

With the exception of language, hemispheric asymmetry has not historically been an important issue in the frontal lobe literature. Data generated over the past 20 years is forcing us to reconsider this position. There is now considerable evidence to suggest to that the left prefrontal cortex is an inference engine that automatically makes simple conceptual, logical, and causal connections to fill in missing information and eliminate uncertainty or indeterminacy. This is a fine-tuning of the "left hemisphere interpreter" account from the callosotomy patient literature. What is new is an understanding of the important contributions of the right prefrontal cortex to formal logical inference, conflict detection, and indeterminacy tolerance and maintenance. This chapter articulates these claims and reviews the data on which they are based.

We conclude by speculating that the inference capabilities of the left prefrontal cortex are built into the very fabric of language, and can be accounted for by the left hemisphere dominance for language. The roles of the right PFC require multiple mechanisms for explanation. Its role in formal inference may be a function of its visual-spatial processing capabilities. Its role in conflict detection may be explained as a system for checking for consistency between existing beliefs and new information coming into the system and inferences drawn from beliefs and/or new information. There are at least three possible mechanisms to account for its role in indeterminacy tolerance. First, it could contain a representational system with properties very different than that of language, and an accompanying inference engine. Second, it could just contain this different representational system, and the information is at some point passed back to the left prefrontal cortex for inference. Third, the role of the right prefrontal cortex may be largely preventative. That is, it doesn't provide alternative representational and inference capabilities but simply prevents the left prefrontal cortex from settling on initial, local inferences. The current data do not allow us to differentiate between these possibilities. Successful real-world functioning requires the participation of both hemispheres.

Keywords: frontal lobes, lateralization, reasoning, problem-solving, decision-making, inference, logic, inconsistency detection, conflict detection, indeterminacy tolerance, uncertainty

`To appear in Grafman & D'Esposito (Eds.) Handbook of Clinical Neurology, Elsevier.`

1.0 Introduction

Some degree of hemispheric asymmetry seems to be a principle of brain organization in most, if not all, species (Denenberg, 1981; Toga & Thompson, 2003). In terms of the human brain, hemispheric asymmetry came to prominence in the 1950s, with the pioneering work by Sperry and colleagues on split brain patients (Gazzaniga, 1995; Sperry, 1982). Since then a number of studies have highlighted differences in hemispheric organization ranging from physiological and structural cellular organization (Glick, Ross, & Hough, 1982; Zilles et al., 1996), to functional differences at the level of sensory motor functions (Amunts et al., 1996; Coghill, Gilron, & Iadarola, 2001), language (Knecht et al., 2000; Levy, 1976; Levy, Nebes, & Sperry, 1971), visual-spatial processing (Christman, 1989; Ratcliff, 1979), attentional systems (Corbetta & Shulman, 2002), emotion (R. J. Davidson, 1992), and complex cognition systems (Gazzaniga, 1985, 1995).

The focus of this chapter is on hemispheric asymmetry in prefrontal cortex for complex cognition functions like reasoning, decision-making and problem-solving.[1] We ask and answer the following questions: (1) Is there robust data to suggest hemispheric asymmetry in the human prefrontal cortex (PFC) for complex cognition? (2) if so, what are some of the functions attributable to left and right prefrontal cortex? (3) What are the underlying mechanisms of this hemispheric asymmetry? We will answer the first question in the affirmative, review some of the recent data supporting this asymmetry, identify the lateralization of certain functions, and then speculate on underlying mechanisms.

In brief, the data suggest that the left PFC is an inference engine set up to reduce uncertainty/indeterminacy by filling in informational gaps by making simple conceptual, logical, and causal connections. The right PFC subserves complex cognition by being involved in formal logical inference, conflict/consistency detection, and indeterminacy tolerance and maintenance. Neither system is dominant for complex cognition. The two systems are complementary and both have unique, critical roles to play in real-world functioning. We conclude by speculating on possible underlying mechanisms for these functions.

2.0 Complex Cognition and Asymmetry: A Brief History

By complex cognition we are referring to the reasoning, problem-solving, and decision-making literatures. The problem solving literature studies tasks such as cryptarithmetic, theorem proving, Tower of Hanoi, and also more open-ended, real-world problems such as planning, design, and even scientific induction, among others (Dunbar, 1993; Goel, Grafman, Tajik, Gana, & Danto, 1997; Goel & Pirolli, 1992; Newell & Simon, 1972). The basic theoretical framework is one of search through a problem space using the formal apparatus of production rules (and more generally, recursive function theory). The reasoning literature is largely focused on

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[1] The important topic of language is taken up in another chapter of this handbook. We will have occasion to discuss the role of language at the end of the chapter when addressing the issue of underlying mechanisms.

deductive inference tasks and draws upon the theoretical apparatus of formal logic (Jonathan Evans, 1983; P. Johnson-Laird, 2006; Rips, 1994). The judgment and decision-making literature uses such tasks as the base rate fallacy and the conjunction fallacy, and draws upon the formal apparatus of probability theory (Tversky & Kahneman, 1974). Collectively, these literatures cover much of what we mean by the colloquial use of the term "thinking." The question of interest is whether there are hemispheric differences involved in these thought processes, particularly with respect to the prefrontal cortex.

If we begin with the split brain patient literature, we find a story of left hemisphere dominance for complex cognition functions, particularly inference. Perhaps the most interesting studies in this regard have been undertaken by Gazzaniga and colleagues. In one classic experiment involving implicit inference (Gazzaniga, 1989), split brain patients were presented with a picture of a chicken claw projected to the right visual field (left hemisphere) and a picture of a snowy winter scene projected to the left visual field (right hemisphere). The patient must then select (one with each hand), from an array of other pictures, which two are related to the projected pictures. The patient selects a shovel with the left hand (because the right-hemisphere, controlling that hand, has viewed a snowy winter scene) and a chicken with the right-hand (because the left hemisphere, controlling that hand, viewed a chicken claw). Upon being asked to explain the choice of the shovel with the left hand (guided by the right hemisphere) the patient's left hemisphere (dominant for language) has no access to the information about the snowy scene viewed by the right hemisphere. But instead of responding "I don't know," the patient fabricates a plausible story, based upon background knowledge, and responds that the shovel is required to clean the chicken coop.

In another simpler paradigm, a picture of a saucepan, followed by a picture of water, is shown to each hemisphere, (Gazzaniga & Smylie, 1984). When the pictures are shown to the left hemisphere, the patient can draw the causal inference of "boiling water". When the pictures are shown to the right hemisphere, the patient cannot draw the inference.

Such findings led to the postulation of the left hemisphere "interpreter," (Gazzaniga, 1995; Wolford, Miller, & Gazzaniga, 2000) (see also (Hagoort, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) for related ideas) a system compelled to connect bits of incomplete information to make sense of the world by locking onto and extrapolating patterns. This system abhors uncertainty, and automatically fills in any gaps with assumptions based upon background knowledge and beliefs, often prematurely and incorrectly. This same literature limited the role of the right hemisphere to little more than organization of visual information (Corballis, 2003) and resulted in a story of left hemisphere dominance for reasoning, problem-solving and decision making.

The split brain patient research was, of necessity, concerned with hemispheres rather than more circumscribed cortical regions. But much of the literature on complex cognition focuses on prefrontal cortex. If we examine the historical literature on prefrontal cortex, at least until the late 1990s, the issue of hemispheric asymmetry is discussed, but certainly has not been a major distinction (like, for example, ventromedial prefrontal cortex and dorsolateral prefrontal cortex). Hemispheric differences have been postulated in dorsolateral prefrontal cortex (DLPFC) with respect to spatial and linguistic working memory (Goldman-Rakic, 1994; Paulesu, Frith, & Frackowiak, 1993). The HERA model predicted hemispheric differences in the encoding and retrieval of episodic memories in prefrontal cortex (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). A few studies identified left prefrontal lesions as differentially affecting the WCST (Drewe, 1974), Tower of London (Shallice, 1982), and the Stroop task (Perret, 1974; Weekes & Zaidel, 1996). A few other studies identified right prefrontal lesions impairing design fluency (Jones-Gotman & Milner, 1977), cognitive estimation (Smith & Milner, 1984), planning and design tasks (Goel & Grafman, 2000), and cognitive tasks (like humour appreciation) requiring the "breaking of mental sets" (Shammi & Stuss, 1999).

A review of 14 patient studies from this period, on the role of prefrontal cortex in planning processes illustrates this point (Bamdad, Ryan, & Warden, 2003; Bechara, Damasio, Damasio, & Anderson, 1994; Burgess, 2000; Colvin, Dunbar, & Grafman, 2001; Dritschel, Kogan, Burton, Burton, & Goddard, 1998; Fellows, 2006; Fortin, Godbout, & Braun, 2002, 2003; Goel & Grafman, 2000; Goel, Grafman, et al., 1997; Miotto & Morris, 1998; Penfield & Evans, 1935; Shallice, 1982; Shallice & Burgess, 1991). Only four of these studies (Colvin et al., 2001; Fellows, 2006; Miotto & Morris, 1998; Shallice, 1982) specifically grouped patients into left and right hemisphere lesions. They reported either no difference in the performance of patients with lesions to left or right PFC (Colvin et al., 2001; Fellows, 2006; Miotto & Morris, 1998), or they reported in fact that the left hemisphere patients did worse than the right hemisphere patients (Shallice, 1982), a finding consistent with the left hemisphere dominance account from the split brain patient literature. A recent meta-analysis of the Tower of London task neuroimaging and patient studies reported similar ambivalent results with respect to hemispheric asymmetry (Nitschke, Köstering, Finkel, Weiller, & Kaller, 2017).

Over the past 20 years, two important factors have contributed to the rethinking of hemispheric asymmetry in prefrontal cortex: (1) The development of *in vivo* functional imaging technologies have allowed us to identify specific contributions of left and right prefrontal cortex to complex cognition tasks. (2) There has been an appreciation of the distinction between ill-structured and well-structured tasks and the realization that neuropsychological test batteries are biased towards well-structured tasks, while real-world problems have both ill-structured and well-structured components. The first factor is self-evident, but the second warrants some discussion. It is addressed in Section 3.2.3.

3.0 Evidence for Hemispheric Asymmetry in PFC: The Last 20 Years

3.1 Functions of Left PFC System

Gazzaniga's conclusion about the dominance and role of the left hemisphere in complex cognition has more recently been associated with left prefrontal cortex (Marinsek, Turner, Gazzaniga, & Miller, 2014; Wolford et al., 2000). The "left hemisphere interpreter" has manifested itself in various ways in left prefrontal cortex, across a range of complex cognition tasks, including deductive reasoning

(Goel, 2007; Prado, Chadha, & Booth, 2011), inductive reasoning (Goel & Dolan, 2004; Reverberi, Lavaroni, Gigli, Skrap, & Shallice, 2005) (Goel et al., 1997), decision-making (DeNeys & Goel, 2011), and drawing simple causal inferences (Roser, Fugelsang, Dunbar, Corballis, & Gazzaniga, 2005).

One way of characterizing the left PFC interpreter in light of these data is as an inference engine focused on reducing uncertainty or indeterminacy by making connections and filling in missing information.[2] There is considerable data to support the following three types of inferences: (i), conceptual/semantic inference (ii) simple logical inference, and (iii) simple causal inference. The data for each is briefly reviewed below.

3.1.1 Conceptual/Semantic Inference

Conceptual/semantic inference concerns relationships between ideas, words and propositions. Such relationships can exist by virtue of logical structure and/or semantic content. The former is discussed in the next section. In terms of semantic content, consider the famous Linda Problem (Tversky & Kahneman, 1974):

> (A)
>
> Linda is 31 years old, single, outspoken, and very bright. She majored in philosophy. As a student, she was deeply concerned with issues of discrimination and social Justice, and also participated in anti-nuclear demonstrations.

From this information participants are much more likely to draw the inference that Linda is active in the feminist movement than the inference that Linda is a bank teller. Neither of these inferences follow logically from the given information, but the former is reliably considered more plausible than the latter, given what we have been told about Linda.

Such content based inferences are invariably inductive inference. They draw upon world knowledge and semantic/conceptual connections and tend to preferentially activate left prefrontal cortex. For example, Goel and Dolan (2004) had participants determine the plausibility of arguments such as B. With respect to PFC, they reported activation in left dorsolateral PFC (BA 9, 8, 45) for inductive reasoning (Figure 1A). Goel et al. (1997) reported similar results with similar material.

> (B)
>
> House cats have 32 teeth;
>
> Lions have 32 teeth;

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[2] The term "uncertainty" is often used in the decision-making literature to convey risk/reward evaluations as a probability. I use the term "indeterminacy" to refer to uncertainty independent of risk-reward evaluations, where there is literally no fact of the matter. For example, given the premises A > B, A > C, what is the relationship between B and C? There are no probabilities to be assigned here. Given this incomplete information, there is no fact of the matter as to the relationship between B and C. It is indeterminate. If uncertainty is understood thus, the two terms are interchangeable.

∴ All felines have 32 teeth.

Another paradigm which draws upon inductive inference is the inclusion fallacy task (Liang, Goel, Jia, & Li, 2014; Osherson, Smith, Wilkie, López, & Shafir, 1990). In this task participants are given arguments such C and D and asked to select which is the stronger of the two.

(C)

Robins secrete uric acid crystals

∴ Birds secrete uric acid crystals

(D)

Robins secrete uric acid crystals

∴ Ostriches secrete uric acid crystals

Participants will sometimes (fallaciously) find the conclusion of argument C stronger than the conclusion of argument D. (This is fallacious because a property cannot be more likely of a whole category then of a member of that category.) The fallacious response is attributed to a belief bias effect. In example, in D, ostriches may be considered to be non-central/peripheral members of the category of birds, so perhaps the generalization does not apply. In such cases, a left frontal-temporal system is activated in response to the belief biased, fallacious choice (Liang et al., 2014).

Other neuroimaging-based studies have examined inductive reasoning by way of analogical mapping. In one study, participants viewed pictures of colored geometric shapes and determined whether the shapes were analogous (analogy condition) or identical (literal condition) compared to a source picture of shapes (Wharton et al., 2000). They reported enhanced brain activation in the medial frontal cortex (BA 8), the left prefrontal cortex (BA 6, 10, 44, 45, 46, and 47), the anterior insula, and the left inferior parietal cortex (BA 40) when subjects made analogical match judgments.

Other studies have examined brain activation associated with judgment of analogous word pairs as in E (Green, Fugelsang, Kraemer, Shamosh, & Dunbar, 2006) and verbal analogies, as in F (Luo et al., 2003).

(E)

Planet : Sun versus Electron : Nucleus

(F)

Soldier is to army as drummer is to band

Green and colleagues (2006) report enhanced activation of a left-sided network of parietal-frontal regions, most notably the left superior frontal gyrus (BA 9, 10) for word pair stimuli (E). Examining analogous concepts (F), Luo and colleagues (2003) reported a network of activation in the left and right frontal lobes (BA 45, BA 47, BA 11) and left temporal lobe/hippocampus (BA 22). These areas are generally consistent with the areas of activation reported for other studies that have examined the neuroscience of induction.

Overall, studies evaluating language based inductive arguments generally indicate activation in large areas including the left frontal and parietal lobes. These regions overlap with the cortical regions involved in deductive reasoning with familiar material (discussed below). However, evaluation of inductive arguments seems to be distinguished from the evaluation of deductive arguments (such as G, K, L, M) by the greater involvement of the left middle frontal gyrus (BA 9) (Goel & Dolan, 2004; Goel, Gold, Kapur, & Houle, 1997).[3]

3.1.2 Simple Logical Inference

Some conceptual connections involve relationships between propositions set up by closed form terms of language. These are more specifically referred to as logical connections. For example, categorical syllogisms deal with quantification and negation involving reasoning with the terms 'All', 'Some', and 'None', as in the following arguments:

(G)

All apples are fruit;

All fruit are nutritious;

∴ All apples are nutritious.

(H)

All a are B;

All B are C;

∴ All a are C.

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[3] Interestingly, in the popular literature on hemispheric lateralization, such content based inferences are usually attributed to the right hemisphere (and formal inferences to the left hemisphere). There is one study (Deglin & Kinsbourne, 1996) which endorses this reverse position, where inferences involving formal logical relationships engage the left hemisphere but inferences involving conceptual or semantic connections are processed by the right hemisphere. No other study has replicated this result.

Both G and H are valid by virtue of their logical form. In terms of validity, it does not matter that one is about apples and the other about A's and B's.

Similarly, arguments such as I and J involve transitive relations that can be hierarchically organized on a linear scale. Again, they are valid by virtue of their logical form, independent of content.

(I)

London is north of Paris;

Paris is north of Cairo;

∴ London is north of Cairo.

(J)

A is north of B;

B is north of C;

∴ A is north of C.

It is the case that prefrontal cortex is engaged in logical reasoning, but selectively (Goel, 2007; Prado, Chadha, & Booth, 2011). For example, linguistically presented logical arguments in the form of categorical syllogisms such as (G & H) activate PFC to a much greater extent than linguistically presented logical arguments involving transitive relations (I & J), which tend to activate parietal cortex, to a greater extent (Goel, 2007; Knauff, Fangmeier, Ruff, & Johnson-Laird, 2003; Prado et al., 2011; Waechter, Goel, Raymont, Kruger, & Grafman, 2013). In cases where prefrontal cortex is engaged, whether it is left PFC, right PFC, or bilateral PFC is a function of content, conflict, and indeterminacy (Goel, 2007). The former is discussed below, the latter two in section 3.2.

Activation in left lateral and dorsolateral PFC (BA 44, 45, 6) is widely reported for syllogistic reasoning tasks in neuroimaging studies (Goel, 2007; Goel, Buchel, Frith, & Dolan, 2000; Goel & Dolan, 2003). One of the few lesion studies of deductive reasoning also reports that patients with left lateral and superior medial frontal lesions performed poorly on elementary deductive reasoning problems (Reverberi, Shallice, D'Agostini, Skrap, & Bonatti, 2009).

All real-world reasoning occurs in the context of beliefs. That is, we do not typically reason about A's and B's but about whether climate change causes hurricanes or whether one should buy a new or used car. The *content effect* is the finding that, despite deductive reasoning being a function of logical form, argument content modulates response. A robust consequence of the content effect is the *belief bias effect*. In reasoning with meaningful content, one will encounter either a congruency or incongruency between the logical response and conclusion believability. Congruent arguments are either valid with believable conclusions (G), or invalid with unbelievable conclusions (K). Incongruent arguments are either valid with unbelievable conclusions (L), or invalid with believable conclusions (M).

(K)
No apples are fruit;
All fruit contain calories;
∴ No apples contain calories.

(L)
All apples are fruit;
All fruit are poisonous;
∴ All apples are poisonous.

(M)
No apples are fruit;
All fruit contain calories;
∴ All apples contain calories.

The belief bias effect has two components (J. Evans, Barston, & Pollard, 1983; Neys, 2012): (i) participants reason more accurately on congruent trials than on incongruent trials; and (ii) on incongruent trials, participants can detect a conflict between the logic of the argument and believability of the conclusion and, on occasion, can suppress the belief-cued prepotent response and engage the formal reasoning system.

The neuroimaging data indicate that the main effect of comparing arguments with meaningful semantic content (such as G) with arguments without semantic content (such as H) results in activation of a left frontal-temporal system (Figure 1b) (Goel et al., 2000; Goel & Dolan, 2003). Comparing arguments without semantic content (H), with logically equivalent arguments with semantic content (G), activates bilateral PFC (Figure 1C), along with bilateral parietal and occipital regions (Goel et al., 2000; Goel & Dolan, 2003).

This is initially surprising. In both cases the arguments are valid, and they are valid by virtue of their logical form (i.e. independent of any content). However, psychologically, the content of the propositions (or absence of content) impacts the conclusions participants are willing to accept (Wilkins, 1928). So the accuracy rate for valid arguments with a believable conclusion, such as G, will be very high, while the accuracy rate of the equivalent argument, in the absence of a believable conclusion, as in H, will be lower (Jonathan Evans, 1983). Some cognitive theories of reasoning recognize this robust phenomenon and, consistent with the neuroimaging data, postulate different cognitive systems for reasoning with familiar material that we have beliefs about, and unfamiliar material that we have no beliefs about (J. S. Evans, 2003).

The involvement of the left frontal system in reasoning about familiar, meaningful content has also been demonstrated in neurological patients with focal unilateral lesions restricted to prefrontal cortex. (Goel, Shuren, Sheesley, & Grafman, 2004) administered the Wason card selection task to such patients and found that they all performed as well as normal controls on the arbitrary version of the task, but unlike the normal controls they failed to benefit from the presentation of familiar content in the meaningful version of the task. In fact, consistent with the neuroimaging data, the latter result was driven by the exceptionally poor performance of patients with lesions to left PFC. Patients with lesions to right PFC performed as well as normal controls.

This has been interpreted in the literature as a difference between contentful and noncontentful reasoning (J. S. Evans, 2003; Goel, 2007). However, rTMS studies suggest even a finer grained distinction. Tsujiia et al. (Tsujii, Masuda, Akiyama, & Watanabe, 2010; Tsujii, Sakatani, Masuda, Akiyama, & Watanabe, 2011) show that rTMS disruption of left prefrontal cortex specifically reduces reasoning accuracy only on a subset of contentful reasoning trials, the congruent trials. If this is the case it suggests that the left PFC's role in logical inference may be limited to belief bias and conceptual connections and simple logical connectives. Arguments involving complex logical connections need to draw upon additional cognitive resources.

One exception to the overall implication of left PFC in deductive reasoning is study by Parsons and Osherson (2001), in which they report that deductive inference is a right PFC function. These results have subsequently been explained as an artifact of a confound in their experimental design (Goel, Stollstorff, Nakic, Knutson, & Grafman, 2009). They used the identical items for both inductive and deductive inference. To do this, the deductive arguments need to be indeterminate (otherwise the deductive response will override the inductive response). The presence of indeterminacy does involve the right prefrontal cortex, and is discussed at some length below.

3.1.3 Simple Causal Inference

A third way in which left PFC fills in gaps is by drawing simple causal inferences. Unlike conceptual and logical relationships which hold between words or ideas or propositions, causal relationships reflect how our mind structures and comprehends the world. For example, there is no conceptual or logical relationship (i.e. by virtue of the meanings of the words) between the brakes of a car, and the car stopping. There is, however, a causal relationship.

In the above experiment involving the "boiling water" task (Gazzaniga & Smylie, 1984), there are no logical or conceptual connections between "saucepan" and "water", leading to the conclusion of "boiling water", but there are relationships stemming from our knowledge of the structure and functioning of saucepans and water. The same holds for "chicken coop and shovel" experiment (Gazzaniga, 1989). There are no logical connections between the two, but they are certainly relationships stemming from our knowledge of causal relationships in the world.

More recent studies suggest that both left and right hemisphere have a role to play in our understanding of causation. For example, Roser et al. (2005) tested two callosotomy patients on perception and inference of causality using a simple billiard ball collision events task and another task involving controlling lights in a room with a switch. They reported a double dissociation, such that, the right hemisphere is very good at analysing perceptual interactions between moving stimuli (i.e. the billiard balls) and extracting causal structure information from these events. The left hemisphere is unable to do this, but rather, specializes in inferring causality from contingencies between events, such as the flipping of the light switch and the brightening of the room.

These data are largely consistent with the characterization of the left PFC as a system dedicated to reducing uncertainty by automatically drawing logical, conceptual, and causal inferences (Gazzaniga, 1995; Marinsek et al., 2014). This function is dramatically illustrated in the split brain patient inference tasks discussed above. It can also be seen in the everyday functioning of normal healthy individuals. For example, while piloting material for a logical reasoning task, we asked participants about the truth or falsity of certain statements such as “the sand on Mars is red.” This is a statement that most people should not have strong beliefs about (due to a lack of factual knowledge). Surprisingly, many people responded confidently. When one participant was asked to explain his “no” response, she replied “there is no sand on mars.” Their inference engine had simply filled in some blanks, resulting in a confident, though perhaps erroneous answer, that could not be justified by the knowledge they possessed.

However, the story of inference is much more complex. In addition to the fine-tuning of the left hemisphere interpreter account there has been considerable recent progress in our understanding of the critical roles played by the right prefrontal cortex in complex cognition.

3.2 Functions of Right PFC System

During the last 50 years of the 20th century it was widely accepted that the right PFC had no role to play in complex cognition, except for visual-spatial organization (Corballis, 2003). It is only within the last 20 years that the advent of in vivo imaging technologies, and an appreciation of the limitations of the problem-solving tasks utilized in neuropsychological test batteries, have allowed us to revise this erroneous conclusion. Much of this research has only been recently assembled and reviewed. The result is a greater understanding of the multiple roles the right prefrontal cortex plays in complex cognition.

The data seem to support three critical roles for the right PFC in complex cognition, namely (i) inference in the absence of familiar conceptual content (right lateral PFC), (ii) conflict/anomaly detection (right dorsolateral PFC), and (iii) uncertainty or indeterminacy tolerance (right ventral lateral PFC). Each is discussed below.

3.2.1 Formal Logical Inference

Logical arguments such as H & J, that lack any meaningful semantic content that participants can have beliefs about, must be evaluated with formal machinery (i.e. based purely on structure). As noted above, while arguments of the form G, K, L, & M result in engagement of left prefrontal cortex, logically identical arguments, lacking familiar content as in H, engage bilateral lateral PFC (Figures 1B & 1C) along with bilateral parietal and occipital lobes (Goel et al., 2000; Goel & Dolan, 2003).

The categorical syllogisms in these studies were presented linguistically. Wendelken and Bunge (Wendelken & Bunge, 2010) used fMRI to examine participants' ability to engage in explicit transitive inference tasks using nonlinguistic/pictorial stimuli. In comparing a three-term relational inference condition with a two-term relational baseline condition they reported activation in bilateral parietal lobes and right rostrolateral PFC (BA 10).

One interpretation of these results would be that, while the left PFC may be necessary and sufficient to deal with logical inference involving familiar material that participants have beliefs about (at least in congruent trials), the right PFC is part of the system required to deal with logical inference in purely formal situations, or situations where there is an incongruency between the believability of the conclusion and validity of the argument (L & M, see below), thus requiring explicit formal evaluation of the argument. Disruption of left PFC functioning would impair the content sensitive inference system, resulting in poor performance on congruent trials. The rTMS data reported above supports this prediction (Tsujii et al., 2010, 2011). It is also consistent with cognitive theories of reasoning that postulate dual mechanisms for reasoning about familiar and unfamiliar material (J. S. Evans, 2003).

3.2.2 Conflict Detection

Conflict or incongruency detection refers to the detection of inconsistency between one's beliefs, beliefs and incoming information, and/or inferred/calculated information. It seems to be a generalized function of the right PFC.

In the context of logical reasoning, we are specifically referring to an inconsistency between a response cued by our beliefs about the world and a response cued by the logic/structure of the argument. Within inhibitory belief trials (as in L & M) the prepotent response is the incorrect response associated with the believability of the conclusion. Incorrect responses in such trials indicate that subjects failed to detect the conflict between their beliefs and the logical inference and/or inhibit the prepotent response associated with the belief-bias. These belief-biased responses activate ventral medial prefrontal cortex (BA 11, 32), highlighting its role in non-logical, belief-based responses (Goel & Dolan, 2003). The correct response indicates that subjects detected the conflict between their beliefs and the logical inference, inhibited the prepotent response associated with the belief-bias, and engaged a formal reasoning mechanism. The detection of this conflict requires engagement of right lateral/dorsal lateral prefrontal cortex (BA 45, 46) (see Figure 1d) (Goel et al., 2000; Goel & Dolan, 2003; Prado & Noveck, 2007; Stollstorff, Vartanian, & Goel, 2012).

These fMRI results have been replicated by rTMS studies demonstrating that stimulation of right PFC specifically impairs performance on incongruent reasoning trials such as L and M (Goel et al., 2000; Goel & Dolan, 2003; Prado & Noveck, 2007; Stollstorff, Vartanian, & Goel, 2012). These rTMS data also show that disruption of left PFC results not only in decreased performance in congruent trials but also *improved* performance in incongruent trials. That is, when the left PFC is impaired, participants are less likely to go with the believability of the conclusion, and recruit other cortical regions to formally evaluate the argument.

One early demonstration of this conflict detection system using lesion data was carried out by Caramazza et al. (1976) using simple two-term reasoning problems such as the following: “Mike is taller than George” who is taller? They reported that left hemisphere patients were impaired in all forms of the problem but – consistent with imaging data (Goel et al., 2000; Goel & Dolan, 2003; Stollstorff et al., 2012) -- right hemisphere patients were only impaired when the form of the question was incongruent with the premise (e.g. who is shorter?).

Similar conflict detection phenomenon can be observed in inductive reasoning, decision-making and problem-solving tasks. For instance, in the inclusion fallacy task (C & D), there is a conflict/tension between fallacious and non-fallacious responses. Detection of this conflict leads to activation in a right frontal-parietal system (Liang et al., 2014).

In terms of decision-making tasks, consider the base rate fallacy task (Kahneman & Tversky, 1973):

> (N)
>
> Participants are told that a jar contains 100 names. 15 of the names are of engineers and 85 names are of lawyers. Each name is associated with a description. A name is randomly pulled from the jar and the following description is read:
>
> Jack is a 45-year old man. He is married and has four children. He is generally conservative, careful, and ambitious. He shows no interest in political and social issues and spends most of his free time on his many hobbies which include home carpentry, sailing, and mathematical puzzles.
>
> The participant is then asked the following question:
>
> Which one of the following two statements is most likely?
>
> a. Jack is an engineer.
> b. Jack is a lawyer.
> c. Equally likely that Jack is an engineer or lawyer.

The base rates point to one response (85% chance that Jack is a lawyer) while the description of Jack is more prototypical of an engineer. This generates a conflict that the subject must recognize and resolve. Is the description sufficiently poignant/salient to overcome the odds in this particular instance?

De Neys et al. (2008) scanned normal healthy volunteers with fMRI while participants engaged in the lawyer-engineer type base rate problems. As in the reasoning paradigm, activation of right lateral prefrontal cortex was evident when participants inhibited the stereotypical heuristic responses and correctly completed the decision making task.

The Rectangle and Polygon Task (Stavy, Goel, Critchley, & Dolan, 2006) provides an example from the problem solving literature. In this task subjects are shown a rectangle followed by a polygon derived from the rectangle by a minor modification (see Figure 1f). They are asked to compare the perimeters of the two figures and determine whether the second is larger than the first. In some trials (congruent condition), the perimeter and area change in the same direction (i.e. both increase or decrease as a result of the modification). In other trials (incongruent condition), the area changes but the perimeter stays the same (for example, when a small square is removed from the upper right hand corner of the triangle). Young adults accurately respond to the congruent trials but many (46%) claim that the perimeter of the derived polygon in the incongruent condition is smaller than that of the original rectangle (Stavy et al., 2006). This response is explained in terms such as "a corner has been taken away", suggesting they're using a strategy that might be referred to as "more A (area) = more B (perimeter)". The data suggest that they do the task by attending to both the area and perimeter of the rectangle. But for most subjects, the area seems to be the more salient feature. In the congruent condition both processing streams result in the same response. In the incongruent condition a conflict arises between the responses generated by processing the area and the perimeter. To generate a correct response in this condition, the conflict must be detected and the salient response based on the area must be inhibited. In Neuroimaging studies of this task (Stavy et al., 2006) found activation in bilateral prefrontal cortex in the incongruent condition compared to the congruent condition, where the conflict between two strategies needs to be detected and overcome.

A final example of the role of right prefrontal cortex in conflict detection is provided by Reverberi et al. (2005). They carried out a revised version of the Brixton Task with neurological patients with focal lesions. In the first half of this task subjects are presented with a series of cards, one at a time. Each card contains a 2 x 5 matrix of numbered circles. One circle on each card is colored blue, the others are white. The position of the blue Circle moves from card to card following one of seven rules. The rule is switched every five to seven cards without warning. Upon being presented with a card of the subject's task is to indicate the position of the blue Circle on the next card, thus indicating their ability to induce the current rule. The second half of the task is similar to the first, except for the following important differences: (i) rules stay active for six to 10 trials and (ii) before the end of the particular series of rule an interfering rule is introduced. This consists of sequence of four cards from the first part (only they contain red-filled circles rather than blue ones). These four cards follow a previously presented rule, but different from the current rule thus introducing a conflict between the interfering rule and the previously active rule. This conflict must be detected, the interfering rule inhibited and response generated based on the active rule. They report that while patients with lesions to left prefrontal cortex show an impairment in rule induction, patients with lesions to right prefrontal cortex are impaired specifically in the rule-conflict condition.

This conflict detection role of right lateral/dorsal prefrontal cortex is a generalized phenomenon that has been documented in a wide range of paradigms in the cognitive neuroscience literature (Fink et al., 1999; Picton, Stuss, Shallice, Alexander, & Gillingham, 2006; Vallesi, Mussoni et al., 2007; Vallesi, Shallice, & Walsh, 2007). Marinsek et al. (2014) have actually suggested that conflict detection, or the resolving of inconsistency, is the main role of the right prefrontal cortex. We are suggesting that it is a very important role, supported by robust data, but one of three known roles.

3.2.3 Indeterminacy tolerance

Section 3.1 highlights the key indeterminacy reduction function of the left PFC interpreter. In a world where time and computational resources are limited, we must of necessity function with incomplete information. In such a context, it is easy to appreciate the value of a system focused on reducing uncertainty by drawing upon outside information and our belief network to make certain inferences to fill in the blanks, (even though they may be premature and incorrect). Indeed, the cognitive decision-making and problem-solving literatures are largely focused on techniques for reducing uncertainty and constraining the problem search space through the introduction of heuristics and biases (Gigerenzer & Goldstein, 1996; Tversky & Kahneman, 1974). Once uncertainty has been eliminated, or at least reduced, the problem can be solved using various computational techniques (Laird, Newell, & Rosenbloom, 1986; Todd & Gigerenzer, 2000).

However, it has also been argued that indeterminacy has a beneficial role to play in real-world problem solving (Goel, 1995, 2014, 2015). This will strike most cognitive psychologists and neuropsychologists as counterintuitive. But the failure to appreciate this critical point stems from an incomplete understanding of the nature of problems and problem-solving. Here we briefly discuss the pervasiveness of indeterminacy in real-world problem solving, and the importance of maintaining it, at least for a certain period of time.

The issue at stake is the nature of real-world problems, and their relationship to tasks used to study problem-solving in the laboratory, and indeed, to test patients in clinical settings. This issue has been a point of debate and contention in the cognitive psychology literature for over 50 years (Reitman, 1964; Simon, 1973). It came to prominence in the neuropsychology literature in the 1990s, with several labs noting discontinuous performance of patients with frontal lobe lesions in neuropsychological test batteries and real-world functioning (Eslinger & Damasio, 1985; Goel, Grafman, et al., 1997; Shallice & Burgess, 1991). In each of these cases, patients performed well on the neuropsychological test batteries, but had difficulty functioning in real-world situations.

Drawing upon the cognitive psychology literature, Goel (2010) proposed that this dilemma from the frontal lobe literature could be explained by seriously considering the issue of structure as a critical component of problems/tasks. It was argued that neuropsychological test batteries were providing a distorted view of problem-solving abilities because they were comprised of only well-structured problems, while real-world problems have both ill-structured and well-structured components.

The terms “well-structured” and “ill-structured” problems originate with Reitman (1964). Reitman classified problems based on the distribution of information within the three components (start state, goal state, and the transformation function) of a problem vector. Problems in which the information content of each of the vector components is absent or incomplete are said to be ill-structured. Goel (1995) noted a number of additional differences, the most important perhaps being the constitutive nature of task constraints in well-structured problems and the non-constitutive nature of task constraints in ill-structured problems.

The Tower of Hanoi problem, a widely used "executive functions" task in the neuropsychology literature, is a typical example of a well-structured task. It is a puzzle consisting of three pegs and several disks of varying size. The goal is to transfer the disks from one peg to another peg under the following three constraints: (1) only one disk may be moved at a time; (2) any disk not being currently moved must remain on the pegs; and (3) a larger disk may not be placed on a smaller disk at any point during the transition. In such tasks the start states (given), goal states (given), and transformation functions (move a disk) are completely specified, and the constraints are logical or constitutive of the task. For example, if I complete the task by placing a larger disk on a smaller disk, on route, I am not doing the task. I have cheated.

Features of ill-structured problems can be illustrated with a simple everyday task like planning a dinner party for some guests. In such a task the start state is incompletely specified (e.g. Should it be lunch or dinner?; Should it be on a Monday or Friday? etc.). The goal state is also incompletely specified (e.g. Do I care whether they enjoy the meal? Should I take into consideration the fact that Mary is upset with John when doing the seating arrangement? etc.). And finally, the transformation function is also incompletely specified (e.g. Should the meal be catered? Should I do a potluck? If I prepare it myself should I use free range chicken? Etc.). Not only are each of these three components of the problem space vector, under specified, they are each negotiable. So, if I invite you to my home for dinner, and then convince you that we should instead grab a quick pizza and go to the new movie playing around the corner, and you agree, there is no sense in which I have cheated or failed the planning task. The selected solution simply lies beyond the (assumed) constraints of the original problem.

In well-structured laboratory problems, given that there is complete/sufficient information in the problem vector to specify a problem space, and the constraints are constitutive or definitional of the task, a simple inference engine like the left PFC interpreter, may be sufficient for successful completion. Real-world problems have both ill-structured and well-structured components. As such, real-world problem solving must accommodate the indeterminacy resulting from incompleteness of information and non-constitutive task constraints.

Interestingly, one approach to dealing with indeterminacy is simply to eliminate it by making some assumptions/inferences (Simon, 1973). So, whether confronted with an ordinary real-world problem like planning a dinner party, or an extraordinary real-world problem like finding a cure for cancer, we could simply to go with what we already know, or what can be inferred from what we know (via the left PFC interpreter). In the mundane case of planning a dinner party, the left hemisphere interpreter would start with knowledge of past parties and follow the conceptual/logical connections to the current situation and could not look beyond (suggested and assumed) constraints. It would be a prisoner of its background knowledge and beliefs. Every dinner party would be similar to the last, with little allowance for the variations and deviations that are the hallmark of human problem solving. In the case of the extraordinary problem-solving situation, the problem solver may not have access to any known solutions (as there may be none), but nonetheless, there will be background beliefs and knowledge from previous experiences that will be mapped onto the problem space. The left hemisphere interpreter, by its acceptance and precise representation of this belief network and task constraints, armed with local semantic, and simple logical and causal connections would confine the problem solver to a particular state space, perhaps precluding the actual solution space.

One way of circumventing such a depressing outcome is to have a complementary system to the left PFC interpreter that serves to maintain any indeterminacy that exists in the task environment (at least for a period of time), and where it does not exist it may serve to actively create it. In both the mundane and novel cases, the introduction of indeterminacy is serving the function of overcoming unwarranted preconceptions based upon prior beliefs and allowing for the exploration of the broader state space. There is evidence that such a system exists and it is housed in right ventral lateral PFC.

Before reviewing some of the evidence, it is worth reminding ourselves why it has taken so long to identify and articulate these functions of the right PFC. The reasons have to do with (1) simply recognizing the important differences between well-structured laboratory problems and real-world problems (Goel, 1995), and (2) coping with the challenges of administering real-world problems in laboratory settings, to say nothing of the much more stringent constraints of brain imaging paradigms. Despite the difficulties, there are now several data points in the literature involving real-world design and planning tasks.

Kowatari et al. (2009) carried out an fMRI study in which novice and experienced designers were asked to “think about new designs” for pens. Their main finding included greater activation in right PFC than in left PFC, in the design component of the task. Furthermore, a correlational analysis using the originality scores of individuals (generated by applying a "good design award criteria" metric) and BOLD signal changes showed a correlation between the left minus right PFC BOLD signal and the originality scores, but not between left PFC or right PFC BOLD signals and originality scores per se. This interesting finding is consistent with our contention that interaction between right and left PFC are critical for real-world problem solving.

Gilbert et al. (2010) administered well-structured and ill-structured versions of a simple design task, involving the arrangement of furniture in a board room, to participants as they underwent MRI scanning. The well-structured version of the task contained specific constraints such as “the two tables face each other” while the ill-structured version contained more open-ended constraints such as “the room should feel spacious.” The main conclusion of the study was that the ill-structured design condition was associated with greater activation in right DLPFC compared to the well-structured condition.

Two patient studies, involving real-world design and planning tasks, have reached the same conclusion. Goel and Grafman (2000) tested a very accomplished 57 year old architect (PF) diagnosed and treated for a right frontal parasagittal meningioma, by requiring him to develop a new design for their lab space, and compared his performance to an age and education matched architect. The control architect began the task by considering abstract issues such as “circulation space” and “social/professional hierarchies,” and then used these abstract concepts to determine arrangements of walls, cubicles, etc. The patient’s sophisticated architectural knowledge base was still intact, and he used it quite skillfully during the problem scoping phase to discuss various aspects of the design. However, he approached the design task at a very concrete level and just rearranged furniture. He generated a quick solution, without abstracting from the particulars and exploring the space of alternatives.

In another study, Goel et al. (2013) administered a real-world planning task to neurological patients with unilateral lesions in PFC and normal controls. Patients with lesions to right PFC generated substandard solutions compared to both normal controls and patients with left PFC lesions. Examination of the underlying cognitive processes and strategies revealed that patients with lesions to right PFC approached the task at an excessively concrete level compared to normal controls, and very early locked themselves into substandard solutions. Patients with lesions to left PFC displayed a trend towards approaching the task at a more abstract level than the controls, and more fully explored solution possibilities. In contrast to both patient groups, normal controls engaged the task at both concrete and abstract levels and easily/judiciously moved between the levels.

One can even get a glimpse of this role of right PFC even in well-structured tasks. For example, broadening the search space on a scrambled words tasks by widening semantic categories words can belong to (e.g., " make the word ‘knife’ with IKFEN"; to "make a word for a kitchen utensil with IKFEN"; to "make a word with IKFEN") reduces task constraints, broadens the problem space, and selectively engages right PFC (Vartanian & Goel, 2005).

(O)

Mary is taller than John;

John is taller than Angie;

∴ Mary is taller than Angie.

(P)

Mary is taller than John;

John is taller than Angie;

∴ Angie is taller than Mary.

(Q)

Mary is taller than John;

Mary is taller than Angie;

∴ John is taller than Angie.

(R)

None of the bakers play chess

Some of the chess players listen to opera

∴ Some of the opera listeners are not bakers.

Even in a classic "left hemisphere" task like logical reasoning, where participants are presented with transitive arguments such as O, P, & Q, that one can have no beliefs about, and must determine if the conclusion follows from the premises, a lesion study shows that patients with left PFC lesions are selectively impaired in trials with complete information (i.e., determinate trials as in O and P) while patients with right PFC lesions were selectively impaired in trials with incomplete information (i.e., indeterminate trials like Q) (Goel et al., 2007). This patient study demonstrates a double dissociation across left and right PFC along the dimension of determinacy. Neuroimaging studies involving similar transitive arguments reveal similar results (see Figure 1e) (Brzezicka et al., 2011; Goel, Stollstorff, Nakic, Knutson, & Grafman, 2009). A study examining deductive reasoning with indeterminate syllogistic arguments like R, also reported activation in right PFC, instead of left PFC (Parsons & Osherson, 2001).

4.0 Frontal Lobe Lateralization Hypotheses

These data, generated over the past 20 years, are forcing us to reconsider the left hemisphere dominance hypothesis and replace it with a frontal lobe lateralization hypothesis (FLLH):

> Left and right prefrontal cortex make differential contributions to supporting complex cognition. The left PFC abhors uncertainty/indeterminacy and tries to automatically fill in the gaps by drawing simple, conceptual, logical and causal inferences from any given information and belief network. The right PFC plays important roles in formal logical inference, consistency/conflict checking, and indeterminacy tolerance. Damage to either system will result in impaired real-world performance, but with different cognitive signatures. Damage to right PFC system will allow the left PFC free reign to prematurely lock on to patterns and solutions; drawing conclusions quickly and confidently, oblivious of inconsistency and logical form. Damage to the left PFC will allow the right-hemisphere system to have more impact. If it remains totally unchecked by the left PFC, the right PFC will display enhanced formal reasoning, conflict detection, and exploration of the problem space, perhaps to the point of not reaching a conclusion. Successful functioning in the real world is a judicious balancing act between these two systems.

5.0 Speculation on Underlying Mechanisms

5.1 Left PFC

We began the chapter by noting that, except for the case of language, hemispheric asymmetry has not historically been a major issue in the frontal lobes literature. But the left PFC dominance for language is widely accepted. Could it be that the left PFC interpreter, or inference engine, is a byproduct of language, and its location in the left PFC is to be explained in the same way? There is a case to be made for such a claim.

The features of the left PFC interpreter that the data reviewed above highlight are its abilities to draw conceptual/semantic, and simple logical and causal inferences. In fact, it seems compelled to do so. Several linguists have argued that our conceptual/semantic, logical, and causal constructs and relationships are built into the very fabric of natural language and derive from it (Lakoff, 1986; Talmy, 1983, 1988, 2003). Thus, it is possible that the causal, logical, and conceptual inferences that come so effortlessly to the left hemisphere do so because it is dominant for language. However, when the task cannot piggyback off the semantic, logical, causal relationships embedded in language, either because of complexity or indeterminacy, additional cognitive resources in the right PFC are engaged.

Many philosophers and psychologists have argued that the structure of language mirrors the structure of human thought, and both are characterized by the properties of productivity, systematicity, compositionality, and inferential coherence (D. Davidson, 1982; Fodor & Pylyshyn, 1988; Penn, Holyoak, & Povinelli, 2008). Productivity refers to the unbounded generative capacity of human language/thought. It is made possible by the recursive application of a finite set of rules to a finite set of symbols. Such a system allows for compositionality and systematicity. Compositionality requires that a primitive symbol make approximately the same semantic contribution to the meaning of every complex expression in which it appears. Thus, the meaning of a complex expression is a function of the atomic symbols and rules of composition of the language. Systematicity is the property of language (and thought) that ensures that our ability to produce/understand certain sentences is intrinsically related to our ability to produce/understand certain other sentences (Fodor & Pylyshyn, 1988). For example, if we understand the sentence/thought "John loves Mary" then we must also understand the sentence/thought "Mary loves John". Inferential coherence requires that similar logical form be dealt with similar inference machinery and entail similar consequences. For example, if one is prepared to infer "John went to the store" from the sentence "John and Mary and Peter went to the store", one must also infer it from "John and Mary went to the store". The inference follows simply from knowing the language. So, the claim is that the inferential capacities of the left PFC follow from these properties of natural language.

To further illustrate this point, let's consider the case of simple transitive inference. There are a number of studies showing that many animals, including chimpanzees (Boysen, Berntson, Shreyer, & Quigley, 1993; Gillan, 1981), pigeons (Delius & Siemann, 1998), and rats (Davis, 1992) can be taught to do transitive inference, or at least behave in a manner consistent with understanding transitive inference. Let's set aside the questions of experimental design and interpretation (Allen, 2006; Delius & Siemann, 1998), and focus on the training regime. It takes a pigeon approximately 1600 trials to behave in a manner consistent with simple transitive inference. How many trials does it take a human subject? If one uses the same training paradigm with the human participants as one does with a pigeon, it takes approximately 800 trials for a human (Acuna, Eliassen, Donoghue, & Sanes, 2002). But when it is explicitly presented, most of us understand transitive inference in one or two trials. What this suggests is that we are capable of learning to do transitive inference in the same manner that a pigeon does, and we can do it in 800 trials as opposed to 1600 trials. However, the more important point is that we have certain cognitive resources - namely language - that a pigeon does not. If we utilize this system we understand simple transitive inference in one or two trials because it is built into the structure of language.[4]

This line of argument would suggest that the structural properties of the symbol system of language give rise to the left PFCs inference capabilities. But what about the right PFC? What is its underlying mechanism? There are several possibilities here

5.2 Right PFC

With respect to the right PFC, we have identified the following three different functions: formal inference, inconsistency or conflict detection, and indeterminacy tolerance. Each is associated with different subareas of right PFC. Unlike the case of the left PFC, there seems to be no obvious single underlying mechanism to account for the several functions. We propose the mechanisms below to account for each function.

5.2.1 Role in Formal Inference (right lateral PFC?)

One surprising finding is the fact that the right PFC is recruited (in addition to the left PFC) for evaluation of logical arguments involving no content cues (like H) and incongruent arguments (L & M) where the belief bias must be suppressed and the argument evaluated formally. Such a finding is actually consistent with the Mental Models theory of logical reasoning (P. N. Johnson-Laird, 1994). On this account, logical inference involves the construction of visio-spatial representations of the information contained in propositions and a search for counterexamples. The right hemisphere recruitment may be indicative of the building of spatial mental models (Corballis, 2003), when linguistic resources are inadequate for the task.

5.2.2 Conflict Detection (right dorsolateral PFC)

The right dorsolateral PFC plays a robust role in detecting inconsistency or conflict, not only in logical arguments (like L & M), but also in decision making and problem-solving tasks. This would require a mechanism to check (1) information coming into the system (e.g. "all apples are poisonous") against existing beliefs[5] (i.e. apples are not

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[4] A detailed illustration of how causal connectives are embedded in language is provided by Talmy (1983).

[5] Occasionally one may also check the belief network itself for inconsistencies, and revise to minimize the same.

poisonous); (2) check conclusions generated by inference processes (e.g. valid in L) against existing beliefs (i.e. apples are not poisonous); (3) check belief-cued conclusion against conclusions based on logical intuitions/form. Where a conflict or inconsistency is detected, a red flag goes up that may require rethinking, revaluation and revision of beliefs and inferences.

5.2.3 Indeterminacy Tolerance (right ventral lateral PFC)

The third role of right (ventral lateral) PFC that we have highlighted is indeterminacy tolerance. There are several possible mechanisms for accounting for this essential function.

First, just like many philosophers and psychologists have argued that the structure of language reflects the structure of human thought, others have argued that, the structure of language captures important facets of human thought, but the structure of human thought is much broader/more flexible than the structure of language (Cassirer, 1944; Goel, 1995; Goodman, 1976; Langer, 1942). They point to other symbol systems like painting, music, dance, sketching, etc. and argue that the structures of these symbol systems are very different from that of language, but also encompass essential aspects of human thought. We cannot express all that we need to express simply in language. We need language, but we also need these other symbol systems to fully express ourselves. Given an account like this, one might argue that these nonlinguistic symbol systems require their own representational systems and inference engine, located in right PFC, and enable/facilitate the right PFC's representation and processing of abstract, vague, ambiguous, indeterminate information. A formal treatment of the properties of some of these nonlinguistic symbol systems is offered in Goel (1995), while the argument that these types of representational systems and inference mechanisms underlie indeterminacy tolerance in right PFC is developed in Goel (2014, 2015). However, it is not the only possibility.

A second possibility is that the right PFC does contain representational systems with different properties than language, allowing for more vague, ambiguous, indeterminate representations, but there is no inference engine associated with this representational system. The information needs to be ultimately sent back to the left PFC interpreter for inference. But this process may allow for the left PFC interpreter to deal with more abstract levels of representations.

A third possibility is that the role of the right PFC is simply one of preventing the left PFC from settling of initial local inferences. That is, it in itself does not offer an alternative representational medium and inferential capabilities. Rather, it simply monitors the inferences drawn by the left PFC interpreter and says "don't stop, keep looking, keep looking…"

The current data are consistent with all three possibilities, and do not allow us to differentiate.

Conclusion

The last 20 years of neuropsychological research are reshaping our understanding of hemispheric asymmetry, for complex cognition, in prefrontal cortex. Our understanding of the left hemisphere interpreter has been refined, and qualified. The left PFC automatically makes simple conceptual, logical, and causal inferences to fill in missing information and eliminate uncertainty or indeterminacy. However, when the inferences are more complex and call upon formal logical reasoning, right PFC resources are required. The right PFC also plays critical roles in detecting conflict and tolerating/maintaining indeterminacy.

We speculate that the inferential capabilities of the left PFC are an outgrowth of its dominance for language. The capabilities of the right PFC need to be explained in other terms. Its role in formal logical inference may be a function of its visual spatial processing abilities. Its role in conflict detection might be explained as a system for checking consistency between existing beliefs, new incoming information, and inferences drawn from beliefs and/or the new information. Several possible explanations are proposed for the right PFC's indeterminacy tolerance capabilities. It may contain a representational system, and accompanying inference engine, with very different structural properties than language. Second, it may contain such a representational system, but not a separate inference engine, so the information goes back to the left PFC for inference. A third possibility is that the right PFC does not provide alternative representational and inference capabilities, but simply prevents the left PFC from settling on initial, local inferences.

Finally, this is not a left PFC or right PFC dominance account of reasoning, problem-solving, and decision making. It is an account whereby each hemisphere is biased towards certain types processing, possibly underwritten by different representational structures and processing mechanisms, and makes unique, complementary contributions. Successful real-world functioning requires the participation of both hemispheres.

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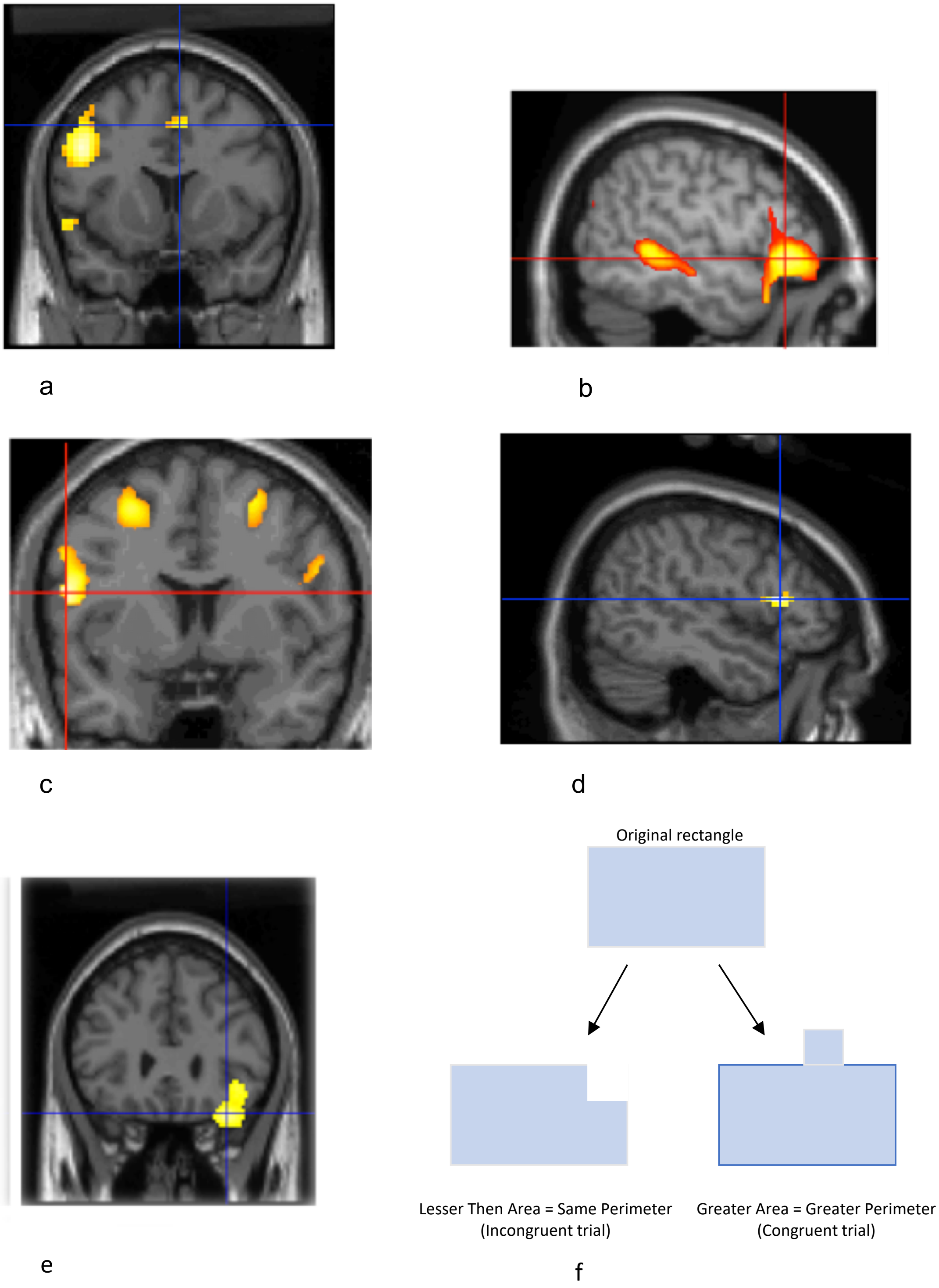
Figures

Figure 1. Areas in PFC activated by different reasoning conditions. (A) Inductive reasoning activates a left DLPFC (Goel & Dolan, 2004). (B) syllogistic reasoning with familiar content that we have beliefs about activates a left frontal temporal system (Goel et al., 2000). (C) syllogistic reasoning lacking any familiar content activates a bilateral frontal system (Goel et al., 2000). (D) conflict between argument validity and conclusion believability activates right DLPFC (Goel et al., 2000; Goel & Dolan, 2003). (E) transitive reasoning involving indeterminate trials with unfamiliar content activates right ventral lateral PFC (Goel et al., 2009). (F) Rectangle and polygon task (Stavy et al., 2006).

Figure 1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Greater Area = Greater Perimeter
(Congruent trial)
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