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Issue: *The Year in Cognitive Neuroscience***Hemispheric lateralization in reasoning**Benjamin O. Turner,¹ Nicole Marinsek,² Emily Ryhal,¹ and Michael B. Miller¹¹Department of Psychological & Brain Sciences, University of California Santa Barbara, Santa Barbara, California.²Dynamical Neuroscience, University of California Santa Barbara, Santa Barbara, California

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A growing body of evidence suggests that reasoning in humans relies on a number of related processes whose neural loci are largely lateralized to one hemisphere or the other. A recent review of this evidence concluded that the patterns of lateralization observed are organized according to two complementary tendencies. The left hemisphere attempts to reduce uncertainty by drawing inferences or creating explanations, even at the cost of ignoring conflicting evidence or generating implausible explanations. Conversely, the right hemisphere aims to reduce conflict by rejecting or refining explanations that are no longer tenable in the face of new evidence. In healthy adults, the hemispheres work together to achieve a balance between certainty and consistency, and a wealth of neuropsychological research supports the notion that upsetting this balance results in various failures in reasoning, including delusions. However, support for this model from the neuroimaging literature is mixed. Here, we examine the evidence for this framework from multiple research domains, including an activation likelihood estimation analysis of functional magnetic resonance imaging studies of reasoning. Our results suggest a need to either revise this model as it applies to healthy adults or to develop better tools for assessing lateralization in these individuals.

Keywords: split brain; unilateral brain damage; meta-analysis

Introduction

Hemispheric specialization is a widely accepted principle of cortical organization in the human brain. However, this specialization is best understood in the context of the overwhelming symmetry evident in the brains and bodies of most organisms, including humans.¹⁻³ For example, the nervous system of most organisms evolved symmetrical bilateral control of both sides of the body in order to move in a linear fashion through a natural environment (unless the organism prefers to move in circles). Likewise, nervous systems evolved symmetrical bilateral sensitivity to predators approaching from either side of the visual field. Across all species, this principle of symmetrical bilateral control and sensitivity is ubiquitous across brain functions and development.

The evolution of hemispheric specializations swam against the tide of this overwhelming symmetry. The two clearest examples of this in the human brain are language processing and handedness.

The lateralization of language processing has been known since the pioneering work of Marc Dax, Paul Broca, John Hughlings Jackson, Carl Wernicke, and others on aphasic patients in the 19th century, showing that brain damage restricted to the left hemisphere in most individuals was associated with deficits in language production and comprehension. Handedness is an even more obvious asymmetry. The great majority of humans are right-hand dominant, and it is clear that this dominance is due to a cerebral asymmetry in the control of the hands rather than to mechanical or structural differences in the hands.⁴ Even though both of these processes are lateralized to the left hemisphere and often assumed to be related, the cerebral dominance for language is only weakly correlated with cerebral dominance for handedness.⁵ There are also well-documented specializations in the right hemisphere, including spatial processing and face perception.⁶⁻⁸

The reasons for hemispheric lateralization and the extent to which it is unique to humans are

not well understood. Anatomical studies of the asymmetry in microcolumns and macrocolumns in cortical regions that support language processing suggest that lateralization may be fixed (or at least, strongly predisposed) in the human brain—that is, early ontogenetic or genetically determined events might have led to asymmetries in cytoarchitecture that in turn led to hemispheric differences in function^{9–11}—although this relationship is not perfect.¹² It has also been suggested that sophisticated functions like skilled manual operations (praxis) and language involve heavy processing demands. Such processing may require localized neural circuitry that is efficiently encapsulated in one region and does not depend on the transfer of information across the corpus callosum.^{3,8} Indeed, several functional specializations may have evolved in this way within the human brain, including face recognition and theory of mind. Precursors of some of these specializations may be evident in other species as well. Corballis⁵ suggests that language may have slowly evolved through a dual-stream system that underlies praxis and communication, leading to the lateralized gestural system that is evident in several primate species. The final step in vocalizing these gestures within hominins may have accelerated this lateralization and opened up the hands for sophisticated tool use and the voice for more expressive communication.

Aside from these specialized brain regions that may be lateralized to one hemisphere or the other, there may also be pairs of identically homologous brain regions (across the two hemispheres) that nevertheless carry out different functions, with one hemisphere biased toward a different processing strategy than the other hemisphere. Indeed, functional magnetic resonance imaging (fMRI) studies of intrinsic brain activity suggest that laterality can vary independently across at least four different brain networks.¹³ This duality of function may be adaptive in that it increases the neural capacity of the brain.^{8,14,15} Indeed, this has often been the argument used to explain language processing in the left hemisphere versus spatial processing in the right.¹⁵ An even more striking example of hemispheric dual function is the unihemispheric slow-wave sleep that has been observed in a number of terrestrial and aquatic animals, a phenomenon in which half the brain engages in deep slow-wave sleep while the other half is awake and alert.^{16,17}

There are also a number of examples across species of hemispheric biases in function. For example, reliable asymmetries have been observed in human brain activity associated with approach and avoidance (or conversely, distinct affective outcomes have been observed in patients with damage to one or the other hemisphere).¹⁸ These findings accord with evidence from the animal literature, including research on nonhuman primates and in rodents.¹⁹ Similarly, “handedness” has been observed across multiple species, including some species of birds and ungulates, along with other behavioral asymmetries such as the direction of a dog’s tail-wag depending on whether it is being approached by an unfamiliar dog or by its owner³ or the direction in which a toad attacks.¹⁴ Asymmetries are also present at the neural level in other species—for example, in the population-coding properties of honeybees’ left versus right primary olfactory centers.²⁰

We suggest this may be the case for reasoning: each hemisphere operates according to different cost functions, which has the effect of predisposing each hemisphere to certain types of processes. That is, rather than asserting that any given process is localized exclusively to a particular hemisphere, we merely claim that the operational principles guiding each hemisphere render it more suitable for certain processes. In much the same way that the right hemisphere has come to be understood to have some limited linguistic capacity,⁵ each hemisphere may be able to perform some of the functions we ascribe to the contralateral hemisphere, but will tend to do so in ways that are inefficient or strange.

The particular distinction at the center of our theory of reasoning is between uncertainty and conflict. We propose that the left hemisphere is primarily concerned with reducing uncertainty, which it does by generating explanations, filling in gaps in information, and drawing inferences, which are all manifestations of the left hemisphere’s guiding principle of eliminating uncertainty. On the other hand, the right hemisphere is primarily sensitive to conflict, which it relieves by abandoning untenable hypotheses, initiating shifts to new hypotheses, and operating in a generally inhibitory or cautious fashion. In the healthy brain, the hemispheres should synergistically cooperate in order to balance the need for fast but flexible hypothesis making. However, when this balance is upset, for example, by damage to only one hemisphere, the behavioral effects will reflect

the unhindered operation of the spared hemisphere, and should have a systematic form depending on which hemisphere is damaged.

Ours is hardly the first theory to propose that each hemisphere operates according to different principles or to point out the effects these differences might have on reasoning. For example, a number of theories have characterized the hemispheres in similar (or at least compatible) ways. Ramachandran²¹ suggested that the left hemisphere is willing to accept minor discrepancies in order to maintain a status quo, and that a “devil’s advocate” in the right hemisphere generates a paradigm shift in the case that the discrepancy exceeds some threshold. Likewise, Corballis² proposed that the left hemisphere is responsible for “generativity,” while the right hemisphere operates according to an analogue mode of representation. On the basis of a comparative psychological approach, Rogers²² concluded that the left hemisphere is used to consider multiple alternatives and choose strategies sequentially, and also in the manipulation of objects, while the right hemisphere operates in a parallel fashion and specializes in rapid, “species-typical” responses. Similarly, Bradshaw and Nettleton²³ asserted that the “analytic” left hemisphere is adept at operating in the sequential or temporal domain (including, e.g., perceiving duration or rhythm), while the “holistic” right hemisphere is characterized by spatial processing. And Beeman and Bowden²⁴ proposed that strength of the left hemisphere is defined by relatively fine semantic coding, while the right hemisphere’s strength draws on coarse semantic coding.

The role of laterality in emotion has also spawned a number of general theories of hemispheric specialization. For instance, the left hemisphere has repeatedly been associated with positive emotional valence and approach behaviors, and the right hemisphere with negative emotional valence and avoidance behaviors.^{25–27} Several theories have proposed that these tendencies are in fact driven by a more basic division, for instance, associating the left hemisphere with “energy enrichment” and the right hemisphere with “energy expenditure;”²⁵ or positing that the left hemisphere acts as a deliberate, conscious approach system (including goal-oriented and exploratory behavior), while the right hemisphere operates in a nondeliberate, nonconscious fashion, and that it is especially attentive to novelty

(or threat), which leaves it better positioned to drive avoidant behavior.”²⁶

It is clear that most of these theories ascribe similar roles to the two hemispheres, which are broadly consistent with the distinctions we make in our own theory. The left hemisphere is consistently identified with local processing (in time as well as possibly in psychological space) and a generally more “acceptant” attitude (e.g., in ignoring conflicting evidence or being approach centric). The right hemisphere is somewhat less clearly characterized, but is nonetheless associated with more global processing, which it may carry out in parallel, and that it is more “skeptical” than the left hemisphere. These commonalities align well with our proposal that the left hemisphere operates in a space defined by certainty rather than conflict—perhaps because its scope is too narrow to detect such conflict—and vice versa for the right hemisphere. These theories exist at different levels of explanation, both in terms of the ramifications of the distinctions they identify and the proposed origins or mechanisms underlying those distinctions, but they all seem to recognize a common truth.

Researchers must be careful, however, to not be too fast and loose with claims about hemispheric asymmetries. Previous claims of asymmetries have been found to be more apparent than real. For example, one of the most prominent theories of memory of the last three decades—the hemispheric encoding/retrieval asymmetry model^{28,29}—has been repeatedly shown to fail to account for the patterns of results from studies of split-brain patients,³⁰ as well as neuroimaging data from healthy adults.^{31,32} It has been proposed that hemispheric effects in memory experiments instead reflect other distinctions, for instance, the nature of the studied material.³⁰ Similarly, theories proposing strict lateralization of functions related to face processing have been refuted; while there may be differences in how faces are processed by each hemisphere,³³ there is clearly some face-processing capacity in each hemisphere.³⁴

In light of the possibility of misconstruing the nature of hemispheric asymmetry in reasoning, clear tests of laterality are needed to verify any such claims of asymmetry. A common theme in the above-mentioned cases of “apparent” laterality has been the diverging conclusions reached when using different research methodologies; in this article, we

review the various lines of evidence regarding the hemispheric laterality of reasoning. In addition to discussing the evidence *per se*, we also point out potential strengths and weaknesses of each line of evidence. We conclude by applying a test of laterality to the neuroimaging evidence using an activation likelihood estimation (ALE) meta-analysis of the existing fMRI literature, the results of which confirm that neuroimaging represents an approach for which especial care is needed when investigating laterality.

Studies of split-brain patients

There is probably no condition more appropriate for asking questions about laterality than the split brain. Split-brain patients are those patients who have undergone corpus callosotomy, a surgical procedure in which the corpus callosum is severed, as a treatment for intractable epilepsy. In these patients, the two hemispheres are almost completely unable to communicate (although the extent of the resection varies from patient to patient, and the anterior and posterior commissures are usually left intact). To the degree that there is competition between the hemispheres in the healthy brain, the split brain allows for investigation of the operation of each hemisphere when freed completely of such competition. Corpus callosotomies also carry lower concern for trauma-induced processes (apoptosis, cortical reorganization, etc.) than the various types of damage present in patients with lesions. The experimental procedures for addressing questions of laterality are also fairly straightforward; the primary concerns are ensuring information reaches the correct hemisphere and finding a suitable means for querying the (language-deficient) right hemisphere.

Some of the earliest evidence regarding the diverging tendencies of the two hemispheres with respect to reasoning comes from studies of split-brain patients conducted by Michael Gazzaniga. For example, Gazzaniga and Smylie³⁵ used a task that required participants to infer the relationship between objects (e.g., a wooden log and a match would lead to the conclusion of a bonfire). The left hemisphere was able to perform the task while the right hemisphere was unable to do so (see also Ref. 36). Moreover, the left hemisphere draws connections between even unrelated objects. In an experiment where each hemisphere independently selected an object based on a cue presented

only to that hemisphere, the left hemisphere was asked to explain the choices of both hemispheres. One subject whose left hemisphere had selected a chicken (in response to a picture of a chicken claw) and whose right hemisphere had selected a shovel (in response to a picture of snow) explained that, "The chicken claw goes with the chicken and you need a shovel to clean out the chicken shed," despite the fact that there was no extrinsic connection between these objects.⁸ The tendency of the left hemisphere to create explanations led Gazzaniga to formulate the idea of the left hemisphere interpreter, which has a propensity to explain everything it encounters.

Although the left hemisphere is able to draw inferences and generate explanations, it is less capable of revising those explanations. When instructed specifically to adopt a new strategy, the left hemisphere seems to be able to do so,³⁷ but there are also cases wherein the left hemisphere perseverates with an explanation even in the presence of new information (but without explicit instructions to update).³⁸ The left hemisphere is also prone to errors of commission. For example, in recognition memory experiments, the left hemisphere falsely identifies related lures as having been studied before, while the right hemisphere correctly rejects these lures.^{39–41} This is again consistent with the idea that the left hemisphere bridges gaps between studied items and related, nonstudied items. The left hemisphere also strives to establish patterns where there are none, even if doing so is suboptimal: in a probability-matching experiment wherein participants were asked to guess which of two stimuli would appear on the following trial, the right hemisphere adopted the optimal strategy (nearly always choosing the more frequent stimulus), while the left hemisphere matched the base rates.⁴² However, note that this behavior is abolished if the stimuli differ in a way to which the left hemisphere is insensitive (e.g., using face stimuli), in which case the right hemisphere actually exhibits matching behavior.⁴³

The available evidence from split-brain patients tells a fairly coherent story regarding the role of each hemisphere in reasoning. The left hemisphere is able to make inferences and to draw connections between distinct pieces of information, but is unable to abandon the explanations it comes up with, either ignoring conflicting information

or expanding the explanation. The right hemisphere is more veridical, and although it did not demonstrate any other specific strengths in regard to reasoning, the deficits demonstrated by the left hemisphere in these tasks suggest that, in healthy brains, the right hemisphere is responsible for halting perseveration of incorrect hypotheses and reining in the left hemisphere's propensity for filling in gaps. As mentioned above, this line of evidence is particularly compelling because of the purity of hemispheric isolation. It is also worth restating that, to the degree that the hemispheres act in opposition in the intact brain, the functioning of each hemisphere in the split brain reflects the operation of that hemisphere released from the influence of the other hemisphere (a point to which we will return later).⁴⁴

Studies of unilaterally brain-damaged (non-delusional) patients

While the surgery that results in the split-brain condition is relatively rare, brain damage or surgical intervention limited to a single cerebral hemisphere is far more common, although correspondingly less homogeneous. The most common causes of unilateral brain damage include stroke and other related ischemic events, various traumatic events such as motor vehicle accidents, and surgical intervention (e.g., to treat epilepsy). The deficits associated with unilateral brain damage are therefore extremely varied, and depend on factors including the extent of the damage, the locus (e.g., involvement of white matter), the age at which damage occurred, and the environment in which it occurred (e.g., in a surgical setting with relatively less extensive damage outside the focally damaged region compared to a traumatic event in which nearly all of cortex may undergo postinjury responses). Despite this heterogeneity, there are a number of phenomena relating to reasoning that have been reliably observed in brain-damaged patients.

Consistent with the results of studies in split-brain patients, patients with right hemisphere brain damage are still able to draw inferences,^{45–50} and in fact are often subject to making the same sorts of hyper-inferential errors as the left hemisphere in split-brain patients.^{42,49} Similarly, patients with right hemisphere damage can be “captured” by initial hypotheses and be unable to update or abandon those hypotheses.^{51–54} Conversely, patients with

left hemisphere damage have difficulty drawing inferences⁵⁰ but remain sensitive to conflict, for example, between real-world knowledge and logic⁴⁵ or semantic inconsistencies.⁴⁷

Despite the general consistency of this evidence, several studies from this domain report findings that are inconsistent.^{53,55,56} In addition to the possibility of cortical reorganization or other compensatory or injury-induced neural changes with unilateral brain damage, we should expect a less consistent effect in terms of how thoroughly the undamaged hemisphere is released from the influence of the damaged hemisphere. Because damage to any particular brain region may be incomplete, it may retain the ability to partially influence the contralateral hemisphere and thereby mitigate the measurable effects of unchecked operation of the contralateral hemisphere. Notwithstanding these concerns, the results from studies of brain-damaged patients are broadly consistent with our theory.

Studies of patients with delusional disorders

Delusional disorders are associated with “fixed beliefs that are not amenable to change in light of conflicting evidence”⁵⁷ and have been consistently linked with a shift in the balance of hemispheric control toward the left hemisphere. Generally, this is the result of damage to the right hemisphere,^{21,44,58–60} but there are also instances of left hemisphere hyperactivity in the absence of right hemisphere damage.^{44,61,62} As with unilateral brain damage that does not lead to delusions, delusional patients are a very heterogeneous group, though they are definitionally united by a common set of diagnostic symptoms.

Once again, the pattern of deficits observed across a variety of classes of delusional disorder are in line with what we predict on the basis of the left hemisphere hyperactivity (or right hemisphere hypoactivity) that seems to underlie most delusions. Delusional patients draw conclusions prematurely^{63–67} and fail to move away from those conclusions appropriately.^{59,68–70} Neuroimaging studies with delusional patients have also demonstrated that the right hemispheres of delusional individuals with intact right hemispheres have lost sensitivity to conflicts between evidence and beliefs.⁷¹ These deficits combine to produce strikingly abnormal behavior. For example, patients with anosognosia will deny

that a limb is paralyzed, even immediately after having been unable to perform a task with the affected limb.⁵⁹

An influential theory of delusions⁶⁸ serves to explain both why delusions arise in these patients and why split-brain (and right hemisphere-damaged) patients are surprisingly free of delusional behavior. This theory hypothesizes that delusions require two factors, of which only one is present in split-brain patients: a dysfunctional belief evaluation system and an impairment that demands explanation. Delusional patients satisfy both factors, insofar as they have hypoactivity in the right hemisphere and the left hemisphere is confronted with information for which it has no schema (e.g., the absence of a limb or degraded input from another damaged neural system).⁶⁸ Delusions in these patients represent the left hemisphere's best attempt to explain such phenomena. On the other hand, split-brain patients (i.e., their disconnected speaking left hemispheres) satisfy the first factor, but in the absence of any such "unexplained" phenomena, we do not expect split-brain patients' left hemispheres to develop delusions.

By linking delusions simultaneously to a leftward shift in the left/right hemisphere balance and to a pattern of deficits characterized by excessive inference making and imperviousness to conflicting information, it is possible to use evidence from studies of delusional patients to address questions of laterality in reasoning. The general conclusions we reach are the same, although the form these deficits take is more extreme than in most non-delusional cases. This may be because these patients are confronted with information for which they have no established model and for which they therefore generate bizarre explanations.^{72,73} However, as with brain damage that does not lead to delusions, there may well be other confounded changes (besides hemispheric asymmetries) that accompany delusional disorders and lead to some of the effects we observe. Moreover, because of their deficits, delusional patients present particular challenges from an experimental standpoint.

Behavioral studies in healthy adults

In healthy adults, the options for assessing laterality are limited. Until the past two decades, virtually the only option was carefully designed behavioral studies. In the intact brain, information travels freely

between the hemispheres, so the outcome measures are generally limited to subtle differences in, for instance, processing speed as a function of presentation lateralization. Moreover, to whatever degree there is tonic (rather than phasic or event-related) influence of one hemisphere on the other, lateralized effects should be yet more muted. However, there is less cause for concern that results may be due to compensatory or other outside factors.

As it relates to lateralization in reasoning, there are several distinct lines of evidence. The first comes from priming studies of making inferences in language tasks.^{24,74} Although limited, this evidence is in line with our predictions, insofar as the left hemisphere was shown to be more involved in inference making than the right hemisphere. A second line of evidence comes from a study using rapid visual half-field stimulus presentation,⁷⁵ which demonstrated a left hemisphere advantage in a visuospatial transitive inference task.⁷⁶ The last two lines of evidence come from the persuasion literature, in which it has been demonstrated that participants are more persuasive when they covertly direct their attention to the left (which causes increased activation in the right hemisphere),^{77,78} and if they are inconsistently handed (which has been shown to correlate with increased right hemisphere activity and increased interhemispheric connectivity⁷⁹).^{80,81} Both of these are likewise in line with our predictions: presuming participants begin with some default belief which they must abandon (i.e., from which they must be persuaded), greater right hemisphere activity (or better communication with the left hemisphere) should be helpful.

Cognitive neuroscience studies in healthy adults

By far the most widely used approach to investigate the localization of cognitive processes in healthy adults is cognitive neuroscience, in particular fMRI, but also including electroencephalography (which we will not discuss here) and transcranial magnetic stimulation (TMS). Neurostimulation methods offer a means to emulate certain types of brain damage, and also lend themselves to causal investigations into the role of particular brain regions. However, suppression or enhancement of any given region is not complete; certain areas are beyond the reach of existing stimulation technologies, and the exact mechanism of some of these technologies is

still not fully understood. As with behavioral studies, there is scant evidence from this domain regarding the lateralization of reasoning, but what there is goes directly against our predictions: disruption of right hemisphere increased (rather than decreased) conflict sensitivity as measured by the belief-bias effect.^{82,83}

Neuroimaging methods are currently far more prevalent than neurostimulation methods, although they too are used only infrequently to address questions of laterality. These methods differ in terms of their spatial and temporal resolution, but nearly all commonly used methods are spatially resolved enough to distinguish between hemispheres. Like neurostimulation, neuroimaging carries the benefit of revealing the workings of the intact brain, although it does not allow for direct experimental control in the same way. However, as with behavioral studies of healthy adults, neuroimaging studies reveal the activity of the hemispheres when they are communicating normally. In fact, the behavioral paradigms used in neuroimaging generally are not designed with lateralization in mind—in that they do not attempt to strictly isolate the processes we believe to be lateralized—so the ability to separate the hemispheres depends entirely on the common logic of neuroimaging that any region active during a task is associated (usually, causally) with performance or processing of that task. Moreover, questions of laterality require direct contrasts between the hemispheres in order to avoid committing the “neuroimager’s fallacy”²⁰⁹—interpreting a difference in significance as implying a significant difference—which very few studies do. We discuss these issues, in addition to several others, in more detail below.

Unsurprisingly, the evidence for our theory from fMRI is somewhat mixed. In line with our predictions, multiple studies have identified left-lateralized activity (based on inspection of the reported peaks) associated with reasoning about past events,¹⁰⁸ making inferences about related sentences,^{47,210–212} attempting to generate explanations,²¹³ and inferring a rule.¹⁷⁸ Conversely, right-lateralized activity has been observed when logic conflicts with prior beliefs,^{49,125,214–216} when participants are preparing for a set shift^{217,218} or receiving feedback necessitating such a shift,²¹⁹ and generally in context monitoring and inhibition,^{56,220,221} including inhibiting outlandish

hypotheses.²²² However, most of this evidence is fairly qualitative and lacks direct contrasts between the hemispheres; there are also studies whose results seem to at least partially contradict our predictions.^{218,223}

Whereas most of the research from the previous lines was directly addressing questions of laterality and is fairly straightforward to combine, the results from fMRI generally lack a focus on lateralization, and because they are presented as a series of peaks of activation spanning the entire brain, it is more difficult to qualitatively assess correspondence between studies. In order to address these limitations, we undertook an ALE meta-analysis of fMRI studies of reasoning. This analysis technique allows us to assemble a quantitative understanding of the cumulative patterns of activation across multiple studies (a summary of the topics covered is given in Table 1). Briefly, ALE treats each study or contrast as providing a Gaussian cluster of activity centered on the reported peak location, with width and height dictated by the sample size of the study; information is aggregated across studies by considering how much activation is present in each voxel.²²⁴

We searched the literature for fMRI studies involving reasoning using the search terms listed in Table 1 in conjunction with the term “fMRI.” Then, two labelers (the first two authors) read redacted versions of each paper (in which the results were removed) and ascribed a label to each fMRI contrast. The labels attempted to describe the cognitive process or processes that the contrast was designed to identify (e.g., “negative feedback processing” or “building a model”). Once all contrasts were labeled, the labelers reconciled their labels to create one set of descriptive labels for each contrast (Fig. S1). ALE analyses were performed on the labels we deemed most relevant. Additional details are provided in the supplementary online appendix; below, we present the results of this analysis.

ALE meta-analysis of fMRI studies of reasoning

Our primary hypotheses concerned the patterns of activity associated with labels related to either hypothesis formation or hypothesis evaluation. Our terms “building a model” and “rule finding” were taken to load on the former, and “statement verification” and “rule checking” on the latter. In addition to the analyses using these core terms, we ran ALE

Table 1. Summary counts of ALE search results

Search term	Search results	Allowed	Not relevant	Excluded	Failed	Used
Abstract reasoning	32	7	4 ^{84–87}	0	0	3 ^{88–90}
Analogical reasoning	25	12	3 ^{91–93}	2 ^{94,95}	0	7 ^{96–102}
Categorical reasoning	7	2	1 ¹⁰³	0	0	1 ¹⁰⁴
Conceptual reasoning	20	6	4 ^{105–108}	1 ¹⁰⁹	0	1 ¹¹⁰
Deduction tasks	7	3	0	0	0	3 ^{111–113}
Deductive reasoning	31	13	1 ¹¹⁴	2 ^{115,116}	1 ¹¹⁷	9 ^{118–126}
Delis–Kaplan	5	2	2 ^{127,128}	0	0	0
Everyday reasoning	15	5	4 ^{129–132}	0	0	1 ¹³³
Inductive reasoning	29	13	2 ^{134,135}	3 ^{136–138}	2 ^{139,140}	6 ^{141–146}
Inferential reasoning	10	4	3 ^{147–149}	1 ¹⁵⁰	0	0
Raven’s progressive matrices	21	13	2 ^{151,152}	4 ^{153–156}	1 ¹⁵⁷	6 ^{158–163}
Remote associate’s test	23	11	8 ^{164–171}	3 ^{172–174}	0	0
Sylogism	11	7	0	0	1 ¹⁷⁵	6 ^{176–181}
Sylogistic	8	3	0	0	0	3 ^{182–184}
Twenty questions test	5	2	2 ^{185,186}	0	0	0
Wason selection	9	5	2 ^{187,188}	0	0	3 ^{189–191}
Wisconsin card-sorting task	70	17	6 ^{192–197}	3 ^{198–200}	0	8 ^{201–208}

NOTE: “Allowed” are papers that passed our initial exclusion screening (see online Appendix); “Not relevant” are those papers for which no contrast was deemed relevant; “Excluded” are those papers that failed our secondary exclusion screening; “Failed” are those papers for which a technical issue prevented inclusion; and “Used” are those papers which contributed at least one relevant contrast (see Fig. S1). Superscript numbers refer to references listed at the end of the paper.

analyses on two other terms—“set-shifting” and “conflict”—which we posited may load more heavily on the right hemisphere than “statement verification” or “rule checking” because they correspond better with our prediction that the right hemisphere rejects (rather than merely checks) incongruent hypotheses. Figure 1 presents the thresholded results for the ALE analyses using each of these labels, while Figure S2 gives unthresholded results. The coordinates for each cluster in Figure 1 are given in Tables S1 and S2.

Although visual inspection of these figures suggests clear patterns of lateralization (or a lack thereof), we conducted a series of *t*-tests to quantify the degree of lateralization in each figure. The tests, the results of which are presented in Table 2, were conducted to test the hypothesis of greater activity in the left hemisphere than the right hemisphere. These tests confirm the general pattern of results evident in the figures: there is strong left lateralization for both “building a model” and “statement verification” frontally, along with moderate right lateralization for “conflict” frontally, striking bilaterality for “rule finding” and “rule checking,” and a lack of any consistent pattern for “set-shifting.”

According to our framework, we predicted left lateralization for the first two labels in Table 2 and right lateralization for the last four. What we observed bears little resemblance to those predictions. In particular, although “building a model” demonstrated the expected left lateralization, “statement verification” exhibited a very similar (rather than opposite) left-lateralized pattern. Similarly, “rule finding” and “rule checking,” which should have opposite patterns of lateralization, were both fairly bilateral. Finally, “set-shifting” and “conflict” were both expected to be strongly right-lateralized, but the former showed no consistent pattern, and although the latter was right-lateralized frontally, this was not significant (after corrections), and the rest of the brain was mixed. However, there are a number of complicating factors that might account for this disagreement.

First, and most obviously, the majority of the tasks we included were not designed to separate out the various processes in which we are interested. Although we attempted to enforce such separation through our labeling scheme and by using exclusive ALE analyses, this process was only an approximation. Also, we did not attempt to exclude other

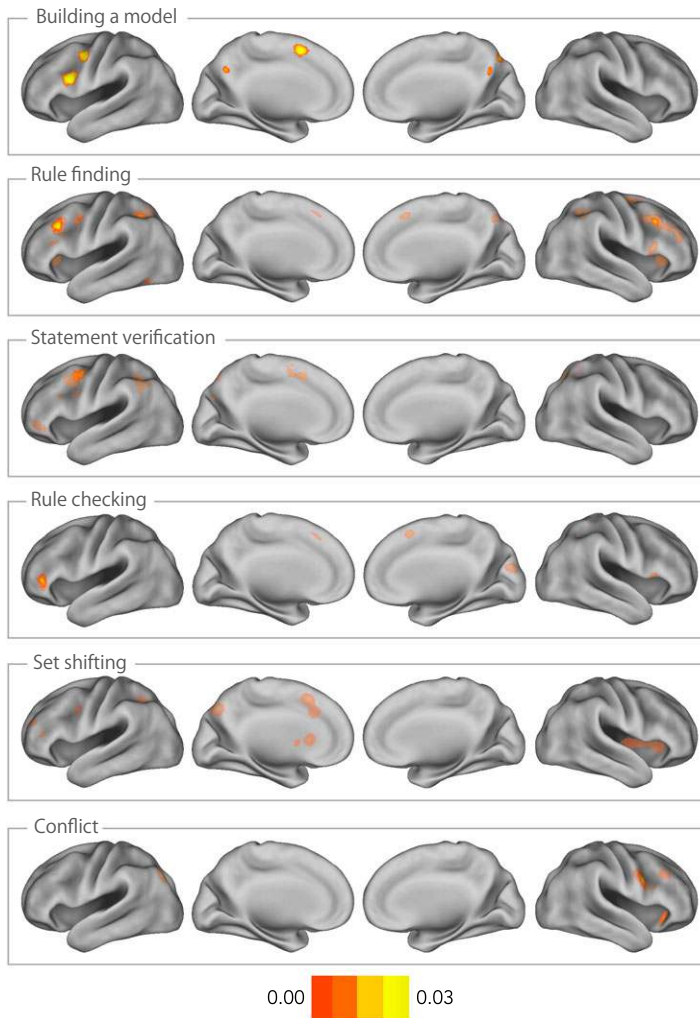


Figure 1. ALE results for each label. Translucent clusters correspond to type II-matched thresholding; solid clusters correspond to type I-matched thresholding. Values are ALE scores.

processes that may have been present in some of the contrasts. For instance, we noted processes associated with decision making, abstract thinking, and cognitive effort, each of which may be bilateral (or lateralized opposite to the primary label) and may therefore give the appearance of bilaterality for the associated label, but did not exclude contrasts with these labels, as doing so would have left us with too few contrasts.

Second, the way in which we applied our labels inadvertently ended up mapping more or less onto a distinction between tasks that relied on linguistic processes and those that relied on spatial or visual processes. For example, most tasks that employed

written syllogisms were given the labels “building a model” to describe the process of creating a cognitive model based on the premises of the syllogism and “statement verification” to describe the process of evaluating the validity of the conclusion. Similarly, tasks such as the Wisconsin card-sorting task (WCST) were given the labels “rule finding” to describe the process of searching for an unknown rule and “rule checking” to describe implementing a rule and using feedback to verify its accuracy. This distinction was unintentional, but may explain the stark divide between these two sets of labels, with the former being strongly left-lateralized (as expected for linguistic processes) and the latter more bilateral.

Table 2. Results of tests of laterality for Figure S2

Label	Frontal	Parietal	Occipital	Temporal	Cerebellar	Subcortical
Building a model	4.722	1.849	3.520	0.482	0.910	2.084
Rule finding	-1.077	-0.310	0.887	0.505	0.329	1.151
Statement verification	3.782	2.698	0.479	1.740	-0.351	-1.776
Rule checking	-0.350	1.247	-0.829	0.896	0.263	0.287
Set shifting	0.574	1.310	2.663	0.649	-2.692	0.445
Conflict	-2.469	2.772	2.987	-1.272	0.892	-0.301

NOTE: *t*-values have been converted to *Z*-values for comparability across regions. Test is of left hemisphere greater than right hemisphere (so positive values denote left > right, negative values right > left). Values in italics are significant at $P < 0.05$, two-tailed, Bonferroni corrected for multiple comparisons.

In addition to this linguistic/nonlinguistic distinction, our labels differed in another way: namely, it is theoretically plausible that during the “statement verification” phase of tasks to which that label was applied (e.g., syllogism tasks), there was still a considerable amount of hypothesis formation ongoing (as the participant attempted to incorporate the syllogism’s conclusion into his/her model, for example), while it seems somewhat less likely that participants in these sorts of tasks were engaging in “statement verification” during the “building a model” phases of these tasks. Likewise, during the “rule finding” phase of tasks given that label (e.g., Raven’s progressive matrices or the WCST), it may be that participants were engaging in a more rapid process of alternating between “finding” and “checking” their rules, but that the “rule checking” phase truly contained relatively less “rule finding.”

Third, the interpretation of blood oxygen level-dependent (BOLD) activity as reflecting causal processing is speculative. Particularly when it comes to regions that are posited to operate in roughly analogous ways and to act on approximately the same input, the assumption that the more active region is the causally responsible region requires careful thought. It may be that greater activity reflects greater (ineffective) effort, for example. Moreover, in the intact brain, even if there existed a situation that loaded purely on the processes of only one hemisphere, we are agnostic to how the hemispheres would interact—perhaps the other hemisphere would adopt a supportive role, rather than either continuing in its normal mode or turning off.

Finally, beyond the limitations of the tasks we considered, our specific label-dependent meta-analysis approach, or the ambiguities surrounding the interpretation of BOLD activity differences in

these situations, it may be that fMRI is fundamentally ill-suited to addressing questions of lateralization in the intact brain. Given the small effect sizes associated with most higher-order processes in fMRI, it may be that the biases in hemispheric dominance during performance of a reasoning task are simply too subtle to be detected using fMRI, even with the power afforded by an ALE approach. Or it may be that the dual effects of hemispheric isolation present in patient studies—pure activation of one hemisphere and release from contribution by the other hemisphere—are responsible for the effects observed in those studies, and that homeostatic processes are powerful enough in the intact brain to prevent any asymmetries detectable by fMRI.

For researchers interested in using fMRI to address questions of lateralization, this is not to say that there is no hope. Indeed, we see several possible ways forward. The most obvious approach is to endorse the assumption that BOLD activity reflects effective processing, and to design a task that separates the processes ascribed to each hemisphere as fully as possible. For example, a hypothetical task that included some events or epochs that loaded entirely on hypothesis formation and others that loaded entirely on hypothesis evaluation would offer a strong test of lateralization in reasoning in the intact brain.

Unfortunately, as stated previously, our framework presumes that both hemispheres will attempt to use all available information. Thus, although they will perform different computations on that information, the net amount of activity in each hemisphere may be similar, even during times when one or the other is ultimately driving behavior. However, even given the limitations of interpreting activity in any such task, it may still be possible to answer

questions of laterality. For example, differences in asymmetry during different events (or from other measures entirely) could be related with, for example, different types of reasoning errors across subjects.

Another approach would be to conduct a meta-analysis using a broader survey of topics. Indeed, reasoning studies may ironically be a suboptimal domain in which to study our proposed primary function of the right hemisphere—that is, to overhaul implausible or inappropriate hypotheses. In most reasoning studies, participants do not need to overhaul their beliefs. Instead, they perform simple evaluations like checking a rule or verifying if a statement matches an inference, which may load onto the right hemisphere according to our theory, but which is likely to do so relatively weakly. One of the strengths of Marinsek *et al.*'s study¹ was that it related evidence from a multitude of tasks to a common set of processes thought to be involved in reasoning. Although this presents challenges—for instance, sifting out the various activation associated with any particular task to identify the activity associated with the putative common underlying process—it might be more straightforward than attempting to parse processes in tasks in which those processes are inextricably linked.

The most obvious remedy for these problems in cognitive neuroscience lies in neuromodulatory techniques, including TMS and transcranial direct current stimulation. Because these methods can (reversibly) emulate brain damage, they allow a direct link between the patient literature and studies of laterality in healthy adults. In fact, these methods allow direct testing of causal questions in a way that is impossible in patients (e.g., by targeting each hemisphere in turn in the same individual⁴⁵). As discussed above, these methods are not without their limitations, but they may nonetheless represent the best path forward for investigating questions of lateralization in healthy adults.

Conclusions

The combined evidence from across multiple methodologies suggests that successful reasoning is the result of the interaction of two lateralized sets of processes. The left hemisphere has consistently been associated with explanation, and the right hemisphere with monitoring and inhibition. There is little question regarding these general

tendencies, particularly when the balance between the two hemispheres is upset. However, it is less clear how individuated the hemispheres are in the intact brain. Although we do not believe that the tendencies we have described are epiphenomenal outcomes of brain damage, it may be that these tendencies are exaggerated in such cases.

The other possible explanation for the results we see in fMRI is methodological. Some isolated fMRI studies do lend support for our framework, so the ambiguous results from our ALE analysis may reflect limitations of the ALE analysis itself—for example, using tasks that failed to sufficiently separate the processes, or settling on a labeling scheme that happened to pit language and spatial processing-related tasks. Alternatively, current fMRI methods may simply be inadequate to detect lateralization, at least without careful attention to issues specific to tests of laterality. Either way, future work is clearly needed before we can fully understand the role hemispheric lateralization plays in reasoning in the intact brain.

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Conflicts of interest

The authors declare no conflicts of interest.

Supporting Information

Additional supporting information may be found in the online version of this article.

Figure S1. Labels associated with every contrast from each “used” paper (see Table 1).

Figure S2. Unthresholded ALE results for each label. Maps show max-projection of ALE scores along the z dimension.

Table S1. Cluster coordinates for “conservative” clusters from Figure 1.

Table S2. Cluster coordinates for “liberal” clusters from Figure 1.

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