A call to action (and perception): Beyond questions of representational format, and toward the functional role of functional circuits in language and cognition

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0. Introduction

Cognitive science has long been concerned with the representational format of thought. This followed naturally from the pervasive view that the goal of cognitive science is not merely to identify the physical mechanisms that instantiate cognition—the implementation—but also to develop functional- or computational-level models of mental representations and processes (Marr, 1982). The reasoning goes that those mental constructs—the functional machinery of cognition—have to be realized in some particular format. Carey (2009) gives voice to this stance when she writes, “A full characterization of any mental representation must specify its format as well as its conceptual role” (p. 457).

Yet there remains substantial disagreement about the representational format of higher cognition. One particularly fierce debate has asked whether representations are “embodied and “modal,” or “abstract” and “amodal.” Proponents of the amodal approach argue that the representations and processes of higher cognition differ in format from the perceptual modalities that activate it and the motor outputs that it can drive (Fodor, 1975; Kintsch, 1998, Newell & Simon, 1972; Pylyshyn, 2002). Proponents of the modal view, in contrast, suggest that at least some representations and processes of higher cognition are not entirely abstracted from their perceptual or motor essences, but have an inherent perceptuo-motor nature. This view is not entirely novel (Hume, 1739; Locke, 1690; see Prinz, 2002), but has experienced a recent resurgence among cognitive scientists (Lakoff, 1987; Johnson, 1987; Barsalou, 1999; Glenberg and Robertson, 2000; among others). This renaissance of concept empiricism has generated a large empirical literature and continues to drive research on language comprehension and production, categorization, reasoning, and mathematical cognition, among other topics (Barsalou, 2010).

This empirical work is often explicitly framed in terms of representational format. Some modal authors characterize their experimental results as specifically conflicting with amodal views of representation (e.g. Glenberg & Robertson, 2000, i.a.); others make the more modest point that their results are predicted by modal but not amodal theories (e.g. Stanfield & Zwaan, 2001, i.a.). The latter rhetoric is more common. Consider an early example, typical of the literature:

“Although the current experiment cannot be taken as an unconditional falsification of amodal symbol systems [...] , it does suggest that
amodal theories, as they stand now, are insufficient to fully explain comprehension and that, moreover, perceptual symbol systems or, at the very least, hybrid systems, are a viable alternative.” (Stanfield and Zwaan 2001, p.156)

Quite recently, however, there has a been some push-back in the literature, with several papers arguing that results purporting to support modal accounts really cannot distinguish between modal and amodal theories, since they are compatible with appropriately extended versions of either (e.g. Mahon & Caramazza, 2008; Dove, 2009; Chatterjee, 2010). These authors have proposed that modal theories of cognition are insufficient and need to incorporate both modal and amodal representations (e.g. Mahon & Caramazza, 2008; Dove, 2009) or admit gradations from modal to amodal symbols (Chatterjee, 2010). If existing empirical work fails to adjudicate between modal and amodal accounts, then these critiques have identified a significant failing.

In this paper, we argue that these criticisms stop short. It’s not just that existing evidence cannot distinguish between modal and amodal representational formats, or that the amodal-modal dichotomy is in need of gradations. Rather, the representational debate is ill conceived and no amount of evidence could ever resolve it. We propose instead that the field would be better served by focusing its attention on questions of mechanism and function (c.f. Bechtel and Wright, 2009). Current evidence demonstrates that brain areas known to subserve perception and action are also activated during higher cognitive processes, such as language comprehension (see Section 2, below). We defend a research program that focuses on the functional role of these specialized brain circuits in higher cognition. That is, instead of representational format, the question that ought to be driving the field is: Which neural circuitry, performing which functions for perception and action, serves what functional role(s) in higher cognitive processes (if any)?

The structure of this paper is as follows. First, we describe the modal and amodal positions in the representational format debate (Section 1). We then canvass the empirical evidence adduced by both sides of the debate, focusing on language research, a particularly contentious area (Section 2). We next argue that the debate is in principle irresolvable (Section 3), and propose that the field should re-orient itself to focus on the functional role of functionally specialized neural populations (Section 4). Finally, we outline some of the promising empirical avenues that may allow us to address this issue (Section 5), and conclude by discussing the potential rewards of this modified approach (Section 6). We focus throughout on language
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research, although the proposal applies broadly to questions of representational format and the neural basis of cognition.

1. The modal/amodal debate

In this section, we briefly review what the various players in the modal/amodal debate mean when they make claims about the format of mental representations. To this end, we give a careful reading of a few illustrative theorists in both the modal and amodal camps.

1.1 The modal position

There are many proponents of the idea that higher cognition is grounded in perception and action. Some of the most fully articulated accounts can be found in the work of Larry Barsalou (Barsalou, 1999; Barsalou et al., 2003; i.a.), Jesse Prinz (Prinz, 2002; i.a.), and George Lakoff and Mark Johnson (Johnson, 1987; Lakoff, 1987; Lakoff & Johnson, 1999, i.a.), so we draw heavily from their work here.

Modal approaches argue that the representations and processes of higher cognition are based in modal systems—those dedicated to perceiving and acting. This is nicely illustrated by Barsalou’s (1999) characterization of the relation between color perception and color concepts. Whether engaged in perception or cognition, Barsalou suggests, the representation of color involves the same neural substrate—in particular, the “neural systems that represent color in perception” (1999, p.578). More generally, the representations underlying higher cognition are grounded in perception because “they are represented in the same systems as the perceptual states that produced them” (p.578). Similarly, Prinz (2002), argues that "concepts derive from perceptual representations" (p. 113), and "are couched in representational codes that are specific to our perceptual systems" (p. 119). And Lakoff & Johnson (1999) write that “An embodied concept is a neural structure that is actually part of, or makes use of, the sensorimotor system of our brains. Much of conceptual inference is, therefore, sensorimotor inference” (p. 20; emphasis ours). In short, all argue that at least some conceptual representations are modal in virtue of their reliance on perceptual systems in the brain.

Modal theories are therefore explicitly reductionist, in the sense that they make claims about the biological substrate underlying cognition. It is a claimed overlap in structure at this level that makes the representational format of concepts perceptual or motor. Implicit in this line
of argument is a commitment to certain neural systems being devoted to perception and action—that is, “modal”—such that using these systems for other cognitive functions like language comprehension makes those latter functions themselves modal.

For instance, Barsalou and colleagues (2003) describe the neural grounding of concepts in perceptual systems by identifying the neural structures hypothesized to serve this function:

Modal approaches represent knowledge very differently [from amodal approaches]. Rather than being transduced into amodal symbols, modality-specific states are captured by adjacent memory systems. Consider visual states (analogous accounts exist for states on other modalities). When a car is perceived visually, a set of neural feature detectors becomes active in the visual system. Conjunctive neurons in a nearby association area then conjoin the active features and store them in memory. Later, in the absence of visual input, these conjunctive neurons partially reactivate the original set of feature detectors to represent the car visually. Such re-enactments or simulations are never complete and can be biased. Nevertheless they provide the cognitive-level representations that support memory, language and thought. (p. 85)

The basic claim of modal approaches, therefore, is that there are perceptual or motor structures\(^1\) in the brain that are also used for conceptual functions, and that this neural repurposing makes those conceptual functions modal. In sloganized form, it states:

**Modal Hypothesis**: Neural machinery that is specifically modal—that is, devoted to perception or action—also plays a functional role in higher cognitive processes.

The Modal Hypothesis, however, has received considerable opposition. We turn now to those criticisms.

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\(^1\) Note that modal accounts often do not specify whether it is conceptual representations or processes that are modal (Machery, 2007). See, for instance, the ambiguity in the excerpt directly above, or the earlier quote from Lakoff & Johnson (1999). Arguably, this is precisely because of the reductionist move these theorists take; at the level of neurons, there are no precise homologues for the computational level distinction between representation and process.
1.2 The amodal position

Modal accounts often provide clear characterizations of what they take the amodal position to be and its differences from the modal position. For instance, Barsalou (1999) contrasts the amodal approach with the modal one in terms of both its processes and its representations:

> Rather than extracting a subset of a perceptual state and storing it for later use as a symbol, an amodal symbol system transduces a subset of a perceptual state into a completely new representational language that is inherently nonperceptual.” (578)

And Barsalou et al (2003) flesh this transduction out in further detail:

> In amodal approaches, sensorimotor representations are transduced into an amodal representation […] that reside[s] outside sensorimotor systems […]. Once amodal redescriptions of sensorimotor states exist, all cognitive processes operate on them to achieve their functions — not on memories of the original sensorimotor states.” (Barsalou et al 2003, p. 85; emphasis ours)

So when Barsalou describes these amodal representations as “inherently nonperceptual,” he means in part that amodal symbols and perceptual representations do not use the same neural systems:

> The amodal symbols that represent the colors of objects in their absence reside in a different neural system from the representations of these colors during perception itself.”(578)

Prinz (2002) has a similar take on the nature of amodal representations, which he describes under the banner of “rationalism”:

> A familiar tradition favored by rationalists is that all mental systems share a “common code” (see Leibniz 1765, Pylyshyn 1978). On this view, perceptual modalities all use the same kinds of symbols as each other and as the more central systems associated with high-level cognition. Call this “common-code rationalism.”” (p.117)
In contrast to this “common code rationalism,” Prinz defends the modalist view that concepts “are couched in representational codes that are specific to our perceptual systems” (ibid, p. 119).

While characterizations of the amodal thesis are commonplace in the writing of its opponents, it’s harder to find explicit advocacy of amodal conceptual representations. One of the clearest such positions, however, is taken by Pylyshyn (2002), who in the context of mental imagery, characterized the amodal position as follows:

The ‘null hypothesis,’ that at the relevant level of analysis—the level appropriate for explaining the results of many experiments on mental imagery—the process of imagistic reasoning involves the same mechanisms and the same forms of representation as are involved in general reasoning, though with different content or subject matter. […] If so, nothing is gained by attributing a special format or special mechanisms to mental imagery. (p.158; emphasis ours)

It appears, then, that the amodal symbols hypothesis—while less often self-consciously articulated—holds that non-perceptual processing is not performed by perceptual systems, but by amodal processes and representations that live outside the perceptual and motor systems. This hypothesis, moreover, is one of several default assumptions made in the literature about representational format—the “null hypothesis,” according to Pylyshyn. At first pass, this amodal hypothesis seems to contrast intrinsically with the modal position.

2. Empirical evidence for and against modal accounts of language use

A large literature has emerged over the past decade purporting to demonstrate that higher cognition is based in perception and action (see reviews in Barsalou 2008, 2010). This includes work on recall, imagery, reasoning, and arithmetic, among others, but likely the richest segment of this literature addresses language comprehension. Studies have demonstrated that processing language about action results in engagement of the motor system (e.g. Glenberg, Sato & Cattaneo, 2008), and processing language about perceptual experience, perceptual systems (e.g., Kaschak et al, 2005). This work is often taken to show that the semantic representations built up during language comprehension are modality-specific and tied to perceptual and motor systems. In this section, we briefly review a sample of prominent studies in this area. We then discuss
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evidence against—and general skepticism about—the view that language comprehension involves modal semantic representations. Readers familiar with this literature may want to skip ahead to Section 2.2.

2.1 Engagement of modal neural systems during language processing

A broad range of experimental techniques in cognitive neuroscience and psychology have been used to investigate the engagement of modal neural systems during language comprehension, including reaction time paradigms, functional magnetic resonance imaging (fMRI), and transcranial magnetic stimulation (TMS). Generally speaking, each technique allows the researcher to infer whether comprehension of language about perception or action interacts with actual action or perception. When such results are found, researchers often conclude that perceptual and motor brain systems play a functional role in language comprehension, and that language comprehension is therefore modal.

A great deal of work in this area has used behavioral paradigms. Reaction time studies typically pair a linguistic stimulus with a nonlinguistic task—either perceptual or motor—and require a speeded behavioral response to either the linguistic or nonlinguistic stimulus. If the compatibility of the linguistic and non-linguistic stimuli has a significant effect on reaction time, this is taken as evidence that language processing has engaged modal brain systems. A seminal study by Glenberg and Kaschak (2002), for instance, showed that comprehending sentences implying action toward (e.g., Courtney handed you the notebook) or away from the body (e.g., You handed Courtney the notebook) selectively affected the time required to launch subsequent arm movements toward or away from the body. In the study, participants held down a central button to trigger visual presentation of a sentence and were asked to make a yes/no sensibility judgment. To respond, participants released the central button and launched an arm movement toward or away from the body in order to press either the “yes” or “no” button., with response direction counterbalanced within subjects. As predicted, after comprehending an “away” sentence, participants were faster to launch an arm movement away from the body than toward the body; for “toward” sentences, this pattern reversed. This “action-sentence compatibility effect” held for both concrete (e.g., You handed Courtney the notebook.) and abstract sentences (e.g., You told Liz the story.). The authors concluded that language comprehension requires perceptual-motor simulation in neural systems responsible for perception and action, and “real bodily action is at the root of meaning conveyed by language” (p. 563). Subsequent behavioral
studies have further explored the highly systematic ways in which the motor system is engaged during language comprehension (e.g., Bergen & Wheeler, 2010; Masson, Bub, & Warren, 2008; Zwaan & Taylor, 2006).

Reaction time studies have also investigated engagement of perceptual systems during language comprehension, with prominent examples coming from studies by Zwaan and his colleagues. In this work, participants hear sentences implying specific perceptual features of some critical object. After each sentence, subjects see a picture of an object and judged whether this object was mentioned in the sentence. In a series of studies that have looked at implied object orientation (Stanfield & Zwaan, 2001), shape (Zwaan, Stanfield & Yaxley, 2002), and visibility (Yaxley & Zwaan, 2007), Zwaan and colleagues have observed faster responses when the relevant perceptual features of the picture matched those implied by the sentence (e.g., faster responses to a picture of an eagle with outstretched vs. folded wings following the sentence The ranger saw the eagle in the sky). Such results are taken to support the notion that “the representation of meaning from linguistic input is a dynamic process involving malleable perceptual representations rather than the mechanical combination of discrete components of meaning” (Zwaan et al., 2002, p. 170). Other behavioral studies have addressed the perceptual basis of linguistic representations of color (Connell, 2007), literal motion (Kaschak et al, 2005) and fictive motion (Matlock, 2004), and the spatial representations of concrete and abstract verbs such as respect and push (Richardson, Spivey, Barsalou, & McRae, 2003), to name a few.

Neuroimaging studies have also supported the engagement of perceptual-motor systems during language comprehension. For instance, comprehending language about effector-specific actions (e.g. actions using the hand, foot, or mouth) selectively activates areas of motor and premotor cortex responsible for observing and executing actions with those effectors (Aziz-Zadeh, Wilson, Rizzolatti & Iacoboni, 2006; Hauk, Johnsrude & Pulvermüller, 2004; Tettamanti et al, 2005). In one study, Tettamanti et al. (2005) presented participants with sentences conveying actions of the hand, mouth, or leg, and found that these sentences, compared to abstract control sentences, activated a left hemisphere fronto-parieto-temporal circuit known to be activated during action observation and execution. While all three effectors exhibited some overlap in activation, the results suggested that sentences describing effector-specific actions selectively activated regions responsible for the motor representation of that effector. The authors concluded that “understanding sentences conveying an action-related content requires the
contribution of sensorimotor circuits, partially overlapping with those active during the execution and observation of the same actions” (p. 278). Similar results have been observed, and similar claims made, regarding language about visual and figurative motion, and brain areas dedicated to motion perception (MT+) (Saygin et al, 2010).

In addition to reaction time and fMRI studies, recent studies using transcranial magnetic stimulation (TMS) have targeted the modality-specificity of language comprehension. TMS is a technique in which an electromagnet is applied to the skull, altering the functioning of a focused cortical region with good spatial resolution (from 7mm to a few centimeters). TMS pulses to primary motor cortex cause motor evoked potentials (MEPs) in the muscles of the associated effectors. Crucially, the amplitudes of these MEPs are modulated by matches between the site of stimulation and the semantic content of language stimuli (Buccino, Riggio, Melli, Binkofski, Gallese, and Rizzolatti, 2005; Oliveri, Finocchiaro, Shapiro, Gangitano, Caramazza, and Pascual-Leone, 2004). More controversially, TMS has also been shown to modulate overt responses to linguistic stimuli, which some argue is stronger evidence that perceptual-motor systems contribute to language comprehension (Willems, Labruna, D’Esposito, Ivry, and Casasanto, 2011). Pulvermüller, Hauk, Nikulin, and Ilmoniemi (2005), for example, had participants perform a lexical decision task in which critical words referred to either leg actions (e.g., kick) or hand/arm actions (e.g., pick). A single subthreshold TMS pulse was applied to hand and leg areas of the left hemisphere 150 milliseconds after the onset of the critical words. Pulvermüller and colleagues found that TMS to the arm area resulted in faster responses to arm than leg words, and conversely that TMS to the leg area resulted in faster responses to leg than arm words. Willems and colleagues (2011) report similar results using repetitive TMS (rTMS) on premotor cortex. These authors conclude that, since the stimulation of motor area affects lexical decision times, the results establish a causal role for the motor system in language comprehension—which, they argue, is not necessarily demonstrated by behavioral and fMRI studies.

Taken together, these studies and others of their ilk attempt to establish overlap between the neural systems responsible for perception and action and those underlying language comprehension. In many cases, the results are taken to indicate a perceptual-motor basis of the semantic representations constructed during language comprehension, in line with theories that place modal representations at the heart of higher cognition. These researchers frequently posit
that language comprehension involves embodied simulations of described situations, and that these simulations (and hence, language comprehension) rely on the motor and perceptual processes connected to the appropriate effectors and sense organs. The proposal, therefore, is that language comprehenders engage a distributed, modal semantic system, the components of which are housed in the same brain areas responsible for the various modalities of perception and motor control.

2.2 Response to the modal evidence

The evidence surveyed above points to the view that, in its most extreme form, takes representations in perceptual-motor systems to exhaust the semantic representations built up during language processing. But there are legitimate reasons to doubt the sufficiency of perceptual-motor systems. Mahon & Caramazza (2008), for instance, argue that modality-specific systems are insufficient to account for all conceptual knowledge, pointing to highly abstract concepts like “incredulous” or “astute” as examples of concepts that lie outside the dominion of sensorimotor representation. Dove (2009: 414-415) articulates the general argument:

All in all, the available evidence suggests that some of our concepts employ perceptual representations—particularly concrete or highly imageable concepts—but fails to support the conclusion that perceptual symbols are the lingua franca of concepts.

Less theoretically, the sufficiency of the Modality Hypothesis would be challenged if lexical or conceptual access were impaired by interference with systems uninvolved in perception and action. Such objections are correct that, if less imageable concepts are not amenable to sensorimotor representation, then the Modality Hypothesis has limited purview.

But these objections attack a modal straw man. It is true that there are proposals on the table for grounding even the most abstract concepts in perception and action (Prinz, 2002, ch. 7; Lakoff and Johnson, 1980; Gallese and Lakoff, 2005; Pezzulo et al, 2011). But crucially, the Modal Hypothesis does not deny that language is subserved by a multifarious network of brain regions, engaged dynamically and opportunistically. Any serious account of access to word meanings or concepts will include roles of varying importance for recall, planning, social cognition, affect, and others. After all, showing that engagement of perceptual and motor
systems is not sufficient for some language behavior would be akin to showing that because lesions to V4 affect vision, the use of primary visual cortex is not sufficient for object perception. Of course it isn’t, and the interesting vision science asks not whether any parts of the vision system are sufficient, but rather what the different parts do. Even arch-modalists Barsalou (c.f. Barsalou et al, 2008) and Prinz (2002, ch. 7) support the involvement of mechanisms that are not properly modal, including symbolic linguistic encoding. Attacks that target sufficiency seem ungenerous to the spirit of the Modal Hypothesis, which focuses not on sufficiency but on the widespread re-deployment of modal brain areas.

More troublesome for the Modal Hypothesis are arguments that target the necessity of modal processes and representations. If these are truly necessary for conceptualization or comprehension, then semantic knowledge should be impaired whenever perceptual and/or motor representations or processing are impaired—and thus, we should not find a double dissociation between semantic knowledge and perceptual/motor knowledge in the corresponding modalities\(^2\). Precisely such a dissociation has been observed, between semantic and motor representations of tool use (for review, see Johnson-Frey, 2004). In conceptual or ideational apraxia, caused by lesions to the parietal-temporal-occipital junction, patients fail to use tools in contextually appropriate ways (e.g. brushing teeth with a comb), but nevertheless remain able to make the fluid hand motions required for tool use (Ochipa et al, 1989). Conversely, patients with ideomotor apraxia—caused by lesions to the left posterior parietal cortex, and/or to the left premotor cortex—retain context-sensitive knowledge of tools’ functions but are unable to perform the appropriate actions with those tools (Geschwind & Kaplan, 1962; Sirigu et al, 1995). These dissociations have been taken as evidence that conceptual knowledge of action is independent of representations of relevant motor skills (Mahon & Caramazza, 2008).

The necessity of perceptual-motor involvement is a legitimate concern for modal accounts. Note, however, that the Modal Hypothesis does not, on its own, entail that perceptual-motor systems are always necessary, only that—when available and appropriately engaged—those systems make specific contributions to, and thus are partially constitutive of, language processing and other facets of higher cognition. In Section 4 below, we argue that a productive account of language and higher cognition should focus on such a mechanistic approach, and thus abandon concerns with the necessity and sufficiency of a particular representational format.

\(^2\) But see Plaut (1995) for reasons to interpret double dissociations with caution.
While arguments invoking necessity and sufficiency are largely orthogonal to the general notion that modal neural systems play some role in language comprehension, there are more serious objections to the modalist view. Mahon and Caramazza (2008) have pointed out that many, if not all, of the experimental results supporting a modal conceptual system are compatible with a completely amodal conceptual system equipped with associative links to perceptual and motor representations. In sloganized form, their argument is as follows:

**Mediating Process Reply:** The observed relation between sensorimotor processing and higher cognitive functioning is due, not to shared representations or processes, but to downstream activation spreading between amodal and modal areas.

According to this Mediating Process Reply, the activation of modal systems by word stimuli, for example, is the result of first activating the associated amodal concept in an amodal system, followed by activation spreading via associative links that mediate between amodal and sensorimotor processes. On this account, sensorimotor systems themselves do not play a causal role in higher cognition; their engagement during conceptual processing is epiphenomenal.

Versions of this objection have been voiced elsewhere (Chatterjee, 2010; Dove, 2009). It is important to note that this argument applies as much to reaction time results as it does to fMRI (Pulvermüller et al., 2005) and some TMS results (Willems et al., 2011). As Mahon and Caramazza (2008) point out, for instance, amodal accounts can even accommodate the facilitation of lexical decisions following TMS to sensorimotor areas (Pulvermüller et al, 2005, Willems et al., 2011), since it is entirely possible that TMS-induced motor activity can spread to purely amodal concepts, activating that amodal representation and producing the observed facilitation of lexical decision times. None of the evidence described in Section 2.1, therefore, can be straightforwardly interpreted as showing a causal or functional role for modal neural systems in conceptual processing.

That is the current state of the field. At this juncture, the modal/amodal debate is at something of an impasse. It is clear that sensorimotor tasks can affect semantic processing, and that semantic processing can engage sensorimotor systems. However, the functional role of this activity remains unclear, and it is unclear what implications these results may have for the format of mental representations. To further complicate matters, there is little agreement on what kind of evidence could in principle resolve this issue. Many theorists look to neuroscience for the crucial
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evidence, yet it seems that any neuroscientific finding that purports to support the Modal Hypothesis could also be explained by a post-hoc amodal Mediating Process Reply. In the next section, we suggest that this impasse is not merely a shortcoming of ingenuity or experimental technology, but a sign that the modal-amodal distinction may not be tenable.

3. The modal-amodal distinction is untenable

Debates surrounding the Modality Hypothesis have largely assumed that the opposing positions are meaningful, coherent, and distinct—that the debate is resolvable in principle, if as yet unresolved. In this section, we challenge this assumption. We consider the criteria used to determine when a brain system is “modal,” and argue that at the neural level this pursuit of labels is quixotic. If questions of representational format are to be adjudicated at the neural level, as they are in the literature concerned with the Modal Hypothesis, then a necessary first step is articulating criteria that can reliably pick out a “modal” neural system. Existing definitions, however, preclude the possibility of such a system playing a role in higher cognition, or fail to characterize the actual activity of those neural systems we intuitively consider “perceptual” or “motoric”. This failure points to the incoherence of debates on the format of cognitive representations, at least when those debates are framed at the neural level. In light of this conclusion, we argue that while recent proposals to marry modal and amodal views do take steps in the right direction, ultimately we must move beyond the notion of modality-specificity when studying how the brain accomplishes feats of higher cognition.

3.1 The brain flaunts the modal/amodal distinction

As discussed in the previous section, the current representational debate appeals explicitly to the brain in determining whether cognitive representations are modal or amodal. Argumentation generally takes the following form: “Engaging representation X activates modal brain system Y; therefore, representation X must be modal.” The argument pivots entirely on the word “modal.” But without an operational definition of what constitutes a modal neural system, one cannot appeal to the brain to determine the modality-specificity of cognitive processes or representations. As Aydede (1999) noted in a commentary on Barsalou’s (1999) original BBS target article, for us to make claims about the perceptual grounding of cognition, “we must have a workable notion of perceptual/nonperceptual systems,” (p. 610)—and according to Aydede,
Barsalou does not supply one. Indeed, Aydede notes that the closest one can get is the circular definition that modal concepts “are represented in the same systems as the perceptual states that produced them” (sect. 1.1, para. 2).

In a response to Aydede’s criticism, Barsalou (1999) appealed to common sense notions of perceptual systems. We quote at length because this gets to the heart of our argument:

Quite remarkably, Aydede claims that there is no way to distinguish perceptual and nonperceptual systems independently of modal and amodal symbols. Given the huge behavioral and neural literatures on perception, this is a rather surprising claim. A tremendous amount is known about the perceptual systems of the brain independent of anything anyone could possibly say about conceptual systems. Clearly, we know a lot about perceptual abilities and the neural mechanisms that implement them. Identifying these abilities and mechanisms independently of perceptual symbols is not only possible but has long since been accomplished in the scientific disciplines that study perception. In defining perceptual symbols, I simply used these well-recognized findings. [...] Perceptual symbols follow the well-trodden paths of perception researchers in claiming that the representational mechanisms of perception are the representational mechanisms of knowledge. What is perceptual about perceptual symbol systems is perception in the classic and well-established sense. (1999b, p.640, emphasis ours)

Whether this “classic and well-established sense” is sufficiently coherent to sustain the “grounding” of conception in perception, however, is the very issue that Aydede raises. Without a precisely articulated account of when a neural circuit qualifies as “modal”, one can only appeal to convention and common sense—notoriously unreliable arbiters of neural architecture.

Since then, few have responded to Aydede’s challenge. Prinz (2002) offers one of the clearest and most cogent responses, a careful account of when exactly a particular neural population counts as a perceptual system or “sense.” He characterizes perceptual systems as dedicated input systems, which he defines as follows:
In saying that senses are *input* systems, I mean that they are systems that receive inputs from outside of the brain. [...] (116, emphasis ours)

In saying that the senses are *systems*, I want to emphasize the fact that they each consist of their own sets of operations and representations, housed in separate neural pathways. Distinguishing separate neural pathways is crucial. [...] To say that senses are systems means that they can be divided up internally, in our case, by distinct collections of cooperative neural populations. (115-116 emphasis ours)

Finally, in saying that senses are dedicated, I mean that each sense responds to a proprietary input class.” (117, emphasis ours)

So a dedicated input system takes a particular class of outside input (e.g. visual input), and processes it in a specific and exclusive neural pathway (e.g. the visual pathway, starting at, say, V1). This position is certainly appealing for its definitional rigor and simplicity, and captures the received wisdom that particular brain regions are responsible for each perceptual modality, others are responsible for action, and so on. Yet, in the light of the very results on conceptual processing that it is recruited to explain, it appears to be untenable. Here’s why.

Consider the process of identifying a particular neural system as perceptual, following Prinz’s criteria. First, it should receive inputs from outside the brain. But there is no reasoned way to terminate the causal chain that begins with sensory input and spreads rapidly throughout the brain. Indeed, Prinz’s first criterion applies to the brain as a whole, including systems that nobody has ever characterized as “perceptual”—systems like Broca’s area and all the rest of the canonical language machinery. Second, the candidate neural system should consist of “separate neural pathways,” “distinct collections of cooperative neural populations.” But again, this does little to distinguish putative perceptual systems from other specialized neural populations, also made up of neurons that “work in tandem” but not in the service of perception. So Prinz’s first two criteria do little to parcel off the perceptual systems from the rest of our neural machinery.

That brings us to Prinz’s third criterion, that a perceptual system needs to be dedicated—that is, to respond to a proprietary input class. And here’s the crux of our argument: We know
that neurons, even in primary perceptual areas, respond not merely to afferent input from specific perceptual organs (e.g. the eyes), but also to efferent input from other cortical sources. After all, this is precisely the finding that drives modal theorist in the first place: that primary perceptual and motor cortices are engaged during higher cognitive functions like recall, imagery, language processing, and so on. What’s more, the activity of primary perceptual cortices “dedicated” to one perceptual sense is modulated by sensory input to other modalities (Ghazanfar & Schroeder, 2006; Kayser & Logothetis, 2007). For instance, both primary auditory cortex and primary sensory cortex have each been shown to respond to stimuli in the other modality: activity in A1 is modulated by tactile stimuli, and activity in S1 by auditory stimuli (Lemus et al., 2010). Such findings led Ghazanfar & Schroeder (2006) to conclude that “...much, if not all, of neocortex is multisensory. This necessarily forces us to reconsider the validity of probing the brain unimodally and suggests a different perspective when considering other aspects of cognition...” (p. 284). We agree. Neurons in “perceptual systems” do more than just process perceptual input. With multisensory processing occurring even in primary sensory cortices, and putative “perceptual” systems responding to rampant cortico-cortical connections, it is likely impossible to define specific neural systems, at least cortical ones, as instantiating a specific perceptual system using a criterion that appeals to proprietariness of input. After all, it is this very input promiscuity that we are trying to explain.

In essence, our objection to Prinz’s third criterion boils down to the question of what it means for a neuron or neural population to respond to input from apparently dissimilar sources. The study of “mirror neurons” is illuminating in this regard. There, the reasoning is perhaps clearer. Suppose a neuron fires both when an animal performs a specific action and when it observes another animal performing the same action (Rizzolatti & Craighero, 2004). What type of cell is that, and how should we characterize its behavior? Is it a motor cell, being used for perception as well—that is, are perceptual representations somehow “motoric”? Is it a perceptual cell, used for motor control as well—that is, are motor representations somehow “perceptual”? Is it a multimodal cell, used for perception and action, or an amodal cell, encoding the action in the abstract? The mirror neuron literature avoids such debates about the format of mirror neuron representation—mere notational negotiations—and focuses instead on the functional contributions of the mirror neuron network (Rizzolatti & Sinigaglia, 2010).
This same logic applies to “perceptual” and “motor” systems that are also activated during non-perception or non-action. Consider for the sake of argument a hypothetical cell that responds to a particular range of wavelengths of light, but also becomes active when a person comprehends a description of color in that range. How should we characterize such a cell? Is it a perceptual cell also used for conceptualization? A conceptual cell also used for perception? A multifunctional cell used for perception and conception? Or an amodal cell that encodes color, independently of whether it’s being perceived or imagined? At the neural level, these labels don’t track meaningful distinctions.

The rampant multifunctionality of perceptual and motor neural systems implies that the very notion of a “modal” neural system is suspect. While we have focused on the account offered in Prinz (2002), our objections are general and apply to any attempt at neural topography that hopes to draw borders around perceptual systems. Neural considerations cannot adjudicate between the possible labels of a mirror neuron—whether motor, perceptual, multimodal, or amodal—and the same applies to neurons involved in both perception/action and conception. And there’s the rub. At the neural level, as presently debated in the literature, the modal-amodal debate—while intuitively compelling—is nothing more than a terminological quibble. When the inputs to a neural system are heterogeneous, as they are in the current debate, the distinction between modal and amodal dissolves at the level of neurons and their functional properties.

3.2 A word about function and teleology

Of course, there may be ways of determining representational format that do not appeal exclusively to neural implementation. Teleological accounts of mental content, for instance, may hold promise for distinguishing modal and amodal systems (Millikan, 1984; cf. Anderson 2010, p. 266). From the perspective of natural selection, the function of a particular organ—or neural region—is determined in light of that organ’s history, its contribution to fitness over evolutionary time. As Sober (2001, p. xi) notes, “Adaptation is a historical concept.” Just as the heart’s function is to pump blood, not to make a lub-dub noise, one might argue on evolutionary grounds that MT+ is modal because, over evolutionary time, its adaptive function was the perception of visual motion.

We are friendly to this project. But this is an entirely different project, however, from the one engaged in by theorists on both sides of the Modal Hypothesis. As revealed by the review of the arguments for and against the Modal Hypothesis, the target of the current debate, in theory
and in practice, is the use and re-use of a particular family of neural systems. The target is not the historical origins of the present-day computational properties of a particular neural region—whether over developmental time, for those of empiricist bent, or over evolutionary time if nativist. The concern is the contribution of particular cortical regions today—more specifically, the possibility that a single cortical region could make contributions to multiple cognitive processes, perhaps as disparate as, say, motion perception and the comprehension of language about motion (e.g. Kaschak et al, 2005). Indeed, both proponents and opponents of the Modal Hypothesis seem to have a tacit agreement about which neural populations should count as modal, notwithstanding the lack of coherent criteria for picking out such populations. Appeals to teleology or adaptive function, therefore, are not germane. In the debate over the modality of mental processing, the players are not cortical historians.

3.3 “Hybrid” positions

In section 2.2, we discussed how much of the current evidence does not adjudicate between modal and (sufficiently elaborated) amodal accounts. We are certainly not the first to recognize this, and other authors have responded by proposing “hybrid” accounts that wed modal and amodal representations (Mahon and Caramazza, 2008; Davies, 2004; Markman and Dietrich, 2000; Dove, 2009; Chatterjee, 2010). Markman and Dietrich (2000), for instance, argue that the amodal view should be supplemented rather than discarded, so that “cognitive models [become] more sensitive to perceptual representation” (p. 475). An illustrative example of a hybrid account is Mahon and Caramazza’s (2008) Grounding by Interaction hypothesis. On their account, a concept has stable and context-independent amodal content, but is also enriched by perceptual-motor content that supports its use in a particular context, at a particular point in time, in a contextually appropriate way. Similarly, Dove (2009) defends a pluralistic view in which separate modal and amodal semantic codes subserve processing of concepts of high and low imageability, instantiated by distinct neural systems. Most recently, Chatterjee (2010) proposes a spectrum of modality, from unimodality to amodality:

“The nervous system has unimodal primary sensory cortices, unimodal association cortices, multimodal cortices as well as structures several synapses removed from sensory inputs and motor outputs that they might be considered amodal.” (p.107)
According to Chatterjee, information is progressively “bleached” of modal content as it is transmitted successively farther from primary sensory areas. He suggests that productive work can be done by framing questions according to several functional-neuroanatomical axes that capture this graded transition from modal to amodal representation—a transition that trades specificity and referential grounding, for flexibility and generative power. Instead of asking whether representations are modal or amodal, Chatterjee (2010) suggests we ask what can be done with representations that are modal and amodal to varying degrees. All these synthetic proposals are meant to account for the empirical results generated by the modal camp while retaining the strengths of amodal approaches.

While these hybrid proposals maintain some version of the modal-amodal distinction that we criticized above (§3.2), they nevertheless push the field in the right direction. Hybrid accounts all share a distrust of unitary, invariant neural systems of conceptual representation, and a commitment to multiple, context-sensitive neural systems. We applaud this focus on variegated, context-sensitive conceptual representation, and the neural systems involved. Rather than attempting to characterize some unitary representational system, a productive research program will investigate how varied cognitive resources support particular cognitive functions in particular contexts. We suggest taking this realization one step further. In the next section, we argue that the study of conceptual processing should abandon the modal-amodal distinction entirely, and focus instead on the functional role of functionally specialized neural circuits.

4. The proposal: Functional roles of functional circuits

We have argued that debates about the modality or amodality of mental representations and processes, if adjudicated at the neural level, are unresolvable. But this does not imply that there is no room to ask how various neural processes, including those also involved in perception and action, contribute to language comprehension and other aspects of higher cognition. In fact, these kinds of questions are essential and productive—if asked in a nuanced way. Instead of investigating the format—modal or amodal—of a mental representation or process, the field will be better served by trying to identify, for particular components of higher cognitive functions, the biological mechanisms that enact those functions. For instance, research on language should focus on asking: What functional role is played by which parts of the brain (and body) in well-defined aspects of language learning, production, and comprehension? This is qualitatively
different from questions about representational format—whether modal, amodal, or both. It’s a question not about format but about mechanisms, and specifically about shared mechanisms. Such questions about mechanism are necessary if we are interested in understanding how we are capable of language comprehension, and of higher cognition more generally.

4.1 Functional roles and the mechanisms of cognition

If we want to know how the brain is capable of higher cognition, we will naturally need to consider a very broad swath of neural territory. Let’s continue with the example of language. Like other complex cognitive behaviors, processing language activates a greedy web of cortical and subcortical areas. The research reviewed in Section 2 above showed that some of those brain areas are also implicated in perception and action, and moreover that their activation is sensitive to linguistic content. We also saw that comprehending language about action and perception interacts with perceiving and acting, so these interactions don’t just take place at the neural level—they also affect behavior. As a result, we take it as uncontroversial that neural resources that are responsible for aspects of perception and action are also active during language comprehension. What remains to be seen is whether their activity is functional or epiphenomenal.

But it is not a stretch to hypothesize—with emphasis on the fact that at present this is merely a hypothesis—that these same regions might indeed play functional roles in language comprehension. This claim is usually implicit in modal accounts. In fact, parts of the brain that serve particular functions for perception and action seem exceptionally well suited to a range of functional roles in comprehension. They are good candidates for producing subjective experiences; if the mechanisms responsible for perception are also responsible for the processes of understanding language about a given percept, then whatever subjective experience one has for the former may also be experienced for the latter. Likewise, if simulated action and perception share neural machinery with real action and perception, then simulated actions and percepts may inherit the mechanisms that perform inferences in response to the genuine article (cf. Grush, 2004), thus supporting inference during language comprehension. And when it gets right down to it, the computational properties of the brain structures responsible for identifying objects and events in perception might make them particularly well suited to represent those same objects and events in their absence, in exactly the way suggested by Barsalou (1999) and others in the modal tradition.
This suggests a mechanistic reframing of the Modal Hypothesis:

**Shared Functional Circuit Hypothesis:** Functional neural circuits—
assemblages of neurons that coordinate to accomplish a particular
function—play a functional role in superficially dissimilar cognitive
tasks.

This *Shared Functional Circuit* approach highlights shared neural machinery between disparate
cognitive accomplishments, and focuses on the functional contributions of that machinery. The
question of functional role, however, is of a very different character from those usually asked in
research undertaken to support the Modal Hypothesis. We’re not advocating asking merely
whether some piece of brain tissue in V1, MT+, or premotor cortex is activated, for whatever
purpose, during a higher cognitive function like language comprehension; this would simply add
to the literature showing that, yes, those cells are active during behaviors other than perception or
action. Instead, we’re arguing that the relevant question is what that neural activity *does*,
mechanistically, for the behavior in question.

Answering this question will require several angles of attack. What properties of the
stimulus, the environment, or the cognizer—their history, their individual characteristics, their
mental or physical state—affect the likelihood that this piece of tissue will be involved? What
leads to the absence of activity? What, functionally, does the presence (or absence) of activity do
to the cognitive process in question? For language comprehension, for example, we might find
that when people don’t use circuits in MT+, they have less detailed mental representations of
described motion, or perhaps they are less able to draw inferences pertaining to the motion of
those objects—two quite different functional contributions that are glossed over in debates
between modal and amodal camps. Instead of debating the representational format of a neuron or
neural system, we need to find out what that cell or system does—the behavioral and cognitive
functions that it enables.

### 4.2 Functional roles of perceptual circuits?

It might be attractive to move toward the functional role of shared functional circuits, and
away from representational format, while maintaining some sense in which those circuits are
perceptual or motor (cf. Gallese and Lakoff, 2005). Suppose we found that some aspect of
language comprehension—the representation of described objects, for instance—was
functionally supported under certain circumstances by parts of V1. We might be tempted to conclude that this was a case in which systems dedicated to perception and action are being re-used functionally for other cognitive purposes. This could be interpreted as big news, in that it would appear to show that some aspect of higher cognition depends on evolutionarily older neural resources originally devoted to vision—and thus, that higher cognition is “modal.” As intuitively appealing as this might be, it amounts to the same line of reasoning that we argued against in Section 3: making format attributions on the basis of shared neural resources, when matters of format dissolve at the neural level. The move to define multifunctional neurons as primarily or intrinsically perceptual or motor is neurally unfeasible.

This isn’t to say that the perceptual or motor contributions of some particular neural circuit are uninformative. On the contrary, if evidence suggests that some functional circuit plays a role in language comprehension but is also functionally implicated in perception or action, then this can provide clues to the functional contribution of this circuit to comprehension. Knowing that MT+ is responsible for motion perception, for instance, suggests that it may play a similar role in language comprehension—such as representing described motion (Saygin et al, 2011).

There’s a delicate balance to be reached here. Researchers need a way to designate certain pieces of brain tissue as being of interest because they have known functions in perception or action, but without problematically having to label them as “perceptual”, “motor”, or “modal”—and importantly, without making claims about format, claims that dissolve at the neural level. With care, however, we can work around this difficulty. Instead of broadly targeting perceptual or motor systems, we can instead focus on specific networks of neurons that serve demonstrated functional roles in processes of perception or action. Without committing ourselves to the origin of this specialization, we take it as given that the adult brain is specialized, with particular neural populations performing particular computations for particular tasks. This specialization may come about by dint of structure, connectivity, training, or a combination of these. The upshot of this, crucially, is that we have neural circuits that perform calculations relevant to effector-specific motor actions in M1, circuits that calculate motion in MT+, and so on.

In place of identifying neurons (or neural systems) as perceptual or motor or amodal tout court, we propose instead to take as the object of neural study functional circuits: connected networks of neurons that demonstrably perform certain functions for given cognitive behaviors.
Observing that some neural circuit performs a given set of computations during perception does not commit us to classifying it as “perceptual.” The focus shifts from identifying format to identifying the computations performed by a neural circuit, and asking whether that functionality is also recruited for other behaviors—and if so, which ones, when, why, and with what consequences.

To be clear, we do not mean to suggest that functional circuits are informationally encapsulated, like Fodorian modules (Fodor, 1983); a functional circuit may be informationally integrated with other circuits. Nor do we mean to reify these functional circuits into a stable ontology of non-overlapping functional circuits, a brain’s bestiary. A given neuron might be seen to participate in more than one functional circuit, depending on context, input from other cortical circuits, or even just the level of analysis relevant for understanding the computations at hand. And the organization of neurons into functional circuits may change over time, throughout development or in response to the current situation. In many ways, we are agnostic about the best way to characterize these functional circuits; indeed, this is the very task at hand. We merely want to suggest that for the purposes of understanding how the brain accomplishes some complex cognitive exploit like language comprehension, neural populations can be fruitfully studied in a mechanistic analysis (Bechtel and Wright, 2009) that pinpoints those neural circuits that make functional contributions—that is, those circuits without which the relevant cognitive processes and their observable products would be different.

So instead of asking whether perceptual or motor systems are involved in language comprehension, we advocate asking: Which functional circuits, perform what functional roles, under what circumstances? In particular, the field appears to be excited by the evidence concerning a subset of functional circuits: those that also contribute to perception or action. Many of these circuits may be involved in a variety of cognitive accomplishments—not solely in action or perception. But this needn’t concern us, since we are not interested in whether any particular circuit should be classified as “perceptual” or “motor,” but instead in its functional contribution, including the sorts of computations it performs. Circuits may have particular functional specializations as a result of having been trained up on certain types of data over the course of development or because of their connectivity shaped in evolutionary time. That specialization allows us to ask whether a functional circuit that spends a lot of its time computing direction of motion from visual input, for instance, also bears some functional load during
language comprehension, either generating motion-related inferences, or preparing for appropriate action, or representing described motion.

How can we find functional circuits of interest? We need to be careful, of course, to avoid purely topographical definitions of circuits, lest we fall into neo-phrenology. That said, the locations of networks of neurons can inform questions about the functional assemblages in which they participate; assuming typical development, neurons in V1 are likely to be attuned to input from the eyes, for instance. But only an analysis of the dynamics of a neural circuit can indicate what it does, and for which cognitive operations. In principle, functional circuits may differ substantially in their promiscuity, from true one-trick functional ponies, only ever engaged for a single type of behavior, to more widely deployed circuits that contribute to a variety of behaviors—although recently authors have argued that the latter are far more common (e.g., Anderson, 2011). The ones most relevant to the question at hand are those keenly tuned to performing specific functions during perceptual or motor tasks, but which also play a functional role in some aspect of comprehension or other conceptual processing.

Adopting this strategy doesn’t lose anything in terms of the broad scientific concerns that drove research on the Modal Hypothesis. And it still allows us to ask the core questions that motivate work on the mind, like how the human brain is able to perform species-unique operations like language comprehension, and whether evolutionarily older brain circuitry used for perception or action has been exapted for language use. But it does so in a piece-by-piece and non-programmatic way, defining circuits by their functions and asking what the (possibly multifarious) contributions(s) are of each functional circuit, within and across behaviors. The late Liz Bates used to say that language is a “new machine built out of old parts” (Bates, 1992). Focusing on functionally defined brain circuits allows us to test this hypothesis in a detailed way, asking whether these old parts (specialized circuits that do certain things in perceptual or motor tasks) are used for other purposes, and what those purposes might be.

There is good reason to be interested in the idea that circuits that perform perceptual or motor functions are also used to perform other cognitive accomplishments. Fortunately, in a framework that seeks the functional roles of functional circuits, we can still make progress on that question without falling into the representational quicksand of labeling particular neurons as modal or amodal. Instead, the Shared Functional Circuit approach offers a more nuanced,
textured account that bears the promise of providing a mechanistic answer, instead of a type answer.

5. Some leading lines of inquiry

If our aim is to determine what functional role (if any) certain known neural circuits play in specific aspects of language comprehension (or any other cognitive function), then this will limit the experimental methods we can conscript for this task. In this section, we outline some design considerations: properties that would allow experimental work to inform the question of shared functional circuitry. We then identify several recent studies that make the most progress in this direction.

5.1 Design features of an experiment on functional role of functional circuits

Much existing behavioral work on language, perception, and action (reviewed in Section 2) uses facilitatory priming of perception or action by language. Well-known examples include sentential priming of picture processing (Zwaan et al., 2002) or manual actions (Glenberg and Kaschak, 2002), among others. Experiments like these may suggest the involvement in language comprehension of circuits that perform perceptual or motor functions, but in themselves they can never identify the functional contribution to language comprehension, if any. Indeed, as discussed, these results are vulnerable to the Mediating Process Reply. It could very well be the case that some other circuitry performs all the relevant computation for language comprehension, and that priming is observed only because of spreading activation to the relevant circuits involved in perception or action.

The same is true for behavioral experiments in which the order of the tasks is reversed, with a perceptual or motor task affecting some subsequent linguistic behavior. For instance, participants might be faster to read and make a judgment about a described action when they have just finished performing that same action. If the sensorimotor behavior reliably activates a given circuit, then a sensorimotor-task-to-language facilitation finding can tell us whether or not a particular circuit can activate the meanings of particular words or phrases—potentially a novel finding in cases like abstract language (e.g. Wilson & Gibbs, 2007). Such findings, however, do not necessarily license the stronger inference that some aspect of language comprehension relies on some part of the neural substrate of the sensorimotor task. Circuits that control the relevant
perception or action could be associatively linked to relevant linguistic circuits—again, the Mediating Process Reply—so the facilitatory priming of language does not demonstrate a functional role of functional circuits. The same holds, importantly, for TMS studies that demonstrate facilitation of language processing by application of a magnetic field to an area believed to house sensorimotor circuits (Pulvermuller et al, 2005; Willems et al, 2011). It could again be the case that increased activation of the sensorimotor circuits lead, through association, to activation of other, language-specific circuitry.

For a similar reason, brain imaging alone cannot tell us whether particular circuits perform a given functional role in language comprehension, and if they do, what functional role that might be. The detection of an increased BOLD signal associated with language of a particular type and in a particular brain region does not imply, as discussed above in Section 2, that there is any functionality to the underlying brain activity for the particular cognitive processes under consideration. Activity in visual areas during language comprehension, for instance, could merely reflect downstream activation that results from, but does not contribute to, the comprehension process. And for that matter, there could well be neural circuitry used for language—but not perception or motor control per se—that is strategically housed in close proximity to circuits that do have sensorimotor functions. The current temporal and spatial precision of brain imaging would not allow us to exclude this possibility, and as a result imaging results are also vulnerable to a Mediating Process interpretation of a sort.

We’ve argued that facilitation effects and brain imaging technologies are inconclusive in that they could be due either to functional engagement of a neural resource or epiphenomenal activity such as that attributed to spreading activation. Although such epiphenomenal activity could incidentally result in facilitation of a subsequent task, the same is less obviously true for interference effects, since certain types of interference effect are thought to reflect competition for the neural resources that play a functional role for a cognitive task (Bergen, 2007). If a cognitive process is inhibited because a particular cognitive resource is unavailable, then we can infer that the process relies functionally on that resource.

More specifically, the key to inferring functional roles for functional circuits involves knockout effects: interference effects in which we observe selectively degraded performance on one task as a result of another task, treatment, or trauma that “knocks out” the ability to use some known neural circuit. The basic logic is to find a way to interfere with a neural circuit that serves
a known function for perception or motor control, for instance, and to determine what other functions (if any) are selectively affected—for instance, accessing the meaning of words or sentences, making inferences, responding appropriately to language, etc. Knockout effects afford clearer inferences about the functional overlaps between linguistic and sensorimotor tasks to the extent that they are known to be due to the unavailability of a particular resource, thus forestalling recourse to a Mediating Processes Reply.

In order to make these inferences, however, two things must be established. First, the sensorimotor task has to affect the specific linguistic manipulation being studied, not just language processing across the board; the same basic logic applies here as to demonstrations of dissociation in general. In practice, this can be established by including a control condition with linguistic stimuli not thought to rely on the relevant functional circuit. For instance, one might want to show that knocking out the neural circuitry that detects motion towards the body interferes selectively with processing sentences related to motion towards the body, and should therefore also include sentences that describe motion away from the body. Even stronger, a double dissociation logic could be used, such that knocking out circuits that detect motion towards or away from the body uniquely interfere with processing sentences about language towards or away from the body, respectively.

Second, it has to be established that the interference effect is indeed interference on the condition of interest, rather than facilitation of the other experimental condition[s]. To continue with our motion example, for instance, we would need a baseline measure that establishes the reaction time to process a sentence (or whatever the dependent measure is) absent the specific knockout manipulation. If reactions in the motion-toward condition are slower than in the baseline condition, but reactions in the motion-away condition are not slower than in their own baseline condition, then this licenses the inference that processing of this particular type of sentence is selectively impaired when the motion-relevant neural circuit is knocked out. Comparison to a baseline condition, therefore, is necessary to distinguish interference from facilitation effects, which are vulnerable to Mediating Process Replies.

The canonical class of knockout effects are neuropsychological lesion studies in which trauma to particular parts of the brain is shown to selectively impair specific cognitive deficits. Imagine a study in which lesions to neural circuits known to play a particular role in effector-specific motor control, are found to impair comprehension of some aspect of language about...
actions using those same effectors but not others. On the basis of this study, we could conclude not only that the lesioned circuits also perform a relevant function for language, but also something about the function performed. But knockout studies need not involve permanent damage to neural tissue. The same logic would apply to a hypothetical study that used TMS to disrupt a localized functional circuit, and as a result impaired not only a perceptual or motor function but also some aspect of language comprehension. And it would also apply to behavioral work, as long as it was possible to behaviorally impede the use of a neural circuit with a known sensorimotor function, and as long as knocking out that circuit again impaired some aspect of a concurrent or subsequent language task.

Alas, there are some further wrinkles. The Mediating Process Reply still potentially applies to some knockout results. For instance, interfering with the use of a circuit with a sensorimotor function (by engaging it in an unrelated sensorimotor task or even possibly through TMS) could again produce downstream activation of a language-specific circuit, and thereby interfere with that language-specific circuit. Thus, simultaneous or subsequent interference on a language task might arise due to downstream knock-out of the language-specific circuit. For instance, if a sensorimotor task requiring motion perception also selectively interferes with concurrent comprehension of motion language (as in Kaschak et al., 2005), then this may be due to the unavailability of the functional circuits responsible for motion perception, as commonly concluded. Alternatively, however, the Mediating Process Reply raises the possibility that the motion-perception task may activate functional circuits that are responsible for motion perception, which incidentally activate other downstream circuitry that represents the concepts AWAY or TOWARD, and—since activating a particular cognitive resource can leave it less available for other tasks—this could therefore leave these latter resources less available for language comprehension. Crucially, however, motion perception and language comprehension would rely functionally on entirely different functional circuits. While this scenario may seem unlikely, it nevertheless reveals that knockout experiments are not unambiguous as to whether or not the “knocked-out” functional circuit is functionally implicated in the secondary linguistic or cognitive task.

There are at least two ways to avoid this doubt and militate against a Mediating Process Reply: use an adaptation paradigm, or include an amodal control task. In an adaptation experiment, one task is repeated or continued until the neural resources subserving the task
become less available for a nontrivial “refractory” period after the task is stopped. A well-known example is motion adaptation, in which viewing motion in one direction for an extended period of time produces a subsequent bias to perceive ambiguous motion as moving in the opposite direction (Mather, Verstraten, and Anstis, 1998). If a language task relies on some of the same functional circuitry as the initial task, then performance on the language task should be selectively impaired during the refractory period.

Adaptation is a clear way to implement a knockout design behaviorally, but how does it evade the Mediating Process Reply? How do we know that interference on a language task is not due to the adaptation of other downstream processes? We reason as follows. As a given circuit starts to habituate to a stimulus—say, as a motion-detecting circuit adapts to a motion stimulus—that circuit begins to fire less. This is the heart of the adaptation paradigm. But, crucially, this habituation will also dampen any potential downstream activation to other circuits. As the first circuit habituates, therefore, these hypothetical downstream circuits—the target of Mediating Process Replies—should receive less input from the first circuit, and would thus be less likely to habituate. Said otherwise, if the initial adaptation task incidentally activates and thus disrupts some downstream circuit, then the demands on this downstream mediating process should decrease as the initial circuitry becomes adapted and thus less reactive to input. So if the interference on the subsequent language task is due to this downstream mediating process, then the observed interference should actually diminish or even disappear with longer adaptation periods. Thus, if an associated linguistic task is inhibited after an adaptation task—and if the inhibition persists or even increases with longer adaptation periods—then we can safely conclude that some of the functional circuitry subserving the original sensorimotor task is also functionally implicated in the linguistic task. Adaption paradigms, therefore, can unambiguously demonstrate shared functional circuitry.

The second way for a behavioral knockout experiment to forestall a Mediating Process Reply is to include an “amodal” control task. If completing a sensorimotor task interferes with a concurrent or subsequent language task, and if this interference is due, as the Mediating Process Reply would argue, to the downstream activation of some language-specific circuit, then qualitatively comparable interference should arise if we activate directly the purported mediating language circuit. Adding a control task that attempts to activate the mediating process can test this possibility. If perceiving motion away from or toward the participant is found to interfere
selectively with their comprehension of language describing motion away or toward, then a control task should attempt to activate the language-specific representations invoked by a Mediating Process Reply—the symbols AWAY and TOWARD, for instance. One way to do this would be to use bimodal stimulus presentation, where the words “away” or “toward” are presented visually while participants respond to sentences presented auditorially. In order to rule out the mediation of language-specific circuitry, we would need to see that the “amodal” control task does not produce the same pattern of results as the sensorimotor task.

The foregoing discussion identified desiderata for experiments that investigate shared neural resources—shared, for instance, by language, perception, and action—that cannot be explained by recourse to downstream activation. A knock-down argument for shared functional circuitry requires experiments that knock-out access to the relevant circuits, and asks how knocking them out affects the relevant behavior. We’ve also argued that behavioral knockout studies ought to additionally incorporate adaptation or “amodal” control tasks in order to deal with potential Mediating Process Replies. Of course, it is unlikely that any such knockout experiment will show a complete inability to understand language, since comprehension is not a unitary phenomenon but the collaborative accomplishment of countless functional circuits; interfering with any particular functional circuit should only dampen, not destroy, language comprehension. The focus is not on necessity for language comprehension writ large, but on the specific functional contributions of specific functional circuits. And interference on a language task, modulated selectively by a concurrent or preceding sensorimotor task, and with the appropriate controls in place, is the kind of evidence necessary to uncover the functional circuits responsible for the varied aspects of language use.

5.2 Some current work

There is a small body of recent work that exemplifies the type of knockout experiment we’ve defended. In contrast to the studies discussed in Section 2, the studies discussed here all used a linguistic task as the dependent variable, looked for (and found) interference in matching conditions, and some also implemented appropriate controls. We highlight them here to suggest both that this type of research is possible, and that early results suggest that neural circuits responsible for perception and action may, indeed, play functional roles in language use.

In one recent study, Meteyard and colleagues (2008) examined the effect of a perceptual task on language processing. Participants looked at random dot kinematograms, in which some
dots moved randomly, and some moved coherently either upward or downward. After looking at a kinematograms, subjects made lexical decisions to visually presented words. Compared with a control condition, viewing coherent motion at subjects' perceptual threshold produced significant interference on incongruent motion verbs. Subjects were slower to respond to verbs describing downward motion like 'fall' after viewing upward-moving kinematograms, but they responded equally quickly to verbs describing congruent motion and to control verbs such as 'eat' and 'kick.' Thus, the effect was interference for incongruent motion verbs rather than facilitation for congruent verbs. This is a relatively straightforward dissociative knockout effect, and it exemplifies many of the desiderata from the preceding section. However, the lack of an amodal control task makes it impossible to rule out the possibility that viewing the kinematograms activated other language-specific circuitry due to downstream spreading activation, which was in turn responsible for the observed decrement in performance.

In a more recent study, Casteel (2011) found interference on language tasks following engagement of the motor system. Casteel (2011) collected reading times for short passages describing motor actions. Before and after reading each passage, participants were instructed to imagine performing (Experiment 1) or to actually pantomime (Experiment 2) a motor action that was either a match or a mismatch for the action that would be described in the written passage. Participants took longer to read passages that matched the action compared to mismatch trials and to trials with no action at all. A third experiment showed that this interference effect disappeared when the action was performed only before reading but not after, leading Casteel (2011) to conclude that it was the maintenance of motor codes in working memory that interfered with language comprehension involving similar movements. This work is suggestive, but again would have been strengthened by the addition of an amodal control task—perhaps a working memory task that required participants to remember the name of the motor action.

Perhaps the result that best fulfills all the design desiderata outlined above is the series of studies reported by Glenberg and colleagues (2008). They adapted the motor system with a repetitive task in which participants moved 600 beads either away from or toward themselves, depending on their condition. After completing this bead task, participants had to judge the sensibility of sentences, including some that described motion away or towards. The bead task selectively interfered with performance on the linguistic task: Sensibility judgments were slower when bead motion and the described motion matched, but otherwise unaffected (or sometimes
slightly facilitated). In addition, the authors further forestalled a Mediating Process Reply with an amodal control task in which participants had to make 600 judgments of whether a visual stimulus was the word “away” or “toward,” or an anagram of that word (e.g., “towrad”); unlike the selective interference observed in the bead experiments, there was no interaction between the motion in the amodal control task (“away” or “toward”) and the motion described by the sentences in the linguistic task.

In sum, researchers are gradually accumulating evidence that certain functional circuits make functional contributions to perception and action, and to the comprehension of corresponding language. Many issues remain to be resolved, including the role of timing in determining facilitation/interference effects, and whether the findings previously observed in facilitation results can also be observed in interference paradigms. We hope that future studies can be strengthened by taking into account some of the design suggestions we’ve made here.

6. Conclusion

Questions of representational format are compelling because they promise to address the workings of higher cognitive functions, like language, including how they emerged over evolution and development. The idea that “modal systems” contribute to higher cognition is a particular compelling answer, one in which the mind is a “new machine built from old parts,” with systems that evolved for perception and action now exapted for use in newer functions like mental imagery, language, or mathematical reasoning. However, we’ve argued here that the attention to representational format cannot live up to this promise—indeed, that the very notion of representational format, as currently used in the debate, is incoherent. Instead, we’ve advocated an alternative approach, one that asks: What neural circuits with known functions—particularly functions in perception and action—are also used for which linguistic (and other higher cognitive) purposes?

This modified approach, while dispensing with issues of format, still allows us to address the mechanisms of higher cognition. And to the extent that it turns out that there are functional circuits that play roles in both sensorimotor and higher cognition, the answer resembles the Modal Hypothesis with which we started. The approach championed by modal theorists is probably a productive way to identify candidate circuits for study, since the evolutionarily older
circuits involved in perceiving and acting are particularly ripe for re-use (Anderson, 2010). It’s also different, though, in several ways.

First, we may discover that the functional circuits reused for language are not limited to ones also specialized for perception or motor control. The early evidence, reviewed above, does seem to suggest a role for such machinery in language comprehension. But language may also recycle entirely different circuits that support functions outside perception and action, like categorization, generalization, binding, representation, etc. A motley crew of functional machinery might well conspire to enable particular aspects of language use; indeed, cultural practices often coordinate diverse cognitive resources to accomplish complex cognitive work (Hutchins, 2010). Mathematics, for instance, may involve the skillful deployment of evolutionarily older circuits that subserve spatial cognition (e.g., Dehaene et al, 1993), but also more evolutionarily-recent abilities like analogical reasoning or conceptual integration (Gentner, 2003; Fauconnier and Turner, 2002; Lakoff and Núñez, 2000). The crucial point is that attending to the functional roles of functional circuits has the potential to explain how, mechanistically, we are able to do things like understand language—regardless of whether those circuits also have roles in perception and action.

Second, the two approaches, modal and functional, differ in the kind of question they ask about this new machine built from old parts. Instead of asking whether language understanding uses modal systems, we now ask what functional roles in the new machine are performed by which circuits, and what other functions those circuits might perform. Because we advocate asking about mechanism and function rather than format, the answers to those questions will follow in kind. If we’re asking about the role in language of circuits that also contribute to perception or action, the type of answer we get will be of the form: such-and-such a neural circuit plays such-and-such a function in language use. For instance, we might find that circuits that are specialized for motion perception play important roles in key aspects of language comprehension, like accessing or representing meaning, performing inference, or generating the subjective experience of comprehension, among others.

The Shared Functional Circuit Hypothesis, therefore, productively reframes the debate so we can ask new question, at once broader and more focused. The answers it invites, framed in terms of the functional roles of functional circuits, can make concrete and constructive contributions to the ongoing science of the mind, contributions that are easily translated into
mechanistic models of language use that make testable predictions. This would be a laudable improvement over the current state of affairs, mired in terminological debates. After all, what better contribution to the study of language and higher cognition than to document, without representational prejudice, the sundry neural resources that combine to create the richness of our mental lives.

References


A CALL TO ACTION (AND PERCEPTION)


