

HHS Public Access

Author manuscript *Can J Exp Psychol*. Author manuscript; available in PMC 2016 January 05.

Published in final edited form as: *Can J Exp Psychol*. 2015 June ; 69(2): 172–178. doi:10.1037/cep0000060.

The Burden of Embodied Cognition

Bradford Z. Mahon

University of Rochester

Abstract

The thesis of embodied cognition has developed as an alternative to the view that cognition is mediated, at least in part, by symbolic representations. A useful testing ground for the embodied cognition hypothesis is the representation of concepts. An embodied view of concept representation argues that concepts are represented in a modality-specific format. I argue that questions about representational format are tractable only in the context of explicit hypotheses about how information spreads among conceptual representations and sensorimotor systems. When reasonable alternatives to the embodied cognition hypothesis are clearly defined, the available evidence does not distinguish between the embodied cognition hypothesis and those alternatives. Furthermore, I argue, the available data that are theoretically constraining indicate that concepts are more than just sensory and motor content. As such, the embodied/nonembodied debate is either largely resolved or at a point where the embodied and nonembodied approaches are no longer coherently distinct theories. This situation merits a reconsideration of what the available evidence can tell us about the structure of the conceptual system. I suggest that it is the independence of thought from perception and action that makes human cognition special— and that independence is made possible by the representational distinction between concepts and sensorimotor representations.

Keywords

embodied cognition; amodal representations; simulation; conceptual representation; neuropsychology

> The sensorimotor system is activated across a range of situations that would not seem to necessitate sensorimotor activation. For instance, regions in and around the motor system are activated when observing actions (Buccino et al., 2001), objects that afford actions (Chao & Martin, 2000), and reading words that denote actions (Hauk, Johnsrude & Pulvermüller, 2004). It is also the case that the state of the sensorimotor system affects cognition. For instance, repeated grasping and moving of objects from a position near to the body to a position far from the body affects judgments about sentences referring to actions (Glenberg & Kaschak, 2002; Glenberg, Sato, & Cattaneo, 2008), and damage to sensorimotor areas may sometimes have some, albeit minimal, effects on conceptual knowledge pertaining to objects and actions (for review and discussion, see Binder & Desai,

Correspondence concerning this article should be addressed to Bradford Z. Mahon, Department of Brain and Cognitive Sciences, Department of Neurosurgery, Center for Visual Science, Center for Language Sciences, Meliora Hall, University of Rochester, Rochester, NY 14627-0268. mahon@rcbi.rochester.edu.

2011; Kemmerer, in press; Mahon & Caramazza, 2008). For instance, damage to early auditory areas can affect conceptual processing of sound-related conceptual knowledge (Bonner & Grossman, 2012; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Trumpp, Kliese, Hoenig, Haarmeier, & Kiefer, 2013). The explanation of those phenomena in terms of the embodied cognition hypothesis states that action and object concepts, as well as many other concepts besides, are represented via sensorimotor information: the motor system is activated during conceptual processing of action verbs (Hauk et al., 2004) because motor activity *is* conceptual activity. According to embodied cognition, conceptual processing uses the same (neural and cognitive) processes as are used in sensorimotor processing. At its core, the embodied cognition hypothesis is the claim that the format of concepts is sensorimotor and not abstract, amodal, or symbolic (for discussion, see Glenberg, 2015; Mahon, 2014).

A useful analogy can be drawn between the putative embodiment of cognition and how a car works. Imagine that the brain were a car: the engine of the car is analogous to central cognitive processes, whereas the drive train and wheels of the car are analogous to the motor system. A naïve observer sees a car for the first time while it is moving. This observer might formulate the hypothesis, akin to the embodied cognition hypothesis: "The functioning of the engine requires that the wheels are turning." Or the even more extreme hypothesis: "There is no 'engine' independent of the wheels—the wheels cause their own motion." Such a hypothesis would be outwardly consistent with observations made while the car is in motion. The theory would also be consistent with the observation that by turning the wheels, you can turn the engine (cf. using the motor system affects judgments of sentences, Glenberg et al., 2008). But then imagine that this naïve observer saw the behaviour of the car when it was taken out of gear and put into neutral: now the engine continues to run, but the wheels are no longer turning. The initial hypothesis about the mechanical interdependence, or representational overlap, between the engine and the drive train/wheels is falsified. The question would then shift to asking how the engine and the wheels, now considered (representationally) distinct processes or systems, are connected and interact with one another.

This analogy clarifies how there is no substantive tension between embodied and nonembodied theories as to the *goal* of thinking: on all views, the merit of our thinking about how to interact with the world is weighed in our actions and by our mind's ability to predict and interpret upcoming sensory events. By analogy, the merit of a car engine is not measured in its ability to "rev" while the car is in neutral—the merit of the engine is measured in how well it moves the car. But that has nothing to do with whether or not the engine and the drive train/wheels are representationally distinct processes. These issues are often conflated in discussions of embodiment, as I would argue occurs, for instance, in Glenberg (2015).

At a broader level, the analogy of the human brain to a car can stand for where we are as a field in our understanding of the relation between concepts and sensorimotor processing we know that the conceptual system can "turn" the sensorimotor system, and the sensorimotor system can "turn" the conceptual system. But we also know that conceptual processing can proceed unencumbered by the representation of the world and the body:

thinking often has nothing to do with the brain's representation of the body or perceptual representation of the world. What does the body have to do with the cognition that was required to invent and build a toaster, or the cell phone, or understand this sentence? Consider the cognitive processes on the part of all the mathematicians, physicists, and engineers who made it possible for an astronaut to tether herself to the space station and repair a broken computer. Where is the body in all of that cognition?¹ This argument applies not only to formal concepts from mathematics or physics but also to the thinking that we do on a daily basis, such as what has been required to read this text to this point. The point is that experiments are not necessary to show what casual observation makes evident: sensorimotor representations offer no obvious purchase for most of human cognition.

Scope of the Current Discussion

The embodied cognition hypothesis has been applied to many domains of cognitive processing, and the empirical evidence discussed here is heavily curated (for broader reviews and diverse theoretical viewpoints, see Allport, 1985; Avenanti, Candidi, & Urgesi, 2013; Barsalou, 1999; Binder & Desai, 2011; Caramazza, Anzellotti, Strnad, & Lingnau, 2014; Chatterjee, 2010; Dove, 2009; Gallese & Lakoff, 2005; Glenberg & Gallese, 2012; Hauk & Tschentscher, 2013; Hickok, 2014; Kemmerer, in press; Kiefer & Pulvermüller, 2012; Lambon Ralph, 2013; Leshinskaya & Caramazza, 2014; Mahon, 2014, in press; Mahon & Caramazza, 2008; Martin, 2007, 2009; Masson, 2015; Meteyard, Rodriguez-Cuadrado, Bahrami & Vigliocco, 2012; Pulvermüller, 2005, 2013; Simmons & Barsalou, 2003; Van dam, van Dijk, Bekkering, & Rueschemeyer, 2012; Willems & Casasanto, 2011; Willems & Francken, 2012; A. D. Wilson & Golonka, 2013; M. Wilson, 2002; Zwaan, 2004, 2014).

The goal here is to highlight an issue that is absent from many discussions of the embodied cognition hypothesis. What is missing is a clear-eyed view of what an alternative explanation of the available experimental facts would look like. Once we identify the alternative to the embodied cognition hypothesis, then we can ask the following: what evidence distinguishes the embodied cognition hypothesis from its alternative? I will argue that when reasonable alternatives to the embodied cognition hypothesis are clearly defined, the "debate" about whether cognition is embodied dissolves: the embodied cognition hypothesis is either demonstrably false or is not coherently distinct from theoretical alternatives (Mahon, 2014). This conclusion frames a new direction: what are the structural and dynamical properties of the interface between concepts and the sensorimotor system? That interface must be such that it can allow for cognitive processes to be *reflected* in sensorimotor activity and sensorimotor processes to *affect* cognition, but also such that cognition is not *limited to* the sensorimotor system.

¹The fact that *some* sensorimotor correlates to *some* formal concepts from physics or mathematics can be demonstrated (e.g., Glenberg, 2015) does not demonstrate that sensorimotor systems are, or even could be generally, the substrate of formal concepts from physics or mathematics.

Can J Exp Psychol. Author manuscript; available in PMC 2016 January 05.

The Alternative to the Embodied Cognition Hypothesis

The core commitment of the embodied cognition hypothesis is that the format of concepts is not abstract, amodal, or symbolic but perceptual and motor. The alternative to the embodied cognition hypothesis is the view that concepts are representationally distinct from sensorimotor information and, as such, are abstract. According to the alternative to embodied cognition, concepts are not *made of* sensorimotor information, although many concepts are *connected to* sensorimotor information. Thus, activating concepts may often lead to the activation of sensorimotor information, and the state of the sensorimotor system can be interpreted by the conceptual system. To illustrate how this alternative can be fleshed out in the context of a specific finding, consider a key piece of evidence for the view that concepts of action words representationally consist of motor information (e.g., Pulvermüller, 2005, 2013). Hauk et al. (2004) found that when participants read action words (e.g., *kick, kiss*), there is activation of the motor system in a somatopically organized manner. Thus, reading the word *kiss* leads to activation of mouth regions of the motor system, whereas reading *kick* leads to activation of leg regions of the motor system. We can formulate two hypotheses to explain those data:

 $H₀$: The activation of motor information occurs after access to the concept corresponding to the word, and the motor activation thus indicates that activation cascades (or spreads) from activated concepts to sensorimotor systems that are connected with those concepts. This hypothesis, which maintains a representational distinction between concepts and sensorimotor systems, is a claim about how information or activation spreads between levels of processing.

*H*1: The activation of motor information *is* conceptual access—the concept of an action word is represented via (i.e., constituted by) information in a motor format that is stored in the motor system. This is the embodied view as it explicitly eschews a representational distinction between concepts and sensorimotor representations.

The widespread acceptance of the embodied cognition hypothesis is based on the implicit rejection of H_0 in favour of H_1 . That rejection was implicit because it was not demonstrated empirically— in fact, H_0 is often not even acknowledged as an alternative explanation, and the data are simply taken to imply H_1 (see, for instance, Gallese & Lakoff, 2005; Glenberg, 2015; Pulvermüller, 2005, 2013; for an elegant empirical test, see Papeo et al., 2014). Regardless of the consideration it has been given, H_0 is a valid account of the data that would need to be excluded before confirming *H*1. What type of evidence would be needed to reject H_0 ? Minimally, one would need evidence either (or both) that:

Supposition (a): Activation does not spread from concepts to input/output representations.

Supposition (b): Damage to motor processes has devastating effects on conceptual processing.

Both suppositions are empirically tractable, and as has previously been argued, neither is tenable (Binder & Desai, 2011; Caramazza et al., 2014; Chatterjee, 2010; Hauk &

Tschentscher, 2013; Hickok, 2014; Mahon, 2015; Mahon & Caramazza, 2005, 2008; Papeo et al., 2014).

Evidence Counter to Supposition (a)

- **•** For example: Dehaene et al. (1998) showed that subliminally presented masked Arabic digits prime the left or right hand (in the context of a task requiring participants to respond with the right hand if the number was greater than 5 and the left hand if the number was less than 5). In other words, even for concepts that have nothing inherently to do with sensorimotor systems, the sensorimotor system can be activated in a task-dependent manner. This is task-mediated stimulus-response mapping—many other similar examples have been demonstrated behaviourally (e.g., Simon & Sudalaimuthu, 1979).
- **•** It is known that lexical semantic representations automatically spread activity to their corresponding phonological representations (e.g., Navarrete & Costa, 2005; Peterson & Savoy, 1998; for a model, see Dell, 1986). The point here is not that there is an equivalence between phonological information and sensorimotor information. Rather, these are clear demonstrations of situations in which central cognitive representations (e.g., lexical semantic representations) automatically spread activity to the input and output representations with which they are connected (in this case, phonology).

These types of considerations imply that we can reject supposition (a) above: it is the case that activation spreads from central cognitive representations to input/output systems.

Evidence Counter to Supposition (b)

• There is a growing literature investigating conceptual processing in individuals who have had a brain lesion that compromised perceptual or motor function. As alluded to earlier, reports indicate that impairments to perceptual or motor function can affect conceptual processing (e.g., Bonner & Grossman, 2012; Kiefer et al., 2008; Trumpp et al., 2013). On the other hand, we also know that, to quote Binder and Desai (2011), "Conceptual deficits in patients with sensory-motor impairments, when present, tend to be subtle rather than catastrophic" (quoted in, and see discussion in, Hauk & Tschentscher, 2013; for review of the evidence from apraxia, see Mahon & Caramazza, 2005, 2008; in the domain of colour, see Stasenko, Garcea, Dombovy, & Mahon, 2014). For instance, patients with certain forms of upper limb apraxia can be impaired for demonstrating the correct manner in which an object should be manipulated and yet remain able to name the object and indicate what the function of that object is (Buxbaum, Veramonti, & Schwartz, 2000; Garcea, Dombovy, & Mahon, 2013; Negri et al., 2007). This dissociation is important and theoretically constraining, because it was the activation of manipulation knowledge (inferior parietal lobule) during naming that was taken to be evidence for an embodied theory of tool concept representation in the first place.

Although much patient-based work clearly remains to be done, the currently available evidence indicates that supposition (b) is not tenable, because sensorimotor impairments do

not impair conceptual processing commensurate with what would be predicted by the embodied cognition hypothesis.

To summarise: The fact that it is independently known that activation spreads from concepts to sensorimotor representations implies that an embodied interpretation of findings, such as those of Hauk et al. (2004), is not supported over alternative accounts. The fact that motor processes can be damaged without dramatically (or even often measurably) affecting concepts directly challenges the core assumption of the embodied cognition hypothesis. The implication of these two inferences, considered jointly, is that we cannot conclude H_1 over *H*0, which means that the embodied cognition framework is, at best, without empirical support over other alternative accounts. In the measure to which those alternative accounts have merits not shared by the embodied cognition hypothesis (such as being able to provide, at least in principle, an account of abstract cognition), I would suggest there is no motivation for retaining the hypothesis of embodied cognition. Finally, neuropsychological data indicate that damaging sensorimotor representations can have little or no effect on conceptual processing for the domain of concepts that (putatively) depends on the damaged sensorimotor information. This implies that the embodied cognition hypothesis does not offer a viable account of how concepts are represented. This conclusion applies with full force to strong formulations of the embodied cognition account of meaning representation, such as advocated for by Glenberg (2015). I have argued elsewhere (Mahon, 2014) that the conclusion applies as well to weaker formulations of the embodied cognition hypothesis.

Complication

The argument outlined to this point has been too charitable on a key issue—namely, the argument has granted that there is in fact decisive evidence that representations that are sensorimotor in their format are active during conceptual processing. However, which activation patterns, or behavioural findings, index the retrieval of information that is in a sensorimotor format? This is an undervalued question, because in order for demonstrations of sensorimotor activation to be evidence for the embodied cognition hypothesis, it must be known that the sensorimotor information is sensorimotor in its format (for discussion, see Caramazza et al., 2014; Hauk & Tschentscher, 2013; Mahon, 2014; Martin, 2009). There are some elegant attempts to empirically disentangle exactly what format of information is indexed by putative sensorimotor activation—for instance, by Simmons et al. (2007) in the domain of colour, Simmons et al. (2013) in the domain of taste, and Postle, McMahon, Ashton, Meredith, and de Zubicaray (2008) in the domain of action words. However, those studies are the exception, rather than the norm. If there is a generalisation that emerges across the studies that have sought a direct test of whether there is overlap between primary sensorimotor processing regions (/processes) and the regions (/processes) involved in conceptual processing, the answer is that there is little if any actual overlap. Or, more precisely stated, where there is overlap, the overlap is over information that most likely is *not* sensorimotor in its format. As a concrete example, Simmons et al. (2007) found that the ventral temporal-occipital region activated by colour perception included, in its anteriormost aspect, a region that was also activated when making conceptual judgments about objects' typical colours. Thus, there is overlap, but it is the opposite of what would be predicted by the embodied cognition hypothesis: the region that is activated during

conceptual processing is also activated during perception, but the region activated during perception is not also activated during conceptual processing (but see Simmons et al., 2013, for overlap that may be as predicted by an embodied account, in the domain of taste).

It is also often the case that the regions activated during conceptual processing are adjacent to regions involved in sensorimotor processing, an observation that broadly motivated the "anterior shift" hypothesis of Martin and colleagues and the sensory/motor model of semantic memory from the same group (e.g., Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Simmons et al., 2007, 2013; for theoretical reviews, see Martin, 2007, 2009; for discussion, see also Mahon, 2015; Thompson-Schill, 2003). There is nothing *embodied* about the proposal of Martin and colleagues because the claim is not that conceptual knowledge is represented in a sensorimotor format. The claim is that the organisation of the conceptual system is shaped, in part, by the organisation of sensorimotor systems (Martin, 2009).

Is Grounded Cognition Embodied Cognition?

The embodied cognition hypothesis is often motivated by the efficacy of its solution to a long-standing issue that is supposed to attend theories of amodal concept representation: how are concepts "grounded" in the sensory/motor systems? In the context of the radical or strong embodied cognition hypothesis, the grounding problem sublimates—there is no grounding problem to be solved, because concepts are already *made up of* sensory/motor information and processes. But how could amodal concepts be grounded in the sensory/ motor systems? Schematically, at least, I would suggest that the answer is not so complex: a line is drawn from the concept to the corresponding sensory/motor information. Pulvermüller (2005) refers to such connections as "neural cell assemblies"; we referred to this type of an approach as "grounding by interaction" (Mahon & Caramazza, 2008; see also Binder & Desai, 2011). The key point is that *connecting* concepts to input/output (i.e., sensorimotor) representations serves to *ground* those concepts—but it does not make those concepts *embodied*.

I would suggest that the so-called grounding problem for amodal concepts is exaggerated, or, at least, the grounding "problem" is no more urgent in the domain of conceptual representation than it is for other cognitive representations. For instance, models of speech processing have long posited an amodal level of word representation that is syntactically specified—termed a *lemma* (e.g., Dell, 1986; Levelt, 1989). Lemma representations of words are abstract in the same way that "concepts" are putatively abstract—neither the representation of a lemma, nor that of a concept, is *constituted* by modality-specific information. However, there is no (and should not be any) concern that lemmas are deracinated from phonology or that we need a new theory of word representation to understand how words can be translated (or "transduced") into phonological information and vice versa. The same considerations should apply to concepts: if the representational format of concepts is not modality specific, then that does not imply that concepts are not grounded. What would imply that concepts are not grounded is if a theory stated that concepts were not connected to input/output systems. But no such theory has ever been entertained: it is in virtue of the (universally posited) *connections* between concepts and sensorimotor systems

Mahon Page 8

that concepts are grounded. There is nothing embodied about claiming that concepts are *connected* to input/output systems because embodiment has to do with the format of conceptual representation.

To summarise: (a) much of the evidence marshaled in support of the embodied cognition hypothesis can be explained by information exchange between amodal conceptual representations and peripheral input/output (i.e., sensorimotor) systems (for discussion, see Mahon, 2014; Mahon & Caramazza, 2008); (b) the available patient evidence falsifies the core prediction of the embodied cognition hypothesis, because perceptual and motor processes can be compromised without compromising concepts (for reviews, see Binder & Desai, 2011; Mahon & Caramazza, 2005); and (c) there is no theoretical need to have concepts be constituted by sensorimotor information in order for them to be grounded—they are grounded because they are connected to sensorimotor information.

I have argued elsewhere (Mahon, 2014) that the only coherent formulation of the embodied cognition hypothesis is as the proposal that concepts are modality specific in their representational format: versions of the embodied cognition that are not committed to the assumption that concepts are sensorimotor in their format are different only in name from so-called disembodied or classic views. If that argument is correct, then any given embodied cognition hypothesis, including that of Glenberg (2015), is (a) vulnerable to the arguments presented here or (b) not coherently different from nonembodied accounts. This conclusion suggests that the "debate" about whether cognition is embodied is resolved, at least in its broad strokes.

The Weight of the Evidence

Glenberg (2015) rhetorically asks, why is it the case that few still believe the world is flat? The answer, of course, is that science overturned long-held assumptions that were based entirely on phenomenological experience. Glenberg's suggestion behind this line of discussion is that to deny that cognition is embodied would be an anachronism like believing that the world is flat. The argument I have outlined addresses the substance of Glenberg's challenge. However, I believe that Glenberg's analogy—that the rise of the embodied cognition hypothesis is akin to the demise of the flat earth theory—is instructive in another way.

To begin: Why would people ever have believed that the world was flat? The answer seems obvious enough: because that is the way it *looks* when you are standing on earth. But already by that point, the flat earth theory had gone astray: the flat earth theory failed to imagine what the earth would look like if it were round. Flat earth believers did not stop to think, but if the earth were round, might it still *look* flat? The paradigm assumption on which the flat earth theory depended was that the evidence for the theory (i.e., the "earth *looks* flat") would not be consistent with the alternative theory (namely, that the earth is round). Of course, however, we now know that was an incorrect paradigm assumption: the earth does look flat, even though it is round. Flat earth believers were thus wrong not only in their theory but also in the weight they gave the evidence for their theory.²

I would suggest that exactly the same situation is occurring right now in our field: many studies are published every year that conclude from (putative) sensorimotor activity to the embodiment of cognition *without considering* how the experiment would have come out if cognition were not embodied. The prejudice of the embodied cognition hypothesis is to have never seriously considered, let alone tested and then rejected, an alternative hypothesis about the format of concept representation. And when we look at the type of evidence that one would want to be in place, minimally, to reject the view that concepts are represented in an amodal format, there is no decisive evidence.

What would a nonembodied view of concepts predict about sensorimotor activation during conceptual processing? It all depends on one's theory of activation dynamics— or information exchange— among representationally distinct processes. There are no theories of conceptual processing that *deny* that activation spreads from concepts to input/output or sensorimotor systems. Therefore, all extant theories that maintain a strict representational separation between concepts and input/output systems would also *predict* that input/output systems can be active during conceptual processing and that the state of input/ output systems can affect cognition. It is absolutely the case that we would not be compelled to expand theories of amodal concept representation in this way were it not for the many elegant findings that can be referred to collectively as the "phenomena of embodiment." However, I would argue that phenomena of embodiment actually have nothing to do with whether cognition is embodied. The substantive issue at stake is not whether the format of concepts is modality specific but the dynamics of activation flow in the system. This is not a dour conclusion—it means that the phenomena of embodiment can be repurposed as clues about how abstract concepts interface with the sensorimotor systems.

Acknowledgments

Preparation of this article was supported by NSF Grant 1349042 to BZM. I am grateful to Arthur Glenberg, Steve Lupker, and Michael Masson for their discussion of these issues at the 24th Canadian Society for Brain, Behavior, and Cognitive Science (CSBBCS) and to Steve Lupker for comments on a draft of this article.

References

- Allport, DA. Distributed memory, modular subsystems and dysphasia. In: Newman, SK.; Epstein, R., editors. Current perspectives in dysphasia. New York, NY: Churchill Livingstone; 1985. p. 207-244.
- Avenanti A, Candidi M, Urgesi C. Vicarious motor activation during action perception: Beyond correlational evidence. Frontiers in Human Neuroscience. 2013; 7:185. [http://dx.doi.org/10.3389/](http://dx.doi.org/10.3389/fnhum.2013.00185) [fnhum.2013.00185](http://dx.doi.org/10.3389/fnhum.2013.00185). [PubMed: 23675338]
- Barsalou LW. Perceptual symbol systems. Behavioral and Brain Sciences. 1999; 22:577–609. [http://](http://dx.doi.org/10.1017/S0140525X99532147) dx.doi.org/10.1017/S0140525X99532147. [PubMed: 11301525]

Binder JR, Desai RH. The neurobiology of semantic memory. Trends in Cognitive Sciences. 2011; 15:527–536. [http://dx.doi.org/10.1016/j.tics.2011.10.001.](http://dx.doi.org/10.1016/j.tics.2011.10.001) [PubMed: 22001867]

 2 Pylyshyn (2003) made this point in the context of the evidence that was brought to bear on the hypothesis that visual imagery involves an analogue medium used in perception (for discussion of the parallels between the imagery debate and the embodiment debate, see Hauk & Tschentscher, 2013). Quoting Pylyshyn (2003), who attributed this story to Wittgenstein: "Two philosophers meet in the hall and one says to the other: '*Why do you suppose people always thought that the sun went around the earth, rather than that the earth was rotating?* The second philosopher replies, '*Obviously because it looks like the sun goes around the earth*.' To which the first philosopher replies, '*But what would it look like if it looked like the earth was rotating?*'"

- Bonner MF, Grossman M. Gray matter density of auditory association cortex relates to knowledge of sound concepts in primary progressive aphasia. The Journal of Neuroscience. 2012; 32:7986–7991. [http://dx.doi.org/10.1523/JNEUROSCI.6241-11.2012.](http://dx.doi.org/10.1523/JNEUROSCI.6241-11.2012) [PubMed: 22674273]
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Freund HJ. Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. European Journal of Neuroscience. 2001; 13:400–404. [http://dx.doi.org/10.1111/j.1460-9568.2001.01385.x.](http://dx.doi.org/10.1111/j.1460-9568.2001.01385.x) [PubMed: 11168545]
- Buxbaum LJ, Veramonti T, Schwartz MF. Function and manipulation tool knowledge in apraxia: Knowing "what for" but not "how.". Neurocase. 2000; 6:83–97. [http://dx.doi.org/](http://dx.doi.org/10.1080/13554790008402763) [10.1080/13554790008402763](http://dx.doi.org/10.1080/13554790008402763).
- Caramazza A, Anzellotti S, Strnad L, Lingnau A. Embodied cognition and mirror neurons: A critical assessment. Annual Review of Neuroscience. 2014; 37:1–15. [http://dx.doi.org/10.1146/annurev](http://dx.doi.org/10.1146/annurev-neuro-071013-013950)[neuro-071013-013950](http://dx.doi.org/10.1146/annurev-neuro-071013-013950).
- Chao LL, Haxby JV, Martin A. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nature Neuroscience. 1999; 2:913–919. <http://dx.doi.org/10.1038/13217>. [PubMed: 10491613]
- Chao LL, Martin A. Representation of manipulable man-made objects in the dorsal stream. NeuroImage. 2000; 12:478–484. [http://dx.doi.org/10.1006/nimg.2000.0635.](http://dx.doi.org/10.1006/nimg.2000.0635) [PubMed: 10988041]
- Chatterjee A. Disembodying cognition. Language and Cognition. 2010; 2:79–116. [http://dx.doi.org/](http://dx.doi.org/10.1515/langcog.2010.004) [10.1515/langcog.2010.004](http://dx.doi.org/10.1515/langcog.2010.004). [PubMed: 20802833]
- Dehaene S, Naccache L, Le Clec'H G, Koechlin E, Mueller M, Dehaene-Lambertz G, Le Bihan D. Imaging unconscious semantic priming. Nature. 1998; 395:597–600. [http://dx.doi.org/](http://dx.doi.org/10.1038/26967) [10.1038/26967](http://dx.doi.org/10.1038/26967). [PubMed: 9783584]
- Dell GS. A spreading-activation theory of retrieval in sentence production. Psychological Review. 1986; 93:283–321. [http://dx.doi.org/10.1037/0033-295X.93.3.283.](http://dx.doi.org/10.1037/0033-295X.93.3.283) [PubMed: 3749399]
- Dove G. Beyond perceptual symbols: A call for representational pluralism. Cognition. 2009; 110:412– 431. [http://dx.doi.org/10.1016/j.cognition.2008.11.016.](http://dx.doi.org/10.1016/j.cognition.2008.11.016) [PubMed: 19135654]
- Gallese V, Lakoff G. The brain's concepts: The role of the Sensory-motor system in conceptual knowledge. Cognitive Neuropsychology. 2005; 22:455–479. [http://dx.doi.org/](http://dx.doi.org/10.1080/02643290442000310) [10.1080/02643290442000310](http://dx.doi.org/10.1080/02643290442000310). [PubMed: 21038261]
- Garcea FE, Dombovy M, Mahon BZ. Preserved tool knowledge in the context of impaired action knowledge: Implications for models of semantic memory. Frontiers in Human Neuroscience. 2013; 7:120. <http://dx.doi.org/10.3389/fnhum.2013.00120>. [PubMed: 23641205]
- Glenberg AM. Few believe the world is flat: How embodiment is changing the scientific understanding of cognition. Canadian Journal of Experimental Psychology. 2015; 69:165–171. [PubMed: 26010024]
- Glenberg AM, Gallese V. Action-based language: A theory of language acquisition, comprehension, and production. Cortex. 2012; 48:905–922. [PubMed: 21601842]
- Glenberg AM, Kaschak MP. Grounding language in action. Psychonomic Bulletin & Review. 2002; 9:558–565. [http://dx.doi.org/10.3758/BF03196313.](http://dx.doi.org/10.3758/BF03196313) [PubMed: 12412897]
- Glenberg AM, Sato M, Cattaneo L. Use-induced motor plasticity affects the processing of abstract and concrete language. Current Biology. 2008; 18:R290–R291. [http://dx.doi.org/10.1016/j.cub.](http://dx.doi.org/10.1016/j.cub.2008.02.036) [2008.02.036.](http://dx.doi.org/10.1016/j.cub.2008.02.036) [PubMed: 18397734]
- Hauk O, Johnsrude I, Pulvermüller F. Somatotopic representation of action words in human motor and premotor cortex. Neuron. 2004; 41:301–307. [http://dx.doi.org/10.1016/S0896-6273\(03\)00838-9.](http://dx.doi.org/10.1016/S0896-6273(03)00838-9) [PubMed: 14741110]
- Hauk O, Tschentscher N. The body of evidence: What can neuroscience tell us about embodied semantics? Frontiers in Psychology. 2013; 4:50.<http://dx.doi.org/10.3389/fpsyg.2013.00050>. [PubMed: 23407791]
- Hickok, G. The myth of mirror neurons: The real neuroscience of communication and cognition. New York, NY: Norton; 2014.
- Johnson-Frey SH. The neural bases of complex tool use in humans. Trends in Cognitive Sciences. 2004; 8:71–78. <http://dx.doi.org/10.1016/j.tics.2003.12.002>. [PubMed: 15588811]

- Kemmerer D. Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but within the context of a flexible, multilevel architecture for conceptual knowledge. Psychonomic Bulletin & Review. in press.
- Kiefer M, Pulvermüller F. Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. Cortex: A Journal Devoted to the Study of the Nervous System and Behavior. 2012; 48:805–825. <http://dx.doi.org/10.1016/j.cortex.2011.04.006>. [PubMed: 21621764]
- Kiefer M, Sim E-J, Herrnberger B, Grothe J, Hoenig K. The sound of concepts: Four markers for a link between auditory and conceptual brain systems. The Journal of Neuroscience. 2008; 28:12224–12230. <http://dx.doi.org/10.1523/JNEUROSCI.3579-08.2008>. [PubMed: 19020016]
- Lambon Ralph MA. Neurocognitive insights on conceptual knowledge and its breakdown. Philosophical Transactions of the Royal Society, Series B, Biological Sciences. 2013; 369:20120392.
- Leshinskaya, A.; Caramazza, A. Organization and structure of conceptual representations. In: Goldrick, M.; Ferreira, V.; Miozzo, M., editors. The Oxford handbook of language production. Oxford: Oxford University Press; 2014. p. 118-133.
- Levelt, WJM. Speaking: From intention to articulation. Cambridge, MA: MIT Press; 1989.
- Mahon BZ. What is embodied about cognition? Language, cognition, and neuroscience. 2015 [https://](https://caoslab.bcs.rochester.edu/pdf/Mahon_InPress_LCN.pdf) [caoslab.bcs.rochester.edu/pdf/Mahon_InPress_LCN.pdf.](https://caoslab.bcs.rochester.edu/pdf/Mahon_InPress_LCN.pdf) [http://dx.doi.org/](http://dx.doi.org/10.1080/23273798.2014.987791) [10.1080/23273798.2014.987791](http://dx.doi.org/10.1080/23273798.2014.987791).
- Mahon, BZ. Missed connections: A connectivity constrained account of the representation and organization of object concepts. In: Margolis, E.; Laurence, S., editors. The conceptual mind: New directions in the study of concepts. 2015.
- Mahon BZ, Caramazza A. The orchestration of the sensory-motor systems: Clues from neuropsychology. Cognitive Neuropsychology. 2005; 22:480–494. [http://dx.doi.org/](http://dx.doi.org/10.1080/02643290442000446) [10.1080/02643290442000446](http://dx.doi.org/10.1080/02643290442000446). [PubMed: 21038262]
- Mahon BZ, Caramazza A. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. Journal of Physiology, Paris. 2008; 102:59–70. [http://dx.doi.org/](http://dx.doi.org/10.1016/j.jphysparis.2008.03.004) [10.1016/j.jphysparis.2008.03.004.](http://dx.doi.org/10.1016/j.jphysparis.2008.03.004)
- Martin A. The representation of object concepts in the brain. Annual Review of Psychology. 2007; 58:25–45. <http://dx.doi.org/10.1146/annurev.psych.57.102904.190143>.
- Martin, A. Circuits in mind: The neural foundations for object concepts. In: Gazzaniga, M., editor. The cognitive neurosciences. 4th. Cambridge: MIT Press; 2009. p. 1031-1045.
- Masson MEJ. Toward a deeper understanding of embodiment. Canadian Journal of Experimental Psychology. 2015; 69:159–164. [PubMed: 26010023]
- Meteyard L, Rodriguez-Cuadrado S, Bahrami B, Vigliocco G. Coming of age: A review of embodiment and the neuroscience of semantics. Cortex. 2012; 48:788–804. [PubMed: 21163473]
- Navarrete E, Costa A. Phonological activation of ignored pictures: Further evidence for a cascade model of lexical access. Journal of Memory and Language. 2005; 53:359–377. [http://dx.doi.org/](http://dx.doi.org/10.1016/j.jml.2005.05.001) [10.1016/j.jml.2005.05.001.](http://dx.doi.org/10.1016/j.jml.2005.05.001)
- Negri GAL, Rumiati RI, Zadini A, Ukmar M, Mahon BZ, Caramazza A. What is the role of motor simulation in action and object recognition? Evidence from apraxia. Cognitive Neuropsychology. 2007; 24:795–816. [http://dx.doi.org/10.1080/02643290701707412.](http://dx.doi.org/10.1080/02643290701707412) [PubMed: 18161497]
- Papeo L, Lingnau A, Agosta S, Pascual-Leone A, Battelli L, Caramazza A. The origin of word-related motor activity. Cerebral Cortex. 2014 Advance online publication. [http://dx.doi.org/10.1093/](http://dx.doi.org/10.1093/cercor/bht423) [cercor/bht423.](http://dx.doi.org/10.1093/cercor/bht423)
- Peterson RR, Savoy P. Lexical selection and phonological encoding during language production: Evidence for cascaded processing. Journal of Experimental Psychology: Learning, Memory, and Cognition. 1998; 24:539–557. <http://dx.doi.org/10.1037/0278-7393.24.3.539>.
- Postle N, McMahon KL, Ashton R, Meredith M, de Zubicaray GI. Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. NeuroImage. 2008; 43:634–644. [http://dx.doi.org/10.1016/j.neuroimage.2008.08.006.](http://dx.doi.org/10.1016/j.neuroimage.2008.08.006) [PubMed: 18786644]
- Pulvermüller F. Brain mechanisms linking language and action. Nature Reviews Neuroscience. 2005; 6:576–582. [http://dx.doi.org/10.1038/nrn1706.](http://dx.doi.org/10.1038/nrn1706) [PubMed: 15959465]

- Pulvermüller F. How neurons make meaning: Brain mechanisms for embodied and abstract-symbolic semantics. Trends in Cognitive Sciences. 2013; 17:458–470. [http://dx.doi.org/10.1016/j.tics.](http://dx.doi.org/10.1016/j.tics.2013.06.004) [2013.06.004.](http://dx.doi.org/10.1016/j.tics.2013.06.004) [PubMed: 23932069]
- Pylyshyn Z. Return of the mental image: Are there really pictures in the brain? Trends in Cognitive Sciences. 2003; 7:113–118. [http://dx.doi.org/10.1016/S1364-6613\(03\)00003-2](http://dx.doi.org/10.1016/S1364-6613(03)00003-2). [PubMed: 12639692]
- Simmons WK, Barsalou LW. The similarity-in-topography principle: Reconciling theories of conceptual deficits. Cognitive Neuropsychology. 2003; 20:451–486. [http://dx.doi.org/](http://dx.doi.org/10.1080/02643290342000032) [10.1080/02643290342000032](http://dx.doi.org/10.1080/02643290342000032). [PubMed: 20957580]
- Simmons WK, Ramjee V, Beauchamp MS, McRae K, Martin A, Barsalou LW. A common neural substrate for perceiving and knowing about color. Neuropsychologia. 2007; 45:2802–2810. [http://](http://dx.doi.org/10.1016/j.neuropsychologia.2007.05.002) dx.doi.org/10.1016/j.neuropsychologia.2007.05.002. [PubMed: 17575989]
- Simmons WK, Rapuano KM, Kallman SJ, Ingeholm JE, Miller B, Gotts SJ, Martin A. Categoryspecific integration of homeostatic signals in caudal but not rostral human insula. Nature Neuroscience. 2013; 16:1551–1552. [http://dx.doi.org/10.1038/nn.3535.](http://dx.doi.org/10.1038/nn.3535) [PubMed: 24077565]
- Simon JR, Sudalaimuthu P. Effects of S-R mapping and response modality on performance in a Stroop task. Journal of Experimental Psychology: Human Perception and Performance. 1979; 5:176–187. <http://dx.doi.org/10.1037/0096-1523.5.1.176>. [PubMed: 528927]
- Stasenko A, Garcea FE, Dombovy M, Mahon BZ. When concepts lose their color: A case of objectcolor knowledge impairment. Cortex. 2014; 58:217–238. [http://dx.doi.org/10.1016/j.cortex.](http://dx.doi.org/10.1016/j.cortex.2014.05.013) [2014.05.013.](http://dx.doi.org/10.1016/j.cortex.2014.05.013) [PubMed: 25058612]
- Thompson-Schill SL. Neuroimaging studies of semantic memory: Inferring "how" from "where.". Neuropsychologia. 2003; 41:280–292. [PubMed: 12457754]
- Trumpp NM, Kliese D, Hoenig K, Haarmeier T, Kiefer M. Losing the sound of concepts: Damage to auditory association cortex impairs the processing of sound-related concepts. Cortex: A Journal Devoted to the Study of the Nervous System and Behavior. 2013; 49:474–486. [http://dx.doi.org/](http://dx.doi.org/10.1016/j.cortex.2012.02.002) [10.1016/j.cortex.2012.02.002](http://dx.doi.org/10.1016/j.cortex.2012.02.002). [PubMed: 22405961]
- Van dam O, van Dijk M, Bekkering H, Rueschemeyer S-A. Flexibility in embodied lexical-semantic representations. Human Brain Mapping. 2012; 33:2322–2333. [PubMed: 21976384]
- Willems RM, Casasanto D. Flexibility in embodied language understanding. Frontiers in Psychology. 2011; 2:116. [http://dx.doi.org/10.3389/fpsyg.2011.00116.](http://dx.doi.org/10.3389/fpsyg.2011.00116) [PubMed: 21779264]
- Willems RM, Francken JC. Embodied cognition: Taking the next step. Frontiers in Psychology. 2012; 3:582. [http://dx.doi.org/10.3389/fpsyg.2012.00582.](http://dx.doi.org/10.3389/fpsyg.2012.00582) [PubMed: 23293620]
- Wilson AD, Golonka S. Embodied cognition is not what you think it is. Frontiers in Psychology. 2013; 4:58. <http://dx.doi.org/10.3389/fpsyg.2013.00058>. [PubMed: 23408669]
- Wilson M. Six views of embodied cognition. Psychonomic Bulletin & Review. 2002; 9:625–636. [http://dx.doi.org/10.3758/BF03196322.](http://dx.doi.org/10.3758/BF03196322) [PubMed: 12613670]
- Zwaan, RA. The immersed experiencer: Toward an embodied theory of language comprehension. In: Ross, BH., editor. The psychology of learning and motivation. Vol. 44. New York, NY: Academic Press; 2004. p. 35-62.
- Zwaan RA. Embodiment and language comprehension: Reframing the discussion. Trends in Cognitive Sciences. 2014; 18:229–234. [http://dx.doi.org/10.1016/j.tics.2014.02.008.](http://dx.doi.org/10.1016/j.tics.2014.02.008) [PubMed: 24630873]