



Representing Motion in Language Comprehension: Lessons From Neuroimaging

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Abstract

A central issue in understanding how language links the mental and the real world is the nature of the mental representations entertained during language processing. Are these mental representations closely linked to the perceptual experiences from which they were formed or are they somewhat removed from them? This review addresses this question by examining studies that have investigated motion verbs and sentences using functional magnetic resonance imaging. These studies tested whether language processing elicits modality-specific brain regions responsive to motion perception. Although the results of these studies are not definite due to the different tasks and analysis techniques utilized, they so far suggest that modality-specific brain regions processing visual motion are not automatically or habitually engaged in language processing. The occasional engagement of visual areas in language processing appears to result from tasks requiring integration of visual and linguistic information or attention to motion-specific features such as direction. The evidence reviewed therefore suggests that although perceptual representations may be flexibly engaged as a function of tasks and contexts, language comprehension in the absence of visual contexts habitually engages experience-based representations of motion events that are one-step removed from visual experiences, even in situations in which imagery is encouraged.

Language is often used to describe objects and events in the world. In this function, words and sentences elicit mental representations of objects and events that have been systematically linked to aspects of experience during the course of learning. A word like *table*, for example, is linked to a mental representation of tables, which in turn, are connected in complex ways to real tables in the world. Likewise, sequences of words, which are combined in systematic ways according to language-specific procedures, are mapped onto mental representations of events and through these representations, to events in the world. A central issue in understanding the role of language in eliciting mental representations of the real world is the nature of the mental representations entertained during language processing. Are these mental representations “true” pictures of the world, or mere ghosts or abstract symbols that have become conventionalized over the years? Are they still closely linked to, or somewhat removed from, the experiences from which they were formed?

It has long been recognized that elements of our experience and knowledge of the world play a role in the representations entertained during language processing (Paivio 1971, 1986). Experiential approaches to cognition, such as probabilistic constraint satisfaction, have emphasized the role of experience-based regularities in processing both form and meaning (MacDonald et al. 1994; Tanenhaus and Trueswell 1995). Experience with both the world and the language, for example, predicts the extent to which readers encounter difficulty in temporarily ambiguous constructions such as *the man examined ... by the doctor*: both the most frequent use of *examined* as main verb and the event

knowledge associated with the examining situation (e.g., who is likely to do what in it) play a role in determining comprehension difficulty (Gennari and MacDonald 2008; Tanenhaus et al. 1989; Trueswell et al. 1993, 1994). Studies of discourse comprehension and memory have also argued that readers establish detailed analogical representations of the situations in the narrative – called *mental models* – , which contain representations of characters, objects, locations, and times of events in the narrative (Bower and Morrow 1990; Zwaan and Radvansky 1998; Zwaan et al. 1998). However, the specific character of these mental representations of the world and in particular, their experiential specificity, remained largely unspecified.

Recent approaches to cognition have argued that semantic representations are embodied and grounded in modality-specific systems that underpin perception, action, and emotions (Barsalou 2003). Perceptual or motor brain states linked to perception and action are said to be re-enacted or simulated when performing conceptual tasks or understanding language. Many behavioral studies have shown effects and interactions consistent with this view. In one seminal study, for example, Glenberg and Kaschak showed that when making semantic decisions about sentences, the motion content of the sentence (e.g., opening a drawer) influenced the time it took to perform the action that indicated the semantic decision in the study (movement toward or away from the participant) (Glenberg and Kaschak 2002). When the action direction and the direction of the sentence motion were congruent, decisions were faster than when they were not. Subsequent behavioral studies have also shown a role for motion and visual perception in language comprehension (Kaschak et al. 2005; Zwaan and Taylor 2006; Zwaan et al. 2002). These demonstrations indicate that there is a relationship between action or perception and language comprehension, and therefore support the claim that language activates traces of sensory-motor experience.

Behavioral demonstrations of a relationship between language and perception do not however explicitly indicate whether perception and language share sensory-based or schematic representations, or whether they are integrated via decision making mechanisms in regions of the brain other than those representing visual or action information. It is possible, for example, that the motion representations elicited by language do not have the same sensory character as those elicited by perception, but that they facilitate (or interfere with) each other in behavior because they feed into brain regions that integrate semantic information when making decisions or planning actions. The expansion of brain imaging studies in recent years has allowed a more direct investigation of this issue by examining the sensory-motor character of the semantic representations entertained during language processing. In particular, the extent to which language and perception share representations can be precisely evaluated by comparing the neural networks involved in each perception and language comprehension. If known perceptual processing regions are involved in language comprehension, this is taken to suggest that perceptually based representations play a role in language processing.

Neuroimaging studies investigating the sensory-motor character of semantic representations have supported different degrees of semantic specificity in language processing. Two different views can be distinguished (Martin and Chao 2001; Pulvermuller 2005). One view – referred to here as *sensory-motor organization theory* – suggests that linguistic and conceptual representations are organized around and distributed along sensory cortices, although linguistic representations need not be identical to perceptual ones (Kable et al. 2002; Martin and Chao 2001). Motion verbs for example engage posterior temporal brain regions that overlap with those elicited by visual perception but are centered more anteriorly: occipito-temporal regions respond to motion perception (area V5), whereas more

anterior temporal regions, such as the posterior middle temporal gyrus (PMTG), respond to both vision and language (see Figure 1). These kinds of finding led to the proposal of a specificity gradient along occipito-temporal structures going from more posterior highly specific perceptual representations to more anterior and schematic event representation, which are also responsive to non-action verbs. This arrangement suggests that semantic representations of motion, and perhaps representations of events more generally, are abstracted or schematized from experience during development and are thus encoded near those sensory regions processing relevant input. In this sensory-motor view, then, linguistic meaning is grounded in sensory-motor representations because these representations provide the organizing principles of conceptual knowledge and the experiences that feed and build them over time, although low-level perceptual motion representations need not be activated by language alone.

Another view – the *strong re-enactment theory* – argues that there are automatic associative neuronal links between words and the experiences they refer to, suggesting therefore that the experiences themselves should be evoked by language. Specifically, Pulvermüller et al. have proposed that action words are learned in the context of action performance

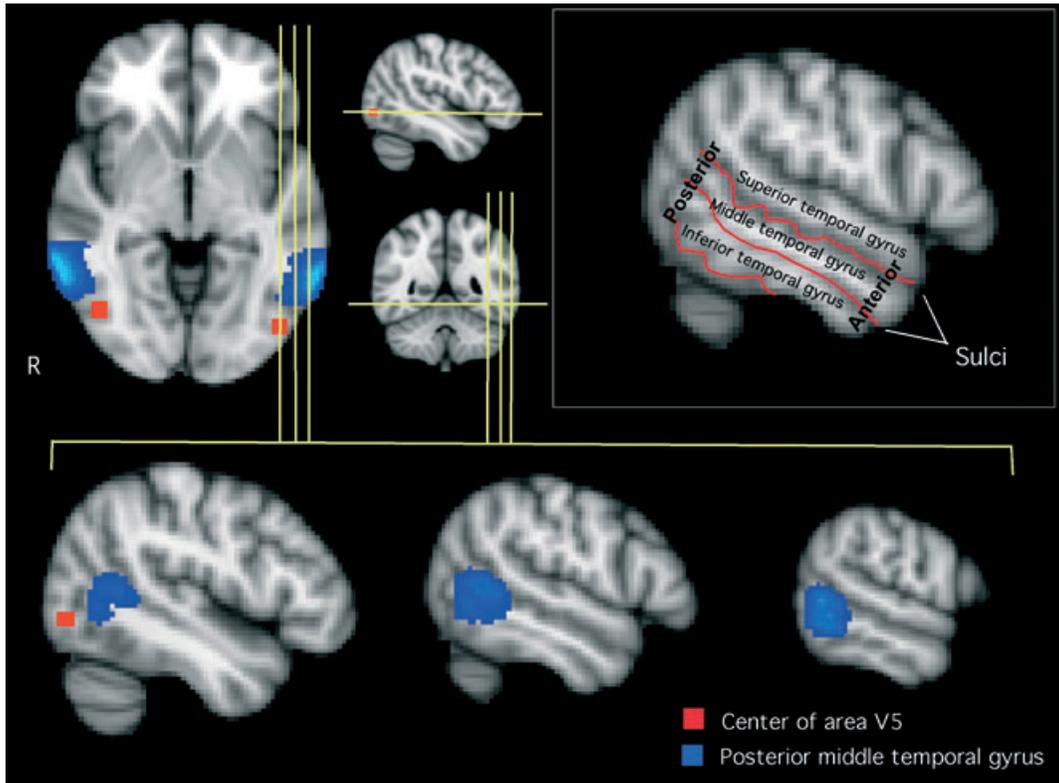


Fig 1. Schematic representation of area V5 and posterior middle temporal gyrus (labeled as *Middle Temporal Gyrus – temporo occipital part* in the Harvard-Oxford Atlas). The center of area V5 is indicated by the small red square. The additional blue region represents the posterior middle temporal gyrus. The top left image shows an axial (horizontal) brain slice located at the level of the horizontal yellow lines in the additional brain views. The vertical yellow lines in the top left image indicate perpendicular cuts shown in the bottom images. Main anatomical landmarks within the temporal lobe are shown in the right top panel. The red lines in this panel display the superior, middle, and inferior temporal sulci.

(Hauk et al. 2004; Markus et al. 2007; Pulvermuller 2005). Hebbian connections between the words and their corresponding action programs are formed due to the near simultaneous firing of neurons in motor and language regions, thus giving rise to distributed neural assemblies linking words and action programs. If similar hebbian links exist between motion verbs and motion perception, that is, if concurrent linguistic and perceptual stimulation during learning gives rise to neuronal connections between words and perceptual experiences, motion verbs should elicit the re-enactment of activity in visual motion processing areas such as V5, rather than more anterior schematic representations in the temporal lobe. On this view, the specificity and perceptual character of the representations elicited by language is greater than those schematic representations proposed by the sensory-motor organization theory, although both these views are experiential in that learning from experience provides the grounding for semantic representations.

In this article, I will review neuroimaging studies investigating motion-related activity in language and perception and highlight some of the difficulties that arise in attempting to determine whether low-level perceptual motion representations are elicited by language. Some of these difficulties are methodological in nature, whereas others are conceptual. For example, it is possible that low-level perceptual associations do not play a critical role in language understanding, even when plenty of experience feeds into linguistic representations during the course of learning. Thus, motion content per se may be necessary but not sufficient to ignite visual perceptual experiences of motion. In what follows, a brief background on motion perception and cognition is given, before moving into language studies. Then, some methodological issues in fMRI research as well as their implication for the conclusions of the reviewed studies are discussed. Finally, different theories of meaning will be considered in the light of these studies.

Motion Perception and Cognition

Numerous studies have reported that moving stimuli, for example, moving dots or gradients, elicit modality-specific activity in an occipito-temporal region when compared to static stimuli (static dots or gradients) (Beauchamp et al. 2002, 2003; Dumoulin et al. 2000; Heeger et al. 2000; Puce and Perrett 2003; Schultz et al. 2005; Servos et al. 2002; Thompson et al. 2005; Tootell et al. 1995a; Zihl et al. 1991). This motion sensitive area is known as area V5 or MT (for middle temporal), although *MT* is a confusing label when applied to humans because V5 is not in the human middle temporal lobe (this label comes from studies investigating motion sensitivity in the monkeys' temporal lobe (Orban et al. 2004)). According to Dumoulin et al. (2000), this area is often found in humans within 1 cm of the ascending limb of the inferior temporal sulcus (ITS), although it can also be located near the ITS or the posterior continuation of the ITS (see Figure 2).¹ As extensively discussed by Dumoulin et al., individuals vary greatly in the location of the brain response to moving stimuli and in the anatomical structures surrounding this region, some of which may be missing altogether. This variability makes this region difficult to identify by visual inspection or by standard analysis methods (see below). Additionally, studies vary on the size of the cluster considered to identify area V5, since large clusters surrounding the peak activity of Figure 2, for example, may extend into the posterior temporal lobe, which makes it difficult to compare across studies.

An important property of V5 is that although it serves the visual analysis of motion, it is susceptible to top-down control and higher level perceptual/conceptual influences: Implied motion, apparent and illusory motion, "moving" sounds, and imagined motion can all elicit significant levels of activation in this area (Goebel et al. 1998; Kaneoke et al.

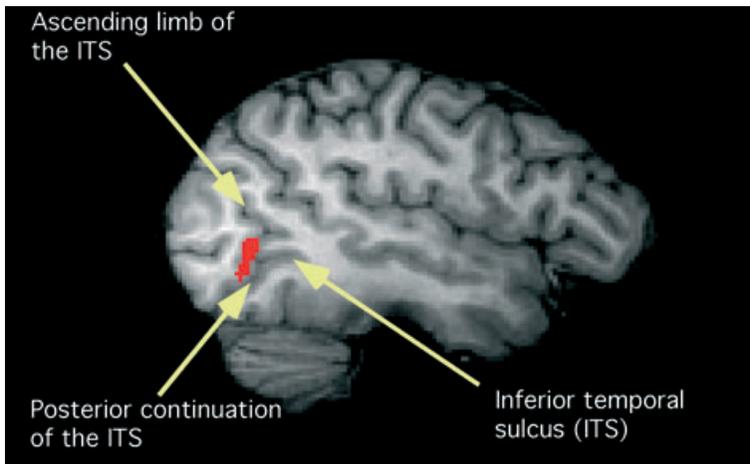


Fig 2. Anatomical landmarks around area V5, as identified by Dumoulin et al. (2000). An individual's response to motion, compared to static images, is shown in red.

1997; Poirier et al. 2005; Tootell et al. 1995b; Zeki et al. 1993). It has been shown, for example, that the V5 complex that is sensitive to visual motion also responds to implied object or human motion in static images of falling objects or performing athletes (Kourtzi and Kanwisher 2000; Senior et al. 2000). Additionally, V5 responds more strongly when participants attend to motion compared to when they do not, even when the visual stimulation is the same (O'Craven et al. 1997). These findings suggest that knowledge of typical human or object movements or expectations of subsequent motions, given a particular still frame, feeds into V5. This property thus raises the possibility that linguistic meaning also influences this region, although the conceptual versus perceptual nature of previous top-down effects remains unclear (e.g., they could reflect visual imagery).

Conceptual and linguistic influences on V5 are indeed possible because this region is often co-activated with more anterior regions of the temporal cortex – the PMTG and the posterior superior temporal gyrus (PSTG) – which are associated with different aspects of (multi-modal) conceptual knowledge (see Figure 1). The PMTG has been claimed to store knowledge of action motion and event structure more generally, because this region responds more strongly to moving tools, compared to static ones (Beauchamp et al. 2002, 2003; Chao et al. 1999; Martin and Chao 2001), and to verbs, compared to other word types (Bedny et al. 2008; Damasio et al. 2001; Kable et al. 2002; Perani et al. 1999; Tranel et al. 2005). This region also plays a causal role in multi-modal event representations, as demonstrated by lesion studies (Tranel et al. 2003). The PSTG, in turn, is thought to encode biological motion or agency and to serve higher order integration functions, because this region differentially responds to biological motion perception, to perception of agency with non-human stimuli and to audio-visual integration (Beauchamp and Beauchamp 2005; Beauchamp et al. 2002, 2004; Blakemore et al. 2003; Calvert 2001; Fritz and Frith 2003; Morito et al. 2009; Puce and Perrett 2003; Schultz et al. 2005; Thompson et al. 2005). These multimodal regions in the posterior temporal lobe may therefore feed information to V5 or together, these regions may be part of a processing network performing both the visual and conceptual analysis of motion stimuli, which may involve audio-visual integration (if present) or more abstract representations of causation/agency.

Motion Language

In language studies, it has been shown that the activity elicited by motion verbs or sentences in temporal regions, compared to verbs and sentences referring to static events, barely overlaps with the identified V5 cluster (Revilla et al. 2008) or is altogether located anterior to it in PMTG, thus suggesting little re-enactment of perceptual features in V5 (Bedny et al. 2008; Kable et al. 2002). Kable et al., for example, presented static images of objects in motion (e.g., a train, a hand slicing bread, ducks walking) or words (*trailing, slicing, following*) in different blocks and compared them to baseline visual patterns. They asked participants to indicate which of the two bottom items on the screen was more related to the top item (matching task). They found that images of objects in motion elicited activity both in V5 and PMTG, whereas motion words elicited activity only in PMTG and other language areas. Bedny et al. (2008) did not find language activity in V5 either using a similarity judgment task, but reports general differences in PMTG between nouns and verbs, thus suggesting that event concepts or grammatical categories may be encoded in PMTG. More generally, numerous language studies using linguistic motion stimuli, but not necessarily comparing language and visual activity, have typically found motion or action sensitivity in PMTG, but no hint of V5 activation (Chen et al. 2008; Gennari et al. 2007; Kellenbach et al. 2003; Noppeney et al. 2005; Tyler et al. 2003; Wallentin et al. 2005).

These findings, however, have been challenged by studies showing V5 modulations as a result of linguistic content. Saygin et al. (2010), for example, report higher activity in V5 when participants are exposed to audiovisual presentation of someone uttering motion and fictive motion sentences (*I drove from Modesto to Fresno* and *The highway runs from Modesto to Fresno* respectively), as compared to static sentences (*Modesto and Fresno are in California*). Participants had to indicate whether the sentences made sense. They found that motion sentences elicited more activity in V5 than fictive motion sentences and that these in turn elicited more activity than static sentences (Saygin et al. 2010). In another study, Rueschemeyer et al. (2010) also report that language modulated activity in V5. In experiment 2, they used semantic anomaly detection on sentences and manipulated the direction of motion: motion toward or away from the self or other people or objects (*the car drives toward you/Maria/the bridge, the car drives away from you*) (Kaschak et al. 2005). Results indicated that all sentence types except for movement away from self elicited significant activation in the region defined as V5. The authors argue that the results reflect top-down modulations on V5 because the described situation requires the listener to track objects' motion to evaluate potential subsequent behavior, as only sentences that appear relevant to the self are simulated.

Although these findings in V5 are in principle consistent with the re-enactment theory, they also indicate other forces at play, since motion content per se is not the driving factor for V5 activity, as it is in visual perception. First, there is the possible modulating influence of attentional factors, as has already been shown in visual perception (O'Craven et al. 1997). Certain aspects of the stimuli such as movement toward oneself or toward other things may cause more attention or arousal, due to the potential for collision and danger. Second, it is possible that simultaneous visual and auditory stimulation in Saygin et al.'s study caused activity in V5, even though there was a sentence type effect. A talking face clearly engages motion perception processing and audiovisual stimulation requires audiovisual integration, which in turn elicits interactions with more anterior temporal integrative regions such as the PSTG. Indeed, studies investigating audio-visual integration (with spoken speech – e.g., syllables, stories and a speaker's mouth as stimuli) have

found activity in V5 and argued for top-down influences from PSTG onto V5 (Calvert et al. 1999, 2000). Interestingly, V5 may be more active in integrating congruent than incongruent audio-visual stimuli, suggesting the possibility that the degree of congruency between the facial movement and the static or non-literal content of the stimulus sentences in Saygin et al.'s study may be responsible for the effects reported. It is therefore likely that language content modulated V5 in this study because it modulated audio-visual integration through interaction with the PSTG, rather than eliciting visual re-enactments of motion. This suggestion is also consistent with other language studies using concurrent visual motion stimulation or naming of visually presented stimuli, which also report activity in V5 (Damasio et al. 2001; Tranel et al. 2005). Whichever the interpretation of these findings, if language truly re-enacts perceptual experiences, and specifically, if there are hebbian connections between words and visual experiences, the strongest test for such re-enactments is the use of linguistic stimulation separate from visual stimulation, as used by Rueschemeyer et al. (Exp. 2), because the words themselves should be able to re-activate these experiences without need of concurrent visual input.

A recent study attempted to shed light on these issues by examining whether higher order representations in temporal cortex as well as low-level representations in V5 were modulated by event properties such as motion and animacy in similar ways to those reported for motion perception above (Humphreys et al. 2010). To this end, the study adapted the blank-screen paradigm used in psycholinguistics eye-tracking studies (Altmann 2004; Altmann and Kamide 2009; Knoeferle and Crocker 2007; Richardson and Spivey 2000). In these studies, participants are first shown an image of a scene such as that in Figure 3. The image is then removed and replaced by a blank screen. Participants then hear a sentence (e.g., *the mechanic will walk towards the airplane*) that refers back to the previously viewed scene. During this time, they launch eye-movements to the now blank locations where the named characters (mechanic and plane) had been, thus suggesting that they interpret the language relative to the mental representation of scene, even when the scene is no longer present. This setting thus encourages visual imagery and relatively constant attention to perceptual memories, which remain the same across experimental conditions and do not include references to the self.

During scanning, participants saw a scene such as that of Figure 3 for 2 s, which disappeared after a variable period. They heard sentences varying in motion content (motion versus static) and in animacy (human versus object), for example, *The mechanic will walk towards the airplane* – Human Motion; *The mechanic is looking at the airplane* – Human Static; *The airplane will taxi towards the building* – Object Motion; *The airplane is stationed near the building* – Object Static. Participants were instructed to fixate on a cross during this time and to press a button only when the sentence did not match the picture, thus encouraging the processing of both the sentence and the scene. This task was preceded by a perceptual task (viewing motion videos of similar content to the sentence stimuli), which served to identify the brain regions targeted in the analyses such as area V5 and regions sensitive to human motion in the PSTG (Beauchamp et al. 2002).

It was found that in V5, language did not appear to recruit low-level motion perception areas. Figure 4 shows the results of this study (see explanation in the associated caption). Motion language recruited posterior superior and middle temporal regions that were also active when observing motion events, but not area V5. In these regions, animacy and motion content (human motion, human static, and object motion sentences) elicited high levels of activation, with only object static sentences showing decreased activity. These group results were further confirmed by analyses in which V5 was separately identified for each individual (this excludes the possibility of lack of power through



Fig 3. Example of visual scene used in Humphreys et al. (2010).

averaging and accounts for individuals' anatomical variability – see below). These results thus suggest that sensory-based representations in motion language do not have the specificity found in visual perception, even when reference to a visual scene was encouraged. Instead, conceptual, rather than perceptual, properties of the events in the temporal lobe, such as agency and movement, appear to be involved in language, as suggested by the sensory-motor organization theory. A summary of studies investigating motion language is provided in Table 1.

Methodological Considerations

One factor that may explain the scarcity and variability of language effects on V5 in the literature is the task and the stimuli used. Task demands and the regularities within the

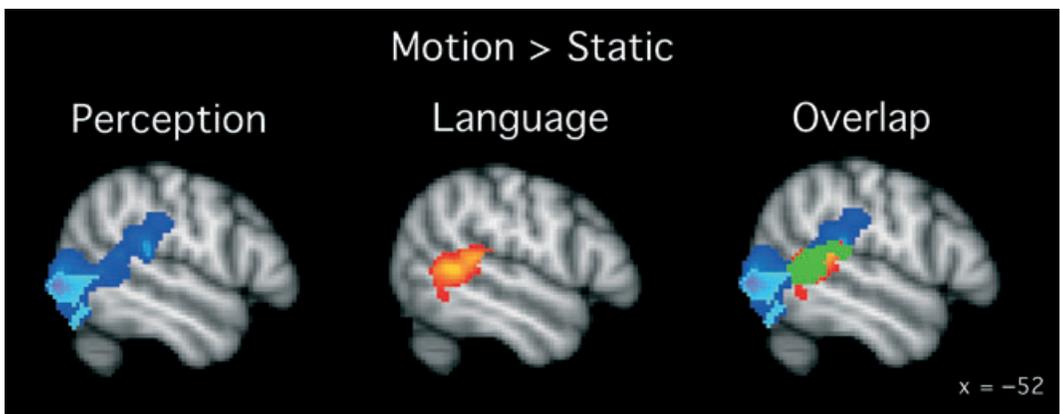


Fig 4. Results from the perceptual and language tasks from Humphreys et al. (2010). The images show activity elicited by motion stimuli, compared to static stimuli both in visual perception and language comprehension. Activity in blue (left image) indicates the perception results, with light blue indicating the strongest cluster responding to motion perception (area V5). Activity in red (middle image) shows the language results and green (right image) indicates the region of overlap between perception and language.

Table 1. Summary of previous studies investigating motion content or audiovisual integration.

Stimulus type	Study	Experimental parameters			Occipito-temporal results	
		Trial stimulus	Task	Comparison	Vision and language	Language
Words	Kable et al. (2002)	Visual words triad: Motion verbs – Nouns	Relatedness judgment	Verbs > Nouns	PSTG/PMTG	PSTG PMTG
	Kable et al. (2005) (Exp. 1)	Visual words triads: Motion verbs – Nouns	As above	Verbs > Nouns	–	PSTG PMTG
	Kable et al. (2005) (Exp. 2)	Visual words triad: Motion verbs – Tools – Animals	As above	Verbs > Nouns Tools > Animals	–	PSTG PMTG
	Bedny et al. (2008)	Auditory word pairs: Verbs (high, low motion) Nouns (high, low motion)	As above	Verbs > Nouns	PSTG	PSTG
	Revill et al. (2008)	Auditory novel motion words Auditory novel non-motion words	Word-visual event matching	Motion > non-motion	Anterior V5 cluster/PMTG	PMTG
Sentences	Rueschemeyer et al. (2010) (Exp. 2)	<i>The car drives towards you/Sam/the bridge</i> <i>The car drives away from you</i> <i>The car looks big</i>	Make-sense judgment	Motion toward self/other > Static	V5 cluster	
	Humphreys et al. (2010)	<i>The mechanic will walk towards the plane</i> <i>The mechanic is looking at the plane</i> <i>The airplane will taxi towards the building</i> <i>The airplane is stationed near the building</i>	Sentence-picture matching	Human motion > Human Static Object Motion or Human static > Object Static	PMTG/PSTG	PMTG/PSTG
	Wallentin et al. (2005)	<i>The man goes into the house</i> <i>The man lies inside the house</i> <i>The pipe goes in the house</i> <i>The pipe lies in the house</i>	Make-sense judgment	Literal & Fictive Motion > Static	–	PMTG

Table 1. Continued

Experimental parameters				Occipito-temporal results		
Stimulus type	Study	Trial stimulus	Task	Comparison	Vision and language	Language
Audiovisual	Calvert et al. (1999)	Hearing numbers + talking face (audiovisual integration) Hearing numbers + static face Visual speaking face	Silent repetition	Audiovisual integration > hearing or viewing	V5, PSTG	
	Calvert et al. (2000)	Congruent narrative + talking mouth (audiovisual integration) Incongruent narrative + talking mouth Auditory narrative alone Talking mouth alone	Passive perception	Congruent audiovisual integration > hearing or viewing	V5, PSTG	
	Saygin et al. (2010)	Auditory sentence + talking face: <i>The deer jumped over the brook</i> <i>The bridge jumped over the brook</i> <i>The deer slept near the brook</i>	Anomaly detection	Motion > Fictive Motion > Static	V5	
	Rueschemeyer et al. (2010) (Exp. 1)	Auditory sentence + static image: <i>The car drives towards you</i> <i>The car drives away from you</i> <i>The car looks big</i>	Direction judgment (of visual motion in catch trials)	Motion toward > Static	V5 cluster PSTG	

PSTG, posterior superior temporal gyrus; PMTG, posterior middle temporal gyrus.

The example stimuli listed are those corresponding to the result contrasts reported, although other type of stimuli may have been interleaved with them. The occipito-temporal results on the right column list the regions activated by either visual or language stimuli or by language stimuli only.

experimental items indicate to participants those aspects of the stimuli that must be attended to in order to perform the task more efficiently. Such tasks and regularities may encourage the retrieval of, and attention to, specific motion features such as manner and direction of motion, which would otherwise not be involved in a simpler language understanding task. Attention to such features may result, for example, from non-literal language uses (fictive motion) in an anomaly detection task, since such uses are initially anomalous in that they mismatch the typical meaning of the verbs with animate agents (*the highway runs ... along the coast* or *the bridge jumped ... over the brook*) (Saygin et al. 2010). Or, it may result from the repetition of the same stimulus type across the experiment (e.g., sentences describing motion away or toward), since such repetition highlights the stimulus differences that make judgments easier (Rueschemeyer et al. 2010). In contrast, making similarity or matching judgments in which two events or words must be compared to a target or to each other encourages schematic representations for global similarity comparisons (e.g., body motion versus hand motion) that may vary from trial to trial, and thus it does not require the consistent use of specific motion features throughout the experiment (Bedny et al. 2008; Kable et al. 2002). Interestingly, making decisions about the relationship between a previously seen picture and a sentence, as in Humphreys et al. (2010), which is known to encourage reference to the mental representation of the picture, did not elicit activity in V5, suggesting that mental imagery is not sufficient to elicit activity in V5.

Another factor that could *in principle* have influenced V5 activations in previous language studies is the analysis method used, although there is no evidence to suggest that this has indeed been the case. As indicated earlier, the anatomical location of V5 varies considerably across individuals. If this region is then localized using the averaged cluster where a group of participants shows high activation for visual motion, as in Rueschemeyer et al. (2010), the resulting activated area may only represent the individuals that happen to anatomically overlap. Moreover, such averages are typically conducted in a standardized brain, which requires the warping of each individual brain into that standard space. This is a noisy process where activity that was in the occipital lobe for a given subject, may end up in the temporal lobe or vice versa (Brett et al. 2002; Swallow et al. 2003). Indeed, methodological studies have shown that statistically grouping (e.g., averaging of activity) across participants to functionally localize V5 is not very reliable (Brett et al. 2002; Swallow et al. 2003). Thus, when linguistic modulations are examined within an area of activation that was localized as V5 via the averaged group activity, contamination from posterior temporal activity is a real possibility.

Additionally, the size of the regions selected to examine language effects – the region of interest – is important. If this cluster is too large, it will include activity from posterior temporal regions anterior to V5, which will then be sensitive to linguistic manipulations. The visual stimuli typically used to localize V5, particularly at the group level, indeed generates a large cluster of activation that extends into the temporal lobe. The averaged activity across a relatively large region of interest then may not result from activity in V5 proper but may in fact be driven by activity in the posterior temporal lobe. Humphreys et al. indeed found overlap between the region responding to language and the large region responding to visual motion at the group level, but this overlap did not include V5 proper (i.e., the stronger bits responding to visual motion) and it was located in the anterior portion of the large cluster responding to motion (see Figure 4), as also reported by Revill et al. (2008).

Taken together, these observations suggest that in commonly used analysis procedures, it is possible to mistakenly attribute language modulations to V5. The strongest demon-

stration of language modulations in V5 is to show that in each individual, the same region (preferably small) that more strongly responds to motion perception (according to an independent localizer scan) is also modulated by the linguistic manipulation. To my knowledge, no study using only linguistic stimulation has provided such a demonstration so far. More importantly, attentional demands may explain the absence or presence of V5 activations in response to linguistic stimuli. Tasks that encourage attention to specific motion features and/or audio-visual integration have reported effects on V5, whereas those requiring global similarity judgments or sentence-picture matching have not.

Discussion

As summarized in Table 1, only a handful of the studies reviewed report modulations in area V5 as a result of linguistic stimulation. None of the word-based studies have found such effects. Studies using audiovisual stimuli (plus others in the literature, e.g., Jones and Callan 2003) often report activity in area V5, even when the stimuli do not include linguistic motion content at all. Such findings suggest that audio-visual integration, rather than reenactment of linguistic motion content, modulates activity in V5. Only two studies – Revill et al. (2008) and Rueschemeyer et al. (2010) – have used sole linguistic stimulation and reported relevant effects, thus suggesting the possibility that linguistic meaning in itself may elicit perceptual re-enactments. In Revill et al. (2008), however, the language activity only minimally overlapped with the V5 cluster and critically, the activation peaks reported for perception and language are arranged from posterior to anterior as in previous studies, suggesting that the found vision-language overlap depended on the chosen cluster size, as discussed above. Moreover, Rueschemeyer et al.'s study clearly indicates that motion content is not sufficient to elicit activity in V5, as only one direction of motion (motion toward) elicited significant activation in V5.

These observations suggest that language effects on V5 do not appear to be automatic or habitual. The fact that only sentential stimuli elicited effects on V5 indicates that those effects are the results of relatively late integration processes (associated with frontal activity) across the sentential words, rather than word associations. Moreover, if task demands and stimulus types can change the nature of the motion representations entertained, as it appears to be the case, perceptually based representations in language comprehension are highly context dependent and the result of attentional or top-down modulations, as argued by Rueschemeyer et al. (2010), rather than inevitable associations resulting from learning. This sharply contrasts with the verb-based evidence offered to argue for the automaticity of motor associations – although the evidence as a whole in this domain is also unclear (Mahon and Caramazza 2008; Papeo et al. 2009; Postle et al. 2008; Raposo et al. 2009). Words implying the use of a body part like *kick*, for instance, very rapidly engage motor regions also involved in planning and performing actions with that specific body-part, even in situations in which participants are asked to ignore the linguistic stimuli and attend to unrelated videos (Hauk et al. 2004; Pulvermuller et al. 2005). Such findings have no parallel in the motion domain. In fact, the absence of V5 activity in circumstances in which motion information ought to be routinely recruited, as in most studies of Table 1, suggests that activity in V5 is not integral to the processing of motion content per se, but rather it results from top-down influences or selective attention, as in perceptual studies.

It is of course possible that some of the studies in Table 1 did not have enough statistical power to show an effect in V5 or that fMRI is simply not sensitive enough to detect transient activation in this region. The verb studies in Table 1 for example may not have

shown activity in V5 because they failed to sufficiently focus on specific motion features by requiring global semantic comparisons. This may decrease the power to detect motion-specific activity by averaging across semantically disparate trials. It is also possible that verb-level and sentence-level representations differ in their degree of engagement of motion features, resulting in stronger, more distributed and detectable activations. These possibilities certainly deserve more investigation but if attention to motion features needs to be increased via stimuli and task designs, or sentential stimuli are needed to elicit effects, it is likely that top-down mechanisms (from temporal and frontal regions) will play a role, making it difficult to determine the associative nature of V5 activations. Different designs or methodologies may thus shed light on this issue.

Even though the evidence so far is inconclusive, there are additional considerations to suggest that low-level perceptual content may not be routinely or automatically engaged in language processing. Visual experiences of motion like those that V5 is sensitive to are not necessarily critical for the child acquiring linguistic concepts such as *push*, *pull*, *hopping*, or *bouncing* because motion per se would not distinguish between their meanings and consequently the properties of the events referred to in the world. Motion is associated with most action words, thus providing frequent but non-diagnostic associations for recognizing or producing a word. This may lead to weaker rather than stronger connections between motion words and motion experiences in V5 because associations that do not help the learner to understand the language and interact with the world may not be reinforced (except perhaps for those involved in the meaning of the word *move*). This is supported by the fact that when monkeys learn to establish novel stimulus-response associations in visual or auditory modalities, these associations are critically linked to task demands (Fuster 2001; Fuster et al. 2000; Quintana and Fuster 1999; Zhou et al. 2007). Using microelectrode cell recording techniques, these studies show that in performing a trained task, neurons in auditory and visual cortices work in tandem with neurons in prefrontal cortex responsible for selective attention, thus implementing the learned stimulus-response association. Therefore, the associative networks that are strengthened during learning are those leading to the achievement of specific task goals. From the point of view of the learner navigating multimodal experiences and acquiring words, such contextual constraints, which include regularities between words and world features, must play a role in determining which associations are strengthened, in the same way that stimulus regularities play a role in statistical learning (Gómez and Gerken 2000). The learner, for example, must figure out what can self-propel and what cannot, what trajectories moving things may take, and how these aspects of events map onto words, rather than simply distinguishing motion from static stimuli. Motion verbs across the world's languages indeed differ in the way they lexicalize motion events so that regular language-specific experience (specific word-to-world mappings) must be extracted from the environment (Gennari et al. 2002). Thus, visual motion perception per se, although a necessary input, may play a less critical role in language learning, leading to associative networks that do not necessarily include V5 but rather other networks responsible for the relevant distinctions between different motion events.

If these observations are correct, conceptual representations of motion need not include modality-specific re-enactments of visual experiences in V5, as long as they preserve features that can be applied to new situations and new uses of words. The evidence reviewed here indeed suggests that modality-specific motion representations in V5 may be invoked by language in circumscribed situations in which attention is drawn to specific motion features, but need not be habitually recruited in comprehending motion

content. In fact, the representations in posterior temporal cortex (PMTG and PSTG), which responds to various stimulus modalities, are the ones habitually shared by language and perception, as indicated by the studies reviewed. These regions appear to encode non-modality-specific schematic properties of events, including their causal structure, since these regions respond to all verbs, irrespective of action content, and to animacy, irrespective of motion content (Bedny et al. 2008; Blakemore et al. 2003; Humphreys et al. 2010; Morito et al. 2009; Rodríguez-Ferreiro et al. 2011).

These considerations are consistent with the sensory-motor organization theory of meaning in that perceptual representations need not be engaged in language processing. They are also consistent with embodied approaches that acknowledge the context-dependent and partial nature of modality-specific representations (Barsalou 2003; Barsalou et al. 2003), although the evidence for modality-specific (visual only) motion representations is inconclusive in language processing. The evidence reviewed, however, is not consistent with strong re-enactment views according to which visual experiences are linked to words via hebbian learning, unless the learning process is further qualified (Hauk et al. 2004; Pulvermuller 2005). Similarly, radical statements claiming that the neural machinery responsible for perceiving and understanding events in the world is engaged during language comprehension (Kaschak et al. 2005) need to be further qualified, as language comprehension by itself does not seem to invariably engage perception-specific machinery.

In sum, the evidence so far suggests that the motion representations entertained during language comprehension are experienced-based, as they have been formed through learning from perceptual input. But they need not require the re-enactment of perceptually specific motion representations as reflected on area V5. Instead, they may be one-step removed from experience and contain schematic properties of actions and events that are relevant for language understanding and its relation to the world. These representations appear organized around modality-specific representations (hence, their proximity to visual cortex) but they are abstracted, generalized or schematized over time through learning. Nevertheless, constraining contexts or task demands, such as the presence of visual stimulation, may cause V5 to cooperate with their neighboring temporal regions during language comprehension, thus resulting in the engagement of perceptually specific representations. This is expected in a flexible and efficient system that is capable of learning and generalization from past experience as well as of recruiting modality-specific information, if so required.

Short Biography

Silvia P. Gennari's research is located at the intersection of psycholinguistics, cognitive science, and cognitive neuroscience of language; she has authored or co-authored papers in these research areas for various journals, including *Cognition*, *Cognitive Psychology*, *NeuroImage*, *Journal of Cognitive Neuroscience*, *Journal of Memory and Language* and others. Her work is focused on the semantic representations entertained in language production and comprehension, particularly in the domain of event structure (event participants, and events' temporal and causal properties). Her current research involves empirical investigations on the representation time, and the relationship between production and comprehension using behavioral and neuroimaging techniques. Silvia received her PhD at Brown University and after holding postdoctoral positions in the US, she moved to the UK, where she currently teaches at the University of York.

Notes

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¹ Previous studies (Watson et al. 1993) have located this region at the junction between the ITS and the lateral occipital sulcus (shown in Figure 2 running horizontally to the left of the V5 area in red), but this latter structure is often absent from individual brains and thus is a less reliable anatomical landmark for identification. Finer distinctions with the V5 complex have also been made in the literature (Dukelow et al. 2001).

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