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**A review of literature on the link between action observation and action language:
advancing a shared semantic theory**

Christel Bidet-Ildi¹, Sophie-Anne Beauprez^{1,2}, Arnaud Badets³

¹ Département des Sciences du sport, Université de Poitiers, Université de Tours,
Centre National de la Recherche Scientifique, Centre de Recherches sur la Cognition
et l'Apprentissage (UMR 7295), Poitiers, France

² Université Lumière Lyon 2, Centre National de la Recherche Scientifique,
Laboratoire Dynamique du Langage (UMR 5596), Lyon, France

³ Centre National de la Recherche Scientifique, Institut de Neurosciences Cognitives
et Intégratives d'Aquitaine (UMR 5287), Bordeaux, France.

Corresponding author:
Christel Bidet-Ildi
CeRCA/MSHS,
Bâtiment A5
5, rue Théodore Lefebvre
TSA 21103
86073 Poitiers cedex 9
Tel.: 33 (0)5 49 45 46 97
christel.bidet@univ-poitiers.fr

Abstract

Understanding each other is a core concept of social cohesion and, consequently, has immense value in human society. Importantly, shared information leading to cohesion can come from two main sources: observed action and/or language (word) processing. In this paper, we propose a theoretical framework for the link between action observation and action verb processing. Based on the activation of common semantic representations of actions through semantic resonance, this model can account for the neurophysiological, behavioral and neuropsychological domains in the link between action observation and language. Semantic resonance is hypothesized to play a role beyond that of the mere observation of others and can benefit future studies trying to connect action production and language.

Keywords: embodiment, action observation, action verb processing, mirror neuron system, semantic resonance.

Introduction

Action observation has immense value for the successful performance of daily life activities (Pavlova, 2012), and it could be the first step in the performance of social behaviors in which intentions and language emerge to reinforce group membership (Gallese, 2008; Rizzolatti & Arbib, 1998; Rizzolatti & Sinigaglia, 2007; Tomasello, 2005). From this perspective, several authors have studied the link between action and language (see Fischer & Zwaan, 2008; Willems & Hagoort, 2007 for reviews). Generally, these studies have largely demonstrated the role of the motor system on language processing through the use of behavioral, neurophysiological or neuropsychological paradigms (e.g., Boulenger et al., 2008; Hauk, Johnsrude, & Pulvermüller, 2004; Papeo, Vallesi, Isaja, & Rumiati, 2009), confirming the view of embodied cognition (Barsalou, 1999, 2008). From this theoretical account, cognition, such as the understanding of the concept “apple”, is not based on stored amodal symbols (Fodor, 1975) but is created from sensorimotor experiences, that is, the smell, the taste or the grasping of the apple (Barsalou, 1999, 2008). Interestingly, the link between action and language also exists when the action is only observed (e.g., Bidet-Ildei, Sparrow, & Coello, 2011), suggesting that motor components are not a prerequisite for the activation of shared action representations between action and language (e.g., Tettamanti et al., 2005). From the theory of embodied cognition, both motor and/or perceptual experience is implied in language processing (Barsalou, 1999, 2008). However, for scholars, shared representations between action and language have been mostly considered as a motor *or* a perceptual approach (Pulvermüller, 2005; Rizzolatti & Craighero, 2004).

Considering the motor approach, it has been suggested that action language shares motor representations with action production (Pulvermüller, 2005; Zwaan & Taylor, 2006; Zwaan, Taylor, & de Boer, 2010). The best empirical evidence for the motor approach is that several

studies have shown that action words and action sentence processing activate the motor cortex in a somatotopic manner (Andres, Finocchiaro, Buiatti, & Piazza, 2015; Buccino et al., 2005; Hauk et al., 2004). For example, Hauk et al. (2004) show that the activation of the primary motor cortex is specific to the body part used in the action described in the verb. Specifically, when participants processed a verb representing an action of the legs (e.g., jump), neuronal activity observed was stronger in the part of the motor cortex that controls leg movements, demonstrating the somatotopy of action-verb processing. Accordingly, motor-related activity for action language would be related to the class of action-verbs considered (Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008). Indeed, depending on the semantic aspects of the action verbs (i.e., action, motion, contact, change of state, tool use), Kemmerer and his collaborators (2008) show that different brain areas are activated and that only action verbs for which the action is incorporated into the meaning of the verb (e.g., running, speaking, cutting) activate motor and premotor cortices. Moreover, some studies have shown that action language processing interferes with action production (Boulenger et al., 2006; de Vega, Moreno, & Castillo, 2013), confirming that both types of processing share common mechanisms. For example, the kinematics of grasping movements are affected when participants must simultaneously process an action verb related to grasping. Finally, studies carried out in patients presenting motor disorders such as Huntington's disease (Peran, Demonet, Pernet, & Cardebat, 2004), amyotrophic lateral sclerosis (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Cousins, Ash, & Grossman, 2018; Grossman et al., 2008; York et al., 2014), progressive supranuclear palsy (Bak et al., 2006; Daniele et al., 2013) or Parkinson's disease (Boulenger et al., 2008; Cardona et al., 2013; Cousins et al., 2018; Fernandino et al., 2013a, 2013b; Ibanez et al., 2013; Peran et al., 2003; Roberts et al., 2017) show that action-verb processing is directly related to the integrity of the motor system. In this

view, action verb understanding would therefore be based on the reenactment of motor programs that imply the execution of action (Pulvermüller, 2005).

In the perceptual approach, however, any shared action representations imply that action language understanding re-activates mainly perceptual representations of actions relating to the understanding of the action goal (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Badets & Osiurak, 2017; Bidet-Ildei & Toussaint, 2015; Rizzolatti & Craighero, 2004; Tettamanti et al., 2005). This approach does not deny motor-component involvement to some degree but strongly minimizes its role in the functional link between action representation and action-word processing. Accordingly, several studies have shown that the understanding of an action sentence is based on a perceptual simulation of the event being described (Kaschak et al., 2005; Zwaan, 2008). For example, when participants listen to the sentence “The ranger saw the eagle in the sky”, they process a picture presenting a flying eagle faster than one showing a perched eagle (Zwaan, Stanfield, & Yaxley, 2002). From this perspective, action language processing activates the mirror neuron system to access the meaning of action, and this mirror neuron system is thought to interpret others’ actions (Rizzolatti & Sinigaglia, 2007). More precisely, the mirror neuron system in humans corresponds to a brain network including fronto-parietal circuits that are activated both when a person takes action or when he/she perceives the same action produced by another (Blakemore & Decety, 2001; Buccino, Binkofski, & Riggio, 2004; Iacoboni & Dapretto, 2006). Classically, this system is known to be implied in imitation, intention understanding, and empathy (see Iacoboni & Dapretto, 2006; Rizzolatti & Craighero, 2004 for review), and it has been proposed that it could also be the origin of human language action understanding (Rizzolatti & Arbib, 1998). In accordance with this view, it has been shown that merely observing actions or reading action sentences can activate common brain networks, including the dorsal premotor cortex, posterior inferior parietal sulcus, medial fusiform gyrus and occipital temporal cortex, suggesting the activation

of some common motor-perceptual brain areas during both activities (Ramsey, Cross, & Hamilton, 2013). Moreover, patients with atypical mirror neuron functioning have difficulty processing action verbs. For example, Moseley et al. (2013) assessed brain activation related to the silent reading of action and object words and measured reaction times in a semantic decision task in high functioning autistic adults and in matched controls. The results show hypoactivity in the inferior frontal gyrus and precentral gyrus during the reading of action words in autistic participants compared with matched control participants. Note that these neuronal areas represent a part of the mirror neuron network. Moreover, reaction times in the decision task were longer for action words than for object words in patients, whereas no difference was seen in healthy controls. Interestingly, precentral activity for action words was positively correlated with the difference in reaction times between action and object words and was negatively correlated with the intensity of the disorder, as measured with the autism spectrum quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), suggesting that patients with autism spectrum disorder present specific difficulties with action verb processing related to specific deficits in social interaction, as hypothesized by the mirror neurons account (Rizzolatti & Arbib, 1998).

In this paper, we compare both approaches, i.e., the motor versus the perceptual approach, through the lens of human action observation. Indeed, even if many studies have assessed the link between human action production and action word processing (see Fischer & Zwaan, 2008; Willems & Hagoort, 2007 for reviews) or between perceptual events and action verb processing (Kaschak et al., 2005; Zwaan & Madden, 2005; Zwaan, 2008; Zwaan et al., 2002), no systematic review has specifically focused on the link between human action observation and action verb processing. Moreover, human action observation is highly relevant for studying the link between action and language because it constitutes the basis for communication and social interactions (Lepage & Theoret, 2007). From a purely theoretical

point of view, it could be argued that the link between action verbs and observation is only a trivial corollary of the main aims of studies on action production and verb processing. Indeed, it has been acknowledged that action observation and action production share many cognitive processing resources (Press, 2011) and that discovering an interaction between verb processing and movement production could result in a similarly trivial assumption for action observation. However, to foreshadow our conclusion, throughout the present article, we will defend the idea that action observation provides a specific opportunity for revealing an important theoretical link between action and language. Specifically studying the link between action observation and action verb processing is relevant from a theoretical and pragmatic point of view. First, action observation capabilities appear much earlier than action production capabilities (e.g., Bidet-Ildei, Kitromilides, Orliaguet, Pavlova, & Gentaz, 2014; Simion, Regolin, & Bulf, 2008), suggesting a key role of action observation in learning (Lepage & Theoret, 2007). Moreover, from a more pragmatic perspective, studying the link between action and language through the use of action observation capacities allows us 1) to focus on the role of action representations without contamination by the peripheral motor system and 2) to modify actions (via video or picture settings) to precisely assess the role of action characteristics in the link between action and language.

Therefore, this review focuses on the link between action and action-verb processing using action observation. The first part of this article provides a model for an overall account of the link between action and action verb processing through the use of shared semantic representations, i.e., the perceptual approach. The second part develops neurophysiological, behavioral and neuropsychological evidences of the link between action observation and action verb processing. The third part reviews specific factors that influence the activation of semantic representations of action. Finally, in the last part of the paper, future directions and open questions are addressed. In this review, we consider experiments that have studied the

role of human action observation in the processing of isolated action verbs but also when action verbs are embedded in sentences.

A tentative model to account for the link between action observation and action verb processing

In agreement with scholars that claim that the mirror neuron system is specifically linked to action language processing using a common perceptual mechanism of understanding (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Badets & Osiurak, 2017; Bidet-Ildei & Toussaint, 2015; Rizzolatti & Craighero, 2004; Tettamanti et al., 2005), here, we propose a tentative model to account for the link between action observation and action language processing.

In this model (see Figure 1), we consider four components: two motor components related to the movement production of an action and to the verbal production of an action word and two perceptual components related to the understanding of the action and the understanding of the action word.

The motor components refer to the motor programming of an action or action word, whereas the perceptual components refer to the perceptions implied by the action or action word and to the understanding of the action or action word. More precisely, if you consider the overt action “run” and the pronunciation of the word “run”, the motor components refer to the programming of the muscles necessary to produce the action (i.e., the motion of the arms and legs) and to the programming of the articulatory movements necessary to produce the sounds associated with the word (i.e., the motion of the tongue, upper and lower lips, etc.). The perceptual components of the action “run” and the word “run” refer to the perceptions associated with the production of the action (i.e., the vision, the sounds and the proprioceptive information associated with the action) and to the perceptions associated with the production

of the word (i.e., the sound, the graphemes, the proprioceptive information related to the production of the word). From this perspective, the different motor components of action and language are linked with their equivalent perceptual components without sharing specific motor representations. However, perceptual components also involve accessing the meaning of the action and action-word. Following the concept of the mirror neuron system theory of language (Rizzolatti, 2005), we consider that shared action representations exist in perceptual components of action and language through the activation of common semantic action representations. Consequently, the meaning of an action or the meaning of an action word could be accessed through the activation of a common semantic representation of the action by semantic resonance. This semantic resonance¹ would be bidirectional in the sense that it would be activated through action processing or action language processing indiscriminately.

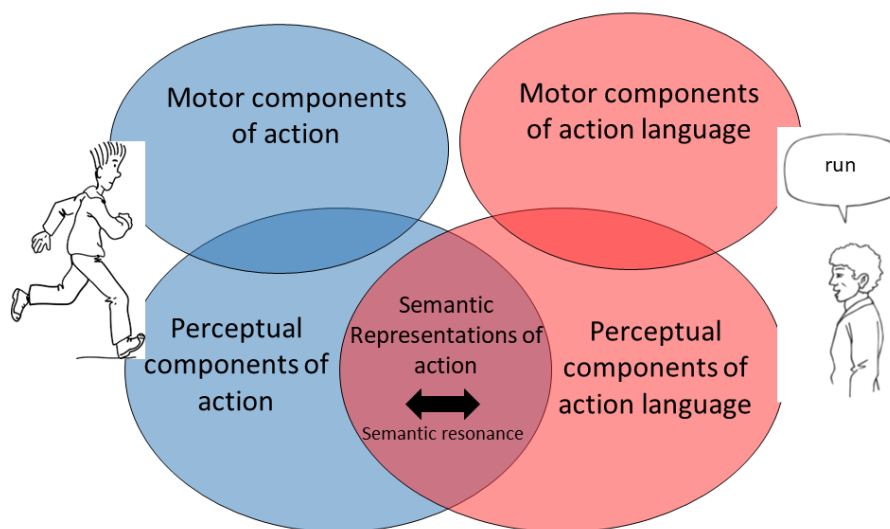


Figure 1: Proposal for a model to account for the links between action and action language processing. The double arrow represents the bidirectionality of the links. Here, we hypothesized that the link between action and language could be based on the activation of common perceptual action representations of actions using semantic resonance. The

¹ The concept of semantic resonance is adapted from the concept of motor and perceptual resonance, which have been proposed by Schütz-Bosbach & Prinz (2007) to account for the relation between action production and action observation.

characters have been selected from the French database Clic images 2.0 (see Clic-Image2-0 – Réseau Canopé <http://www.cndp.fr/crdp-dijon/clic-images/>).

Therefore, in our example, the word “run” and the action “run” would be understood by activating a common semantic representation of the action "to run". This semantic representation could be activated by the production or the observation of the running action or by the reading, hearing or pronunciation of the verb “run”. Following this model, we should probably find a strong link between action observation and action language processing related to the activation of the mirror neuron system.

Presenting this evidence is the aim of the next section. Specifically, we present neurophysiological, behavioral and neuropsychological studies that demonstrate that action observation and action verb processing are based on a common mechanism.

Demonstration of the link between action observation and action verb processing

The existence of the link between action observation and action verb processing was first suggested through brain investigations (Tettamanti et al., 2005). Later, this link was studied with a behavioral approach that assessed possible functional links between the mechanisms of action and language (Bidet-Ildei, Sparrow, et al., 2011). Moreover, thanks to this approach, it was possible for studies to demonstrate that the link is bidirectional, demonstrating that action observation can influence action verb processing (Liepelt, Dolk, & Prinz, 2012) and that action verb processing equally modifies action observation (Bidet-Ildei, Sparrow, et al., 2011). Finally, studies in patients have confirmed the relevance of this functional link by demonstrating the effectiveness of action observation in recovering language (Marangolo et al., 2010).

Neurophysiological investigations

Considering the well-known similarities in brain activation for action production and action observation (see for example Aziz-Zadeh & Ivry, 2009; Grézès & Decety, 2001 for reviews), brain studies focusing on the action-language link do not usually find a difference between action production and action observation activities. In an fMRI experiment, Tettamanti and his collaborators (2005) demonstrate that listening to action-related sentences specifically activates the left fronto-parieto-temporal network, which is usually engaged in action execution and observation, suggesting that the mirror neuron system is directly involved in action language processing (see also Aziz-Zadeh & Damasio, 2008). Interestingly, the neurophysiological similarities between action observation and action verb processing was also tested directly in an fMRI study (Aziz-Zadeh et al., 2006). In this experiment, the authors asked 12 participants to read action sentences that involved different parts of the body (mouth, hands, or feet) and then to observe actions that involved the same parts of the body. Individual comparisons of cerebral activations related to these two tasks allowed us to show similarities in the activation of the left pre-motor cortex, confirming the involvement of action perception circuits during the observation of actions and action sentence processing (see also Pulvermüller, 2018; Pulvermüller, Moseley, Egorova, Shebani, & Boulenger, 2014).

Electrophysiological studies also confirm that similar mechanisms underlie action observation and action verb processing by demonstrating that both activities cause mu and beta rhythm suppression at fronto-central sites (Moreno, de Vega, & León, 2013; van Elk, van Schie, Zwaan, & Bekkering, 2010), suggesting that accessing action meaning involves the same brain mechanisms (i.e., the activation of the mirror neuron system) independent of the modality of the action presentation (action observation vs. action language, see also Ramsey et al., 2013). Interestingly, accessing action representations would occur during the integration

of words in the sentences (Moreno et al., 2015). Indeed, in this study, Moreno and his collaborators analyzed the time frequency in mu rhythm suppression during action (“You will cut the strawberry cake”), abstract (“You will doubt the patient’s argument”) and perceptive (“You will notice the bright day”) sentences. Their analysis shows that mu rhythm suppression during action sentences appeared late in the sentence, that is, while participants were reading the first or the second noun in the sentence, suggesting that motor-related activation during action sentences is, in fact, related to the perceptual / semantic integration of words across the sentence (see also Beauprez, Laroche, Perret, & Bidet-Ildei, 2019).

In summary, several studies have shown that both action language processing and action observation are based on common brain activations using the mirror neuron system, confirming the special link between the observation of actions and the use of action verbs. However, at this point, it is difficult to distinguish if shared action representations are situated mainly in motor or perceptual components because the mirror neuron system involves, by definition, both motor and perceptual aspects (Schütz-Bosbach & Prinz, 2007). However, all of these studies on motion observation suggest that overt behavior and associated motor components are not necessary to reveal functional interactions between action and language processing.

In the next part of the paper, we review some behavioral experiments that have specifically assessed the link between human action observation and action verb processing, and we emphasize the bidirectional aspect of the link (see Figure 1).

Behavioral investigations

Interestingly, several studies have shown that action verbs and action sentences can affect visual judgments of actions. For example, it has been shown that the visual anticipation of action is modified depending on language processing (Springer, Huttenlocher, & Prinz, 2012;

Springer & Prinz, 2010). Considering this view, through three experiments, Springer et al. (2010) demonstrated that the precision of visual action anticipation, i.e., the capacity to predict the next component in an action sequence (Graf et al., 2007), was dependent on the category of the word presented in the prime (concrete noun vs. action verb, static vs. dynamic action verb, and slow vs. fast action verb), suggesting the existence of a link between the simulation of the action and the understanding of the word. Moreover, the link between action language processing and action observation has been demonstrated through the use of the point-light display paradigm (PLD, Johansson, 1973). The PLD paradigm consists of presenting and recognizing an action represented by a sequence of animated dots representing the dynamics of the limbs. The PLD paradigm is largely used in experiments that are interested in the mechanisms involved in action observation recognition (e.g., Bidet-Ildei, Chauvin, & Coello, 2010), and it is known that the interpretation of PLDs involves action representations mainly at a perceptual level, that is, the well-known biological perception mechanism (see Bidet-Ildei, Orliaguet, & Coello, 2011; Blakemore & Decety, 2001; Casile & Giese, 2005; Pavlova, 2012 for reviews). Interestingly, it has been shown that the capacity to detect a PLD within 55 masking dots is significantly improved when participants read a congruent verb in the prime. For example, the response times to detect a point-light running action are approximately 50 ms faster when participants read the verb “run” in the prime than when they read a non-congruent verb (e.g., “throw”) or a non-action verb (e.g., “think”), suggesting that action observation and action language processing are based on a common mechanism (Bidet-Ildei, Sparrow, et al., 2011, see Figure 2A). This idea was specifically investigated in a study that directly compared both tasks (Bidet-Ildei & Toussaint, 2015). In this experiment, Bidet-Ildei & Toussaint (2015) asked 24 participants to perform a lexical decision task and an action decision task. Specifically, in the lexical decision task, the participants had to decide if a sequence of letters corresponded to a French word, and in the

action decision task, the participants had to decide if a point-light display represented a human action. The results show that response times for pseudo-stimuli (i.e., no existing words or no human actions) were slower than those observed for valid stimuli (i.e., existing words or existing human actions) in both action language and action observation tasks, suggesting that these activities share common mechanisms. Accordingly, correlation analysis has shown a specific link between response times when judging action verbs and response times when judging point-light actions, whereas the correlation was not significant between response times when judging nouns and response times when judging point-light actions. This result suggests that judgments of action verbs and the judgments of PLDs are processed similarly by biological perception mechanisms.

Otherwise, the inverse relationship was also demonstrated. Indeed, some studies have shown that action perception can directly affect language processing. In this view, observing a movement of the opening or closing of a hand directly affects the time it takes to pronounce the verb “open” or “close”, suggesting the existence of crosstalk between action observation and action verb production at a semantic level (Liepelt et al., 2012). In agreement with this observation, observing a PLD representing a human action (and, thus, the biological perception mechanism) directly affects the time needed to process an action verb (Beauprez & Bidet-Ildei, 2017; Troyer, Curley, Miller, Saygin, & Bergen, 2014). Beauprez et al. (2017) showed that a lexical decision task was performed faster when the verb was congruent with the point-light action presented in the prime, whereas no facilitation was shown for the presentation of non-congruent actions or point-light displays of shambled movements (see Figure 2B). This result suggests that the biological perception mechanism can directly influence judgments of action verbs.

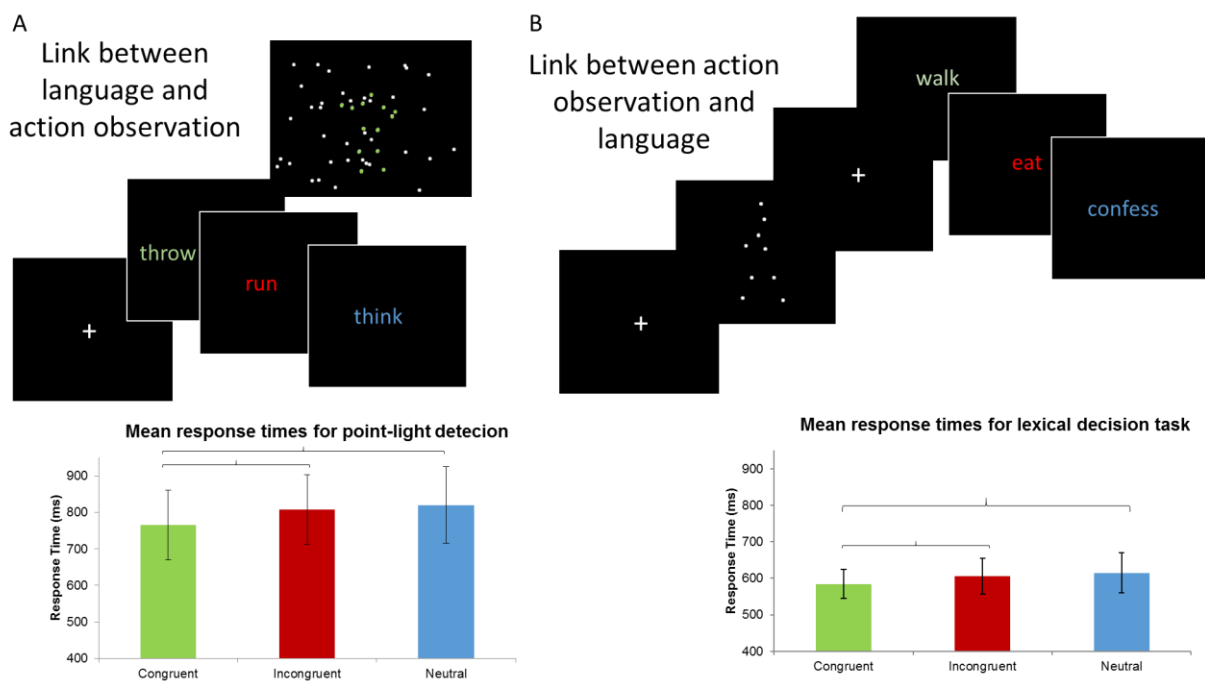


Figure 2: Procedure and results obtained in an experiment testing the link between language and action observation (A) and an experiment testing the link between action observation and language (B). The graphs represent the mean response times for each condition. Error bars represent the 95% confidence intervals. Braces represent significant differences at $p < .05$. Regardless of the modality of the priming task, the results showed better performance when the verb and the point-light action were congruent than in the two other conditions when they were not (adapted from Bidet-Ildei et al. 2011 and Beauprez & Bidet-Ildei., 2017 with permission).

Taken together, these studies demonstrate that action observation and action language processing influence each other, suggesting that action observation and action verb processing are probably based on the activation of common perceptual representations (Bidet-Ildei, Sparrow, et al., 2011; Bidet-Ildei & Toussaint, 2015; Liepelt et al., 2012; Zwaan & Taylor, 2006). Moreover, in accordance with our model (see Figure 1), these experiments confirm the bidirectionality of the link between action observation and action language processing and suggest some specific commonalities between action observation and action verb processing (Bidet-Ildei & Toussaint, 2015). These results are largely compatible with the idea of the activation of a common perceptual/semantic representation via semantic resonance.

The next part of the review presents results from studies in patients that directly suggest a common mechanism between the understating of action and the understanding of action language.

Neuropsychological investigations

The existence of the link between action observation and language has also been demonstrated in studies in patients. Indeed, some studies in patients with aphasia (i.e., patients presenting specific deficits in language processing mainly resulting from an ischemic stroke in the frontal lobe of the left hemisphere) have shown that difficulties in language processing can be related to difficulties in action interpretation (Arévalo et al., 2007; Saygin, Wilson, Dronkers, & Bates, 2004). In one experiment, Saygin et al. (2004) measured the performance of 24 non-fluent aphasic patients in the production and comprehension of language and in the understanding of action pictures compared to that in age-matched controls. In a portion of aphasic patients, especially patients with severe symptoms, the results show specific difficulties both for linguistic and nonlinguistic tasks associated with brain damage in linguistic areas (i.e., anterior superior temporal lobe and anterior insula) and, in accordance with the perceptual approach, in the anterior portion of the inferior parietal lobe, which is a part of the mirror neuron system.

Moreover, the link between action observation and language processing has been shown by highlighting the beneficial impact of action observation therapy for the rehabilitation of patients with language disorders such as non-fluent aphasia (see Marangolo & Caltagirone, 2014 for a review). In this context, it has been demonstrated, for example, that intensive rehabilitation (i.e., three 30- to 45-minute sessions per day for two consecutive weeks) based on the observation of human actions significantly improved the production of verbs in patients with non-fluent aphasia, with effects lasting for at least two months after the end of treatment (Marangolo et al., 2010). Thus, these results confirm the link between action observation and

the processing of action verbs and clearly highlight the potential of action-oriented rehabilitation to restore function in those with language disorders. Interestingly, improving the verbal performance of patients would be constrained by the type of actions presented. Thus, the presentation of human actions (such as "walking") would significantly improve the capacity to produce action verbs, whereas other actions (e.g., animal or mechanical actions) would not (Marangolo, Cipollari, Fiori, Razzano, & Caltagirone, 2012). There is, thus, specificity in the action-language link for actions linked to those included in the motor repertoire of the participants. This specificity could be used as evidence that the motor component is essential in the link between action and language. Indeed, we can hypothesize that only human actions are efficient because participants can simulate these actions at the motor level. However, this specificity could also be simply explained by the perceptual experience of the participants, which is likely stronger for human actions than non-human actions. This point will be further discussed in the final section outlining future directions.

Taken together, neurophysiological, behavioral and neuropsychological findings reinforce the idea that action observation and action language processing are based on common perceptual mechanisms through the activation of similar action semantics. These results are largely compatible with our conception of the existence of shared action semantic representations between action and language. In the next section, we focus on the specific factors that influence the link between action observation and action language processing.

Factors in the link between action observation and action language processing

Though a large body of evidence underlies the link between action and language, several studies have questioned the automaticity of the link by demonstrating that some factors relating to action, to language or to individual characteristics can directly affect the link between action observation and language processing. In the next section, we review these

factors, including language characteristics, action characteristics, action experience, and task specificity.

Language characteristics

One of the first factors studied was the role of semantic context during action verb processing. To investigate this factor, several studies assessed the implication of action during action verb processing according to the semantic characteristics of the sentence in which the verb was included (Bidet-Ildei, Gimenes, Toussaint, Almecija, & Badets, 2017; Bidet-Ildei, Gimenes, Toussaint, Beauprez, & Badets, 2017; de Vega et al., 2014; Troyer et al., 2014). While some studies have clearly shown that semantics can affect peripheral motor reactions (i.e., grip force) to action verbs (Aravena et al., 2014, 2012), works focusing on the role of action representations show more varied conclusions. For example, using fMRI, De Vega and his collaborators (2014) compared brain activation related to action sentence processing associated with factual (“Given that it was my birthday, I unwrapped the gifts”), negative (“Given that it was not my birthday, I didn’t unwrap the gifts”) or hypothetical (“If it had been my birthday, I would have unwrapped the gifts”) semantic contexts. They show that all conditions activated perceptual regions, suggesting that the mirror system is involved during the processing of action verbs even when verbs are presented in abstract contexts.

Similarly, Troyer et al. (2014) demonstrated that judgments of point-light actions share common representations with the understanding of action sentences whether sentences are literal (“The teacher was ambling toward the school”) or metaphorical (“The story was ambling toward its conclusion”), even if neural mechanisms could be less specific in the metaphorical context. This result suggests that common representations can be involved in action observation and action verb processing regardless of the context of the action verb presentation but that the link between both activities could be relatively substantial. This view

was confirmed by Bidet-Ildei et al.(2017), who demonstrated that the ability to detect a PLD among 55 scrambled moving dots is improved when the participants listened to a congruent action verb in a plausible sentence in the prime (e.g., The neighbor is running in the garden). When a congruent action verb is included in an implausible sentence (e.g., The garden is running in the neighbor), the effect of congruence persisted, but it was weaker, suggesting that the plausibility of the sentence context can affect the link between action verb processing and the biological perception mechanism (see Figure 3A). Interestingly, the effect of context has also been found when we contrast the practicability to perform the action described in the sentence. Indeed, Bidet-Ildei et al. (2017) have shown that listening to an action verb does not influence the detection of a congruent PLD if the verb is included in a sentence that describes pain (e.g., “The animator is walking on thistles”). This result suggests that the effect of context found in the link between action verb processing and action observation could be related to the capacity to activate the perceptual representation (here, the pain) associated with an action verb.

Globally, this finding demonstrates that the semantic context of action verb presentation affects the link between action observation and language. However, even if the link is weaker, it still persists, even when action verbs are presented in negative, metaphorical, hypothetical or impossible sentences, suggesting that the ability to simulate a motor action is not essential in the link between action observation and language. This idea largely supports our model suggesting that it is not the motor components but the perceptual components that are at the basis of the link between action and language.

Note that this type of modification in language context directly disrupts the relationship between action production and language (Aravena et al., 2014, 2012; Zwaan et al., 2010). If these findings could be related to the use of different types of processing for the link between action observation and language and action production and language, they could also be

explained by the fact that the link between action observation and language is stronger than the link between action production and language. Indeed, if we hypothesize that the link between action and language is based on the activation of shared perceptual action representations, it is obvious that the activation of the motor component system during action production necessitates more evoked activation (because this motor activation would just be a correlate of the activation of semantic action representation). It is, therefore, evident that small perturbations in the action word presentation can directly disrupt the link between action production and language, whereas the link between action observation and action language can be maintained.

The role of action characteristics

Recently, some works have focused on action characteristics (Beauprez & Bidet-Ildei, 2018; Beauprez, Bidet-Ildei, & Hiraki, 2019; Beauprez, Toussaint, & Bidet-Ildei, 2018; Beauprez, Laroche, et al., 2019). From this perspective, action characteristics refer to the factors that can modify action recognition, such as kinematics (e.g., Martel, Bidet-Ildei, & Coello, 2011; Meary, Kitromilides, Mazens, Graff, & Gentaz, 2007), orientation (e.g., Pavlova & Sokolov, 2000; Simion et al., 2008; Sumi, 1984), context (e.g., Amoruso, Finisguerra, & Urgesi, 2016; Amoruso & Urgesi, 2016; Van Overwalle & Baetens, 2009) or agent (e.g., Matsuda, Hiraki, & Ishiguro, 2016; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). Indeed, by investigating the effects of priming with PLD on action verb processing in three experiments, Beauprez & Bidet-Ildei (2018) have shown that action kinematics, but not action orientation, are crucial in the link between biological perception mechanisms and action verb processing. During these experiments, participants had to perform a semantic decision task (i.e., decide whether a verb implied a movement of the body) after seeing a biological or modified PLD. The modifications could concern the kinematics or the orientation of the action. When

kinematics were greatly modified (i.e., the inverse of the biological motion), the facilitation normally observed when participants had to process an action verb after seeing a congruent PLD disappeared. Interestingly, the absence of a facilitation effect occurred only when crucial limbs related to the action were affected (e.g., the legs in the verb “run”). In contrast, the modification of the orientation (e.g., showing an upside-down point-light action) or a small modification in the kinematics (constant velocity) had no effect on the link between action observation and action verb processing. Globally, these results show that the strength of the action-language relationship can be affected by a large modification in the action kinematics (inverse tangential velocity). This finding could be compatible with the motor approach because this effect is only observed when the main joints used in the production of the action are affected. However, this effect could also be related to a perceptual gap between the observed action and the perceptual action representation, which could be compatible with the perceptual approach. In agreement with this latter hypothesis, the results show that the link between action observation and language can persist even when the observed action cannot be simulated at the motor level (upside-down movement or constant velocity), which confirms the idea that the motor component is not essential in the link between action observation and action language processing.

Other studies have shown that the context of the action is also crucial in the relationship between action observation and action verb processing (see Figure 3B). For example, Beauprez et al. (2018) have demonstrated that observing an action in an unusual context (e.g., a woman writing on a pig’s back) does not facilitate the subsequent judgment of congruent action verbs (e.g., “write”), whereas the same action produced in a usual context (e.g., a woman writing on paper) does. For the authors, this effect was probably due to a default to access to the semantic representation of the verb when the action is embedded in unusual context. In agreement with this finding, Beauprez et al. 2019 compared the topographical

patterns of activities when humans observed an action embedded in usual or unusual contexts and showed that the main differences between the usual and unusual observed actions appear during the semantic access of the verb and the motor preparation of the answer. Finally, the agent that makes the action can also affect the link between action observation and action verb processing. Supporting this view, Beauprez et al. (2019) have shown that presenting videos of Nao, a robotic agent performing an action, does not affect the subsequent processing of action verbs. In contrast, an effect appears when the agent producing the action is a human. Interestingly, this effect is not systematic but seems to be dependent on familiarity with the robotic agent. Therefore, in the Japanese population, which is familiar with robots, or in French people, who are familiar with Nao robots, actions made by the robotic agent can prime the subsequent processing of action verbs. As it is not likely that humans can simulate actions as robotic agents, this effect is therefore more compatible with a perceptual approach. Indeed, we can suppose that perceptual experiences with robotic agents can modify the semantic representations of actions, leading to the strengthening of the link between action and language. For example, we can assume that people who are familiar with robotic agents associated the production of cleaning by both the robotic agent and the human agent with the verb “to clean”.

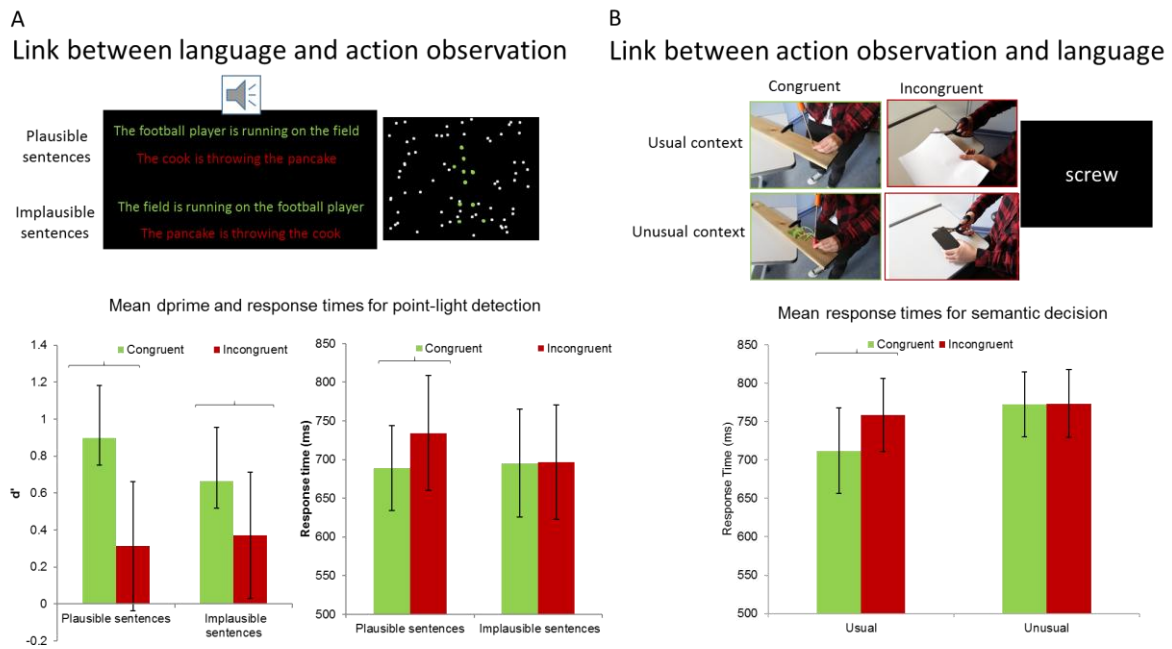


Figure 3: Procedure and results obtained in experiments testing the effect of context on the link between language and action observation (A) and on the link between action observation and language (B). These experiments compared the performance for congruent (when the action and the verb are the same) and incongruent (when the action and the verb are different) trials in different contexts of language (plausible vs implausible sentences, A) or action (usual vs unusual actions, B) presentation. The graphs represent the mean performances in the different conditions. Error bars represent 95% confidence intervals. Braces represent significant differences at $p < .05$. Globally, the results show that context affects performance in both tasks (adapted from Bidet-Ildei et al., 2017 & Beauprez et al. 2019 with permission).

The role of experience

Some authors have shown that motor experience can directly affect the link between action observation and action verb processing. Indeed, motor activation related to action language processing is stronger when participants have motor experience with the action (Fargier et al., 2012; James & Swain, 2011; Lyons et al., 2010; Tomasino, Guatto, Rumiati, & Fabbro, 2012; Tomasino, Maieron, Guatto, Fabbro, & Rumiati, 2013). For example, by using fMRI, Lyons et al. (2010) have shown that ice hockey experts show more neural activation in the left inferior frontal gyrus and in the left dorsal premotor cortex when they have to silently read

action sentences related to ice hockey practice, revealing that the motor repertoire directly intervenes in action language processing. Moreover, the effect of motor experience could be dependent on the feasibility of the action and the context (Tomasino et al., 2012, 2013). Indeed, when experts have to silently read impossible action sentences associated with positive commands, activation in the primary motor cortex and premotor cortex decreased (Tomasino et al., 2013). Interestingly, the effect of experience was also demonstrated in motor learning studies (Fargier et al., 2012; James & Swain, 2011). Indeed, mu rhythm desynchronization, which is an index of mirror-related activity (e.g., Virji-Babul et al., 2008), appeared during the processing of new verbal stimuli, but only if these stimuli had been previously associated with an action in the learning phase. This result suggests that motor associations between verbal stimuli and actions are crucial to the link between action and language (Fargier et al., 2012). However, motor practice does not seem essential. Actually, visual familiarization with the action of a non-human agent was sufficient to activate motor representations during action verb processing (Beauprez, Bidet-Ildei, & Hiraki, 2019). Recently, a study has directly tested the role of motor and observational experiences in the link between action observation and action-verb processing by comparing the priming effect induced by unusual actions before and after a learning phase consisting of motor practice or the observation of unusual actions (Beauprez, Blandin, Almecija, & Bidet-Ildei, submitted). In agreement with previous studies, unusual actions did not prime action verb processing before training (Beauprez et al., 2018; Beauprez et al., 2019). However, after practice or the observation of unusual actions, the facilitation effect was present, suggesting that motor and visual experiences are crucial in the activation of motor representations related to action verb processing.

Globally, these experiments suggest that motor or visual experiences can affect the link between action observation and language. Thus, it is difficult to disentangle motor or

perceptual approaches. Indeed, considering the motor approach, we can speculate that the effects of motor experience are directly related to the capacity to simulate the action at the motor level. This view could also account for the effect of observational learning because it is known that observation and production are based on similar mechanisms (Press 2011). However, these effects could also be related to the perceptual approach, in which motor practice could hone the perceptual experience of participants to reinforce the semantic representation of actions. In this sense, we can speculate that the effect shown in experts in a particular motor action could be due to the activation of a correlated motor component that can intervene in the link between action and language when motor expertise is strong. This idea is compatible with the hypothesis that motor simulation does not accompany systematic action verb processing (Tomasino & Rumiati, 2013; Willems, Toni, Hagoort, & Casasanto, 2010).

The role of the task

Finally, several studies have shown that the task performed by the participants helps determine the activation of the link between action and language (Papeo et al., 2009; Spunt & Lieberman, 2012). Indeed, Papeo and collaborators have studied brain activity in the primary motor cortex related to action verb processing. In this work, they compared the performance on a semantic decision task (i.e., deciding whether a verb is action-related) or a syllabic decision task (i.e., deciding how many syllables the verb has) while transcranial magnetic stimulation was applied to the primary motor cortex. The results show that both reaction times and accuracy differ based on the function of the task, suggesting that the involvement of the primary motor cortex is not automatic during action verb processing but is dependent on the task performed by participants. In agreement with this finding, Spunt and Lieberman (2012) have shown that the activation of the mirror neuron system related to action sentence

understanding fluctuates based on whether participants focus on the action implementation (How did the person perform the action?) or the action motivation (Why did the person perform the action?). Specifically, they showed that the understanding of action motivation is more associated with the activation of a mentalizing system (i.e., a system devoted to the understanding of mental states), whereas the understanding of action implementation is more associated with the activation of the mirror neuron system. Interestingly, in the left hemisphere, the activation of the mirror neuron system (namely, the posterior part of the inferior frontal gyrus, ventral premotor cortex, anterior part of the intraparietal sulcus, rostral inferior parietal lobule and dorsal premotor) did not differ when the action was presented visually or in a sentence, suggesting that both tasks are based on the same mechanism.

Together, these studies challenge the motor approach by demonstrating that the recruitment of motor components in action verb processing is not systematic but is instead related to the specifics of the task. Moreover, the common brain network associated with the processing of action verbs or action observation is compatible with the perceptual approach, since it is suggested that action observation and action verb processing are based on the use of common semantic action representations.

In summary, many studies have shown that the observation of actions and the processing of action verbs maintains a bidirectional relation based on the activation of common perceptual representations (Aziz-Zadeh et al., 2006; Bidet-Ildei, Sparrow, et al., 2011; Bidet-Ildei & Toussaint, 2015; Tettamanti et al., 2005). Interestingly, the activation of these representations is flexible and dependent on many characteristics. Specifically, the strength of such representations is related to the characteristics of the action verb presentation (i.e., the semantic context and the category of the verbs), the characteristics of the action presentation (i.e., the kinematics of the action, the context of the action and the agent producing the action), the personal characteristics of the subject (their motor and visual experiences and

their familiarity with the action) and the task itself (i.e., action vs non-action related task), resulting in evidence for both a lack of connection and a strong connection between action observation and action verb processing. Figure 4 shows the model proposed in Figure 1, with the addition of modulators to increase or decrease the activation of the semantic representations of the action.

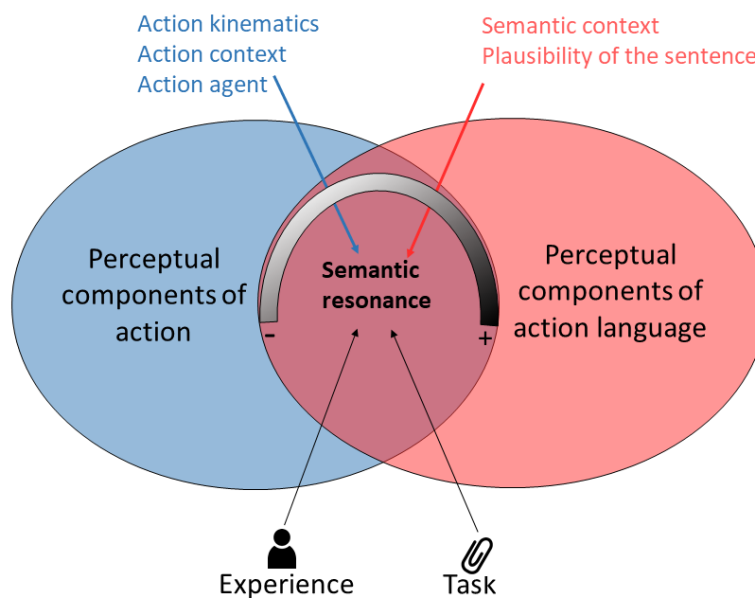


Figure 4: The model proposed in Figure 1, with the addition of a gradient that can regulate the intensity of the semantic resonance (i.e., the activation of action semantic representations) depending on the action characteristics (in blue), language characteristics (in pink) and external characteristics (individual experiences or task).

Open questions and future directions

In this paper, we reviewed several lines of evidence showing a strong link between action observation and action verb processing, demonstrating that each activity influences the others. This result is clearly compatible with the view that the link between action and action verb processing is based on the bi-directional activation of common perceptual representations that

share action meaning between activities (Aziz-Zadeh et al., 2006; Badets & Osiurak, 2017; Bidet-Ildei & Toussaint, 2015; Rizzolatti & Craighero, 2004). For us, this shared perceptual representation could be represented by the semantic representations of actions, which is evoked through the use of semantic resonance (see Figures 1 and 4). Moreover, considering the original paradigms, the link between action observation and action verb processing has been specified, which is now thought to be flexible and mainly dependent on a gradient intensity related to action, language and individual characteristics (see Figure 4). Importantly, even though we consider that action observation and action word processing are related through the mechanism of semantic resonance, in the present model, this mechanism is not necessarily related to the conscious recognition of action. Indeed, the experiments testing the effects of the action characteristics in the link between action observation and action verb processing have clearly demonstrated that this link was independent of the explicit recognition of action. For example, in an unusual context (Beauprez et al., 2018; Beauprez, Laroche, et al., 2019), with inverse kinematics (Beauprez & Bidet-Ildei, 2018) or with robotic agents (Beauprez, Bidet-Ildei, et al., 2019), perceived action is always well recognized, even though the link between action observation and action verb processing substantially decreases.

However, some questions remain open. For example, we may wonder what the exact role of the mirror neuron system is.

Some authors suggest that the activation of the mirror neuron system could directly intervene in the retrieval of the meaning of the word (Barsalou, 2008; Beauprez & Bidet-Ildei, 2018; Bidet-Ildei et al., 2011; Fischer & Zwaan, 2008; Rizzolatti & Craighero, 2004; Zwaan & Taylor, 2006), whereas others suggest that this effect is just an epiphenomenon that accompanies accessing the meaning (Bedny & Caramazza, 2011; Caramazza, Anzellotti, Strnad, & Lingnau, 2014; Mahon & Caramazza, 2008). One way to better understand these

alternative hypotheses could be to more systematically study action verb understanding in populations presenting atypical functioning in the mirror neuron system, such as in patients with autism (Dapretto et al., 2006; Manuel de Vega et al., 2019; Martineau, Andersson, Barthelemy, Cottier, & Destrieux, 2010) or schizophrenia (Enticott et al., 2008; Mehta, Thirthalli, Basavaraju, Gangadhar, & Pascual-Leone, 2014). Indeed, if the mirror neuron system is directly involved in the retrieval of the meaning of action verbs, we should find atypical performance in action verb understanding in these patients related to difficulties in the interpretation of visual actions. Moreover, if we consider that the mirror system is directly implicated in the retrieval of word meaning, social factors such as group membership or social stereotypes should modulate the link between action observation and action verb processing. For example, related to the fact that perception–action coupling is limited to the in-group (Gutsell & Inzlicht, 2010), we could suppose that the visual presentation of an action realized by an out-group person would activate the semantic representations of action less strongly, resulting in a weak link between action observation and action language processing.

Moreover, it could be suggested that semantic resonance can account for the link between action production and language. Indeed, several studies have shown that action production and action language processing are directly linked (notably with studies that demonstrate the specific activation of the primary motor cortex during action verb processing; (e.g., Hauk et al., 2004). Traditionally, these results have been explained by the use of a motor simulation to access the meaning of an action word (e.g., Pulvermüller, 2005). However, these results could also be explained through the gradient of semantic resonance, with the idea that action language processing activates semantic action representations that may or may not activate the motor component of action, i.e., a motor simulation of the action. This idea would be compatible with the view that common representations of action are more perceptual than motor (Caramazza et al., 2014) and could explain how conscious awareness (Bottini, Bucur,

& Crepaldi, 2016) and strategy (Tomasino & Rumiati, 2013) can directly modulate the intervention of a motor simulation. One way to separate these conceptions would be to directly compare in the same participants the priming effect of action production and action observation on action verb processing. If the link between action and language is based on the activation of shared perceptual representations of the action meaning (and not on motor representations), we can hypothesize that the link between action observation and action verb processing should appear earlier and should be stronger than the link between action production and action verb processing.

Conclusion

In this paper, we present and defend the perceptual explanation of the link between action and language through the activation of common semantic representations that are used both to understand the behavior of others and to understand language. Specifically, we challenge this model with literature outlining studies of the link between action observation and action language processing, and we emphasize the compatibility of the model with the results in the literature. Clearly, behavioral, neurophysiological and neuropsychological studies reveal that motor components are not essential in the link between action and language and that action processing and language observation share common semantic representations. The main points that we have raised in our review are that (1) action observation and action language are based on common perceptual features, (2) the common semantic representations between action and language contain action and language characteristics, and (3) the link between action observation and action language processing is flexible and depends on individual experiences and the task itself. Future studies should determine how this model can account for the literature on action production and language and how the link between action and language is related to social interactions. The next theoretical step will be to parsimoniously

reconcile the motor and the perceptual approaches through a broader perspective to delineate and understand their specific roles in the functional link between action and language.

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