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Brain dynamics in the comprehension of action-related language. A time-frequency analysis of mu rhythms

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ABSTRACT

EEG mu rhythms (8–13 Hz) recorded at fronto-central electrodes are generally considered as markers of motor cortical activity in humans, because they are modulated when participants perform an action, when they observe another's action or even when they imagine performing an action. In this study, we analyzed the time-frequency (TF) modulation of mu rhythms while participants read action language ("You will cut the strawberry cake"), abstract language ("You will doubt the patient's argument"), and perceptive language ("You will notice the bright day"). The results indicated that mu suppression at fronto-central sites is associated with action language rather than with abstract or perceptive language. Also, the largest difference between conditions occurred quite late in the sentence, while reading the first noun, (contrast Action vs. Abstract), or the second noun following the action verb (contrast Action vs. Perceptive). This suggests that motor activation is associated with the integration of words across the sentence beyond the lexical processing of the action verb. Source reconstruction localized mu suppression associated with action sentences in premotor cortex (BA 6). The present study suggests (1) that the understanding of action language activates motor networks in the human brain, and (2) that this activation occurs online based on semantic integration across multiple words in the sentence.

Introduction

Action-related language is currently an active field of research within the so-called embodied semantic approach to linguistic meaning. This approach claims that meaning is grounded in our perceptive and motor interactions with the world. From a neurobiological point of view, embodied theories postulate that language comprehension partially relies on modality-specific neural systems for perception and action (Barsalou, 1999; Barsalou et al., 2003; Barsalou, 2008; Damasio et al., 2004; Fischer and Zwaan, 2008; Glenberg and Gallese, 2011; de Vega et al., 2008). Neuroimaging studies have reported activations in the motor and premotor brain regions during the comprehension of action-related language. Some of these studies found motor activation when people process action verbs presented in isolation (Hauk and Pulvermüller, 2004; Pulvermüller, 1996; Pulvermüller et al., 2005; Rizzolatti and Luppino, 2001), and others have found similar motor activation when people process action-related sentences (Aziz-Zadeh et al., 2006; Moody and Gennari, 2010; Raposo et al., 2009; Tettamanti et al., 2005; Urrutia et al., 2012; De Vega et al., 2014).

Such results have been taken as evidence that motor networks in the brain are involved in the processing of action-related language, although some important issues still remain unsolved (de Vega et al., 2008; Mahon and Caramazza, 2008). One of these issues is the need to determine whether language-induced motor activations are exclusively lexical or are dependent to some extent on the semantic context. One possibility is that the activation of the motor cortex occurs automatically about 150–200 ms after the onset of action verbs, as part of their lexical processing (Pulvermüller et al., 2005; 2009; Boulenger et al., 2006; Buccino et al., 2001; Nazir et al., 2008; Sato et al., 2008). Another alternative is that the activation of the motor cortex associated with reading is a non-automatic, context-dependent process, involving *lexical–semantic integration* across the sentence. The latter proposal is based on neuroimaging (Moody and Gennari, 2010; Schuil et al., 2013; Raposo et al., 2009; Urrutia et al., 2012), and brain stimulation studies (Cacciari et al., 2011; Buccino et al., 2005; Tomasino et al., 2008; Papeo et al., 2009). For example, in a fMRI experiment Raposo et al. (2009) reported that action verbs activate motor regions when they appear in concrete literal sentences (e.g., kick the ball), whereas the

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same verbs in idiomatic sentences do not activate motor regions (e.g., kick the bucket). In the same vein, Cacciari et al. (2011) employing single-pulse TMS on the left leg-related motor cortex while participants read leg-related action verb embedded in sentences, reported modulations of cortico-spinal excitability only when the action verbs appeared in a literal or metaphorical context, but not when the same verbs appeared in idioms.

Given the poor temporal resolution of hemodynamic neuroimaging and single-pulse TMS techniques, the above studies of language comprehension mainly provide a neuroanatomical view on motor activation in the brain. The present study uses a different strategy by recording moment-to-moment changes in mu and beta oscillatory rhythms in the EEG, which are generally considered as markers of motor processes in the brain (Pfurtscheller, 1992; Pfurtscheller et al., 1997; Pfurtscheller and Lopes da Silva, 1999). Mu rhythms are 8–13 Hz oscillations generated in the motor and premotor cortex, which provide a high-resolution window onto the temporal dynamics of motor activation (Gastaut, 1952; Muthukumaraswamy et al., 2004). Specifically, mu synchronization reflects neural activity correlating with a deactivated motor cortex, whereas mu suppression or desynchronization can be attributed to an increase in neural activity of the motor and premotor cortex (Kuhlman, 1978; Pfurtscheller et al., 1997). Thus, these rhythms become suppressed or desynchronized when participants move, observe other's movements, or imagine their own movements, especially if these movements are manual (Cochin et al., 1998; McFarland et al., 2000a, 2000b; Pfurtscheller et al., 2006; Pineda, 2005).

Recently, some studies have reported that mu rhythms, and to some extent beta rhythms, can also be modulated by action-related language. Thus, Moreno et al. (2013) asked their participants to listen to sentences referring to manual actions (e.g., Now, I cut the bread) or abstract sentences (e.g., Now, I doubt the plan), and also to watch video clips of an actress performing simple manual actions. The results indicated that both action language and action videos caused mu (8–13 Hz) and low beta (15–20 Hz) power suppression at fronto-central electrodes, whereas abstract language did not, confirming that understanding action language activates motor networks in the brain. However, Moreno et al.'s study did not allow for assessing the temporal evolution of the mu and beta rhythms. In another study, van Elk et al. (2010) used time-frequency analysis while participants read action sentences and observed larger suppression in mu and beta rhythms in response to the action verb ("swimming") paired with an animal agent (e.g., duck) compared to a human agent (e.g., the woman), suggesting that motor resonance is a context-dependent and integrative phenomenon, as it depends on the previously mentioned agent. One drawback of the study, however, is that the absence of non-action sentences as a contrasting condition does not allow the conclusion that these time-resolved mu and beta rhythms are exclusively modulated by action language. A different research strategy was employed by Fargier et al. (2012). They trained participants to associate new words with action related videos or with visual motion videos in two sessions. After the second training session they found mu suppression for action-associated words presented alone at fronto-central sites.

The present study goes one step further than the previous brain dynamics studies on action language. Our first goal was to determine whether motor processes in the brain are specific to action language. We therefore examined the modulation of mu and beta rhythms by contrasting action sentences with non-action sentences. Specifically, we employed three types of contents: action sentences referring to concrete manual actions, abstract sentences referring to mental states or processes, and perceptive sentences referring to sensory events. All sentences were written in the second person because the pronoun "you" most likely induces an egocentric perspective (Brunyé et al., 2009), and in the future tense because preparing to perform an action elicits stronger motor activity than an action already performed (Candidi et al., 2010). We expected to find mu and beta modulation (suppression) in action sentences but not in abstract sentences, confirming our previous findings (Moreno et al., 2013). We were however particularly interested in the contrast between action sentences and perceptive sentences, which to our knowledge has never been used in conjunction with an analysis of EEG oscillations. One possibility is that only action sentences modulate mu rhythms, which would indicate that motor cortical activity is very specific to the semantics of action sentences. A second possibility is that perceptive sentences also modulate mu rhythms to some extent, perhaps because the sensory processes described by the sentences also involve motor actions like head movement or body postural changes, or because perception and action are closely related processes in the brain. If this is the case, then we should observe equally strong mu and/or beta suppression for the action and the perception conditions over sensorimotor electrodes. Finally, given that perceptive sentences describe mostly visual events, we may also expect differential activation of cortical areas responsible for visual processing (i.e. occipital and inferior-temporal lobes), thereby producing differential alpha suppression over these areas (Bastiaansen and Brunia, 2001; Pulvermüller et al., 1999; Klimesch et al., 2007; Weisz et al., 2011; Woertz et al., 2004).

Our second goal was to examine whether the activity in the motor cortex is exclusively triggered by the action verbs, involving purely lexical and automatic motor resonance, or whether motor cortical activity requires the integration of linguistic units (verb + noun in our materials) to build up a specific motor simulation of the complete action. With this aim in mind we employed time-frequency analysis (hereafter TF) of mu and beta rhythms across the whole sentence. The action sentences in this study were written in such a way that the action was not entirely specified at the verb, but was completed by the two nouns that immediately followed the verb (see Table 1). If mu/beta suppression occurs exclusively at the action verb this would support the idea that modulation of motor activity is purely lexical. By contrast if mu/beta suppression occurs in the nouns following the verb, we can assume that if a context is supplied, modulations of motor activity result from integration of meaning across the sentence.

We also presented participants incongruent action sentences to have additional information about the integration of meaning across sentences. Incongruent action sentences used the same verbs as congruent action sentences, but they included an object name that made them non-sensical. Processes of semantic integration have typically been associated with the N400 ERP component, a negative deflection found over centro-parietal electrodes, peaking approximately 400 ms after word onset (Kutas and Hillyard, 1984). We therefore could expect an N400 effect after the onset of the noun directly following the verb where the sentence congruence or incongruence emerges.

Table 1
Example stimulus materials. The verb, the Noun1 and the Noun2 are marked in bold.

Congruent Action sentences	
Spanish	**Abrirás** la **puerta** de la **habitación**
English	You **will open** the **door** of the **room**
Congruent Perceptive sentences	
Spanish	**Escucharás** la **orden** del **maestro**
English	You **will hear** the **teacher's command**
Congruent Abstract sentences	
Spanish	**Dudarás** del **diálogo** del **paciente**
English	You **will doubt** the **patient's dialog**
Incongruent Action sentences	
Spanish	**Abrirás** el **color** del **techo**
English	You **will open** the **color** of the **roof**
Incongruent Perceptive sentences	
Spanish	**Escucharás** el **retrato** del **álbum**
English	You **will hear** the **photo** of the **book**