



Event-related desynchronization of mu and beta oscillations during the processing of novel tool names

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ABSTRACT

According to the embodied cognition framework, the formation of conceptual representations integrates the type of experience during learning. In this electroencephalographic study, we applied a linguistic variant of a training paradigm, in which participants learned to associate novel names to novel tools while either manipulating or visually exploring them. The analysis focused on event-related desynchronization (ERD) of oscillations in the mu and beta frequency range, which reflects activation of sensorimotor brain areas. After three training sessions, processing names of manipulated tools elicited a stronger ERD of the beta (18–25 Hz, 140–260 ms) and the lower mu rhythm (8–10 Hz, 320–440 ms) than processing names of visually explored tools, reflecting a possible re-activation of experiential sensorimotor information. Given the unexpected result that familiarized pseudo-words elicited an ERD comparable to names of manipulated tools, our findings could reflect a suppression of sensorimotor activity during the processing of objects with exclusively visual features.

1. Introduction

The semantic memory system contains our knowledge about the world. It provides the basis for many complex behaviors, from the categorization of stimuli to the communication with others. The neural underpinnings of semantic knowledge are still a matter of debate. Theoretical approaches range from amodal/symbolic (e.g. Fodor, 1975) to strongly embodied theories (Gallese & Lakoff, 2005; Glenberg, 1997; Glenberg & Kaschak, 2003). They form the extremes of a continuum of theoretical accounts, with the former postulating a complete independence, the latter a complete dependence of semantic processing on modality-specific systems (e.g. sensory but also motor and emotional; for reviews see Binder & Desai, 2011; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). According to more moderate accounts, semantic processing is associated with (Mahon & Caramazza, 2008; Patterson, Nestor, & Rogers, 2007) or partially relies on (Barsalou, 2008; Pulvermuller, 2001) modality-specific systems, in coordination with higher order convergence zones (Binder & Desai, 2011; Meteyard et al., 2012). The exact role of modality-specific systems, however, is still debated. The focus of the debate concerns the hypothesis put forward by embodied accounts that the representation and retrieval of semantic knowledge partially reactivates the respective modality-specific networks that were active during the original experience with the concepts' referents (Barsalou, 2008; Meteyard et al., 2012;

Pulvermuller, 2001). Focusing on knowledge about manipulable objects such as tools, their function, manipulation, and motion can be considered as particularly relevant types of experiential information (Beauchamp & Martin, 2007), which are thus supposed to become an integral part of the tool concepts' neuronal representation (Kiefer & Pulvermuller, 2012).

The role of experience postulated by embodied cognition accounts has been supported by neuroimaging studies on conceptual processing of familiar tools. They revealed an activation of a left-hemispheric fronto-parietal network, which comprised, among others, action-related areas underlying object manipulation as well as areas subserving functional knowledge (Canessa et al., 2008; Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Dekker, Mareschal, Johnson, & Sereno, 2014; Devlin, Rushworth, & Matthews, 2005; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Perani et al., 1995; Simanova, Hagoort, Oostenveld, & van Gerven, 2014). Results were similar when conceptual representations were accessed either via tool pictures or tool names (for reviews see Cappa, 2008; Noppeney, 2008). Patients with lesions in this network were shown to be impaired in their ability to generate or imitate tool-directed movements (Buxbaum, Shapiro, & Coslett, 2014) and showed deficits in conceptual processing of action-features in an object identification task (Lee, Mirman, & Buxbaum, 2014).

The role of experience in acquiring and processing conceptual representations, however, can more directly be tested by applying

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training protocols on unfamiliar objects. In this case, concept acquisition takes place in a laboratory environment, and the modalities of experience can be experimentally controlled. Manipulation training studies showed an activation increase in a distinctive, action-related fronto-parietal network for processing pictures of knots (Cross et al., 2012) or novel tool-like objects (Bellebaum et al., 2013; Ruther, Tettamanti, Cappa, & Bellebaum, 2014; Weisberg, van Turenout, & Martin, 2007).

The timing of the recruitment of modality-specific brain regions is of particular importance in order to unravel the nature of their contribution to conceptual processing (Kiefer & Pulvermüller, 2012). Using electroencephalography (EEG) and familiar object concepts, object-category selective effects were seen between 110 and 250 ms after the presentation of words or pictures referring to tools vs. other objects in event-related potentials (ERPs; Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Proverbio, Adorni, & D'Aniello, 2011). In an extensive training study with novel objects and their names, the early P1 ERP component reflected a functional experience-dependent priming effect of object category names on the processing of pictures of novel objects already 117 ms after stimulus onset (Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007). In this study, a source analysis linked ERP components between 270 ms and 400 ms to the premotor cortex for categories defined by object function. ERP studies thus provided evidence of an early experience-dependent recruitment of motor areas during conceptual processing, suggesting that conceptual information is grounded in modality-specific regions (Kiefer & Pulvermüller, 2012).

An EEG-based measure often linked to the activation of (primary) sensorimotor areas is the suppression of the so-called mu rhythm in the alpha frequency range of 8–12 Hz and frequencies in the beta range of 13–35 Hz (Neuper, Wortz, & Pfurtscheller, 2006). The mu rhythm itself reflects an idling state of reduced activity of the sensorimotor cortex (Kuhlman, 1978) whereas the beta rhythm has been linked more closely to the primary motor cortex (Jasper & Penfield, 1949). Consequently, electro- and magnetoencephalographic studies showed that mu and beta rhythm suppression occurs before and/or during active movement (Chatrian, Petersen, & Lazarte, 1959; Pfurtscheller & Neuper, 1992; Pfurtscheller, Stancak, & Neuper, 1996; Salenius, Schnitzler, Salmelin, Jousmaki, & Hari, 1997). There is evidence that it also occurs during movement observation (Babiloni et al., 2002; Caetano, Jousmaki, & Hari, 2007), and movement imagination (Pfurtscheller, Brunner, Schlogl, & Lopes da Silva, 2006; Pfurtscheller & Neuper, 1997). Studies combining electrophysiological measures and functional magnetic resonance imaging could further show that the mu and beta frequency are inversely related to activation within sensorimotor and motor areas in movement execution and imagery (Bonstrup, Schulz, Feldheim, Hummel, & Gerloff, 2016; Formaggio, Storti, Cerini, Fiaschi, & Manganotti, 2010; Jancke, Lutz, & Koeneke, 2006; Pfurtscheller, 2001; Ritter, Moosmann, & Villringer, 2009; Yin, Liu, & Ding, 2016).

In the context of conceptual processing, the perception of familiar tool pictures (140 ms after stimulus onset) or reachable and graspable objects in a virtual reality environment (300 ms after stimulus onset) elicited a mu rhythm suppression (10–12 Hz in Proverbio (2012); 8–12 Hz in Wamain, Gabrielli, and Coello (2016), respectively). The perception of manipulable objects in different contexts elicited beta (12–16 Hz and 20–25 Hz) suppression in sensorimotor areas after 400–600 ms (Natraj et al., 2013). Further, the beta band (16–24 Hz) desynchronization differentiated between meaningful and meaningless object-directed movements (van Elk, van Schie, van den Heuvel, & Bekkering, 2010). Notably, action-related language processing also appears to recruit sensorimotor areas, as mu and beta frequencies were modulated within 500 ms after the stimulus presentation (Alemanno et al., 2012; Moreno, de Vega, & Leon, 2013; Moreno et al., 2015; Niccolai et al., 2014; van Elk, van Schie, Zwaan, & Bekkering, 2010; for a review on beta oscillations see Weiss & Mueller, 2012).

For experience-induced novel tool representations, effects on mu rhythm suppression have been found as well. Ruther, Brown, Klepp,

and Bellebaum (2014) reported a stronger suppression during the processing of object pictures in the lower mu frequency band (8–10 Hz), which occurred over central electrodes after observational manipulation training as compared to visual exploration training. A potential criticism when using tool pictures as stimuli is that the visual input might prime actions afforded by the objects (e.g., Tucker & Ellis, 2004), especially as embodied conceptual action-information cannot be disentangled from affordances (Glenberg, 1997). To address this issue, the present study applied a linguistic variant of the training paradigm with novel tool-like objects (from now on referred to as tools; Bellebaum et al., 2013; Ruther, Brown, et al., 2014; Ruther, Tettamanti, et al., 2014). As described above, linguistic stimuli can indeed access conceptual representations of tools as well as action verbs in semantic memory, while their visual appearance does not carry any motor- or action-related information.

In this linguistic variant of the training paradigm, we let our participants form conceptual representations of novel tools through either active manipulation or visual experience. Meanwhile, they learned a pseudo-word assigned to each tool, which served as the tool's name. In a post-training EEG session, we applied a linguistic task to investigate whether the processing of the newly learned names recruits sensorimotor areas differentially, depending on whether the names referred to tools associated with either active manipulation or visual experience in the learning phase. In order to examine the time-course of the recruitment of sensorimotor areas in the processing of the novel tool names, we applied the event-related de-/synchronization method (ERD/ERS; Pfurtscheller & Lopes da Silva, 1999) on mu and beta frequency bands measured via EEG.

We hypothesized to find a stronger sensorimotor activation, reflected in mu and beta desynchronization, during the processing of names of actively manipulated tools compared to the names of tools that were only visually explored as well as to familiar pseudo-words without any object-association. For the mu frequency, we expected experience-dependent effects to occur especially in the lower range (8–10 Hz), which is thought to be less movement-type-specific than the upper range (10–12 Hz) (Pfurtscheller, Neuper, & Krausz, 2000), as the objects we used required different manipulations (see also Ruther, Brown, et al., 2014). For beta, we analyzed the 18–25 Hz beta frequency band since comparable ranges showed the strongest response in conceptual action-language processing (Moreno et al., 2013; Schaller, Weiss, & Muller, 2017; van Elk, van Schie, Zwaan, et al., 2010). Finally, the high temporal resolution of the ERD/ERS method is critical for assessing whether the recruitment occurs during early conceptual word processing or in a later, post-conceptual phase (according to embodied and disembodied theories, respectively; for a discussion, see Mahon & Caramazza, 2008). In addition, we considered also the temporal alignment of mu and beta effects. Sebastiani et al. (2014) showed a dissociation of these two frequency bands during action execution and observation and interpreted it in terms of different underlying motor-activation processes. The literature on action-language processing is contradictory with respect to the relative timing of mu and beta desynchronization (compare e.g. Niccolai et al., 2014; van Elk, van Schie, Zwaan, et al., 2010), so that this aspect was of particular interest for the present study.

2. Method

2.1. Participants

Twenty-three healthy German native speakers took part in this study. One participant had to be excluded from data analysis due to performance at chance level in the EEG task (mean accuracy = 48.2%). This resulted in a sample of 22 (six men) healthy young adults aged between 19 and 31 years ($M = 23.3$ years, $SD = 3.7$ years) without a history of psychiatric or neurological diseases. All participants reported to be right-handed, as indicated by the Edinburgh Handedness

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