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Language and action in Broca's area: Computational differentiation and cortical segregation

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ABSTRACT

Actions have been proposed to follow hierarchical principles similar to those hypothesized for language syntax. These structural similarities are claimed to be reflected in the common involvement of certain neural populations of Broca's area, in the Inferior Frontal Gyrus (IFG). In this position paper, we follow an influential hypothesis in linguistic theory to introduce the syntactic operation Merge and the corresponding motor/conceptual interfaces. We argue that actions hierarchies do not follow the same principles ruling language syntax. We propose that hierarchy in the action domain lies in predictive processing mechanisms mapping sensory inputs and statistical regularities of action-goal relationships. At the cortical level, distinct Broca's subregions appear to support different types of computations across the two domains. We argue that anterior BA44 is a major hub for the implementation of the syntactic operation Merge. On the other hand, posterior BA44 is recruited in selecting premotor mental representations based on the information provided by contextual signals. This functional distinction is corroborated by a recent meta-analysis (Papitto, Friederici, & Zaccarella, 2020). We conclude by suggesting that action and language can meet only where the interfaces transfer abstract computations either to the external world or to the internal mental world.

1. Introduction

The relation between language and action has been approached in the past years from radically different points of view. Embodied Cognition, for example, has postulated that language processing might be achieved through mental simulations of motor contents taking place in the motor system at the cortical level (Fischer & Zwaan, 2008). According to this view, sentence comprehension is related to neural representations that are inherently semantically coherent with the action evoked by the main verb (Barsalou, 1999; Gallese, 2008; Glenberg & Gallese, 2012; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012; Pecher, Boot, & Van Dantzig, 2011; Pezzulo, Candidi, Dindo, & Barca, 2013; Taylor & Zwaan, 2008; Zwaan, 2016). A hallmark finding in this respect is the action-sentence compatibility effect (ACE; Glenberg & Kaschak, 2002), which shows that the behavioral response to a certain action is slowed down when the movement implied by the sentence and the intended movement promoted by the action are incompatible with each other. Albeit stimulating a large body of research, ACE and other motor simulation-related findings in the Embodied Cognition literature (Fischer & Zwaan, 2008) remain confined to a very narrow space of language use. Real-life sentences as well as single words do not transparently map onto actions and thus they are hardly expected to generate motor-related simulations (Goldinger, Papesh, Barnhart, Hansen, & Hout, 2016; Papesh, 2015). Moreover, language use can be considered by itself only a narrow definition of language, as it refers almost exclusively to the symbol-meaning mapping (Sonesson, 2008; Violi, 2008; Zwaan, 2014), without taking into consideration other and equally fundamental computational features of language intended as a system (Fitch, 2011).

A second large class of motor-language mapping theories that has received considerable attention in the last decades posits the existence of common syntactic combinatorial capacities—neurally rooted—at work during the processing of both linguistic structures and movement-goal combinations (Greenfield, 1991; Pastra & Aloimonos, 2012; Pulver-müller, 2014). This view has brought to the hypothesis that action might constitute the biological prerequisite for language to emerge (Fujita, 2009; Maffongelli, D'Ausilio, Fadiga, & Daum, 2019; Roy et al., 2013), following the idea that some basic mechanisms governing the syntax of

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sequential events might be shared across different cognitive domains. In this position paper, we specifically focus on this proposal by raising a number of issues, which we believe need to be carefully addressed:

- (i) How do we characterize language syntax?
- (ii) What features of language syntax are shared with action syntax (if any)?
- (iii) Are action and language implemented similarly at the cortical level?

In addressing these questions, we redefine the space in which action and language can be considered to interact. In Section 2.1 and in Section 2.2, we take a critical look at those theoretical accounts that have attempted to establish a mirror link between the formal structures of language and action. In Section 3.1 and in Section 3.2, we extend our analysis to the neural mechanisms for language and action processing. We first review some of the main findings that led to the identification of the language network in the brain, especially concerning the syntactic operation Merge. We then discuss these findings in the light of current neural models for action processing at the cortical level. We focus on the functional segregation of posterior sub-regions within Broca's area as recently suggested in a meta-analysis of experiments on actions (Papitto, Friederici, & Zaccarella, 2020). In particular, our aim is to discuss this study in a broader context, by addressing how these results can inform the action-language debate. In Section 4, we conclude this work by suggesting both a theoretical and a cognitive outlook for reconsidering the relationship between the two domains in a proactive perspective.

2. Language, action and their computational features

2.1. A theoretical account on language

One major point of divergence in cognitive sciences is that of the definition of language (Bolhuis, Tattersall, Chomsky, & Berwick, 2015). Functionalist views consider language as a symbolic mapping between content and signs being used to communicate complex states of affairs among conspecifics (Reboul, 2015). On this account, all the other animal species use language, given animals' capacity to communicate rather complex meanings through specific movements or vocalizations (e.g., Ralls, Fiorelli, & Gish, 1985). Such a definition can in principle however limit possible considerations into the hypothesis that human language is an enhancement of previously attested systems of communication (Sapir, 1921). Already more than fifty years ago, researchers started to look at diverging points between humans and other animal species using language as an empirical divide (e.g., Hockett, 1959). Our current knowledge allows us to separate language as a communication tool from language seen as a computational cognitive system (Fitch, 2017, 2020). According to the last definition, human language consists of a core computational system that is independent from speech, thus accounting for the fact that (i) it is possible for humans to transfer the linguistic system into other modalities such as signed or written languages (Berwick, Friederici, Chomsky, & Bolhuis, 2013; Trettenbrein, Papitto, Friederici, & Zaccarella, 2020), and that (ii) the vocal tract of other species is in principle fully suitable to produce speech sounds (Fitch, de Boer, Mathur, & Ghazanfar, 2016). An empirical hypothesis put forward in linguistic theory is that the computational system for language might be constituted by a simple recursive combinatorial operation-canonically known as Merge-enabling humans to combine word-like syntactic objects-the lexical items-into hierarchies of phrases and sentences (Chomsky, 1995; Friederici, 2020). The lexical items can be described as bundles of features consisting of both category features (Noun, N; Verb, V; etc.) and selectional features (transitivity, inflection, etc.). Formally speaking, Merge can be seen as a simple syntactic operation forming a new set {a, b} out of two more basic syntactic objects a and b, where one of the two basic objects satisfies some feature requirement of the other-e.g., the requirement of a transitive verb to have a direct object merged with it (Chomsky, 1995). This is canonically also known as external Merge. The newly formed set can in turn be input to a new Merge operation, where *c* is merged with $\{a, b\}$ to output the set $\{c, \{a, b\}\}$ b}} to satisfy further feature requirements. Depending on the syntactic nature of the objects forming the set (i.e., single items, already-formed phrases, or a combination of both), one of the two objects qualifies as the head of the set, thus standing in an asymmetric relationship with the other object. While omitting detailed formalisms, the determination of the head within the set may additionally trigger displacement phenomena. This is also known as internal Merge, a ubiquitous property of language, by which an element is found in a certain position, although it is interpreted somewhere else in the structure (see Moro, 2000). As an example, in the question [Which book] did you read?, which book is interpreted as the object of the verb read, although it is found in a different position within the clause. At the same time, the asymmetric relationship established by the head determines the label of the constituent resulting from the set (i.e., Labeling). In some versions of the Strong Minimalist Thesis (SMT), Labeling is separated from Merge, as a prerequisite for the conceptual-intentional system (see below; Berwick & Chomsky, 2017; Chomsky, 2013; Rizzi, 2016; but see Hornstein, 2009 for a different account). Phylogenetically, recent attempts propose that the basic syntactic objects themselves might be the result of some combinatorial operations merging atomic features together (Fujita, 2017). The Merge-based syntactic system is proposed to interface with two different systems, once all feature requirements are fulfilled: the sensory-motor and the conceptual-intentional systems (Berwick et al., 2013; Bolhuis, Tattersall, Chomsky, & Berwick, 2014; Fujita, 2014; Lasnik, 2002). Through the sensory-motor interface, mental expressions organized into syntactic relationships are linearized according to the modality of use (e.g., speech, writing or sign). Through the conceptualintentional interface, syntactic relationships map to semantic-pragmatic features representing concepts and intentions (Berwick et al., 2013). On this account, the interpretation of linguistic strings cannot be fully captured by properties of the sequential linear order, but rather by the hierarchical structural relations between the phrases assembled by Merge (Everaert, Huybregts, Chomsky, Berwick, & Bolhuis, 2015). Textbook examples are ambiguous linguistic strings, where the same linear order permits multiple interpretations, depending on the way phrases are hierarchically assembled together. Thus, a sequence like black coffee mugs can either be perceived as [black [coffee mugs]] (i.e., coffee mugs which are black-colored) or as [[black coffee] mugs] (i.e., mugs for black coffee). Overall, linguistic strings can be then thought of as the output of a core computational system, including a recursive operation that works on language-dedicated categorical/lexical features, that maps syntactically-specified objects (words, phrases) into structural hierarchies (for a recent account on how the computational system might be split into internal subroutines; see Goucha, Zaccarella, & Friederici, 2017).

While the interfaces are shown to be shared with other domains and with other animal species, the computational core is suggested to be uniquely human (Hauser, Chomsky, & Fitch, 2002). In this respect, empirical evidence showing nonhuman capacity to process sequential structures via language-like hierarchies remains debatable. Indeed, the successful processing of the artificial grammar trials tested in these studies can be solved by invoking simpler cognitive processes that apply over arbitrary sets of symbols, including memorization strategies, visual symmetry or acoustic similarities between test and familiarization trials (Ferrigno, Chevette, Piantadosi, & Cantlon, 2020; Fitch & Hauser, 2004; Heimbauer, Conway, Christiansen, Beran, & Owren, 2018; Jiang et al., 2018; Saffran et al., 2008; Sonnweber, Ravignani, & Fitch, 2015; Wang, Uhrig, Jarraya, & Dehaene, 2015; for a critical review see Beckers, Berwick, Okanova, & Bolhuis, 2017). Nevertheless, artificial grammar learning studies in nonhuman primates and other animals continue to provide fundamental advancements to our knowledge of the limits of sequence processing abilities in our ancestors (Murphy, 2020; Petkov & Ten Cate, 2020).

Limiting our considerations to the human species, the concept of hierarchy has received renewed attention following recent accounts of Lashley (1951)'s seminal work, which led to the investigation of common types of structural hierarchies in various cognitive domains beyond language (Fitch & Martins, 2014; Greenfield, 1991; Rosenbaum, Cohen, Jax, Weiss, & Van der Wel, 2007; for an application of Lashley's proposal to nonhuman species behavior, see Byrne & Russon, 1998). Previously, it was believed that behavior could be explained sequentially, in simple stimulus-response associations (e.g., Washburn, 1916). Lashley questioned this assumption by addressing how the domains of action, music and language can be characterized by sustained plans in which every step promotes the accomplishment of a specific plan, thus moving away from behaviorism. These domains have been extensively discussed both at the cortical level, regarding the possible involvement of similar resources as language in processing hierarchy, and at the computational level in the way they resemble linguistic structures to establish relationships between internal elements (e.g., determiner and noun in language compared to tool and object in actions; Friederici, 2020; Jeon, 2014; Tettamanti & Weniger, 2006; Varley, Klessinger, Romanowski, & Siegal, 2005). We will now turn to the debate concerning action and language, where refined formal accounts of action grammars have been living a stronger encouragement and a consequent refinement, also in evolutionary terms.

2.2. A theoretical account of action

With respect to the motor domain, actions can be conceptualized as hierarchies having goals and sub-goals (Pastra & Aloimonos, 2012; Pulvermüller, 2014). If you want to drink a glass of water, you would need to postulate various steps between you wanting the glass of water and you drinking it (e.g., grasp the bottle, open the bottle, pour the water, put down the bottle, grasp the glass, open your mouth, and only finally drink). These steps are applied to accomplish an initial and conscious goal state (Jeannerod, 2006). The fact that goals and sub-goals are not unconsciously processed, as they guide behavior, is already limitative to action hierarchies. In language, hierarchies are not constrained by the presence or absence of (sub-)goals and are processed in an automatic and unconscious fashion. When wanting to pour water into the glass, you might forget to open the bottle. Therefore, you would need to on-line restructure your action syntax to match the goal, for the reason that your sub-goal (e.g., pouring) did not produce the expected result (e.g., water in your glass). Following the metaphor, either you forgot to fulfill a syntactic requirement while planning the overall action or you correctly planned your action but while performing it you forgot to perform that single step and left empty a syntactic requirement (e.g., because of distraction). In language, there is no goal to be achieved if not the correct application of some structural relationship, which is however a biological requirement and not a conscious one (Moro, 2008). In this respect, human language faculty does not include structures that are considered impossible for the human repertoire and that cannot be learned by infants (Friederici, Chomsky, Berwick, Moro, & Bolhuis, 2017; Moro, 2008). Similarly, it has been argued that "action grammar production rules express the fact that no matter how simple or complex an action is, it has a compulsory goal specifier and a compulsory tool complement" (Pastra & Aloimonos, 2012). However, if a goal specifier is a mandatory requirement for an action, can it be left unaccomplished, as in the example above? Or differently stated, how can we not open a bottle if our planned goal is to drink water, and still have a well-formed action hierarchy? We argue that whatever the action production rule might be, its nature appears to be only constrained by causal/physical properties, which can be restructured in time (Mars, Piekema, Coles, Hulstijn, & Toni, 2007). This has little if no similarity with the way Merge outputs well-formed hierarchies in language, on the basis of relationships between lexical/categorical features. This kind of observation, we believe, still leaves the parallelism between action and language a metaphor at most, since physical causality in action does not seem to equate the abstract requirements for correct structure derivation under Merge in language (Berwick & Chomsky, 2017; see also Boeckx & Fujita, 2014; Moro, 2014a, 2014b).

Nonetheless, different accounts on action syntax have been recently proposed (Fujita, 2009, 2014; Pastra & Aloimonos, 2012; Pulvermüller, 2014; see also Fujita, 2016 for a multidomain analysis of Merge and Labeling via Minimal Search). One formal attempt to describe actions using a SMT-derived theory argues that Merge can be applied to form an action of the type [extend hand [grasp with hand knife [cut with knife bread]]], which depicts the action of cutting some bread with a knife (Pastra & Aloimonos, 2012; see Fig. 1B).

In this action, the set {cut with knife, bread} constitutes an example of a merged element, where {cut with knife} represents an action-tool structure, and {bread} is an object complement. The newly formed set is then merged to other elements to reach the full action described above, in a similar fashion as proposed also by Pulvermüller (2014). However, given this action, constraints apply only in the sense that it is physically impossible to cut the bread if not grasping the knife beforehand. Furthermore, Pastra and Aloimonos (2012) seem to introduce a counterintuitive element in their analysis of a minimalist grammar of action. In defining the relationship between a grammatical sentence and an action, they argue that "for a grammatical sentence, all words must agree. Similarly, in action, all sub-actions must agree in terms of the final goal to be served". However, they also mention that interrupting the action of grasping a glass by starting to grasp an unrelated element (e.g., a ball) and only then going back to grasp the glass should represent a type of true recursion as in embedded sentences of the type The cat the boy saw left. It seems reasonable to argue that grasping a ball is not in "agreement" with the final goal of grasping the glass. A similar observation would lead to the conclusion that this action is following another impossible rule and it has little to do with the role of the phrase [the boy saw], embedded in the previous sentence. On the other hand, we know that the action just described is somehow physically possible and, as humans, we stop constantly to do something else. Thus, there are two different conclusions that we can trace from this parallel: either (i) an action is not determined by its goal (a conclusion that runs against most action theories) or (ii) an action is defined by its goal but then each action represents a detached element and true embedding is impossible. This issue is not trivial because it questions the definition of what we can consider to be an action. Let us observe a similar case: you are peeling an apple. After you peeled half of it, you start drinking some water from your glass. Now that you are not thirsty anymore, you can go back to peel your apple. How many actions are these? It is hard to say, following a goal-based definition of action (Pastra & Aloimonos, 2012). Indeed, each sub-step of an action could already be considered as a whole action itself (Clark, 2013). The considerations in Clark (2013) are not only useful in determining the boundaries of actions but also in finding an appropriate definition of action hierarchy as pertaining to predictive processing mechanisms: "motor intentions actively elicit, via their unfolding into detailed motor actions, the ongoing streams of sensory (especially proprioceptive) results that our brains predict". The hierarchy here is a composition of different levels of action modelling, from high-level symbolic representations to low-level movement feature representations. Each level of the hierarchy translates motor states, such as action goals, into predictions, both proprioceptive (i.e., concerning the consequences of an action in relationship to a goal) and exteroceptive (i.e., concerning the sensory features of the external environment; Pesquita, Whitwell, & Enns, 2018; Picard & Friston, 2014). Adapting an example taken from Ondobaka, Kilner, & Friston (2017), in order to fulfill our goal of grasping a cup, two types of predictions need to be generated: (i) a proprioceptive one, related to the consequences of moving the arm in the direction of the cup and grasping it; and (ii) an exteroceptive one, related to external (action-relevant) features such as the location of the cup, or its configuration with respect to the hand.

In this context, predictive processing can be informative in identifying the type of hierarchy attested in the action domain, this way



Fig. 1. Phrase-structure tree for the sentence: "*the man grasps a knife*" (A) and Action parse tree for the act of "*grasping a knife with the hand*" (B; adapted with permission from Pastra & Aloimonos, 2012). S = sentence; DP = determiner phrase; D = determiner; NP = noun phrase; N = noun; VP = verb phrase; V = verb. A = action primitives; A' = action structures; A'' = maximal projection of an action structure; E'' = maximal projection of an entity structure.

shifting the focus from language-like structures to specific processing mechanisms. Predictive processing accounts link the generative model of the world and the sensory inputs it predicts by using statistical regularities processed by the brain (Kanai, Komura, Shipp, & Friston, 2015; Keller & Mrsic-Flogel, 2018; Kwisthout, Bekkering, & Van Rooij, 2017; Wiese, 2017). In other words, an agent represents the structure of the world with an internal model, which can be considered as an approximation of how its sensations are generated (Sales, Friston, Jones, Pickering, & Moran, 2019). To be more specific, the brain processes sensory inputs by taking into account their inherent ambiguity. This is achieved through generative models representing the causes underlying sensory events. However, even different causes can produce almost identical effects to us. This leads the brain to continuously create hypotheses of how causes generate an input, and these hypotheses are tested against sensory evidence (Hohwy, 2013; Walsh, McGovern, Clark, & O'Connell, 2020). Prediction errors are then sent to various levels of the processing hierarchy in order to adjust the internal model (Wacongne et al., 2011). This is equivalent to saying that "the brain is a statistical organ predicting worldly states that generate its sensory inputs" (Kanai et al., 2015). However, at this point we are not considering independent computational cognitive systems such as language (Bolhuis et al., 2014), but we are "at the productive interface of brain, body, and social and material world" (Clark, 2008). Following from this, we would claim that the concept of hierarchy cannot be easily integrated in the action domain if not extending its definition and placing it where interfaces lie.

Indeed, in the embodied account, language-considered not as an abstract system but as a communication tool (Borghi et al., 2019; Borghi, Scorolli, Caligiore, Baldassarre, & Tummolini, 2013)-would use hierarchically structured predictions to accomplish smooth social interactions (Clark, 2016). Thus, once we are at the sensory-motor interface and at the conceptual-intentional interface, predictive processing mechanisms for language might emerge, generating predictionrelated hierarchies and not syntactic ones. As an example, looking at the sensory-motor interface, there is evidence suggesting on-line prediction generation concerning auditory consequences of speech before production (Bourguignon et al., 2020) and at different stages of speech processing (Donhauser & Baillet, 2020; Hovsepyan, Olasagasti, & Giraud, 2020; see also Poeppel & Assaneo, 2020). Similar findings were shown to involve the conceptual-intentional interface as well (e.g., see García & Ibáñez, 2016). It has also been put forward the idea that language acts as an artificial context "helping constrain what representations are recruited and what impact they have on reasoning and inference" (Lupyan & Clark, 2015). Overall, what is relevant here is that predictive mechanisms can be easily applied to language; however, it seems that this is only possible once that language meets the external/ internal world. Therefore, what we have suggested to be the only form of hierarchy in the action domain might also be present in other domains, including language. Note, however, that syntax as the core computational mechanism remains out of the frame. As a matter of fact, syntactic-specific hierarchy might only be attested in language but not in

other domains.

Considering action hierarchy as a non-structural property would also prevent us from questioning the presence of Merge in non-human primates. Fujita (2014) postulates the existence of Merge-like operations in non-human species as evolutionary antecedents to linguistic Merge. This conceptual step was introduced in order to account for the fact that chimpanzees are able to crack nuts with a stone anvil and a stone hammer—merged as {HAMMER, {NUT, ANVIL}}—but they are unable to produce or comprehend linguistic recursive structures (Fitch & Hauser, 2004; Wilson et al., 2013). However, we believe this theoretical overspecification to be unnecessary. Non-human species possess to a certain extent human-like causal cognition (McCormack, Hoerl, & Butterfill, 2011) and they are able of processing conceptual structures of the type actor-action-goal (Berwick & Chomsky, 2011). There is no need to postulate Merge-like operations, but predictive operations suffice as non-human species are also able to generate perception-like states and therefore to adjust their actions in a flexible and adaptive way (Clark, 2013; Gowaty & Hubbell, 2013). The emergence of language, until further evidence will be provided, might still be considered as a sudden and human-only phenomenon (Berwick et al., 2013; for a recent debate on the issue see Berwick & Chomsky, 2019; Martins & Boeckx, 2019).

Finally, further attempts to link theoretical accounts on language with action processing have been made by work on X-bar schema applications to action syntax (Knott, 2012, 2014). X-bar theory is the theory of syntax that was developed within the transformational grammar tradition, now abandoned in favour of more recent Mergebased approaches to language (Chomsky, 1970; Fukui, 2011). Adopting this theory, Knott (2012, 2014) maintains a well-known distinction between Phonetic Form (PF) and Logical Form (LF), the latter being an abstract syntactic level of grammatical representation interpreted by the semantic component (Fox, 2008). Knott (2012, 2014) claims that LF of a sentence describing a goal-directed action is equivalent to the sensorimotor processes involved in the same action. In this context, however, the X-bar schema is considered as the primitive structural unit in LF representations, although SMT assumes that LF and PF must be considered as interface conditions and not levels of representations (Chesi, 2012). More importantly, Knott's considerations are also limited to one example of action-sentence coupling, which corresponds to (i) the act of grasping a cup and (ii) a sentence of the type *The man grasps a cup*. This limits the parallelism between action and language to the realm of goal-directed actions, not being able to provide a full account that takes into consideration also abstract sentences.

Summing up, actions do not seem to rely on sets of unconscious relationships, but on causal/physical properties as well as on statistical regularities—not relevant for language syntax (Everaert et al., 2015; see also Huettig, 2015; Huettig & Mani, 2016)—and hierarchicallyorganized levels of mental representations. These representations can be considered as elements of memory (Grafman, 2002), and they are probabilistic and action-oriented (Clark, 2015), as they combine prior beliefs about the world and the motor system (Clark, 2016).

3. Language and action processing in the brain

3.1. BA44 and its involvement in the action and language domains

Recent models of language processing identify specific brain structures that are highly responsive to linguistic inputs (Friederici, 2002, 2011; Hagoort, 2019; Matchin & Hickok, 2020; Matchin & Wood, 2020; Poeppel, Emmorey, Hickok, & Pylkkanen, 2012; Poeppel & Hickok, 2004). These structures include Broca's area, in the left inferior frontal gyrus (IFG), parts of the middle temporal gyrus (MTG), the superior temporal gyrus (STG), and the inferior parietal and angular gyrus, located in the parietal lobe. Different linguistic functions can be allocated to different structures and cortical networks (Friederici, 2011). Of central relevance here is Broca's area, given that its involvement in different cognitive domains has brought to the question of whether

language is a unique and unprecedented human faculty or whether it shares evolutionary and/or structural properties with other human faculties (Binkofski & Buccino, 2004; Fadiga, Craighero, & D'Ausilio, 2009; Grafton & Hamilton, 2007; Leslie, Johnson-Frey, & Grafton, 2004; Martins, Bianco, Sammler, & Villringer, 2019; Nishitani, Schürmann, Amunts, & Hari, 2005; Wakita, 2014). At the cytoarchitectonic level, Broca's area can be differentiated in two neighboring regions: Brodmann Areas (BA) 44 and 45 (Amunts & Zilles, 2012; Brodmann, 1909). The more anterior BA45 has been often associated to the processing of various types of semantic information during different tasks and manipulations such as plausibility judgment or semantic acceptability (Bookheimer, 2002; Caplan, Chen, & Waters, 2008; Friederici, 2011; Hagoort, 2005; Hagoort & Indefrey, 2014; Zhu et al., 2009). The more posterior BA44 has been conversely strongly associated to the processing of syntactic hierarchies (Zaccarella, Schell, & Friederici, 2017). Activity in the area has been found for the processing of simple two-word syntactic phrases (e.g., the cat), where a single Merge operation is applied, and when more complex structures involving recursive applications of Merge are tested, regardless of the presence of concurrent semantic information (Dapretto & Bookheimer, 1999; Heim, Opitz, & Friederici, 2003; Kang, Constable, Gore, & Avrutin, 1999; Opitz & Friederici, 2004; Zaccarella & Friederici, 2015, 2017; Zaccarella, Meyer, Makuuchi, & Friederici, 2017; Zaccarella, Schell, et al., 2017). These findings support the view that both simple and complex syntactic constructions share the same basic operation in language, as proposed by the SMT (Berwick et al., 2013; Bolhuis et al., 2014; Chomsky, 2010).

Trying to map a similar cortical network to other aspects of human cognition, language and non-language domains show only few overlapping brain areas when dealing with hierarchical structures in the corresponding domain. For example, a study conducted on patients sharing brain lesions in canonical language areas showed that, while linguistic processing was affected by the lesion, solving mathematical expressions was a still preserved ability. This leads to the conclusion that mathematics as a faculty is not directly dependent from Broca's area (for a more complete discussion on the issue, see Friederici, 2020). When exclusively focusing on the action domain, the picture seems to be already rather complex. BA44 activity has been linked to: (i) observation of object-directed and non-object-directed actions (Baumgaertner, Buccino, Lange, McNamara, & Binkofski, 2007; Cattaneo et al., 2007; Lui et al., 2008), (ii) execution of grasping or reaching movements involving both complex or small objects (Binkofski et al., 1999; Di Bono, Begliomini, Castiello, & Zorzi, 2015; Ehrsson, Fagergren, & Forssberg, 2001), (iii) action imitation (Nishitani & Hari, 2000), and (iv) pantomimes of tool use (Goldenberg, Hermsdörfer, Glindemann, Rorden, & Karnath, 2007). In the following, we will review some of those studies investigating underlying structural relationships between language and action processing, and how these might be reflected at the neural level.

In a recent study, Roy et al. (2013) suggested that actions share with language long distance dependencies, which need to be processed in order to account for the accurate execution of a task. For example, when displacing an object from one point to another, weight information can be thought of as moving from the reach phase (sub-phase 1 of the overall action) to the move phase (sub-phase 2). Roy et al. (2013) focused on children affected by Specific Language Impairment (SLI). SLI is a developmental disorder diagnosed when language in a child does not develop normally and the difficulties cannot be accounted for by physical abnormalities or brain damage. It is usually diagnosed when language skills are significantly below non-language skills, and it affects all areas of language (e.g., morphology, phonology and syntax; Webster & Shevell, 2004). In the present case, all children were diagnosed with a dysphasia affecting syntactic aspects of their language (in production rather than comprehension), together with additional phonological or lexical deficits. The authors employed a task in which subjects had to reach and move an object, in two different experimental conditions: in one condition, object weight was known prior to execution; in the other condition, it was unknown until the object was grasped. They

hypothesized that SLI children should not be able to transfer object weight information from one sub-phase to the other, since it is a syntactic-like process. Indeed, they showed that SLI children had shorter latencies at both sub-phases (reach and move) when object weight was known in advance, with respect to when it was unknown. On the other hand, typically developing children were affected by the presence or absence of weight information only in the move sub-phase, showing that they were able to transfer information from one step to the other. According to the authors, this difference in performance is due to a reduced ability for SLI children in processing hierarchical syntactic structures also in the action domain, in which features of the object have to be transferred from one level of the hierarchy to the other. However, if it is true that SLI children are able to process juxtaposed linguistic structures but not embedded ones, as originally assumed by the authors, the presence of a juxtaposed motor condition, where embedding is not crucial for action execution, was not part of the experimental manipulation. Moreover, it is known that SLI children are often affected by comorbid motor deficits (Finlay & McPhillips, 2013; Webster, Majnemer, Platt, & Shevell, 2005), which might have an impact on more basic sub-phases of action configurations before object contact (Weir, MacKenzie, Marteniuk, Cargoe, & Frazer, 1991), without the need to resort to syntactic-like transfers of such information from one sub-phase to the other.

Specifically focusing on BA44, two related studies on action sequencing have been conducted. In Fazio et al. (2009), an action comprehension test was administered to frontal aphasic patients showing BA44 damage and to healthy subjects. Participants were shown a video and then they were asked to re-order four pictures extracted from the video in the right temporal order. The authors observed that aphasic patients were impaired in performing the task. Interestingly enough, patients were selectively impaired in sequencing pictures representing only actions performed by a human agent (e.g., grasping a bottle) but not in those representing a physical event (e.g., a bicycle falling). One important limitation regarding this study concerns however the localization of the lesions. Aphasic patients' lesions, while being centered on left BA44, extended to adjacent cortical areas (see also Clerget, Winderickx, Fadiga, & Olivier, 2009; Fitch & Martins, 2014). In Fazio et al. (2009), all six patients had lesions extending to the insula, and five of them reported lesions in temporal regions as well. This makes it difficult to trace any reliable conclusion on the specific role played by BA44 in processing action sequences. Clerget et al. (2009) adapted the paradigm described in Fazio et al. (2009) to a virtual lesion study on healthy individuals, employing repetitive transcranial magnetic stimulation (rTMS) to interfere with BA44 activity. They observed that subjects were still able to perform correctly the sequencing task, but their reaction times (RTs) were significantly slowed down. The effect was restricted to biological actions (i.e., those performed by a human agent), but it was observed only when the action involved an object. Such a specificity would imply that Broca's area is somehow involved in processing goal-related features of actions but also intermediate steps leading to the final goal. While the results of Fazio et al. (2009) are difficult to discuss for lesion-related limitations, Clerget et al. (2009) already provide a context in which some preliminary conclusions on the relationship between language and action can be traced, given that RTs were decreased only for the biological-transitive condition. It seems indeed that some exclusively motor-related properties of the action itself (biology and transitiveness) are involving BA44. However, if the action domain shares syntactic structures with language, there is no reason to postulate that transitive and intransitive (i.e., non-object-directed) actions should differ in this respect. Furthermore, it appears that the location of stimulation reported in Clerget et al. (2009) could not be uniquely assigned to BA44, but rather laying on the borders between BA44 and BA45 (Amunts et al., 1999, 2004; Eickhoff et al., 2005).

In a functional Magnetic Resonance Imaging (fMRI) study on hierarchically-structured actions, different strategies for building motor sequences were used (Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni,

2006). In this experiment, participants were shown videos in which three cups were manipulated. The strategies employed for manipulation were of three types: (i) seriated pot, (ii) seriated subassembly and (iii) stacked subassembly. In the seriated pot strategy, one cup at the time is moved as a single element. This is the simplest action that can be performed with the objects provided. The second one is the seriated subassembly strategy and it requires a sort of Merge-like operation: first, one cup is moved into another cup; second, the new set of assembled cups is moved into the third cup. The third strategy is the most complex one and it consists in creating a non-seriated hierarchical structure. Two cups are merged together and then they are stacked on top of a third one. Comparing observation to rest, the authors found that only the simplest condition (seriated pot) activated consistently left BA44. In the other two conditions (seriated and stacked subassembly), exclusively its right homologue resulted as being involved in the observation task. Rather than structure, also in this study, activity within the left IFG seems to be triggered by motor features of the action itself. In fact, the seriated pot strategy is also the one that required less time in order to be performed by participants in a behavioral action execution task. This suggests that this strategy was the simplest among the three and the one to which participants could probably relate the most in the observation task as matching their predictions on the unfolding of the action sequence.

An fMRI study conducted by Koechlin & Jubault (2006) employed actions structured according to three different levels: (i) single motor acts, consisting of simple button presses; (ii) simple action chunks, which include sequences of single motor acts; and (iii) superordinate action chunks, which are composed of simple action chunks. The authors found involvement of left BA44 in the initiation and termination of simple action chunks and in the transition from one simple action chunk to another one. These results would seem to support the idea that BA44 activity in language increases as a function of complexity, while in the motor domain it conversely increases for the simplest action sequences, as it is in this case (see also Jeon & Friederici, 2013). In fact, Koechlin & Jubault (2006) showed that processing of the higher-level superordinate chunks leads to the involvement of left BA45. Coherently, it was recently developed a model focusing on these level-structured features of behavior, i.e. the Hierarchical Error Representation (HER) model (Alexander & Brown, 2018). In HER, information is processed in a hierarchical fashion in the sense that for each level of the model (i) predictions are sent to lower levels and (ii) prediction errors are passed to higher levels to reflect the discrepancy between the predicted outcome and the actual one. Alexander & Brown (2018) put forward the hypothesis that these two continuous processes might take place in the PFC and they accordingly tested HER on the results obtained by Koechlin et al. (2003). Employing this model, the authors found activations in the rostral and caudal regions of the PFC as more information was provided by a contextual cue and thus suggested that HER is able to account for such an increase implementing predictive processing information; i.e., if more information is provided than more potential errors need to be accounted for by the model. Overall, what is relevant here is that activity within BA44 increases when few prediction errors need to be accounted for, i.e. at the low levels of the behavioural hierarchy (Koechlin & Jubault, 2006; Koechlin et al., 2003; Koechlin & Summerfield, 2007). This is in direct contrast with language research. In this domain, BA44 activity is responsive both to low and high levels of the syntactic hierarchy (Zaccarella, Meyer, et al., 2017), but its involvement increases as a measure of syntactic complexity (Friederici, Fiebach, Schlesewsky, Bornkessel, & Von Cramon, 2006; Jeon & Friederici, 2013).

Compared to Koechlin & Jubault (2006), that only used simple motor sequences, another fMRI study employed hierarchical rules to generate action sequences (Martins et al., 2019). Crucially, when contrasting hierarchically and sequentially organized finger tapping sequences, the authors failed to report any involvement of Broca's area for the more complex condition. In order to account for the lack of Broca's area activation, the authors suggested that this region might be processing hierarchies of action goals rather than the underlying ways in which the action is structured (coherently with what outlined in Tettamanti & Moro, 2012). This would be consistent with the result observed in Clerget et al. (2009), in which only object-directed actions were affected by rTMS. However, this brings us to the conclusion that a type of hierarchy, in which the notion of goal has to be accounted for, is a non-linguistic hierarchy. As previously mentioned (Section 2.1), it could be argued that it is our predictions that are inherently structured (Clark, 2016). This statement can also be tested at a more fine-grained level, within BA44 itself and across domains.

It was already proposed that BA44 and the ventral premotor cortex (PMv) in BA6 are involved in extracting inherent hierarchical sequential structures and in combining them with prior knowledge in order to form "structural expectations regarding the ongoing sequential event", especially when passively attending certain actions (Fiebach & Schubotz, 2006). A meta-analysis on action domains, however, collapsing data from 416 experiments on action, failed to report activity within left BA44 for the observation task (Papitto et al., 2020). Convergence in BA44 was found exclusively for action execution, imitation and motor imagery. This result thus suggests that structural expectations are likely to be created when the structure of the action has to be accessed and performed (overtly or not) in form of a mental representation. Here we consider mental representations to be involved in abstracting information from events and in selecting the same information from memory whenever it is needed, for guiding or creating constraints on actions (Papitto et al., 2020; Wood & Grafman, 2003). Analogously, mental representations are long known to involve the frontal lobe to a various extent. The prefrontal cortex (PFC) is often considered to be organized in a hierarchical way, following a rostro-to-caudal gradient (Badre, 2008; Badre & D'Esposito, 2007, 2009; Badre & Nee, 2018; Koechlin et al., 2003). Within the PFC, anterior regions are thought to be involved in abstracting rules, while posterior regions are involved in selecting premotor representations based on the information provided by contextual signals, of the type also of stimulus-response associations (Koechlin & Jubault, 2006; Koechlin et al., 2003; Koechlin & Summerfield, 2007).

At a finer-grained resolution, the neuroanatomical convergence in left BA44 for action execution, imitation and imagery that we found across studies in Papitto et al. (2020) was specifically localizable in the most posterior portion of BA44 (pBA44), tangent to BA6, and it was clearly separated from a more anterior sub-region (aBA44), which was conversely linked to language processing (Clos, Amunts, Laird, Fox, & Eickhoff, 2013) and more specifically to the syntactic operation Merge (Zaccarella & Friederici, 2017; Zaccarella, Schell, et al., 2017). Thus, our results localize motor-related activity within pBA44, where contextual signals are integrated into motor representations. This subdivision of BA44, based on functional grounds, is coherent with (i) a receptor-based parcellation of Broca's area, in which density profiles of different neurotransmitters in post-mortem brains were assessed (Amunts et al., 2010; Zilles & Amunts, 2018); as well as with (ii) cytoarchitectonic studies looking at the cellular composition of the region (Amunts et al., 2010; Amunts & Zilles, 2012; Zilles & Amunts, 2018).

In the same study (Papitto et al., 2020), we used Meta-Analytic Connectivity Modeling (MACM) in order to extract co-activation patterns of the two BA44 sub-regions (Robinson, Laird, Glahn, Lovallo, & Fox, 2010; Yu, Barron, Tantiwongkosi, Fox, & Fox, 2018). Languagerelated aBA44 showed mostly a fronto-temporal network of coactivations. These include: (i) the superior temporal gyrus, involved in semantic processing, especially in presence of auditory stimuli (Friederici, Rueschemeyer, Hahne, & Fiebach, 2003); (ii) the middle temporal gyrus, mostly associated with processing syntactic ambiguity and making semantic judgements (Wei et al., 2012; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011); (iii) left inferior frontal clusters, spanning over BA47, already found in a previous coordinate-based meta-analysis investigating neural correlates of language processing (Zaccarella, Schell, et al., 2017); and (iv) right IFG, consistently with previous models postulating right-hemispheric processing of contextual information and semantic knowledge as well as prosodic information

(Jung-Beeman, 2005; Skeide & Friederici, 2016; Van Ettinger-Veenstra, Ragnehed, McAllister, Lundberg, & Engström, 2012; see Fig. 2).

On the other hand, the network derived from the motor-related pBA44 seed includes: (i) the precentral gyrus, suggested to host motor representations and associated with motor execution of skilled actions (Ahdab, Ayache, Brugières, Farhat, & Lefaucheur, 2016; Dubbioso, Sørensen, Thielscher, & Siebner, 2019; Hopkins et al., 2017); (ii) the left primary somatosensory cortex (BA2), previously found for finger-related motor processing both in execution and perception (Berlot, Prichard, O'Reilly, Ejaz, & Diedrichsen, 2019; Case et al., 2016); (iii) bilateral inferior parietal lobule (BA40), shown to be involved in computing and strengthening sensory-motor associations as well as generating motor intentions (Mattingley, Husain, Rorden, Kennard, & Driver, 1998; Meltzoff & Decety, 2003); (iv) the inferior temporal gyrus, attested in more abstract motor tasks such as coding manipulable objects (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Perani et al., 2001); and (v) cerebellum and putamen, respectively hypothesized to have a role in coordinated movements such as bimanual hand movements (Ramnani, Toni, Passingham, & Haggard, 2001) and in the motor learning process (Steele & Penhune, 2010; see Fig. 2). The functional specialization of the two co-activation networks seeding in BA44 is reflected in the distinct behavioral profiles resulting across experimental tasks during the MACM analysis (Fig. 3). Thus, it appears that the segregation across action and language is not only based on theoretical grounds. Rather, functional co-activation patterns-possibly along functional and cyto- /receptor-based parcellations-support the idea that the two domains involve separable processes, which might be differentially implemented at the cortical level.

To sum up, motor tasks activating left BA44 rely on manipulations that are not strictly speaking syntactic. In the action domain, the region seems to encode biological and goal-oriented actions (Clerget et al., 2009; Fazio et al., 2009) and relatable action sequences (Molnar-Szakacs et al., 2006)-but not hierarchically more complex ones (Martins et al., 2019; Molnar-Szakacs et al., 2006). In accounting for the distinction between aBA44 and pBA44, we thus believe that pBA44 is encoding representations, in the form of probabilistic and action-oriented memories, as suggested earlier when introducing the theoretical account of action (Clark, 2015). This hypothesis seems to be met, for example, in the seriated pot strategy in Molnar-Szakacs et al. (2006), which was the strategy the most participants chosed to use in the execution task. During the observation task, when seeing the same strategy being used, no prediction error had to be created since the prediction matched the action. On the contrary, representations of the pot strategy were even reinforced through repeated exposure to the same strategy (Grafman, 2002).

3.2. Temporal dynamics: a comparison on violations

Event-related brain potentials (ERPs) also contribute to our understanding of the relationship between action and language and the way they unfold in time. Event-related brain activation becomes obvious through the application of electroencephalography (EEG) and magnetoencephalography (MEG), which measure brain activity in the range of milliseconds. Studies in both action and language domains report early (before 200 ms) and late (after 300 ms) ERP components when processing sequences that contain rule-based errors. These components can differ in terms of topography and/or timing of corresponding underlying computations. In the next paragraphs, we will try to give a comprehensive picture of the main findings characterizing the two domains, the various components attested for different experimental manipulations and their main features.

For language, the first sentence-level syntactic ERP component is an early left anterior negativity (ELAN), occurring between 120 and 200 ms after the onset of the word carrying category information (Friederici, 2011; Friederici, Wang, Herrmann, Maess, & Oertel, 2000; Hahne & Friederici, 1999; Hasting, Kotz, & Friederici, 2007). This ELAN effect



Fig. 2. Overview of significant clusters from a Meta-Analytic Connectivity Modeling (MACM) analysis comparing co-activation patterns of two meta-analytically defined sub-regions of BA44: anterior BA44 (language-related) and posterior BA44 (actionrelated). Connectivity profile for anterior BA44 > posterior BA44 (blue; image adapted with permission from Papitto et al., 2020). Connectivity profile for posterior BA44 > anterior BA44 (red). Coordinates are in the MNI space. *BA* = Brodmann Area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 3. Behavioral profiles (Action, Cognition and Perception) for the two coactivation networks seeding in BA44 according to the MACM analysis in Papitto et al. (2020; *Appendix A – Supplementary Data*), across functional studies included in the BrainMap database (brainmap.org). Anterior BA44 (blue); Posterior BA44 (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and the underlying process are considered to be highly automatic. One such study, in which the proportion of correct sentences and sentences with phrase structure violations was varied, showed that the ELAN was not affected by the high vs. low amount of violations occurring during the task (Hahne & Friederici, 1999). Worth mentioning is that a similar ERP component has been reported for young children as well. In a recent study, two-year-old children were required to listen to grammatical and ungrammatical sentences. When exposed to ungrammatical sentences, the children were shown to share a similar left anterior negativity as the adults and—as a consequence—the occurrence of some similar syntactic computations (Brusini, Dehaene-Lambertz, Dutat, Goffinet, & Christophe, 2016; however, see Oberecker & Friederici, 2006). An ERP component often following the ELAN is a late effect called P600, a positivity which occurs around 600 ms after violation onset. This late centro-parietal component is considered a correlate of integration processes at the sentence level of syntactic and semantic information, reflecting also difficulties in mapping linguistic information onto world knowledge (Friederici, 2011). The P600 effect is less automatic than the ELAN as it varies as a function of violation probability, suggesting different levels of processing (Hahne & Friederici, 1999). Thus, the two ERP components might reflect two different abstract levels of language processing: the ELAN is a syntactic phenomenon related to the inability of structure building, the P600 reflects integration processes at the interface system (Friederici & Weissenborn, 2007).

In the action domain, various paradigms involving structure violations have been used to test similarities between action and language syntax (Balconi & Canavesio, 2015; Maffongelli, Antognini, & Daum, 2018; Maffongelli et al., 2015, 2019, 2020; Sammler, Novembre, Koelsch, & Keller, 2013). Closer to the language-based studies discussed so far, two recent studies are worth mentioning, which we believe might open to new possible comparisons of the on-line unfolding mechanisms at work for action and language processing. Maffongelli et al. (2015) proposed a paradigm in which sequences of actions were structurally manipulated by scrambling the canonical order of the action sequence. Participants were shown, for example, a slide-show presentation of a making-a-coffee scene, where the picture of pouring coffee powder into a moka pot was shown before the picture of pouring water into the same pot. Intriguingly, the results showed an early centro-frontal negativity in a similar time window to that of the ELAN, namely 100-250 ms after the presentation of the sequential violation. The authors also reported a late anterior positivity effect, occurring between 300 and 750 ms, similar to a P600 effect. In a second study, the same authors used TMS over the left sensorimotor cortex to gain additional specificity on the link between the area and error detection processing in action sequences (electrod C3; Maffongelli et al., 2020). The findings replicated the early errordetection component found in Maffongelli et al. (2015), and they further showed a facilitatory effect reflected in faster RTs reported for the error detection task.

So far, the ELAN component for language has been localized in the temporal cortex and in the inferior frontal cortex or in the temporal cortex only, using MEG and dipole source localization (Groß et al., 1998; Herrmann, Maess, Hahne, Schröger, & Friederici, 2011; Herrmann, Maess, Hasting, & Friederici, 2009; Knösche, Maeß, & Friederici, 1999). On the other hand, the localization of the early component reported for

action processing-recorded from a wide centro-frontal region of interest-still awaits further investigation. The P600 effect detected during processing structural violations in action sequences does not have a centro-parietal distribution (as in language experiments; e.g., see Hahne & Friederici, 1999) but again an anterior one, as a possible reflection of action-specific processes, already hypothesized by Maffongelli et al. (2015). Future works should clarify the different functional nature of the early ERP components for action and language, where the first is an error-detection effect processed by sensorimotor regions and the second is a category violation effect involving inferior frontal and temporal regions. It is possible indeed that violations are recognized at a similar time-window but recruiting different cortical networks. This would not go against our assumptions that language and actions are computationally segregated. As a matter of fact, ELAN is a violation-related component operating with phrase structure rules; on the other hand, an action-based violation-related component might be driven by "temporal rules" (Maffongelli et al., 2015), which could in turn cause a mismatch between what observed and the created expectations on the unfolding structure of the action. Postulating different violation-related mechanisms does not seem at odds also with similar studies in the context of music. Using EEG and MEG, it was shown that musical violations in chord progressions lead to an ERP component similar to ELAN, however in the right hemisphere, i.e. the early right anterior negativity (ERAN; Koelsch, Gunter, Friederici, & Schröger, 2000; Maess, Koelsch, Gunter, & Friederici, 2001). Further investigating how these violation-based effects can be distinguished will improve our understanding of action violations, especially concerning automaticity and localization.

4. Conclusions

In this position paper, we addressed the relationship between action and language as two domains for which hierarchical structures are assumed from two different but interrelated points of view. For language, it was shown that the syntactic core should be considered as domain-specific. Actions can be characterized by hierarchical relationships; however, these do not follow the same principles ruling the recursive structure of language. Specifically, we propose that hierarchy in the action domain lies in predictive processing mechanisms mapping sensory inputs and statistical regularities of action-goal relationships, and not in the structure itself (Kanai et al., 2015; Keller & Mrsic-Flogel, 2018). Differences between language and action were then attested at the cortical level. Broca's area sub-regions might be involved in different computations across the two domains. We argue that anterior BA44 is one main hub where the syntactic core for language can be localized, whereas posterior BA44 is recruited in selecting premotor mental representations based on the information provided by contextual signals. Such a distinction is corroborated by further parcellation studies and MACM analyses (Papitto et al., 2020). Moreover, electrophysiological components might also be taken into account in order to disentangle processes in the two domains leading to early anterior negativities when observing incongruent action sequences or when listening to categorical violations in language. However, further studies are needed in order to localize these violation-related effects. To conclude, action and language share features of pivotal importance but, instead of looking at actions as hierarchical structures, a shift must be undertaken. As a matter of fact, action and language can meet only where the interfaces transfer abstract computations to either the external world or the internal mental world (Berwick et al., 2013). Thus, while syntax should be framed as a language-specific computational system, both action and language might share prediction-driven processes, once language computations are transferred to the conceptual-intentional or to the sensory-motor interface (Lupyan & Clark, 2015).

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CRediT authorship contribution statement

Emiliano Zaccarella: Conceptualization, Writing - original draft. **Giorgio Papitto:** Conceptualization, Writing - original draft, Funding acquisition. **Angela D. Friederici:** Conceptualization, Resources, Writing - review & editing, Funding acquisition, Supervision.

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