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Brain Rhythms in Object Recognition and Manipulation

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Brain Rhythms in Object Recognition and

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Brain Rhythms in Object Recognition and Manipulation

Copyright Statement

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Abstract

Our manual interactions with objects represent the most fundamental activity in our everyday life. Whereas the grasp of an object is driven by the perceptual senses, using an object for its function relies on learnt experience to retrieve. Recent theories explain how the brain takes decisions based on perceptual information, yet the question of how does it retrieve object knowledge to use tools remains unanswered. Discovering the neuronal implementation of the retrieval of object knowledge would help understanding praxic impairments and provide appropriate neurorehabilitation.

This thesis reports five investigations on the neuronal oscillatory activity involved in accessing object knowledge. Employing an original paradigm combining EEG recordings with tool use training in virtual reality, I demonstrated that beta oscillations are crucial to the retrieval of object knowledge during object recognition. Multiple evidence points toward an access to object knowledge during the 300 to 400 ms of visual processing. The different topographies of the beta oscillations suggest that tool knowledge is encoded in distinct brain areas but generally located within the left hemisphere. Importantly, learning action information about an object has consequences on its manipulations. Multiplying tool use knowledge about an object increases the beta desynchronization and slows down motor control. Furthermore, the present data report an influence of language on object manipulations and beta oscillations, in a way that learning the name of an object speeds up its use while impedes its grasp.

This shred of evidence led to the formulation of three testable hypotheses extending contemporary theories of object manipulation and semantic memory. First, the preparation of object transportation or use could be distinguished by the synchronization/desynchronization patterns of mu and beta rhythms. Second, action competitions originate from both perceptuo-motor and memory systems. Third, accessing to semantic object knowledge during object processing could be indexed by the bursts of desynchronization of high-beta oscillations in the brain.

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Acknowledgements

Authors' Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

A programme of advanced study was undertaken. Relevant scientific seminars and conferences were regularly attended at which work was often presented and several papers prepared for publication.

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"Science sans conscience n'est que ruine de l'âme"

Rabelais in *Pantagruel*, 1532.
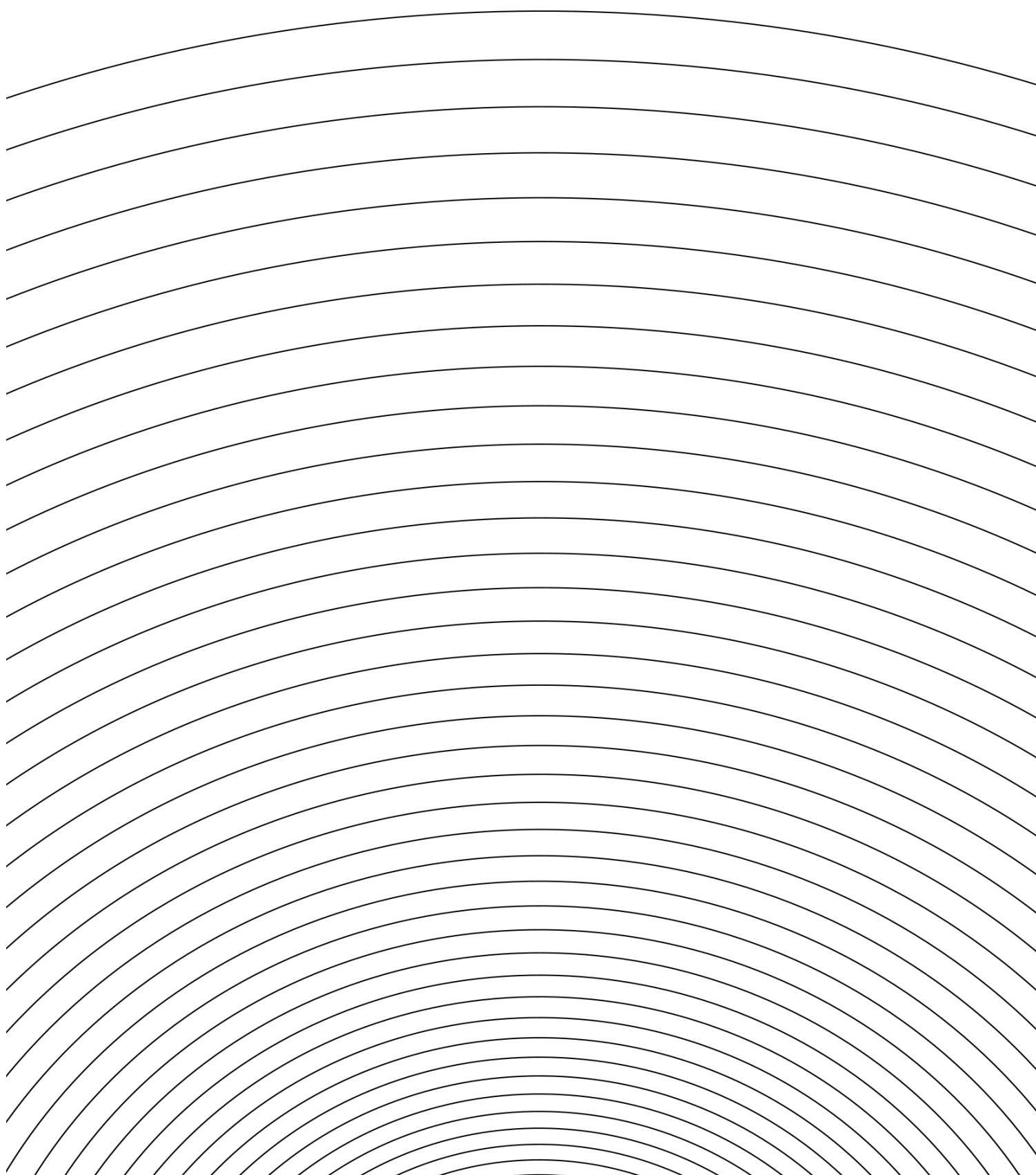
1. General Introduction

1.1. What are the neural bases of human tool use?

As important as our language, complex tool use is an endowment in human culture and the basis for the development of modern technologies (Vaesen, 2012). These linguistic and tool use skills may share a common origin in human history (Arbib, 2011). Consequently, one could ask whether they share characteristics in the way they are implemented in our nervous system. A plethora of neuroimaging studies using functional magnetic resonance imagery (fMRI) informs us what brain structures are involved prior to and during the manipulation of tools in various contexts. However, very few studies used electro/magnetoencephalogram (EEG/MEG) recordings to tell us when and how (i.e. the timings and neural dynamics) these structures are involved. Therefore, we will explore the question of what mechanisms the human brain uses in everyday-like situations when we have to recognise and manipulate objects and tools.

Very few theories on human tool use have been proposed during the last twenty years. Some directly relate to tool use (eg. Buxbaum, 2017; Buxbaum & Kalenine, 2010; Fagg & Arbib, 1998; Johnson-Frey, 2004; Orban & Caruana, 2014; van Elk, van Schie, & Bekkering, 2014), whereas other models have indirect assumptions about tool manipulations (Cisek, 2007; Cisek & Kalaska, 2010; Hart & Kraut, 2007; Kraut, Calhoun, Pitcock, Cusick, & Hart, 2003). We will now introduce and discuss some of these theories and their implications in the understanding of complex tool use in humans before bringing novel insights.

1.2. The emergence of the Affordance Competition Hypothesis and its underpinnings for object manipulation

The early work on the neural bases of human behaviours conceived multiple stages of information processing: perception, cognition, and action (Newell & Simon, 1972). According to this view, the brain would first build and select 'What to do' from an abstract internal representation of an element of the external world (Marr, 1982), for instance 'grasping a spoon'. Then, it would specify 'How to do' this action: effector, trajectories, rotations, and so on, of the limb. As in engineering control theory, the central nervous system is perceived as a problem-solving machine generating behaviours. The inputs of the machine come from the perceptual organs and internal models, which then feed (cognitive) processes commanding actuators (muscles). Regrettably, such a hypothetical functioning of the brain was hardly accommodated by the ecological and evolutionary reasons for its emergence.

The contemporary brain theory on the perception-cognition-action processing of Paul Cizek was inspired by the primary work of James Gibson (1979) on ecological perception and the concept of affordance. An affordance can be defined as the opportunity of action the environment offers to an animal: the size of a branch allowing the monkey to climb on, the shape of a steering wheel allowing us to grab uni- or bi-manually, the geometry of the ground informing either it is walkable on or not, etc. This conception brought the idea that the brain operates an action-oriented perception: perceiving the key elements of the environment to act upon. Seminal perspective on the brain visual system proposed that there are two distinct visual streams: a ventral pathway which encodes the 'What' about the visual inputs (for stimulus recognition for instance) and a dorsal pathway which encodes the 'Where' in the space the visual stimuli are located (Ungerleider &

Mishkin, 1982). Their combination would allow to build a global representation of the external stimulus to interact with.

Following the concept of affordances, Milner and Goodale (1995) reformulated the dorsal stream as processing the 'How' rather than the 'Where', because spatial information is of primary importance to prepare and control how actions must be realized. Thus, from an action-oriented perception view, the dorsal stream would process the visual affordance provided by the environment. A few years later, Fagg and Arbib (1998) proposed that the parietal lobe within the dorsal pathway processes the multiple affordances (opportunities of action) extracted from perceptual inputs and exchanges this information with the premotor cortex to generate possible actions. Neurophysiological data reported by Cisek and Kalaska (2005) revealed that the dorsal premotor cortex (PMd) in primates are not only in charge of the planning and execution of action but also encode the selection of action. Thus, the functioning of the PMd illustrates an overlapping of cognitive (decisional) and action (motor computations) processing (see Cisek, 2005 for a review).

This research paved the way for Paul Cisek to develop the Affordance Competition Hypothesis (ACH; Fig. 1; Cisek, 2007; Cisek & Kalaska, 2010) which proposes an alternative to the sequential view of sensorimotor control for visually-guided actions. Instead of having a neural machine computing inputs and outputs as linear sequences, our brain would process information simultaneously via multiple feed-forward and predictive feedback loops. Two fundamental operations are implemented in distinct but overlapping brain networks. On one hand, the selection of an action (or 'What' to do) would involve the ventral stream, temporal lobes, prefrontal cortex, basal ganglia, and parieto-frontal loops. On the other hand, the specification of an action (or 'How' to do) relies on the dorsal stream, posterior parietal and caudal frontal cortex, which converts, for instance, the perceptual information about an object into possible motor plans. The brain

representations of an action would be largely distributed over these structures and involved in both the preparation and execution of that action. Hence, we could have a clear functional overlapping within parietal and frontal cortices, both in charge of selecting and specifying the parameters of actions to execute.
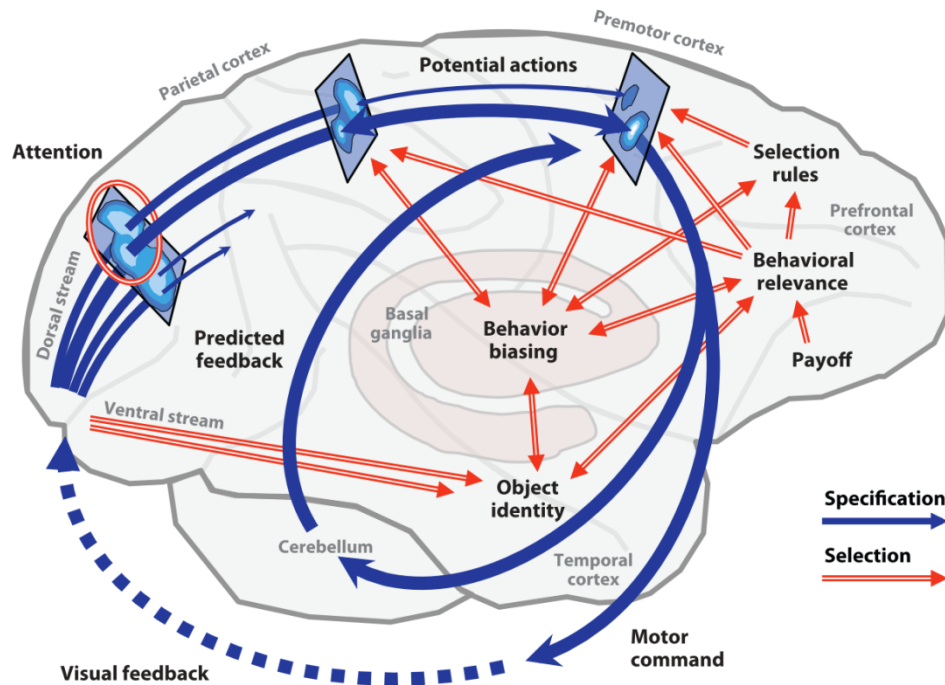
Fig. 1 The Affordances Competition Hypothesis. Potential actions visually afforded by an object are continuously evaluated to build motor plans and re-evaluated over time. The specification of an action (blue arrows) occurs within the dorsal stream converting multiple visual information into potential motor parameters competing for implementation. The selection of action (red arrows) involves the ventral stream and cortico-subcortical connections, gathering information about the appropriateness of potential actions and biasing their processing in fronto-parietal areas (adapted from Cisek & Kalaska, 2010).

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In the ACH theory, each area encodes information used for multiple potential actions, represented as patterns of tuned activity within distributed cells assemblies, working similarly to probability density functions. However, within each area only one information (the most suitable in a given situation or context) is forwarded, leading to the competition between multiple action representations at multiple hierarchical levels. The simultaneous processing of action selection and specification bring important testable hypotheses, such as the re-selection and re-specification (or switching) of motor plans during motor execution, recently validated (Gallivan, Barton, Chapman, Wolpert, & Randall, Flanagan, 2015; Gallivan, Logan, Wolpert, & Flanagan, 2016). In the context of object manipulation, scarcely discussed in the literature (e.g. Rounis & Humphreys, 2015), this means that the selection and implementation of a tool use occur during its recognition but also its reach and grasp, rather than fully planned during action preparation.

To our concern, the ACH theory does not consider the multitude distinctions of affordances discussed in contemporary literature, which extended the seminal Gibsonian perspective on the phenomena. Indeed, many conceptions have been made, opposing structural versus functional affordances (Kalénine, Wamain, Decroix, & Coello, 2016; Mizelle, Kelly, & Wheaton, 2013), variable versus stable affordances (Borghi & Riggio, 2009), perceived versus acquired (Frey, 2007) or learnt affordances (Antunes et al., 2015; Montesano, Lopes, & Bernardino, 2008; Yasin, Al-Ashwal, Shire, Hamzah, & Ramli, 2015). This glossary representing sub-categories of affordances rely on one major difference: the affordances intrinsic to the object (e.g. its shape and size) decoded by the actor's perceptual systems and the affordances extrinsic to the object but dependent on the actor's experience and encoding-retrieval processes of object and action knowledge. Hence, the fundamental difference relates to the fact that some affordances depend on memory processes. The affordances intrinsic to the object represent the actions of grasping our mobile phone given its

geometries. The affordances extrinsic to the object correspond to the consequences of pressing buttons or touching the screen of that mobile phone, which rely essentially on acquired knowledge throughout our multiple experiences. Moreover, our ability to use tools and modern technologies is determined by our ability to memorize object knowledge, such as 'Why' and 'How' we manipulate various objects such as keyboards, remote controllers, construction tools, stethoscope, keys, musical instruments and so on. This differentiation between sub-types of affordance draws the following question: what role does our semantic memory play regarding objects and tools in the selection and production of their manipulation?

1.3. The Two Action Systems theory to describe object manipulation

Understanding how the brain encodes and accessed to semantic knowledge about objects and actions is critical for clinicians facing patients with tool use impairments. Based on a clinical double dissociation, Daprati and Sirigu (2006) proposed that our everyday manipulations of objects can be separated into two categories relying on two brain systems: grasping an object to move it or to use it as a tool. On one side, authors reviewed that patients with visual agnosia, a disorder of object recognition due to lesions of the visual stream or occipito-temporal (Milner et al., 1991), have preserved abilities to grasp and move objects. This means that the processing of visual affordances would be sufficient for an object grasp and transportation. On the other side, patients with optic ataxia, an impairment expressed as difficulties to visually guide effectors and therefore grasp objects due to lesions of the occipito-parietal dorsal stream (Battaglia-mayer & Caminiti, 2002), can correctly recognize objects and tell how to use tools. Thus, we note a possible dichotomy in the cortical processing of intrinsic and extrinsic affordances.

Daprati and Sirigu proposed that affordance processing and semantic memory about object involve two neuronal routes rather independent, as suggest the clinical double dissociation. Depending on the goal of the action, moving an object necessitates the activation of a 'Grasp' system. Using a tool requires the activation of a 'Use' system, which integrates stored semantic knowledge (about the functional hand posture for instance) into motor computations. The 'Grasp' system would be quickly and automatically activated at the perception of an object, whereas the 'Use' system would be activated only when a tool use is intended.

As discussed in the ACH theory, these ideas suggest that perceptual and cognitive processing is tightly related to the action domain, such as the visualization and manipulation of an object. Plus, object knowledge plays a role in motor processing. However, here Deprati and Sirigu propose that object manipulations could not rely solely on on-line processing of affordances, in a way that the production of tool use requires the acquisition and retrieval of object knowledge accumulated over experience. This proposal led Laurel Buxbaum and Solène Kalénine to elaborate the Two Action System theory (2AS; Buxbaum & Kalenine, 2010) to formulate novel hypotheses on the neurocognitive bases of skillful tool use.

The theoretic goal of the 2AS model and its extension (2AS+; Fig. 2; Buxbaum, 2017) is to seat action semantics and praxic skills within the embodied cognition framework: the idea is that the body is the pillar of perception, cognition and action processes (Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012; Wilson, 2002). Therefore, it extends the previous opinions on the role of the visual system in hosting action representations. The framework tries to answer the question of whether action information is a component of embodied object representations. It is based on preceding dual visual streams models (e.g. Milner & Goodale, 1995; Ungerleider & Mishkin, 1982) and Rothi's model of limb praxis (Gonzalez Rothi, Ochipa, & Heilman, 1991), which proposes that action can

involve either a "direct/motor" route or an "indirect/semantic" route. Here, Buxbaum and Kalénine advance a functional neurocognitive implementation of two types of object manipulation.

First, a 'Structure' action system extracts the geometrical properties of the object during its on-line viewings (visual affordances), such as the shape and the size but also the presence of a handle and its location and orientation in space. This 'Structure' system is implemented in the bilateral dorso-dorsal visual stream, involving the bilateral intraparietal sulci (IPS) and the dorso-lateral parieto-frontal network. For example, a simple grasp of an object would be automatically computed within this system.

Second, a 'Function' action system stores and extracts information derived from multiple effector-object interactions, leading to the formation of long-term representations. Thus, this system features a memory component (i.e. the 'manipulation knowledge') allowing us to learn and remember how to perform actions. For instance, it would be responsible for the molding of a tripod grip for skillful writing with a pencil. During motor preparation, the manipulation knowledge generates motor predictions about desired body states, while sensory predictions are used to minimize the error in motor commands. The system is implemented in the left-lateralized ventro-dorsal visual stream, including the left superior temporal and inferior parietal cortices. Here, the theory discerns that the 'Structure' system automatically potentialises non-tool use actions derived from perceptual inputs, whereas the 'Function' system retrieves the functional manipulation when congruent with the action goal or intention.

On the question of whether any object-related action information can be an embodied component of object representations, the authors argue that the evidence provided by the literature highlighted that only functional manipulation (i.e. tool use) are embodied components of object concepts. This means that our everyday functional and structural (e.g. grasp-and-move) manipulation

of objects shape the way these objects become represented in distinct brain systems, but also that only functional tool use relies on sensorimotor simulation of previous experience (i.e. a crucial phenomenon for embodiment theorists). Therefore, some or most representations of tool use are parts of the semantic memory system.
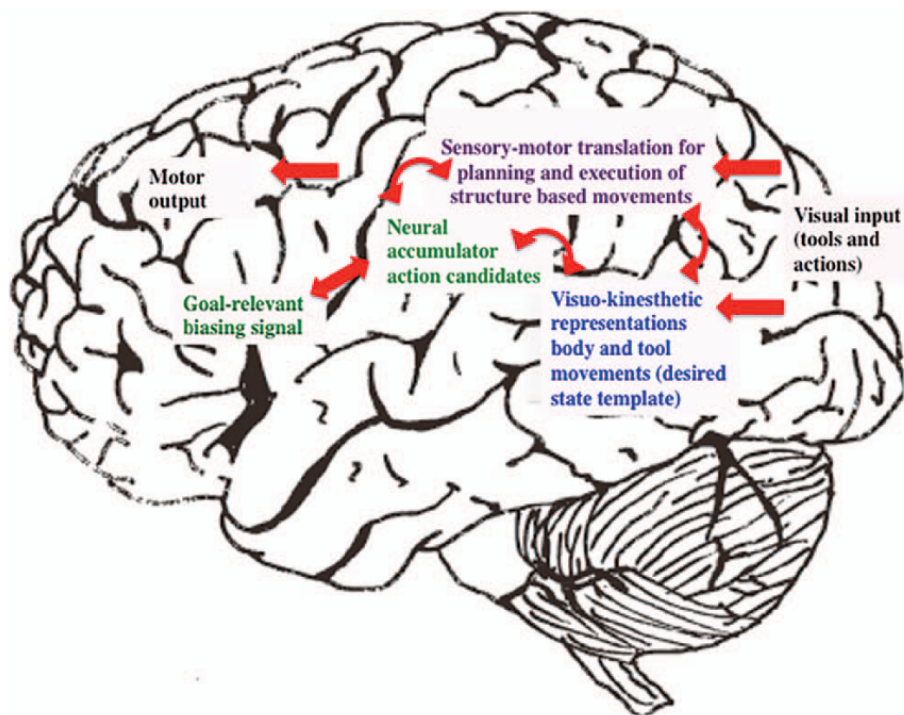
Fig. 2 The Two Action Systems Plus (2AS+) model. The left-lateralized posterior temporal/inferior parietal system allows the storage of abstract, multimodal manipulation knowledge (blue; 'Function' system), which provides sensorimotor inputs to the bilateral fronto-parietal network enabling the production of tool use. This sensorimotor information is complemented with the continuous flow of visual and somatosensory inputs processed within the dorsal pathway (purple, 'Structure' system). The 2AS+ model completes the 2AS model in proposing a sub-mechanism allowing for the selection of object manipulation (green). The

manipulation knowledge (e.g. a functional handgrip) concerning feasible object-directed actions activated by the current task settings is accumulated in a temporary 'buffer' located in the left supramarginal gyrus. The inferior frontal cortex biases the competition of these potential object manipulations for motor execution (black; adapted from Buxbaum (2017).

In contrast with the ACH theory, the 2AS model doesn't detail how these different action representations, within the structural and/or function systems, are selected for further processing when there are multiple possibilities. This would be the case when, for instance, we have to mold a tripod grip to use the pencil over all the other grasps structurally afforded (e.g. pinch grips). More importantly, the ACH theory does not dissociate the activation of object knowledge depending on the action goal, because action selection aggregates multiple sources of information disregarding the action ('Structural' or 'Function') systems. This divergence will be discussed in the following chapters.

A recent study began using event-related potentials (ERP) analysis of EEG recordings to investigate the structural and functional action representations during object recognition (Lee, Huang, Federmeier, & Buxbaum, 2017). The results suggested that, in a task consisting of evaluating the relatedness of two objects visually presented, structural information was activated at first. Thus, when no object manipulation is intended, the 'structure' system is indeed activated rapidly, during the first 150 ms of object processing. Whereas ERP analysis reveals the time course of activation of neural representations, the characteristics of the neurophysiological mechanisms remain unclear. Nevertheless, extending the EEG analysis to the time-frequency domains could bring complementary information about how object knowledge encoded in distributed cell assemblies becomes accessed for the recognition or preparation of functional actions.

1.4. The Neural hybrid model of Semantic Object Memory

Since Hans Bergers' (1929) discovery of the existence of brain rhythms, neuroscientists tried to explain how behaviours are generated by the combination of different EEG rhythms, such as delta (~1-4 Hz), theta (~4-8 Hz), alpha (~8-13 Hz recorded over posterior sites), mu (~8-13 Hz recorded over central sites), beta (~13-30 Hz) and gamma (~30-80 Hz). These oscillations represent a wonderful tool for cell assemblies to communicate with each other (Buzsáki & Draguhn, 2004; Buzsáki & Wang, 2012; Siegel, Donner, & Engel, 2012; Wang, 2010).

Throughout this dissertation, we will review how these different brain rhythms relate to various information processing, from perception to motor functions and language comprehension. For instance, Pulvermüller, Lutzenberger and Preissl (1999) revealed that the semantic processing of words involve high-beta rhythms. On this assumption, the authors presented to participants action verbs associated with strong motor association and nouns associated with strong visual associations. They revealed a double dissociation in the ~30 Hz EEG oscillations, with enhanced responses in cortical sites (electrodes O1/O2) for the nouns and enhanced responses in central sites (electrodes C3/C4) for the action verbs. This rose the question of whether fast brain oscillations can have a functional role in the reactivation of semantic representations.

A few years later, Slotnick, Moo, Kraut, Lesser and Hart (2002) asked an epileptic patient to read a pair of words and press a button when the combined words evoked a third object (e.g., the words 'desert' and 'hump' combine to activate 'camel') or refrain the response when they did not evoke anything (e.g., the words 'bullets' and 'milk' do not activate any third object). Hence, only in the former case, the participant recalled the object from semantic memory. While performing this task, the participant's EEG and implanted electrodes in the bilateral thalamus were recorded. The

authors reported a drop of low-frequency (7-8 Hz) signal power and an increase of fast-frequency (21-34 Hz) signal power in both thalamic and scalp occipital electrodes when the participant recalled an object. In favour of a thalamocortical synchronization mechanism during object semantic retrieval, they also reported phase-locked responses of EEG responses between these thalamic and occipital electrodes. In parallel, other fMRI studies validated the activation of this thalamocortical network for object retrieval (Kraut, Kremen, Moo, et al., 2002; Kraut, Kremen, Segal, et al., 2002). Hence, the global activation of distributed semantic memory representations could rely on these high-beta rhythms (Pulvermüller et al., 1999; Slotnick et al., 2002).

The body of work and accumulation of other evidence in the literature guided Hart, Kraut and colleagues (Hart & Kraut, 2007; Kraut et al., 2003) to develop the neural hybrid model of semantic object memory (referred here as the NSOM theory for clarity), which account for the storage and retrieval of knowledge of both feature- and category-based object representations at a neurophysiological level. The authors proposed that components of object memory are stored within specific systems (e.g. visual features of an object in the visual system) and re-activated via thalamocortical synchronization at around 30 Hz. In accordance to this view, naming visualized pictures of tools activates the left premotor region (Martin, Wiggs, Ungerleider, & Haxby, 1996), suggesting an automatic activation of stored motor information in semantic memory during object recognition. Unfortunately, the NSOM theory attracted minor attention and, therefore, lacks of substantial support from the cognitive neuroscience community. But as Engel & Fries (2010) noted more recently, there is also a clear lack of theoretical hypotheses about why neurons oscillate and what are the functions of these oscillations. These authors proposed that beta oscillations would signal a status quo within sensory and motor circuits. In other words, the stability of beta rhythms would reflect the expected maintenance of a state (e.g. keeping the arm still), whereas the

perturbation of the beta rhythms would indicate a predicted change of the perceptual and/or motor states. This means that instructing someone to perform a given object manipulation (e.g. via an auditory cue indicating what to do) would also elicit this perturbation of beta rhythms. Thus, recent ideas are not in opposition with the NSOM theory that ~30 Hz oscillations could reflect a thalamocortical mechanism serving semantic cognition. Actually, they could complement each other. The perturbation of high beta rhythms may reflect the change of perceptual and motor states via semantic memory activations. However, this remains untested. What we do know is that the concept of object semantic knowledge is vague, as described by Daprati & Sirigu (2006): "Knowledge about an object's use is a broad concept. It means being able to report (i) what the object is used for and how it is operated, (ii) the context in which it is used, and (iii) how the hand and fingers should be positioned when directly interacting with it" (p. 267).

In accordance with the main interests of this thesis, the NSOM theory proposes that ~30 Hz EEG responses indicate thalamocortical connections mediating features binding during semantic memory recall. In this sense, the thalamus would play a role in multimodal semantic processing during object recall, co-activating spatially distributed cortical representations of object features. In our collaborative quest to comprehend the neural bases of complex tool use, one could ask whether these ~30 Hz high-beta oscillations might play a role in re-activating functional action representations, allowing us to know 'What' is the function of a given object or 'How' to manipulate it.

1.5. Scope of this thesis

Here we are asking how and when does the brain retrieve the learnt properties of tools. The ACH theory suggests that object knowledge is automatically recruited for the manipulation of a tool,

whereas the 2AS theory proposes a relatively more goal-depend type of activation (i.e. structural or functional manipulation). To investigate these inconsistent claims, we make the temporary assumption that the ~30 Hz EEG signal reflects the activation of object knowledge, as suggested in the NSOM theory. Using a novel approach combining EEG recordings with tool use training in virtual reality, we report five experiments testing the neural activation of tool knowledge during recognition, action preparation and selection processes. To build a better understanding of how and when the brain retrieves tool knowledge, we addressed the following questions.

1.6. Are beta rhythms sensitive to the preparation of structural and functional tool manipulations?

In the 2AS model, performing known functional actions (i.e. tool use) with an object requires the retrieval of stored information about how to grasp and manipulate it. Simpler structural actions (e.g. grasp-and-move) do not require this retrieval, as they are intrinsically dependent on the object processing (e.g. extraction of visual affordances). How does the brain re-activate this stored information specific to the preparation of tool use?

The neural mechanisms allowing for the preparation of tool use remain largely unknown for multiple reasons. Classical experimental setups, that assess the activation of tool use knowledge, involve visually presented objects to discriminate (e.g. studies on the compatibility effect – the orientation of the handle of a tool to the right facilitates motor responses with the right hand). This entails at least three limitations. First, they are unable to disentangle the information processing related to the object recognition from the motor planning for object manipulation (e.g. Jax & Buxbaum, 2010, 2013; Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007; Osiurak, Roche, Ramone, & Chainay, 2013). Second, tool use information evoked during object recognition is object-dependent,

such as multiplying the number of objects does not only raise the variability of different functional information that is retrieved but also the structural information that is extracted. As an attempt to counter this problem, using novel objects allow to control the former limitations but is not enough to control the latter one (for attempts see Creem-Regehr, Dilda, Vicchrilli, Federer, & Lee, 2007; Kiefer et al., 2007; Ruther et al., 2014; Weisberg, Van Turennout, & Martin, 2007). Third, so far very few studies involved real object manipulations (e.g. Brandi, Wohlschlager, Sorg, & Hermsdorfer, 2014; Hermsdorfer, Terlinden, Muhlau, Goldenberg, & Wohlschlager, 2007; van Elk, van Schie, van den Heuvel, & Bekkering, 2010), such as most of the investigations require pressing buttons or merely pantomimes object use (e.g. Chen, Garcea, & Mahon, 2016; Goldenberg, Hermsdörfer, Glindemann, Rorden, & Karnath, 2007; Moll et al., 2000) or grasping objects (Jax & Buxbaum, 2010, 2013; Osiurak et al., 2013).

Chapter 2 will describe an attempt to counter these limitations in neutralizing the object recognition processing and investigating the neural rhythms and behavioural timings involved in the preparation and execution of tool use and tool transportation. In accordance with the NSOM theory, we tested whether the ~30 Hz beta rhythms reflect the activation of object manipulation knowledge required for the preparation of tool use. The EEG results will question the relation between the beta rhythms and the activation of the 'Function' and 'Structure' action systems during motor preparation. Furthermore, behavioural data will lead to discussing the ACH model, arguing that studies measuring the time to initiate an action (but not the time necessary to execute that action) are bringing partial information on the unfolding motor planning prior and during the performance of object-based or object-directed actions.

1.7. Are beta rhythms reflecting the activation of tool use knowledge during object recognition?

The particularity of a tool is that it is associated with the production of an end-goal. However, to reach this end-goal some instances of tool use require a specific manipulation (e.g. opening a lock with a key) and others do not (e.g. placing a bucket in a location to collect water). The critical feature of the latter case is that the tool use relies mainly on structural information about the object, whereas the former case requires access to manipulation knowledge. Consequently, this questions the relationship between tool use actions and abstracted manipulation knowledge, which existence is contested by the partisans of the reasoning-based approach of tool use (Badets & Osiurak, 2015; Goldenberg & Hagmann, 1998; Jarry et al., 2013; Osiurak & Badets, 2016; but see Buxbaum, 2017 for a commentary). These examples highlight that all tools are not the same. Thus, is the association of manipulation knowledge to a novel tool considerably influenced by its groundings in brain action systems?

In Chapter 3, we investigate whether the ~30 Hz beta rhythms reflect the activation of stored functional and manipulative information about a tool during its recognition, independently of the preparation of tool use. We emphasize the role played by learning action information in the grounding of object knowledge in action systems. Buxbaum and Kalenine (2010) commented in the 2AS theory that an "… open question is whether passive viewing of objects may under any circumstance induce motor resonance phenomena without a prior intention to act in object-compatible ways" (p. 214). As a partial answer, we provide evidence that object knowledge is recruited independently from the end-goal of the action, which also supports the ACH theory proposing an automatic activation of object knowledge for action selection. We report

supplementary proof of the NSOM theory that high-beta rhythms may reflect this activation of this object knowledge.

1.8. Are beta rhythms sensitive to the activation of multiple tool use representations?

In the 2AS theory, even though structural and functional action systems interact with each other, the activation of one system can impedes the other one (Jax & Buxbaum, 2010; Kalénine et al., 2016; Wamain, Sahaï, Decroix, Coello, & Kalénine, 2018). In other words, structural and functional tool manipulations compete against each other, as formulated in the ACH theory in a broader sense. Wamain et al. (2018) showed that EEG power of mu rhythms recorded over central sites and alpha rhythms recorded over posterior sites is sensitive to this between-systems competition occurring for object associated with distinct structural and functional manipulations. However, no beta rhythms analysis has been reported in this study. Could high-beta oscillations reflect the recruitment of multiple tool use knowledge?

In chapter 3, we investigate two critical processes happening prior to tool-directed actions: 1) the recognition of the tool leading the activation of associated representations, and 2) the selection of competing for tool use representations for the performance of functional manipulations. More precisely, we ask whether the retrieval of single or multiple tool use knowledge rely on mu rhythms solely or on additional beta rhythms. The modulation of ~30 Hz beta rhythms depending on the amount of tool use knowledge activated during tool recognition would provide further support to the NSOM theory. Also, does the selection of tool use representations rely on distinct or similar mu/beta rhythms mechanisms? The reported behavioural data extent the ACH theory to the domain of object manipulation and demonstrate an existing interference within the 'Function' action system.

1.9. Could language help the grounding of novel action information in embodied action systems and reflected in beta rhythms?

Often discussed as two characteristics of humanity our complex tool use and language skills may have emerged from a common origin (Arbib, 2011) and share brain structures according to neural reuse theories (Anderson, 2010; Gallese, 2008). Remarkably, both tool use and communicative gestures strongly depend on representations located within the left parietal lobe (Frey, 2008). For the philosophe Guy Dove, abstract concepts such as object labels are 'neuroenhancements' linking lexical, semantic and motor brain representations (Dove, 2018). Associating novel names to a novel knot modifies the activity in the left IPL during the following perception of the knot (Cross et al., 2012), suggesting that, as functional manipulation knowledge, linguistic object knowledge is part of embodied representations. A recent study showed that attaching a label to a novel object while learning its manipulation induce mu and beta rhythms perturbations in the subsequent reading of that label (Bechtold, Ghio, Lange, & Bellebaum, 2018). As far as we know, no one explored the impact of learning such object labels in the selection of structural and functional actions. Could high-beta rhythms reflect a reinforced activation of functional object representations by linguistic knowledge?

In Chapter 5, we review the functional role of linguistic object knowledge on perception and cognition and bring evidence to extend it to the action domain. The 2AS model claims that only functional action information is integral parts of embodied object representations. Given the semantic aspects of an object label, knowing this linguistic knowledge might influence functional action specifically. To go further, it could even impede the activation of the 'Structure' system while strengthening the activation of the 'Function' system. For the ACH theory, any object property (and

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possibly linguistic) facilitating the action selection would be activated and bias the competition both prior to and during the action. In accordance with the NSOM theory, such augmented activation of semantic object representations should be reflected in the power of ~30 Hz beta rhythms. Striking results will question these theories.
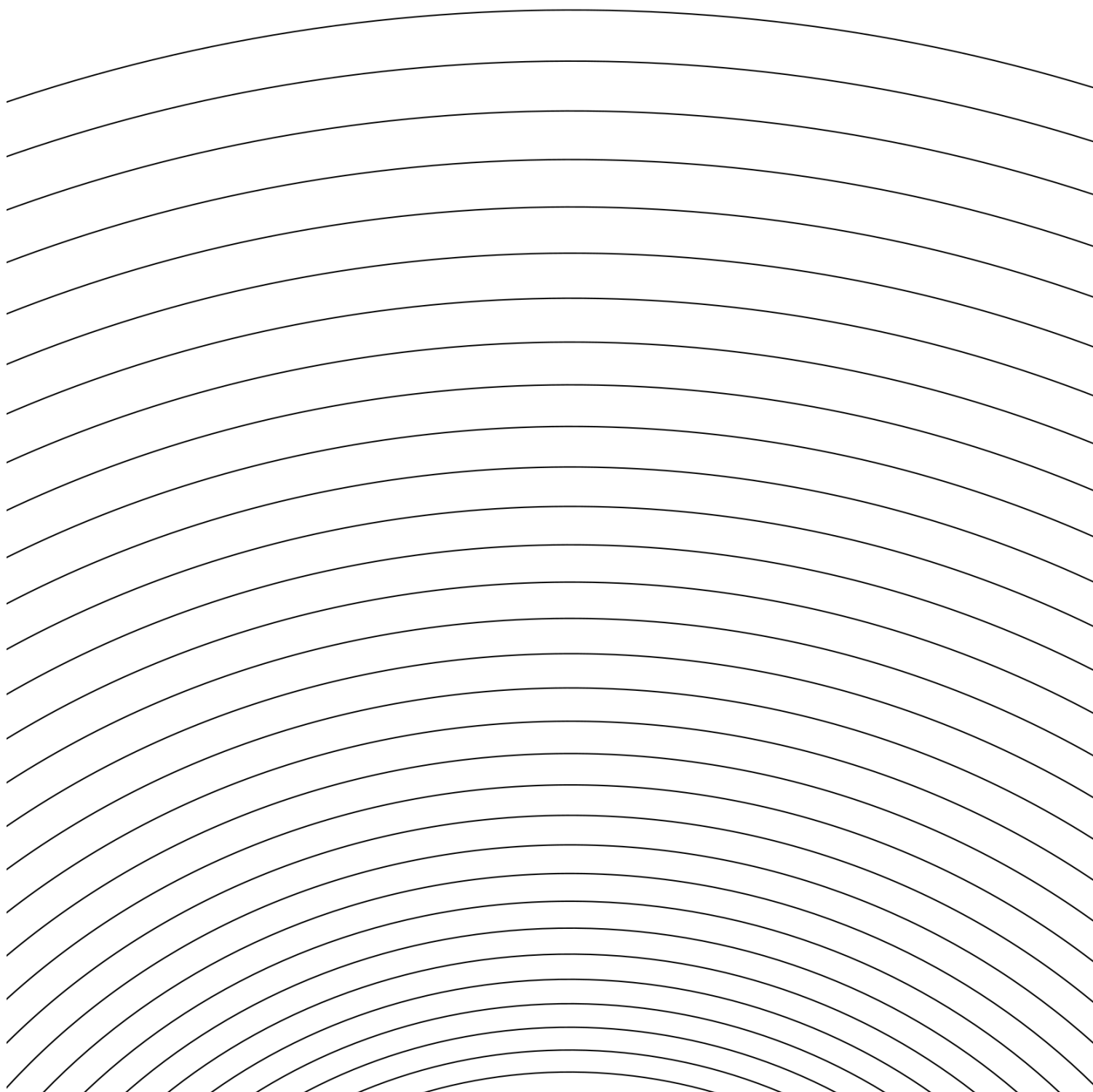
2. Beta rhythms in the preparation of structural and functional tool manipulations

A video demonstrating the experiment is accessible via the QR code at the bottom of the page, or by clicking on the following link: https://www.youtube.com/watch?v=Y20SEX14Az4

2.1. Chapter Abstract

Manipulating a tool to use it requires to inhibit visually afforded (structural) manipulation. In a recent study, the ~20 Hz beta-band power reflected the selection of a structural grasp (Turella et al., 2016). Still remains the question of how does the brain select a stored tool use manipulation from memory.

Combining EEG recordings with an original virtual reality paradigm, we investigated the selection of tool transportation and tool use. In comparison with the selection of tool transportation, we found a left-lateralized decrease of beta-band power peaking at around 25-30 Hz and 100 ms from the initiation of tool use selection. Subsequently, the analysis revealed a bilateral increase in beta-band power peaking at around 15-25 Hz and 200-400 ms from a cue onset. These results indicate that the selection of tool use or move induces different dynamics of beta rhythms in widespread neuronal networks.

2.2. Introduction

The ability to manipulate objects is one of the most important skills in our everyday life. The mechanisms the central nervous system employs have been highly discussed and investigated during the last 10 years. While we use our hands to move objects from one location to another or to give

them to other people, we also manipulate them to achieve higher goals depending on their specific functionality. Whereas a simple object grasp can be based on visual inputs only, such as the geometrical structure of an object, tool use requires the re-activation of learnt information derived from action experiences. Grasping to move and use objects involves distinct cognitive mechanisms implemented in distinct neuroanatomical pathways (Binkofski & Buxbaum, 2013; Daprati & Sirigu, 2006; Jax & Buxbaum, 2013). Preparing an object grasp involves the bilateral dorsal visual streams, also called 'Structure' system (Buxbaum & Kalenine, 2010), whereas preparing an object use requires the additional activation of the left ventro-dorsal pathway, named 'Function' system. Supporting these distinctions, lesions of these streams can lead to ideomotor apraxia, with patients having degraded abilities to use objects while leaving their ability to grasp and transport objects preserved (for a review, Buxbaum, 2001). Recently discussed, such praxic deficits could be explained by a deficit of action selection (Jax & Buxbaum, 2013; Rounis & Humphreys, 2015). Here, we investigated the cognitive mechanisms involved in the selection of tool use.

What cognitive mechanisms would allow for efficient selection of object manipulations? The affordance competition hypothesis (ACH; Cisek, 2007; Cisek & Kalaska, 2010) proposed the selection and specification of action parameters are highly parallelized computations rather than sequential processes. This way, the perceptual processing of an object leads to the simultaneous consideration of multiple action components, such as grasping with the left or right hand to move or use that object. In favor of this view, multiplying objects affordances slow down the motor preparation to grasp and use these objects (Jax & Buxbaum, 2010). So far, the EEG alpha/mu rhythms (~8-13 Hz) appeared to index the extraction of these structural object affordances (Proverbio, 2012; Wamain, Gabrielli, & Coello, 2016; Wamain, Sahaï, Decroix, Coello, & Kalénine, 2018).

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Neuroimaging studies revealed that selecting between left and right hand for finger tapping (Haaland, Elsinger, Mayer, Durgerian, & Rao, 2004), reaching and grasping movement (Gallivan, McLean, Flanagan, & Culham, 2013; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011) or pantomiming tool use (Johnson-Frey, Newman-Norlund, & Grafton, 2005; Moll et al., 2000) rely on a fronto-parietal action network highly left-lateralized. Whereas temporo-parietal structures, such as the middle temporal gyrus (pMTG) and anterior intraparietal sulcus (aIPS), activates motor programs to grasp and move or use objects, the action network, including the supramarginal gyrus (SMG), inferior frontal gyrus (IFG), and superior longitudinal fasciculus (SLF) may implement the selection between the move or use motor programs (Watson & Buxbaum, 2015). Moving and using tools require this left-lateralized action network, and in particular during motor preparation (Brandi et al., 2014). Also, it has been found that right-lateralized parieto-frontal areas represent 'abstract' hand actions, that are independent of the hand performing the action (Gallivan, McLean, et al., 2013). This question the neuroanatomical extend of the action network in bi-lateralized areas, perhaps under the dependence of the complexity of the hand actions. Overall, these reported studies describe well the neural implementation of praxic skills. However, to our concern, when and how these structures are activated to form complete motor plans to execute, such as tool use, remains largely unknown. Therefore, we investigated the motor preparation to manipulate a tool using EEG recordings, which provide precise temporal information about the bilateral activation of action networks.

A well-known EEG marker of sensorimotor processing is the beta-band oscillations. The beta-band activity is intriguing, as numerous studies revealed its involvement in distinct domains of cognitive processing, such as action selection (Brinkman et al., 2016), motor preparation and control (Androulidakis, Doyle, Gilbertson, & Brown, 2006; Kilavik, Zaepffel, Brovelli, MacKay, & Riehle,

2013; Pogosyan, Gaynor, Eusebio, & Brown, 2009; Rubino, Robbins, & Hatsopoulos, 2006; Turella et al., 2016; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010), motor imagery (Brinkman, Stolk, Dijkerman, de Lange, & Toni, 2014; McFarland, Miner, Vaughan, & Wolpaw, 2000), but also language (Bechtold et al., 2018; He et al., 2018; Schaller, Weiss, & Müller, 2017; van Elk, van Schie, Zwaan, & Bekkering, 2010; Weiss & Mueller, 2012), action semantic (van Elk, van Schie, van den Heuvel, et al., 2010) and memory (Hanslmayr, Spitzer, & Bäuml, 2009; Hanslmayr, Staudigl, & Fellner, 2012; Supp et al., 2005). More generally, beta oscillations reflect the activation of task-relevant representations (Haegens, Vergara, Rossi-Pool, Lemus, & Romo, 2017; Spitzer & Haegens, 2017). To unfold the functional role of beta-rhythms, it has been proposed that multiple sub-rhythms reflect different cognitive processing, divided in "low" (13-20 Hz) and "high" (20-30 Hz; Weiss & Mueller, 2012), "slow" (12-20 Hz) and "fast" (12-28 Hz; Zhu et al., 2010), β_1 (13-18 Hz) and $\beta_{2/3}$ (18-30 Hz; Schaller et al., 2017) or beta 1 (~15 Hz) and beta 2 (~25 Hz) frequency ranges (Cannon et al., 2014). Thus, the last 20 years of research on the different beta range activities did not provide yet a consensus on the functional roles they play in cognitive and motor processing.

In one hand, the NSOM theory proposed that the retrieval of object properties relies on ~30 Hz high-beta/low-gamma thalamo-cortical activities (Hart & Kraut, 2007; Kraut et al., 2003; Slotnick et al., 2002). Such ~30 Hz activities could reflect the activation of learnt grasp and tool use representations during motor preparation. On the other hand, a recent MEG study using a movement-delayed paradigm revealed that beta oscillations below ~20 Hz recorded over premotor and parietal areas encodes more abstract (hand-independent) grasp information than simpler reaching movement (Turella et al., 2016), but only starting from 750 ms of initial motor preparation. Hence, it remains unclear which high or low beta rhythms encode complex motor information, such

as tool use actions in comparison with simpler tool transportation. Similarly, the timing and the topography of the beta activities in the bilateral action systems for tool use and transportation remains unknown. In the present study, we investigated the involvement of these beta-range frequencies at multiple sites of the parieto-frontal action network during the motor planning of immediate grasp-and-use and grasp-and-move manipulations of a tool.

We hypothesized that ~30 Hz beta-band power reflects the activation of learnt motor representations required for the performance of tool use. To test it, we compared human EEG signals of real grasp-and-use and grasp-and-move actions, allowing to distinguish tool use-related information from reaching and grasping information processing for simpler tool transportation. To neutralize the effect induced by the knowledge, recognition, and affordance of objects, participants manipulated a novel and unique "dual-use" tool (Fig. 3) in immersive virtual reality, composed of two distinct functional parts: a blade allowing a 'cutting' tool use and a flat part allowing a 'crushing' tool use. The onset of a coloured virtual cylinder indicated whether participants had to grasp-and-move the tool with either hand (a control 'Move' condition; Fig. 4) or to grasp-and-use the tool with either hand to cut or to crush the cylinder ('Use' condition). Here, we predicted that the activation of complex tool use representations, rather than simple grasp representations, rely on ~30 Hz beta rhythms rather than lower beta rhythms (Turella et al., 2016). In accordance with the NSOM theory (Hart & Kraut, 2007; Kraut et al., 2003; Slotnick et al., 2002), the activation of tool use representations occurring within the left-lateralized 'Function' system (Buxbaum & Kalenine, 2010) should involve ~30 Hz beta rhythms. Alternatively, the presence of these rhythms in the bilateral 'Structure' systems would reflect the processing of geometrical affordances rather than the access to learnt tool use representations. Such EEG modulations would have multiple consequences on the 2AS theory (Buxbaum & Kalenine, 2010). Distinct beta sub-rhythms could allow dissociating the

'Function' and 'Structure' systems to use or move the tool, respectively, but also indicate the precise temporal profiles of activation of these systems. Finally, we looked at behavioural timing to perform the use and move of the tool, generally pointing out that the former requires more extensive motor planning, but so far only investigated with dominant hand actions (Chainay, Bruers, Martin, & Osiurak, 2014; Jax & Buxbaum, 2010; Osiurak et al., 2013; Valyear, Chapman, Gallivan, Mark, & Culham, 2011).

Fig. 3 Visual representation of the manipulated object. The object composed of an edge and a flat part to afford the actions of cutting and crushing.

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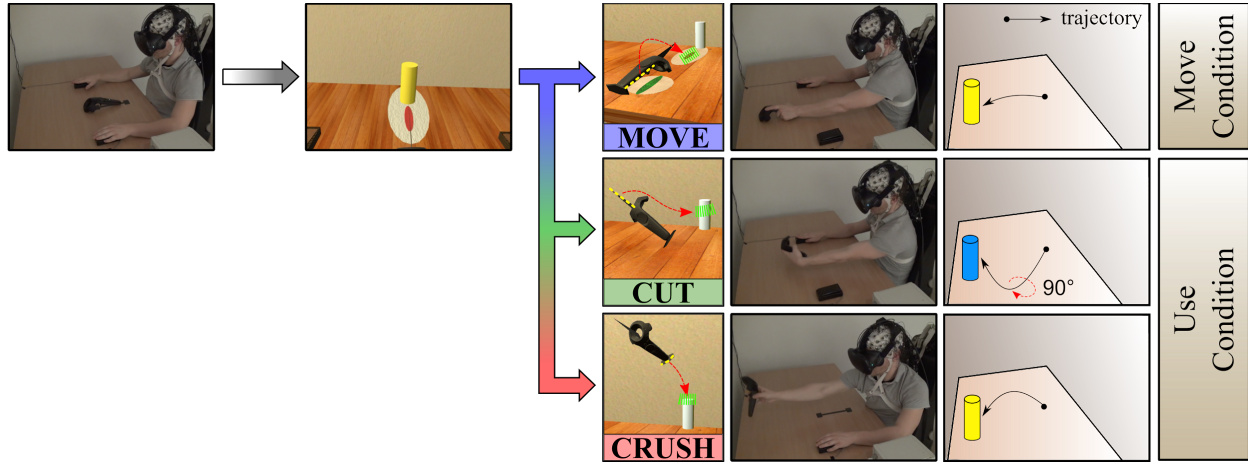
Fig. 4 Experimental design. A depiction of the physical and virtual environment and the experimental procedure for the move, the cut and the crush actions with their associated kinematic trajectories.

2.3. Method

2.3.1. Participants

Thirty-five adults' volunteers (mean age = 22 years old, range 18-34, including 6 males) from the University of Plymouth participated in the study in exchange of course credit. All participants reported being right-handed and having normal vision. Due to the use of a Virtual Reality headset, participants wearing correction glasses were not accepted. Five participants were removed, two for equipment failure and three for excessive electroencephalogram artefacts. The experimental procedure and written consent form for this study were approved by the ethics committee of the University of Plymouth and conform with the 2008 Helsinki Declaration.

2.3.2. Procedure

The experiment used the Unity software (Unity technologies, version 5.3.4f1) to create the virtual environment and the HTC Vive (HTC Corp.) headset and controllers. Participants were seated in a chair next to a desk, wearing both the EEG and VR headsets. Two-button boxes were placed on the desk and connected to the computer to detect the movement onset and the hand used. The virtual environment was composed of two small wooden textured boxes, a pale, a yellow and a green area on a table with wooden textured. The size and height of the room, virtual table and boxes were equivalent to the physical setting of the laboratory space. The visual representation of the VR controller has been modified to appear as a novel tool (Fig. 3) to control a possible effect of familiarity. Participants were asked to produce three different types of action with the VR controller located immediately in front of them on a table. The three possible actions were moving, cutting and crushing (Fig. 4). The tool was composed of an edge and a flat part, in order to afford the actions of cutting and crushing. We created a unique novel tool in order to control the influence of previous experience and of the geometrical properties of the object on semantic and affordances processing. The experiment involved two blocked within-participant conditions, namely, Move and Use. In the Move condition, the participant was required to grasp the controller and move it to an area on the table indicated in red immediately in front of the controller. This movement was initiated by the appearance of a coloured cylinder directly placed directly in front of the red area. The colour of the cylinder indicated the hand used to perform this action (e.g. blue for the left hand and yellow for the right hand). In the Use condition, the participants had to either cut or crush the cylinder. The colour of the cylinder informed the hand needed to grasp the controller and also the use action that was required (to cut or to crush). For a given participant, each of the actions would be consistently associated with a particular hand. For instance, a blue cylinder could have indicated

to respond by cutting it with their left hand and a yellow cylinder to respond by crushing it with their right hand. In order to elicit specific hand grip depending on the action to perform, cutting the cylinder required a left to right horizontal movement and a rotation of the edge to the left of 90 degrees $\pm$ 50 degrees. The experimental design used both hands in order to control possible differences of familiarity to cut with the left hand and crush with the right hand. In both conditions, trials were initiated by the appearance of a white fixation cross at the same location as the cylinder. To start a trial, the participant had to place both hands at rest on buttons place to the left and right of the controller and fixate their gaze on the cross for 1000 ms. Gaze fixation to the cross was established by tracking the orientation of the head through the sensors of the VR headset. When initiating a trial, the fixation cross would disappear, to be replaced by a coloured cylinder at a jittered SOA of between 1500 ms and 2000 ms. Once the participants had completed their action the cylinder disappeared, and the participants were instructed to place the controller back on the start position (indicated by a green area).

Both the move and use blocks consisted of 100 trials each, with random ordering of the two trial types in each block (blue or yellow cylinder) and random ordering of blocks for each participant. The left/right-hand association with crush/cut actions was also randomised for each participant, as was the association with the colour of the cylinder and left/right-hand grasp. Prior to each of the two experiment blocks were two training blocks of 10 trials each. These instructed the participant on the procedure and action associations with the cylinder condition and provided training for movement or use actions. In both cases, active tracking of the controller allowed for positive and negative feedback during training. During the experiment blocks, only negative feedback was provided for incorrect actions (e.g. cutting instead of crushing the cylinder). In total the average

duration of the experiment was 40 minutes, and breaks were provided every 33 trials during the experiment blocks.

2.3.3. Behavioral and electroencephalographic recording

The release of one of the button boxes was used to calculate the movement onset and the hand used to manipulate the object. The grasp onset latencies were calculated from the onset of the movement of the controller, and action latencies when the controller completed the action. These events were used to calculate the following latencies, as follows: a) Initiation time, as the time between the movement onset and the stimulus onset; b) Grasping time, as the time between the movement onset and the grasping onset; c) Execution time, as the time between the grasping onset and the action onset. EEG data were collected from 61 actively amplified Ag/AgCl electrodes (actiCAP, Brain Products, Gilching, Germany) mounted on an elastic cap and following the standard International 10-20 montage. Electrode impedances were kept below 20kΩ and referenced to the left mastoid. The signals were amplified using a BrainAmp MR Plus amplifier (Brain Products) and continuously sampled at 500 Hz. The virtual environment and the EEG recording were running on different computers connected via a homemade parallel port-USB adaptor. Separate ERPs were then time-locked to the stimulus onset.

2.3.4. Data analysis

Only successful trials during the test phases were used for the behavioural and EEGs analyses. Successful trials were defined as trials where participants realized the correct action with the correct hand and initiated the action after 200 ms of stimulus presentation. We used RStudio (v. 0.99.489) and the lme4 (v. 1.1-12) package to perform linear mixed-effect models analyses of the behavioral data to control the variability of the performances between participants and during the experiment (e.g. faster performance over time). Separate models were used to compare the Initiation,

Grasping and Execution Times as a function of the Condition (Move or Use). The strategy used for the following modelling was to maximize the complexity of the structure to control for a maximum of variance while keeping converging models given the size of our dataset. Our fixed effect was the Condition and we entered both the condition and by-participants varying intercepts and slopes and by-task order (administration order of the task) varying intercepts. Visual inspection of residuals plots did not reveal any violation of the assumptions of application. P-values were obtained by likelihood ratio tests of the full model against the null model, with and without the effect of the Condition, respectively (formula of the full model: lmer(ReactionTime ~ Condition + (1+Condition|Participant) + (1|TaskOrder). Pseudo-R-squared effect sizes were estimated with the r.squaredLR function of the MuMIn (v. 1.15.6) packages and planned comparisons were analysed with the glht function of the multcomp (v. 2.2.1) package.

EEGs were analysed using Brain Vision Analyzer (Brain Products, Munich, Germany, v. 2.1) and filtered offline with a 0.1 Hz high pass filter, a 30 Hz low pass filter and a 50 Hz notch filter. Electrodes were re-referenced offline to the average of left and right mastoids activity (TP9 & TP10) and the fronto-central electrode AFz was used as the ground. Separate ERPs were calculated on events time-locked on the stimulus onset. Artefact rejections discarded 19% of the stimulus-locked trials. Individual electrodes with excessive artifact were substituted using topographic interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). Time-frequency representations (TFRs) were calculated for each segment of the ERPs by convolving Morlet wavelets with a width of seven cycles and a frequency range of 14 to 35 Hz. TFRs were then re-segmented to a period 200 ms before the time-lock and 800 ms to remove edge effects inherent in wavelet analyses of segmented data and focus analyses on the temporal period of interest. TFRs were represented in terms of the percent of power change relative to the average power calculated over the initial 200 ms baseline.

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Given that participants' responses were around ~ 600 ms, we focused our analysis on the first 500 ms following the stimulus onset.

Data were analysed using separate pairwise t-tests across all electrodes and all data points comprised in the first 500 ms following the stimulus onset and the 14-35 Hz frequency range comparing the Move and Use actions. To avoid correction for multiple comparisons these analyses were conducted using the cluster randomisation technique of Maris & Oostenveld (2007). Two-tailed t-tests were performed, comparing each electrode-time sample pair for each condition (move or use actions). Those samples with t statistic above the significance threshold ($P < .05$) were clustered together in spatial and temporal terms. Each cluster was based on a minimum of eight samples and used for the subsequent cluster analysis. The t statistic at a cluster-level was calculated as the sum of the t statistic of all electrode-time samples of a given cluster. Then, for the cluster analysis, the cluster with the largest t statistic was selected for a Monte-Carlo simulation. This means, each of the original pairs of t-tests sample that compose the cluster was repeated 1000 times, with permutations of each paired samples randomly assigned between the two conditions. It generated a Monte-Carlo distribution of summed t statistic corresponding to the null hypothesis. A Monte-Carlo p-value was calculated as the ratio of the 1000 summed t statistics in the random distribution that was above the cluster-level t statistic. This p-value was considered significant above $P < .025$. The ERPs were computed by averaging artefacts-free segments for each participant and each condition (Use versus Move).

2.4. Results

2.4.1. Behavioural results

On average, participants picked up the object with the correct hand 95.72% of the test trials and performed the correct actions 99.69% of the test trials. Movement onsets superior to 3000 ms (0.06% of trials) and both grasping and action onsets superior to 3500 ms (0.06% and 1.4% of trials, respectively) from the test phases were discarded as representing outliers, leaving 6281 valid trials.

At first, we looked at participant's time required to prepare and initiate the reach of the tool from the cue onset. The analysis of mixed-effect models revealed a main effect of the task (Chi^2 (2) = 6.9041, R^2 = .0019, P = .02; Fig. 5) and the effector (Chi^2 (2) = 6.5441, R^2 = .0011, P = .01). Surprisingly, participants were slower to initiate the reach of the tool when intended to move (M = 598 ms; SD = 186 ms) rather than to use it (M = 589 ms; SD = 171 ms), as found in (Osiurak et al., 2013) in another move-use task. More evident, participants were faster with the right dominant hand (M = 601 ms; SD = 180 ms compared to the left hand (M = 586 ms; SD = 177 ms). No significant interaction effect was present (Chi^2 (2) = 0.056, R^2 < .0001, P = .81).

We then evaluated the time participants required to grasp the tool from the initiation of the reach, triggered by the release of the press button. Our statistical tests reveal a main effect of the task (Chi^2 (2) = 56.022, R^2 = .0109, P < .001) and the effector (Chi^2 (2) = 61.145, R^2 = .0119, P < .001). Again, participants were slower to grasp the tool when intended to move (M = 797 ms; SD = 207 ms) rather than to use it (M = 779 ms; SD = 206 ms). However, they were slower to grasp with the right hand (M = 799 ms; SD = 212 ms) in comparison with the left hand (M = 778 ms; SD = 200 ms). Again, no significant interaction effect was present (Chi^2 (2) = 1.3514, R^2 = .0002, P = .24).

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Finally, we analysed the execution times, the time participants required to move or use the tool with either hands once the tool handled, to see whether participants were particularly faster to perform a skilled tool use with their dominant hand compared with the non-dominant hand or the move manipulation. The models revealed both significant differences for the task (Chi^2 (2) = 32.418, R^2 = .0056, P < .001) and the effector (Chi^2 (2) = 4.7979, R^2 = .0008, P = .02). Once the tool grasped, participants were faster to move (M = 371 ms; SD = 256 ms) compared to use the tool (M = 401 ms; SD = 191 ms) and faster with the right dominant hand (M = 392 ms; SD = 219 ms) than the left hand (M = 379 ms; SD = 233 ms). The interaction effect was not significant (Chi^2 (2) = 1.727, R^2 = .0003, P = .18).
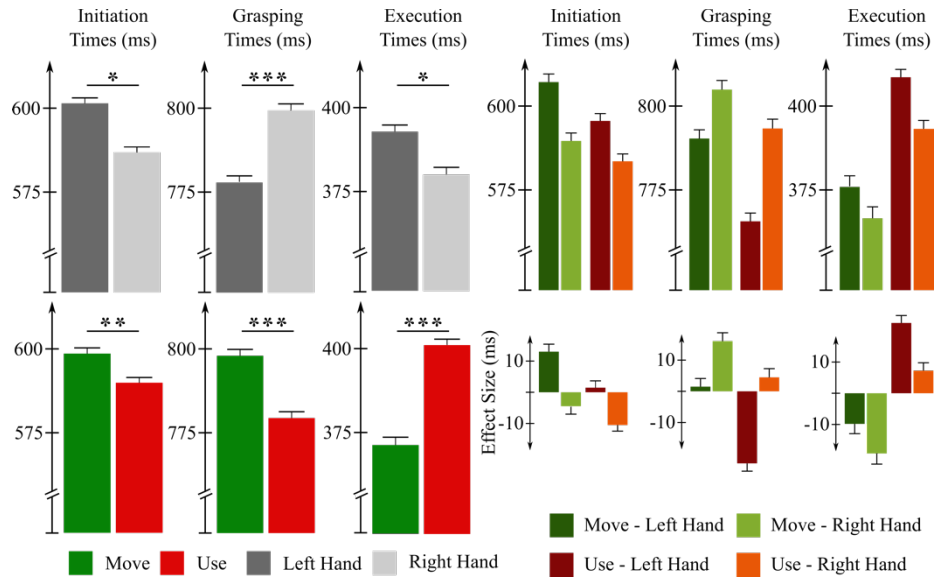
Fig. 5 Behavioural results. Reaction latencies for Initiation Times, Grasping Times (i.e. reach-to-grasp motor sequence) and Execution Times (i.e. from the moment the object is grasped to the moment the object is transported or used). Error bars represent one standard error. * P < 0.05; ** P < 0.01; *** P < 0.001.

2.4.2. EEG results

The EEG analysis time-locked at stimulus onset is represented in Fig. 6. The randomization technique revealed two significant clusters of data points. A first cluster concerned the 0-150 ms time-window, where the decrease of beta power was more important for the tool use compared to the tool move (frequency-interval 22-35 Hz; time-interval 0-155 ms; P = .002). A second cluster concerned a later 150-500 ms time-window, indicating a less important beta power decrease when participants required to use rather than to move the tool (frequency-interval 15-35 Hz; time-interval 55-500 ms; P < .001).

The greater beta power decrease for tool use (cluster 1) is predominant in the left hemisphere (Fig. 7). The peak of the difference occurred at 100 ms post-stimulus onset, around 25-30 Hz over the left dorsal fronto-parieto-occipital electrodes sites (e.g. FC1, FC2, CP1, CP2 and PO3; Fig. 5).

In opposition, the lesser beta power decrease for the tool use (cluster 2) mainly occurred in the right hemisphere. The peak of the modulation occurred in the first 200-400 ms from stimulus onset, between 15-25 Hz, and in the right dorsal parieto-occipital areas (CP2, P2, O2, PO4), widespread to the electrodes located over right ventral pathway (e.g. P8). Notably, no beta power modulation has been revealed in bilateral temporal electrodes sites (T7, T8).

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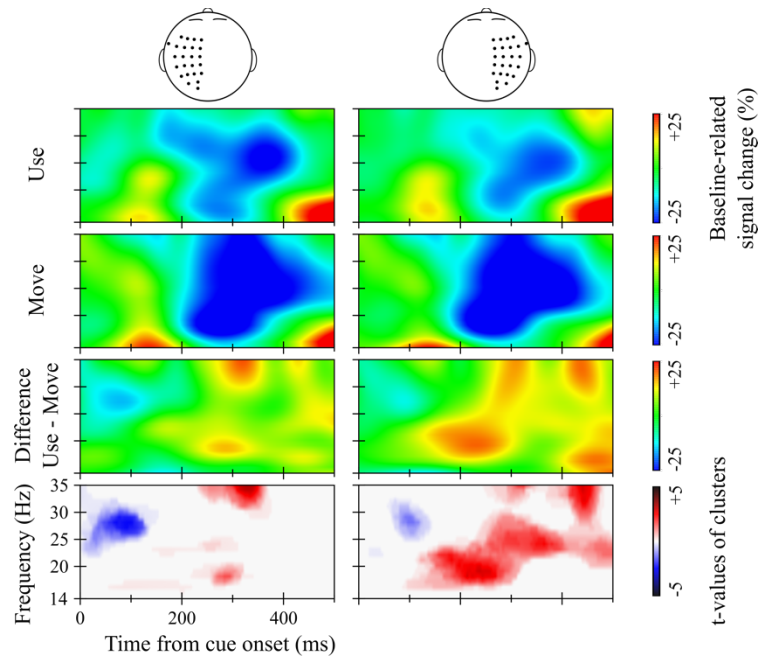
Fig. 6 Results of the time-frequency analysis by hemispheres. The early (0-150 ms) beta-band power at around 25-30 Hz is particularly reduced in the left hemisphere when required to use the tool. Following beta-band power in the 16-30 Hz range is less reduced in the right hemisphere when required to use the tool.
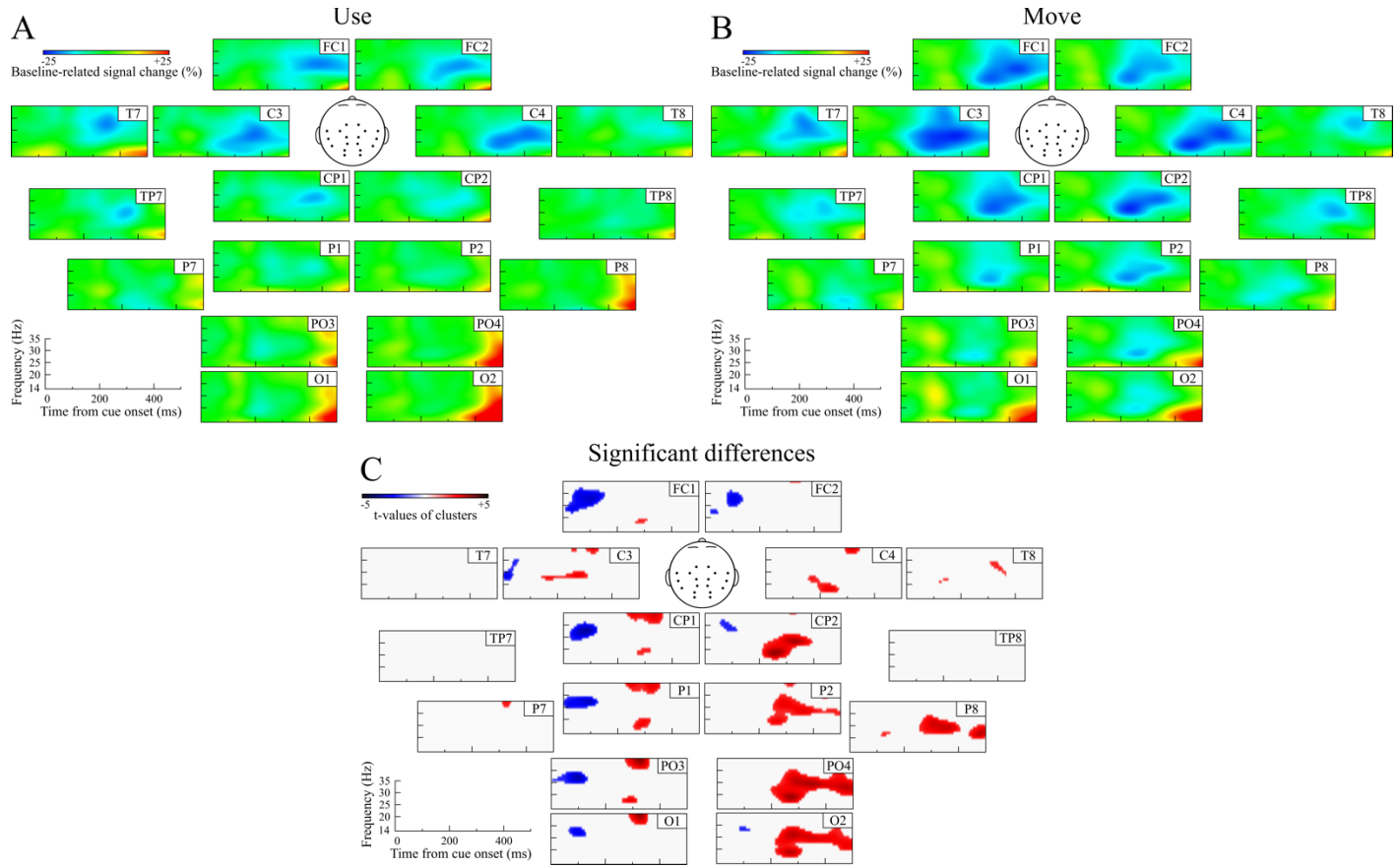
Fig. 7 Results of the time-frequency analysis in the beta range by electrodes. A representative subset of electrodes is displaying the 14-35 Hz beta power from cue onset for the tool use (A) and move (B) conditions. The time-frequency representations of significant beta modulations (C) reveal that the early greater power decrease (blue) for the tool use appears left-lateralized, whereas the latter weaker power decrease (red) appears bilateral.

2.5. Discussion

Previous studies evaluated the geometry-based and function-based object manipulations through the move-use paradigm, where participants were asked to grasp an object as if they were

going to move or use it. In some of these studies no move or use of tools is actually performed (e.g. Jax & Buxbaum, 2010), whereas in others the participants did (Chainay, Bruers, Martin, & Osiurak, 2014; Valyear, Chapman, Gallivan, Mark, & Culham, 2011). For instance, Osiurak, Roche, Ramone, & Chainay (2013) where participants had grasped a pan to hit a ball. These studies report that the preparations to transport objects require less time than those to use them. The debated conclusion drawn from these data is that the integration of object knowledge for tool use is more cognitively demanding than transporting an object, the latter simply requiring to process the geometries of the object. Neuroimaging data that could support this argument have shown that motor preparation and execution when using objects increases activation of the superior frontal gyrus and the superior parietal lobule when compared to the transportation of objects (Brandi, Wohlschlager, Sorg, & Hermsdorfer, 2014). In this Experiment 1, we present data providing a contrasted interpretation of the preparation and execution of tool use and transportation. Here, independently of the hand laterality, the preparation of tool transportation requires more extensive preparation and execution time than tool use. The difference in reach-and-grasp timings reported here support the ACH model (Cisek, 2007; Cisek & Kalaska, 2010) suggesting that action preparation unfolds during motor control, whereas the absence of the effect would have support non-parallelized but sequential mechanisms of action. In our experimental settings, this result may be explained by the physical constraints of the two actions, such as the recipient of the tool transportation (see Osiurak et al., 2013 for a similar consideration). Indeed, using the tool involved the interaction of a virtual target, whereas moving the tool required the consideration of the physical table. If this experimental feature explains the relatively long reaction times for the tool transportation, this interference would be more important than the selection between the tool use (cut or crush) actions. Indeed, as these functional actions have common motor properties, they represent important action competitors to

select (Cizek, 2007) and should slow down the motor preparation and execution. Therefore, we believe in an alternative interpretation, considering that functional actions are prevalent in tools compared to structural actions, such as they are fundamental properties and therefore prepared at first, as suggest our EEG results.

Our behavioural data revealed that participants were faster to initiate the reach of the tool with their right (dominant) hand. But strikingly, the reach-and-grasp movements of the tool were also slower with their right hand. This could possibly reflect the specificity of the dominant hand for precise motor function (e.g. handwriting). Then, the action execution is faster with the right hand, most likely due to the habit to manipulate tools with the dominant hand in right-handed people. Further investigations are needed to comprehend why object manipulations with the dominant hand are slowed down, independently of the object knowledge and affordances.

The 2AS model (Buxbaum & Kalenine, 2010; see also Binkofski & Buxbaum, 2013; Sakreida et al., 2016 for discussion) proposed that different neuronal activations emerge for simple object grasp and complex object use. An outstanding question is how does the brain select the multiple motor sequences composing an object-directed action? In this study, we asked the two following questions. First, could the ~30 Hz beta rhythms, proposed to reflect the retrieval of object semantic memory (Hart & Kraut, 2007; Kraut et al., 2003; Slotnick et al., 2002), also represent the activation of the 'Function' tool use system? Second, when this system is activated during the preparation of functional actions? Our EEG results indicate that the preparation of complex tool use reduces the early (0-150 ms) beta power on the 25-30 Hz range. This transient modulation occurs specifically within the left dorsal (possibly corresponding to the 'Function') system, from occipital to premotor areas, but also over the right premotor cortex. Similarly, a previous study has pointed out that beta rhythms were involved in semantic object manipulations (van Elk, van Schie, van den Heuvel, et al.,

2010). Thus, we propose that the 'Function' system involved in the preparation of tool use (Buxbaum & Kalenine, 2010) could rely on neuronal activations paced at ~30 Hz, involved in the retrieval of object knowledge (Hart & Kraut, 2007; Kraut et al., 2003; Slotnick et al., 2002).

Our experiment supports the idea that beta rhythms reflect the activation of grasp action representations, revealed in Turella et al. (2016). However, we found here that effector independent action representations encoded in beta rhythms can be recruited way before ~800 ms when subjects are instructed to perform immediate-response (in comparison with delayed-response) to a cue. Whereas the authors found that grasp movements modulated 10-20 Hz beta activity compared to simpler object reach, and in particular in the right hemisphere, here performing complex tool use actions rely on beta rhythms over 20 Hz. However, the results from Turela et al. (2006) support the idea that < 20 Hz beta rhythms reflect the preparation of structural grasps, and possibly the activation of the 'Structure' system proposed in the 2AS theory. Indeed, in the following 200-500 time-window, tool use actions involved more signal power below 20 Hz recorded over bilateral sites than the tool transportation. This would indicate that preparing a tool use activated the 'Structure' system to a lesser extent than tool transportation did (i.e. reflected in less decreases of signal power). An alternative interpretation but still supporting our proposal is that the late beta modulation reflects the inhibition of this system when required to perform the tool use. An important role of the dorsal visual stream is to translate visual information into motor plans, for example when the orientation of an object would favorize a specific hand to grasp. The effect found in Turella et al. (2006) may reflect the reinforced activation of the 'Structure' system when participants intend to object grasp rather than simpler reach. However, we observe here that the complexity of the motor plan appears to raise the power of the beta rhythms.

Assuming that beta rhythms are involved in activation of the 'Function' and 'Structure' action systems, the present results suggest that the 'Function' system is not necessarily activated after the 'Structure' system, but may depend on situational and contextual characteristics, as discussed Borghi and Riggio (2015). This could be the case when people cannot pre-select a hand or a specific manner to manipulate an object prior to movement initiation. Our beta modulations during tool use preparation occur before 400 ms, known to be a critical timing for semantic processing (Jackson, Lambon Ralph, & Pobric, 2015; Kiefer et al., 2007; Supp et al., 2005; van Elk, van Schie, & Bekkering, 2008; van Elk, van Schie, van den Heuvel, et al., 2010). Hence, these results suggest that tool use representations are activated quicker than previously thought, possibly during the first 100 ms of motor preparation. Also, different beta frequencies, even dough partially overlapping, may differentiate the activation of these two systems. Beta frequencies at around ~30 Hz may reflect the activation of the 'Function' system, dedicated to the processing of semantic tool use representations, whereas the activation of the 'Structure' system may rely on lower ~20 Hz beta oscillations. Clearly, further investigations are needed to confirm this distinction.

In conclusion, the present study provides new insight on hypotheses regarding the neurocognitive dissociation of structural and functional action systems, based on the move-use paradigm (Brandi et al., 2014; Chainay et al., 2014; Jax & Buxbaum, 2010; Osiurak et al., 2013; Valyear et al., 2011). In contrast with the prevailing findings of the literature, our experiment illustrates that a functional action (i.e. an instance of tool use) can be initiated and performed faster than a structural action, questioning the move-use dichotomy and its applications. Our EEG analyses revealed two time-windows of particular interest. During the first 150 ms of the motor preparation, a decrease of 25-30 Hz beta power prior tool use could reflect the activation of the left-lateralized 'Function' system. Afterward, lower beta activities (16-25 Hz) could reflect the

activation of the bilateral 'Structure' system. We believe in a possible functional dissociation between high and low beta rhythms and their involvement in the preparation of functional and structural object-directed actions, respectively. We will come back on that statement and the move-use paradigm in Chapters 5 and 6.
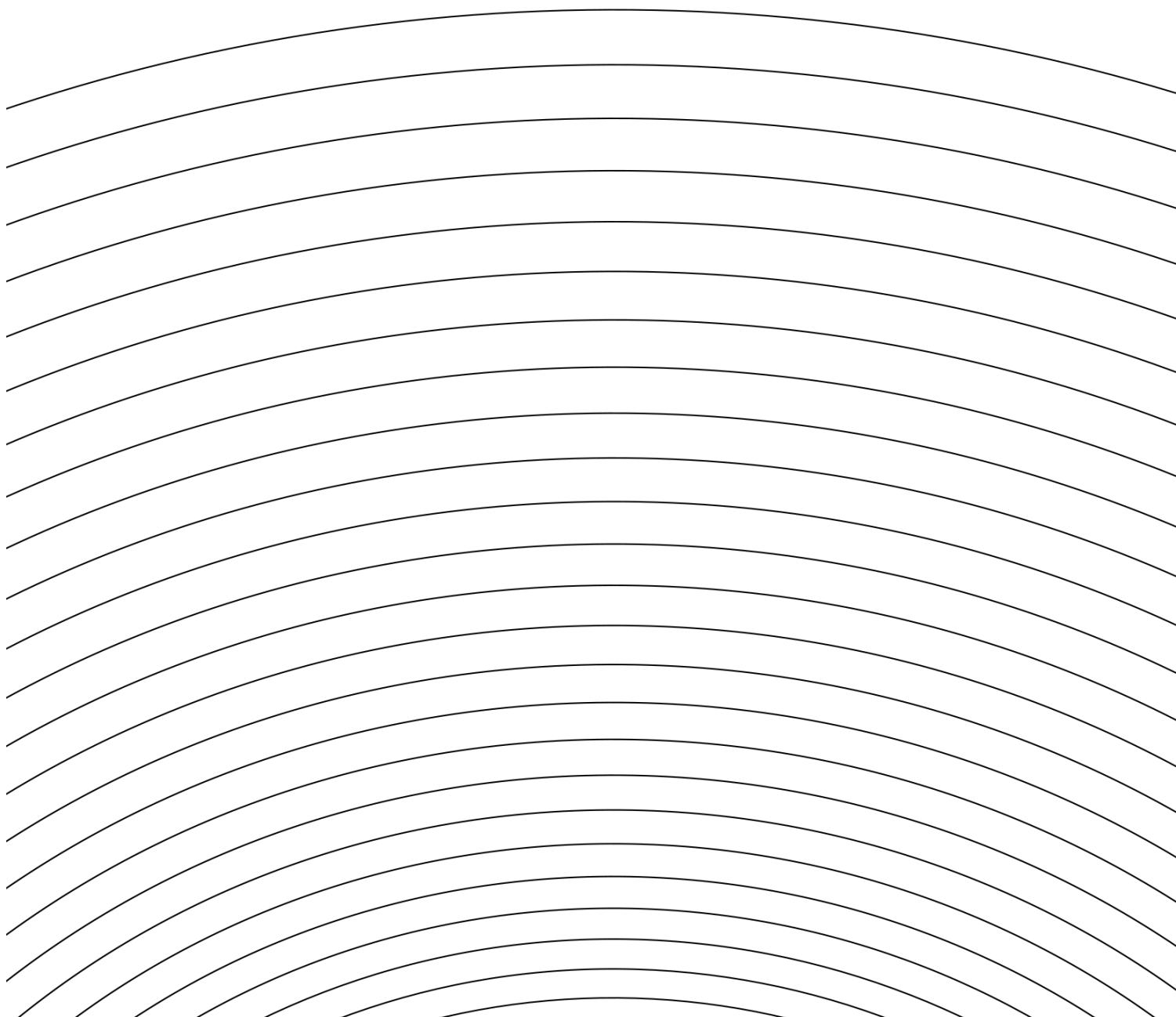
3. Beta rhythms in the activation of functional and manipulation knowledge during object recognition

A video describing the work done in this chapter can be seen via the QR code at the bottom of the page or the following link: https://www.youtube.com/watch?v=5e4BmL8MSG4&t=22s

3.1. Chapter Abstract

What makes an object a tool is its association to a specific function to reach an end-goal. However, all tools do not rely on motor knowledge ('How') to perform a functional action. In one hand, using a key requires remembering what action (turning inside a lock) to execute its function (opening a lock). On the other hand, using a bucket does not require this remembrance to execute its function (collecting water), given that the action is directly afforded by the structural properties of the bucket (grabbing the bail handle). Theoretically, this means that the first category of tools is embodied in brain action systems rather than semantic systems. Oppositely, the second category of tools should be represented in semantic systems rather than action systems.

We investigated whether different cortical ~30 Hz beta-band power could reflect the activation of functional and/or manipulative object information during object recognition through two training studies. We found that 1) learning the function of a novel tool activates frontal representations at 400-740 ms, whereas 2) learning both function and action information (i.e. a tool use) activates left-lateralized parieto-occipital representations at 340-640 ms. Consequently, our knowledge about tools reflects the way they are represented in the brain and influence the EEG ~30 Hz beta responses.

3.2. Introduction

Using objects and tools requires access to the manipulative and functional information associated with them. For instance, using a hammer involves specific motor parameters, such as the appropriate palmar hand grip and tool use (a forward swinging movement of the forearm). It also requires access to semantic associations such as the object-targets (usually nails) and the perceptual expectations of the action (e.g., the sound and vision of hammering; Humphreys et al., 2010; Orban & Caruana, 2014; Vaesen, 2012). This manipulative and functional information emerges from our action experiences and is encoded in sensory-motor neuronal assemblies (Kiefer & Pulvermüller, 2012; Kiefer et al., 2007). Whereas manipulative information seems automatically activated when viewing tools (Borghi et al., 2007; Proverbio, Adorni, & D'Aniello, 2011; Tucker & Ellis, 1998 ; see also Borghi & Riggio, 2015 and Osiurak, Rossetti, & Badets, 2017 for reviews), the recruitment of functional information appears task-dependent (Daprati & Sirigu, 2006; Kiefer & Pulvermüller, 2012). For instance, Lindemann, Stenneken, van Schie, and Bekkering (2006) showed that participants were faster to respond to a word related to an upcoming object-based action to perform (e.g. responding to the word *mouth* while preparing to bring a cup to the mouth) compared to an unrelated word. This effect vanished when participants had to prepare a simple lift of the finger. Hence, meaningful actions involve a semantic activation that meaningless actions don't require, which support the selection-for-action principle (Allport, 1987) suggesting that only relevant information is recruited to prepare a given action. However, such data appear in opposition with the affordance competition hypothesis (ACH; Cisek, 2007; Cisek & Kalaska, 2010), proposing that non-motoric information (e.g. the semantic properties of a tool) is recruited to bias motor decisions

upon multiple manipulations available. This would mean that the semantic properties of an object are constantly into play when required to manipulate it.

We use everyday tools to obtain a particular end-goal. Theories of cognitive embodiment posit that cognitive processes are rooted in perceptual and motor neural circuits (see Meteyard et al., 2012, for a recent review). Our common tools are embodied concepts, given that we associate specific actions (i.e. a tool use) along with semantic (e.g. a goal or a function) properties. Hence, these objects and tools are represented in perceptuo-motor brain systems given their strong association with action (Brandi et al., 2014; Hermsdorfer et al., 2007). For Buxbaum and Kalenine (2010), only the representations within the tool use systems are embodied components of tools. However, distinguishing tools from non-tool objects is not clear. Any objects can be used as a tool without a particular tool use, theoretically resulting in 'disembodied' brain representations – tool representations independent from a specific action. This is the case of the meaningful transportation of a bucket to collect water, an argument in favour of the reasoning-based approach of tool use (Badets & Osiurak, 2015; Goldenberg & Hagmann, 1998; Jarry et al., 2013; Osiurak & Badets, 2016). Thus, a plethora of studies investigated how tools are embodied in perceptuo-motor systems, whereas such 'disembodied' tools category has been left aside.

Here, we tested where and when disembodied semantic representations of a tool are activated during its perception. To do so, we created two novel objects in immersive virtual reality that participants grasped and moved from one location to another. The use of virtual reality and novel objects assured the participants remembered only the information they were taught, thus neutralizing unrelated factors (e.g. object features, prior knowledge). At the middle of the experiment, participants learnt the semantic functionality of one of the two objects – the object is a

key opening a box when transported to a specific location. We compared participants' EEG before and after the training during the perception of the 'key' tool and the non-tool object.

Little is known about how, in a given task, the brain re-activates such semantic representations of objects and tools, but recent progress in cognitive neuroscience highlighted functional roles of beta (13-30 Hz) oscillations. Beta-band activity reflects top-down information processing (Engel & Fries, 2010; Wang, 2010). In the predictive coding framework, beta-band oscillations are proposed to communicate top-down sensory predictions (Arnal & Giraud, 2012). This beta-band activity appears involved in memory (Hanslmayr et al., 2009) and objects semantics processing, especially in the 400 ms following object viewing (Supp et al., 2005). Performing functional hand postures of tools (van Elk, van Schie, van den Heuvel, et al., 2010) and retrieving object's weight upon viewing (Quandt & Marshall, 2014; Quandt, Marshall, Shipley, Beilock, & Goldin-meadow, 2012) are reflected in the modulation of beta-band power. These results are in accordance with a neural model of object semantic memory, proposing that neuronal activities paced at ~30 Hz can represents thalamo-cortical activity re-activating object representations from memory (Kraut, Calhoun, Pitcock, Cusick, & Hart, 2003; Slotnick, Moo, Kraut, Lesser, & Hart, 2002; see also Pulvermüller, Lutzenberger, & Preissl, 1999). Recently, Spitzer & Haegens (2017) proposed that beta-band activity reflects the re-activation of cortical representations necessary to accomplish a task. Altogether, the ~30 Hz beta-band activity represents a reliable marker of retrieval of semantic object knowledge.

We examine the EEG ~30 Hz beta-band power, and in particular its decrease (Hanslmayr et al., 2012), as an index of object semantic processing to asks when and in what cortical system the semantic representations of a tool become activated. Many studies reported that temporal (Joseph, 2001; Kiefer & Pulvermüller, 2012) and occipitotemporal (Cichy, Pantazis, & Oliva, 2014; Gallivan,

Adam McLean, Valyear, & Culham, 2013; Lingnau & Downing, 2015; A. Martin et al., 1996; Noppeney, 2008; Orban & Caruana, 2014) cortex represent the core of semantic representations of tools and actions. Other studies revealed that parietal (Chao & Martin, 2000; Cross et al., 2012; Johnson-Frey, 2004) and frontal areas, such as the left premotor areas, encode how tools are used (Chao & Martin, 2000; Joseph, 2001; Martin et al., 1996; Noppeney, 2008). Previous EEG studies reported both fronto-central and occipito-parietal activations sensitive to learnt conceptual representations of novel objects within the first 200 ms of object processing sites (Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Kiefer et al., 2007). Hence, turning an object into a tool might re-activate semantic representations around these cortical sites and timings during subsequent tool recognition. Would non-motor semantic representations of a novel tool be grounded within frontal (i.e. encoding tool use) or occipitotemporal (i.e. encoding actions, motions, colors) brain systems? The presence of ~30 Hz modulations would support the NSOM theory (Kraut et al., 2003). We tested the hypothesis that a beta-band modulation would occur within the first 400 ms, indicating the activation of functional representations of tools, concomitant and possibly playing a role in object recognition (see Kutas & Federmeier, 2011, for a review; Supp et al., 2005). A subsequent beta-band effect would indicate that the retrieval of semantic information about a tool occurs post-recognition, probably during the motor preparation to transport the tool. Alternatively, the absence of beta-band modulations would suggest that semantic knowledge is recruited for the preparation of tool use only but not mere recognition or tool transportation (Lindemann et al., 2006).

3.3. Methods

3.3.1. Participants

Twenty-four adult volunteers (mean age = 20.1 years old, range 19-27, including 5 males) from the University of Plymouth participated in the study in exchange for money or course credit. All participants reported being right-handed and having normal vision. Due to the use of a VR headset, participants wearing correction glasses were not accepted. Two participants were removed for excessive electroencephalogram artefacts. The experimental procedure and written consent form for this study were approved by the ethics committee of the University of Plymouth and conform with the 2008 Helsinki Declaration.

3.3.2. Experimental setup and procedure

The experiment used Unity software (Unity technologies, version 7.1.0f3) to create the virtual environment and the HTC Vive (HTC Corp.) headset and controllers. Participants were wearing both the EEG and VR headsets and were seated in a chair next to a desk. A button box was placed on the desk situated on the right side of the participants and connected to the computer to detect movement onsets. The virtual environment was composed of a small wooden textured box, a white and a red dashed area situated on the table, a big box situated in front of the participant and a small black cube on their left (Fig. 8A). The size and height of the room, virtual table, and the button box were fitted to the dimensions of the physical environment. For a comfortable position of the hand on the button box, the distance between the chair and the desk was adjusted for each participant. Participants were instructed to manipulate a VR controller, visually represented by two possible 3-D models (Fig. 8B).

Brain Rhythms in Object Recognition and Manipulation
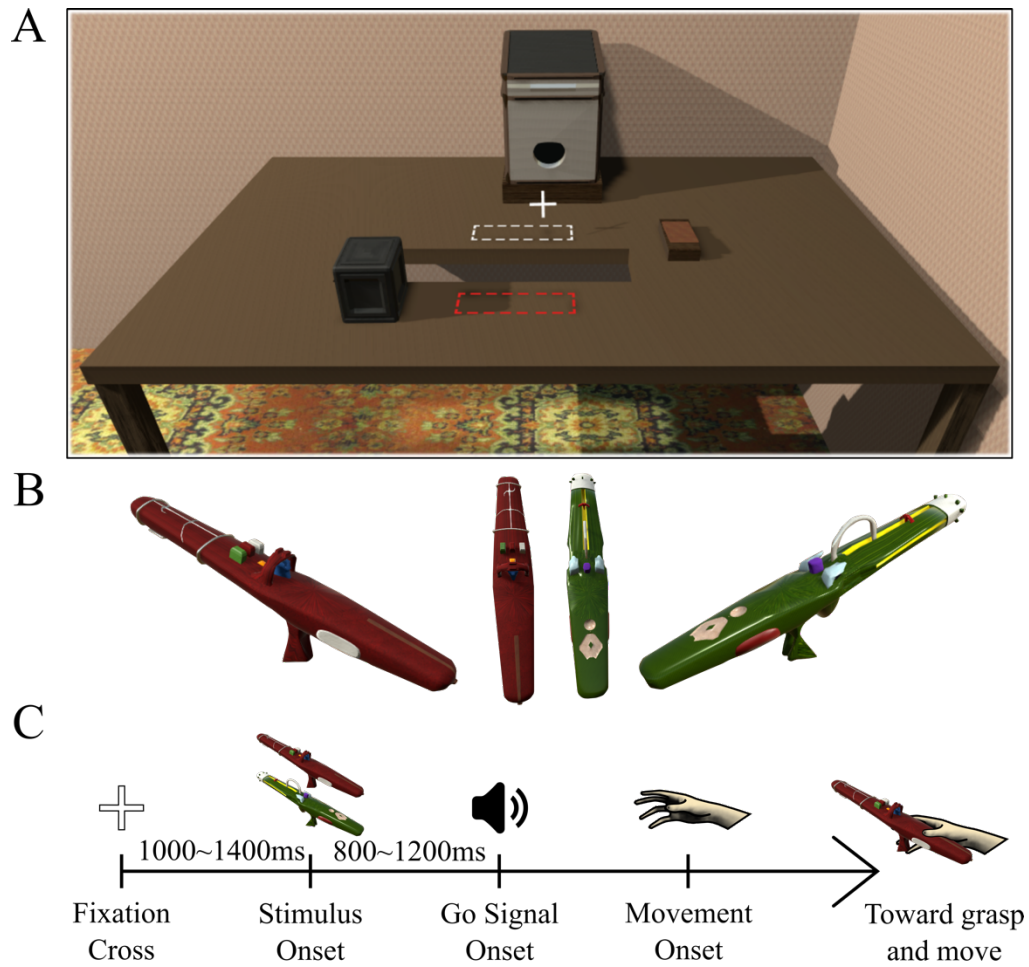
Fig. 8 Experimental design. (A) The virtual environment perceived by the participants. (B) The two possible visual representations of the stimuli-objects manipulated during the experiment. (C) After viewing a fixation cross, one of the two objects randomly appeared. After a time-interval between 800 ms and 1200 ms, participants heard a tone (i.e. the go-signal) and had to grasp and move the object as fast as possible.

The experiment was divided into three phases termed as pre-training, training, and post-training phases which consisted of 120 trials, 50 trials, and 120 trials, respectively. The trials for the pre-training and post-training phases were divided into four blocks of 30 trials. The training phase was divided into two blocks of 25 trials. After each block of trials, a time break was proposed to the participant and the VR headset was removed if desired. The pre-training period was used to control the possible effects of visual attention and familiarity with the two stimuli and the task on the EEG activities. The trial procedure is depicted in Fig. 8C. At the beginning of each trial, the participant had to place the right hand on the button box and look at the white fixation cross situated in the front of him/her, at the location of the invisible controller. After 1000 ms, the fixation cross disappeared. Subsequently, one of two visual representations of the controller appeared after a random time-interval between 1000 ms and 1400 ms. Participants were instructed to prepare to grasp-and-move the controller from the white to the red area after hearing a tone (i.e. go-signal) triggered after a random time interval between 800 ms and 1200 ms. We used this delayed response paradigm to prevent contamination of the EEG signal from movement-related effects. Once the controller was placed on the red area, next to the black cube, the participant was instructed to return it to the white area. The 3-D model of the controller then disappeared. The black cube had no other importance in the experiment. The motor task had to be performed as fast as possible. If the button box was released before the onset of the go-signal, the participant received a written feedback about their performance on a virtual panel at the end of the trial, reminding him/her to move only after the tone. At the end of each trial, participants were instructed to put their right hand back on the button once they were ready to start a new trial. Participants were instructed to avoid movements and eye blinks during the trials, especially before the go-signal. They were able to move freely between trials. The visual representation of the controller was randomly assigned to each trial.

During both pre-training and post-training phases, participants had to grasp-and-move the two stimuli without distinction. The purpose of the training phase was to transform the representation of one of the two objects into a tool (i.e. a key that opens the box on the table). The object trained was randomly assigned to each participant at the beginning of the training phase. In the training phase, the participants were instructed to grasp-and-move the object and the tool. The tool opened the box when it was transported on the red area, whereas the non-tool object did not trigger any sound or animation. Hence, participants associated with the tool the function 'a key that opens the box' without additional manipulation.

3.3.3. Behavioural and electroencephalographic recording

The release of the button box was used to calculate the movement onset of the participant. Then, the tool or object being lifted was detected and used to calculate the grasping onset. The action onset was calculated when the tool or the object was transported to the red area. The stimulus onset (i.e. tool and object apparition) and movement onset were used to time-lock ERD/ERS analysis. The timing of the motor action was segmented and calculated as follow: a) Initiation times, as the time between go-signal onsets and movement onsets; b) Grasping times, as the time between movement onsets and grasping onsets; c) Execution times, as the time between grasping onsets and action onsets. We evaluated these time intervals depending on the stimulus-object during the post-training phase of each condition. EEG data were collected from 61 actively amplified Ag/AgCl electrodes (easyCAP, Brain Products, Gilching, Germany) mounted on an elastic cap and following the standard International 10-20 montage. Electrode impedances were kept below 20 kΩ and referenced to the left mastoid. The signals were amplified using a BrainAmp MR Plus amplifier (Brain Products) and continuously sampled at 500 Hz. The virtual environment and the EEG recording were run on separate computers.

3.3.4. Data analysis

Only successful trials during the pre- and post-training phase were used for the behavioural and EEGs analyses. Successful trials were defined as trials where participants initiated the action after the go-signal onset. We used RStudio (v. 0.99.489) and the lme4 (v. 1.1-12) package to perform linear mixed-effect models analyses of our behavioural data. The strategy used for the following modelling was to maximize the complexity of the structure to control for a maximum of variance while keeping converging models given the size of our dataset. Given the high variability in the pre- versus post-training phase, expressed as decreases of behavioural timings for the post-training phase, only post-training behavioural data have been considered for statistical testing in order to obtain converging models. These models compared the initiation, grasping and execution times as a function of the stimulus (tool or non-tool object). We entered the stimulus as a fixed effect and by-participants random intercepts and slopes. Visual inspection of residuals plots did not reveal any violation of the assumptions of application. P-values were obtained by likelihood ratio tests of the full model against the null model, with and without the effect of the stimulus, respectively (formula: lmer(ReactionTime ~ Tool + (1+Tool|Subject)). Pseudo-R-squared effect sizes were estimated with the r.squaredLR function of the MuMIn (v. 1.15.6) packages.

We analysed the EEGs with Brain Vision Analyzer (Brain Products, Munich, Germany, v. 2.1) and filtered off-line with a 0.1 Hz high pass filter, a 50 Hz low pass filter, a 50 Hz notch filter and downsampled to 80 Hz. Electrodes were re-referenced off-line to the average of left and right mastoids activity (TP9 & TP10) with the fronto-central electrode AFz used as the ground. Due to the friction of the VR headset with the anterior electrodes during the task, the electrodes Fp1, Fp2, Fpz, AF7, AF8, AF3 and AF4 were removed from the analysis. Signals were time-locked to the stimulus onset. At first, for each participant we computed the event-related potentials (ERP) time-

locked to the stimulus onset, including a time-window of 1100 ms, starting 300 ms before the stimulus onset and ending 800 ms after this onset. Baseline correction was performed on the first 200 ms before the stimulus onset.

A semi-automatic artefact rejection procedure was run on the ERPs to exclude segments violating the following parameters: maximal allowed voltage step of 50 µV/ms, maximal voltage differences allowed of 100 µV within 200 ms intervals, maximal/minimal allowed amplitude of ± 100 µV/ms, and minimum amplitude of 0.5 µV within 100 ms intervals. These parameters were slightly adapted manually for each participant to maximize the signal-to-noise ratio, resulting in a total of 32% of segments rejected. Individual electrodes having greater than ~10% of rejected segments were removed from analyses and substituted with topographically interpolated replacements (Perrin, Pernier, Bertrand, & Echallier, 1989).

After artifact rejection, we evaluated event-related power changes using the ERD/ERS (Event-Related Desynchronization/Synchronization) method (Pfurtscheller, 1992; Pfurtscheller & Lopes, 1999). Each trial was band-pass filtered for the beta frequency band (25-35 Hz; as in Pulvermüller et al., 1999) and then squared to produce power values ($µV^2$). These squared values were then averaged and converted in the percentage of power change (as in van Elk, van Schie, van den Heuvel, et al., 2010) relative to the average power calculated over the baseline period. These ERD/ERS signals were smoothed using a running average time-window of 137 ms (as in Ruther et al., 2014).

In order to control for the effect of the familiarity to the grasp-and-move task and increase the signal-to-noise ratio within each condition, we computed the difference of ERD/ERS for each stimulus (tool and non-tool object) in pre- and post-training phase, such as: training effect = (tool $_{post-training}$ – tool $_{pre-training}$) – (non-tool object $_{post-training}$ – non-tool object $_{pre-training}$). Therefore, for each

participant, the ERD/ERS training effect of each stimulus and condition was kept for statistical analysis.

To avoid multiple comparisons, we carried out pairwise comparisons analyses based on the cluster randomisation technique of Maris and Oostenveld (2007) within each condition. Two-tailed t-tests were performed across all electrodes and all data points comprised in the first 800 ms following the stimulus onset and the 25-35 Hz frequency range comparing the two objects. Those samples with t statistic above the significance threshold ($P < .05$) were clustered together in spatial and temporal domains. Each cluster was based on a minimum of eight samples and used for the subsequent cluster analysis. The cluster-level t statistic was calculated as the sum of the t statistic of all electrode-time samples of a given cluster. For the cluster analysis, the cluster with the largest t statistic was selected for a Monte-Carlo simulation. Thus, each of the original pairs of t-tests sample that compose the cluster was repeated 1000 times, with permutations of each paired samples randomly assigned to the tool or the non-tool object. It generated a Monte-Carlo distribution of summed t statistic corresponding to the null hypothesis. A Monte-Carlo p-value was calculated as the ratio of the 1000 summed t statistics in the random distribution that was above the cluster-level t statistic. This p-value was considered significant at $P < .025$. Averaged TFRs were re-plotted as t-values in the time-electrodes domain, derived from t-tests against baselines of zero. Finally, Monte-Carlo simulation of pairwise t-tests was conducted to compare the tool and the non-tool object and plotted in the time domain on topographic maps.

3.4. Results and Discussion

We discarded 7.42% of the trials where participants initiated the action before the go-signal onset. Mixed-effects models did not reveal any significant timing differences in terms of initiation,

grasping and execution times, between the tool and non-tool object in the post-training phase. The tool did not elicit different initiation times (Chi^2 (1) = 2.888; R^2 = .0019; P = .0892), grasping times (Chi^2 (1) = 1.796; R^2 = .0008; P = .1801) or execution times (Chi^2 (1) = 1.9639; R^2 = .0009; P = .1611) compared to the object.

ERD/ERS time-locked to the stimulus onset resulting from the grand-averages and the cluster-randomization technique is represented in Fig. 9A. The analysis revealed an increase of beta-band power for the tool compared with the non-tool object (Fig. 9B; time-interval 400 to 738 ms; P = .003) over the right fronto-central electrodes (F2, F4, FC2, FC4, FC6). This suggests that the ~30 Hz activity recorded over fronto-central areas, possibly related to the right premotor cortex, appears sensitive to the stimulus category. Hence, this first results contrast with recent studies suggesting that functional knowledge about objects and tools are represented within left temporal areas (e.g. Almeida, Fintzi, & Mahon, 2013; Chen, Garcea, & Mahon, 2016).
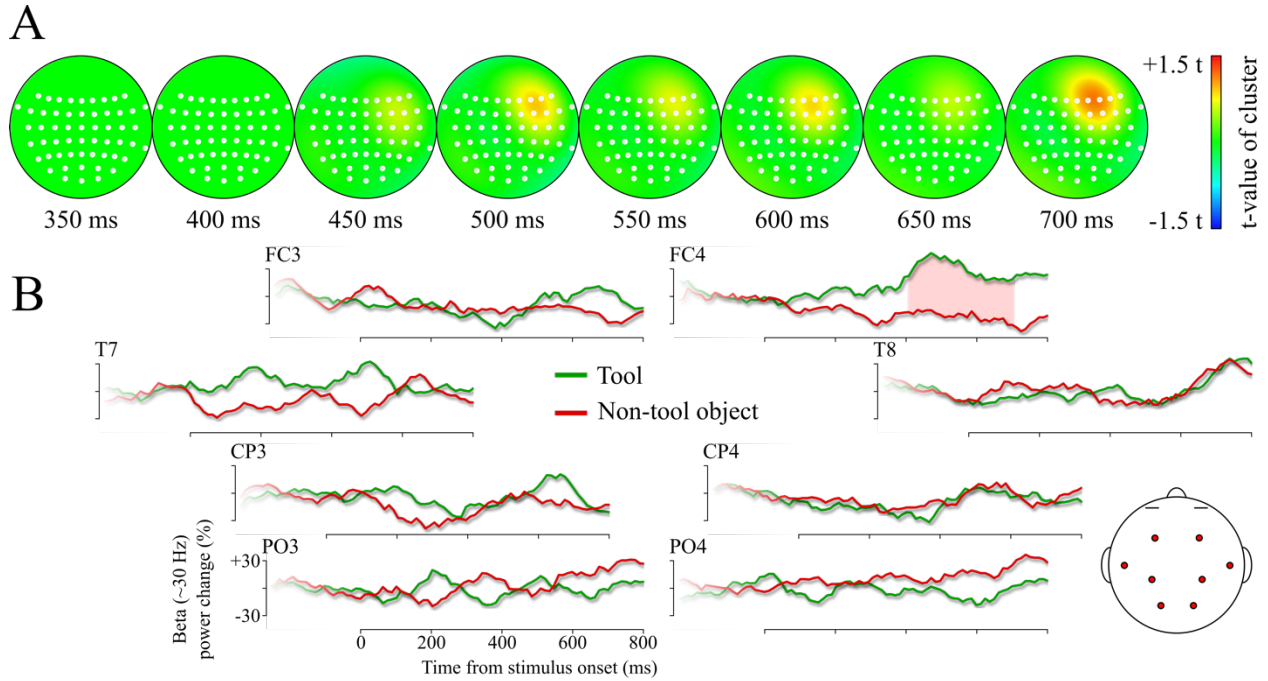
Fig. 9 Beta power differences pre- and post-training. (A) Topographic maps of the beta (25-35 Hz) ERD/ERS time-locked to the stimulus onset and based on the difference of signal post- minus pre-training for the tool and non-tool object. The significant cluster resulting from the cluster-randomization technique, represented in summed t-values, appeared in fronto-central electrodes from ~400 ms following stimulus onset. (B) A representative subset of electrodes across the scalp comparing the ERD/ERS post- minus pre-training for the tool (green) and non-tool object (red). The red area in electrode FC4 represents the significant increase of beta power for the tool (P = .003).

In this Experiment 2, we used virtual reality to train participants to learn the function of a novel tool and compared the beta-band power before and after a semantic training through EEG recordings. In everyday life, we can use an object as a tool without the requirement of a specific tool use manipulation to solve a problem. This is what happens when we transport a glass to collect

dripping water or an elongated object to push/reach something else. Hence, this follows the definition of a tool as a particular entity allowing us to solve a problem (see Osiurak & Badets, 2016, defending a reasoning-approach of tool use), which do not necessarily involve manipulation knowledge. Here we asked whether the ~30 Hz cortical rhythms re-activate such 'disembodied' tool use representations.

Most importantly, the presence of the ~30 Hz modulation related to the semantic training support the NSOM theory (Hart & Kraut, 2007; Kraut et al., 2003; Slotnick et al., 2002), proposing that accessing semantic properties of a tool rely on cortical re-activation of object representations paced at ~ 30 Hz, known as high beta/low gamma rhythms.

Our data revealed that some tool function representations are located in right fronto-central cortical sites, located around the premotor area, and therefore question whether purely semantic tool information is embodied in action systems. Participants retrieved this tool-related information relatively late, at around 400 ms from stimulus onset. Thus, these representations might not be crucial for tool recognition, but rather automatically accessed following recognition. Kiefer et al. (2007) found that function knowledge about novel tools was reactivated within the first 200 ms of object perception, but only for participants knowing how to pantomime the tool use. Therefore, our results are interesting as no motor knowledge about the tool use was learnt during the training phase. Also, it may suggest that our late fronto-central beta modulation might reflect a strengthen motor resonance phenomena: the view of the tool implied a simulation of the functional transportation to open the box.

Here, the functional information is not necessary to perform the transportation of the tool, yet it is activated. Thus, our result defies other proposals that the activation of functional information about a tool is task-dependent (Daprati & Sirigu, 2006; Kiefer & Pulvermüller, 2012;

Lindemann et al., 2006). Rather, it supports the ACH model of action selection (Cisek, 2007; Cisek & Kalaska, 2010), suggesting that object knowledge is automatically recruited when a motor interaction occurs. This model would predict that, when a tool use is associated with a novel tool, it would compete against and interfere with the selection of other tool manipulation, such as its transportation. This first experiment was not designed to test such a hypothesis. Hence, we decided to conduct a second experiment allowing to test the possible interference of manipulation (tool use) knowledge in the performance of tool transportations.

Also, it is quite remarkable the EEG analysis revealed a modulation in fronto-central areas rather than occipitotemporal cortex, the latter being known for storing multiple types of object knowledge (Cichy et al., 2014; Gallivan, Adam McLean, et al., 2013; Lingnau & Downing, 2015; A. Martin et al., 1996; Noppeney, 2008; Orban & Caruana, 2014). In the following experiment, we tested whether training the participants to associate a tool use (i.e. opening the box with a key-like movement instead of a transportation) would re-activate occipitotemporal representations. Our reasoning is the following: if tool use representations are re-activated via ~30 Hz activity during the preparation of non-tool use (transportation) actions, it would suggest these representations are somehow task-relevant, possibly in participating in the elaboration of motor decisions. This would vanish the distinction between task-relevant and task-irrelevant motor information, as learnt motor information may always be used for action decision (Cisek, 2007; Cisek & Kalaska, 2010). We predicted that learning a tool use would induce more important beta-band power decrease during motor preparation, especially in left temporo-parietal and ventral visual areas, known to represent manipulation, function and more generally object knowledge (Almeida et al., 2013; Boronat et al., 2005; Buxbaum, 2001; Buxbaum, Kyle, Tang, & Detre, 2006; Buxbaum & Saffran, 2002; Canessa et al., 2008; Cross et al., 2012; Culham & Valyear, 2006; Gallivan, Adam McLean, et al., 2013; Lingnau

& Downing, 2015; M. Martin et al., 2016; Mizelle et al., 2013; Noppeney, 2008). The modulation in sensorimotor areas would suggest that the functional affordance is prepared rather than simply retrieved for decision making. Given the ACH, the tool use action would represent a competitor to inhibit and thus delay the preparation and execution of the grasp-and-move actions. Following an 'additive model' of tool processing, the right fronto-central modulation found in the Experiment 2 would still occur. However, an additional and earlier activation in posterior sites would suggest these representations are particularly crucial for tool recognition.

3.5. Method

3.5.1. Participants

Twenty-five adult volunteers (mean age = 21.1 years old, range 19-29, including 8 males) from the University of Plymouth participated in the study in exchange for money or course credit. All participants reported being right-handed and having normal vision. Due to the use of a VR headset, participants wearing correction glasses were not accepted. Four participants were removed for excessive electroencephalogram artefacts. The experimental procedure and written consent form for this study were approved by the ethics committee of the University of Plymouth and conform with the 2008 Helsinki Declaration.

3.5.2. Experimental setup and procedure

In comparison with the Experiment 2, the only difference concerned the training phase. Here, the participants were trained to execute a challenging key-like movement with one of the two objects. At the commencement of the training, a very brief video was depicting the use of the tool to learn and perform. The participants were instructed to perform the tool use when the tool appeared and the grasp-to-move action when the non-tool object appeared. The tool use learnt by

the participants was a series of three rotations (i.e. left, right and left again) of the tool in the hole of the wooden box to open it. The rotations were restricted by the respective angles: turn the controller 90° to the left, then turn 180° to the right, and finally turn 90° to the left back to the center, with a precision of $\pm$ 10°. Exceeding $\pm$ 10° of precision resulted in a failure to open the box and consequently of the trial. After the rotations, a button must be pressed to open the box, constraining the hand grip associated with the tool use. At the end of a failed trial, participants received a feedback advising which rotation was performed incorrectly, assuring motor learning. If the button was pressed after the rotations were done correctly, a simple animation showed the box opening accompanied by a sound. Thus, during the training of the tool use with specific manipulation condition, participants associated the tool with motoric information (e.g. hand grip, wrists rotations, pressing a button) and the function information 'a key that opens the box'.

3.5.3. Data analysis

The analysis of behavioural and EEG data was the same that in Experiment 2. The semi-automatic artefact rejection procedure performed on ERP rejected a total of 34% of the trials from the pre- and post-training phases.

3.6. Results and Discussion

We discarded 4.85% of the trials where participants initiated the action before the go-signal onset. During the training phase, participants succeed in performing the challenging tool use in 38.5% and 50.7% of the trials in the first and second trial blocks, respectively. Mixed-effects models did not reveal any significant timing differences in terms of initiation, grasping and execution times, between the tool and non-tool object in the post-training phase. As in Experiment 2, the tool did not elicit different initiation times (Chi^2 (1) = 2.559; R^2 = .0015; P = .1097), grasping times (Chi^2 (1) =

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2.425; $R^2 = .0014$; $P = .1193$) or execution times (Chi^2 (1) = 0.09; $R^2 < .0001$; $P = .763$) compared to the non-tool object. We expected delays of reaction times with the tool compared with the non-tool object when a particular manipulation was learnt, indicating a competition between multiple action components (Cisek, 2007; Cisek & Kalaska, 2005, 2010), such as handgrips, as found in previous studies (Jax & Buxbaum, 2010, 2013). Indeed, participants reported using a different hand grip to perform the tool use during the training phase. However, we did not find such behavioural lag and propose two possible explanations. First, our delayed-response paradigm used a pre-tone period which could have been long enough to plan robust motor decisions. Second, task-irrelevant action competitors do not interfere with motor planning and control in a repetitive task, such as their effect is minimized with the task experience. Considering only our behavioural data, the study supports the literature suggesting that knowledge about objects is selectively activated upon task requirements (Daprati & Sirigu, 2006; Lindemann et al., 2006). However, our EEG analysis challenges this claim.

ERD/ERS time-locked to the stimulus onset resulting from the grand-averages and the cluster-randomization technique is represented in Fig. 10A. The cluster-randomization technique revealed a significant decrease of ~30 Hz beta-band power for the tool compared with the non-tool object (Fig. 10B; time-interval 338 to 638 ms; $P < .001$) over the left parieto-occipital electrodes (Pz, P3, P5, PO7, PO3, POz).
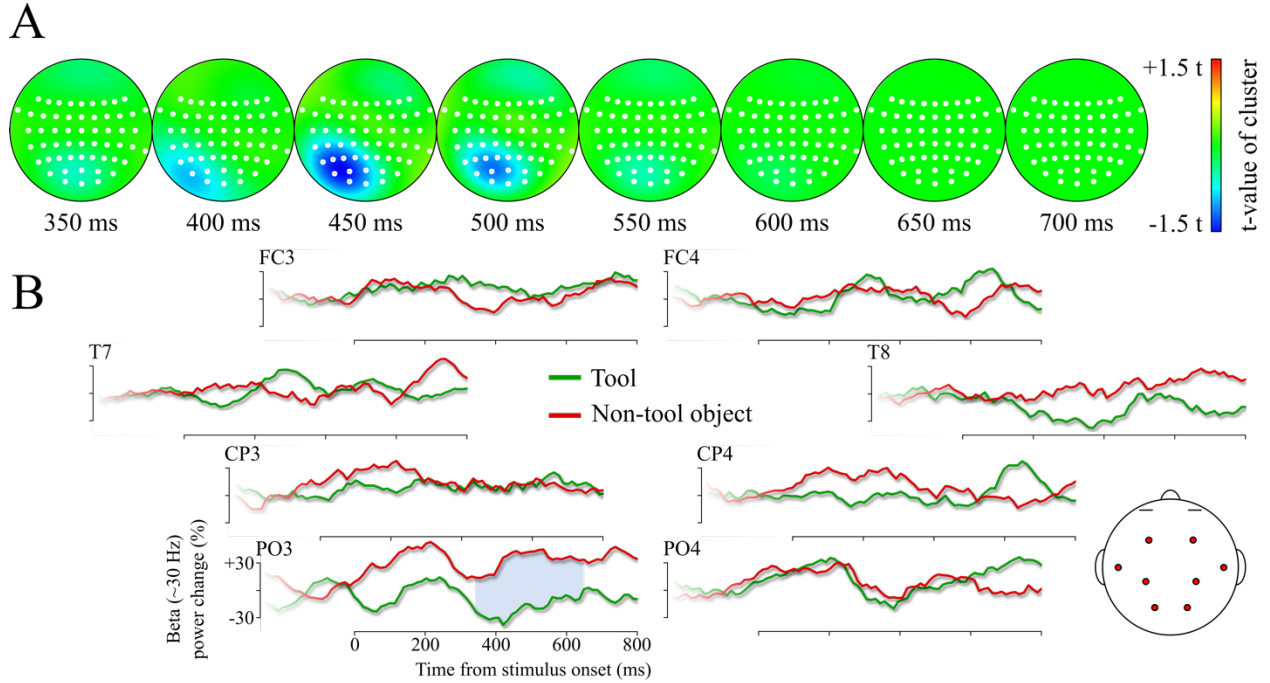
Fig. 10 Beta power differences pre- and post-training. (A) Topographic maps of the beta (25-35 Hz) ERD/ERS time-locked to the stimulus onset and based on the difference of signal post- minus pre-training for the tool and non-tool object. The significant cluster resulting from the cluster-randomization technique, represented in summed t-values, appeared in parieto-occipito electrodes from ~340 ms following stimulus onset. (B) A representative subset of electrodes across the scalp comparing the ERD/ERS post- minus pre-training for the tool (green) and non-tool object (red). The blue area in electrode PO3 represents the significant decrease of beta power for the tool (*P* < .001).

In contrast with our behavioural data, this parieto-occipital activation supports the ACH model, such as 'a priori' task-irrelevant tool use representations appear activated. This decrease of beta-band power reflects the activation of the ventral and dorso-ventral action systems (Binkofski & Buxbaum, 2013; Brandi et al., 2014; Buxbaum, 2017; Chao & Martin, 2000).

This result extends previous work suggesting that the mere perception of tool re-activates tool use representation within the ventral visual stream (Almeida et al., 2013). Here, we provide evidence that ~30 Hz beta oscillations may play a mechanistic role in the re-activation of action representations within this pathway and occurring during the first 400 ms of object processing. This relatively late activation may be explained by the 'task-irrelevant' aspect of this information, such as functional hand postures or tool use motion, for object transportation. As Lee et al. (2017), we do not believe that the activation of tool use representations is incidental or a by-product of object processing, but rather fundamental to elaborate potential motor plans. Such mechanisms would allow fast switching of motor plans, for example deciding to use the tool during its reach.

In a task requiring to actually perform the tool use, we would expect an earlier decrease of beta-band power recorded over parieto-occipital electrodes sites. Hence, further studies are needed to clarify whether the automatic activation of tool use representations would occur early when required by the motor task.

Surprisingly, the centro-frontal modulation found in Experiment 2 vanished when the participants learnt the actual tool use manipulation. A possibility is the semantic characteristics associated with the tool become of different nature (i.e. strongly 'embodied') when associated with a specific action. In this sense, our data support theories of embodiment suggesting that our motor experience with an object guides the encoding of conceptual knowledge ('what is a tool?') within perceptual and action brain systems (Martin, 2007) , which contrast with other amodal accounts of object and tool representations (Caramazza & Mahon, 2003; Caramazza & Shelton, 1998; Cross et al., 2012).

3.7. General Discussion

In Experiments 2 and 3, we attempted to investigate how the brain constructs *de novo* object knowledge, and more particularly what happen after we learnt the function and/or the manipulation of a novel tool. Most of the studies investigated where manipulation and function knowledge about tools are represented in the brain, but how this knowledge is retrieved is still unknown.

Using EEG recordings allowed us to distinguish the timing of activation of these two types of semantic information, barely investigated so far (Kalénine, Mirman, Middleton, & Buxbaum, 2012). We found that learning manipulation and function information, previously considered as task-irrelevant when intended to grasp and transport a tool, induced a ~30 Hz beta-band decrease, most likely reflecting the retrieval of this stored information (Hanslmayr et al., 2009, 2012; Hart & Kraut, 2007; Slotnick et al., 2002). Thus, as predicted, the beta-band power decreased with the addition of a novel motor program to the action repertoire of the tool. The statistical tests did not revealed this effect when no novel manipulation was learnt. The modulation started ~300 ms from tool perception and peaked around 400 ms, a critical timing for semantic processing (Jackson et al., 2015; Kiefer et al., 2007; Supp et al., 2005; van Elk et al., 2008; van Elk, van Schie, van den Heuvel, et al., 2010). Also, it occurred in left occipito-parietal areas, which suggest this information was re-activated but not prepared by the motor system. Thus, we believe that even when repetitive non-tool use manipulations are intended, visual and proprioceptive tool use representations are 'ingredients' influencing motor decisions.

Overall, our results are accommodated by multiple theoretical frameworks. Semantic information about objects and tools is typically considered as information represented in a declarative format in the ventral system (Almeida et al., 2013; Binkofski & Buxbaum, 2013;

Buxbaum, 2001) and memory processing related to stimuli as reflected in beta-band oscillations (Hanslmayr et al., 2009). However, it is important to notice that the representation of the tool use knowledge within the ventral stream occurs only when the novel tool is embodied (Experiment 3). The results also support the sensitivity of the left parietal lobe in representing novel objects associated with motor components (e.g. novel tying knots) but not linguistic-semantic knowledge (Cross et al., 2012). Our present study reports that such semantic processing upon visual object perception and beta-oscillations are associated. The beta-band power modulations fit the mechanistic view of beta-band oscillations as top-down processes (Arnal & Giraud, 2012; Engel & Fries, 2010; Spitzer & Haegens, 2017; Wang, 2010) reflecting the integration of semantic tool information into motor computations.

However, the sensory-motor account of conceptual knowledge proposes that semantic knowledge about objects and tools is represented in sensorimotor areas (Beauchamp & Martin, 2007; Kiefer & Pulvermüller, 2012; van Elk et al., 2014). Our results contrast with this claim, as the re-activation of a learnt motor program did not re-activated motor areas and suggest a more distributed view on semantic tool use representations (for a review see Yee, Chrysikou, & Thompson-Schill, 2013). For instance, the distributed hub-and-spoke model of semantic memory (Patterson, Nestor, & Rogers, 2007) proposes that the cognitive task induces the re-activation all object properties (e.g., visual, auditory, praxic) in memory. But, these re-activations are based on the statistical organization of our experience with the task. Keeping this, it can explain why the beta-band modulation in temporal areas was only revealed when function knowledge was learnt – it was possibly extinguished over time starting from the end of the training phase.

The frontal beta-band increase found when transporting the tool was associated with the visual consequences of the box opening, which is in other words, the mapping of the grasp-and-

move action with sensory expectations (i.e. audio-visual experience of the box opening). However, after the training, participants were informed the box would no longer open during the experiment. It has been proposed that selection of motor parameters results from the simulation of available action-outcome pairs (e.g. pressing a button to turn on lights; Wolpert & Ghahramani, 2000). Thus, our frontal beta-band increase may also reflect the action-outcome remapping, correcting the discrepancy between the sensory predictions and the motor specifications to move the tool, which means, at a higher representational level, detaching the functional properties from the tool. Further investigations are necessary to disambiguate this possibility.

The ACH theory has been mostly evaluated and validated in simple motor tasks such as reaching behaviours in monkeys (Cisek & Kalaska, 2005) and humans (Gallivan et al., 2015, 2016). We believe that it is of major importance to evaluate the model in a wider perspective such as the manipulation of objects (for an interpretation of limb apraxia in the ACH framework, see Rounis & Humphreys, 2015). To conclude, we tested the hypothesis that learnt manipulative and functional information about tools is re-activated to bias the action selection. In line with our hypotheses, the results suggest that manipulative information is automatically recruited when intended to grasp-and-move tools and reflected in the ~30 Hz beta-band power recorded over left parieto-occipital areas. This activation occurs in the 300 ms following the tool perception. For the first time, these neurophysiological data suggest that the integration of tool use knowledge into a decision-making process might be task-independent and reflected in the beta-band rhythms. We believe the present evidence contribute to a better understanding of how learnt tool information is accessed during object recognition, gifting us our everyday praxic skills.

Brain Rhythms in Object Recognition and Manipulation
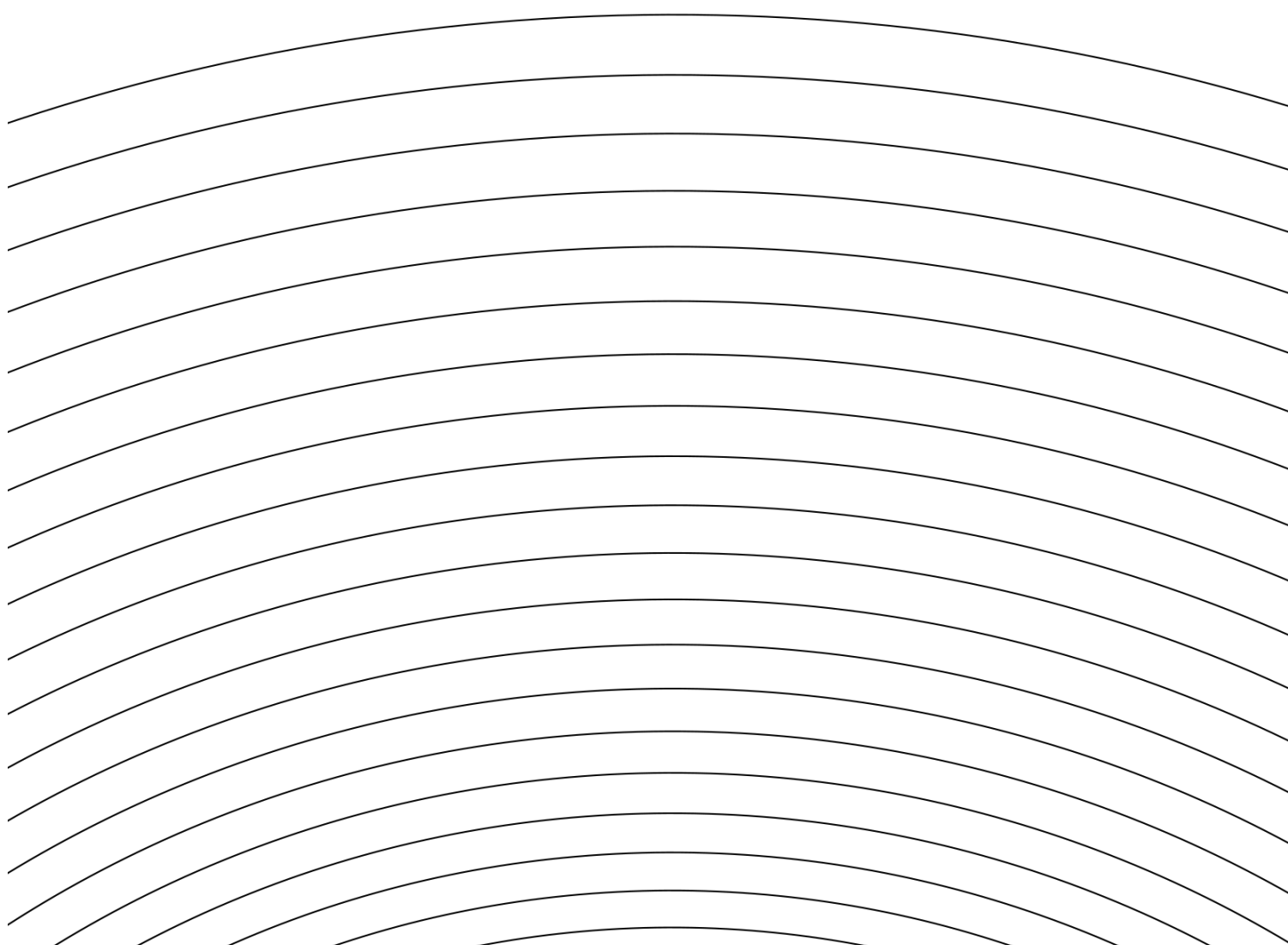
4. Competition between object-based functional affordances: the role of mu and beta EEG rhythms

A video describing the experiment can be visualized via the QR code at the bottom of the page or the following link: https://www.youtube.com/watch?v=g5Ge4gh4ZgE

4.1. Chapter Abstract

Intending to manipulate a tool always requires solving the question of 'How' to do it. Tools are particularly tricky as the cognitive system needs to choose between actions they perceptually afford (e.g. by the structure of the object) and actions they remind (e.g. a tool use learnt over many exposure or practice). The EEG power of mu and alpha rhythms reflects the competition between the two brain systems implementing these structural and functional actions. A remaining question concerns whether this competition also occurs between functional actions retrieved from memory – this is what happens when intended to manipulate a tool with multiple uses as mobile phones. Hence, the following investigation tested whether there is competition between multiple tool use and the involvement of beta-band rhythms in it.

The analysis revealed that, indeed, the competition between multiple tool use induced a decrease of 28-40 Hz signal power at 400-480 ms and an increase of 21-28 Hz signal power at 470 to 565 ms from tool perception. These beta modulations were accompanied by an earlier increase of 11-14 Hz mu-band power. Therefore, the activation of multiple tool use representations recruits the conjunction of both sensorimotor mu and beta rhythms.

4.2. Introduction

Learnt object-based actions derive from experience and are afforded during visual processing of objects and tools (Bub, Masson, & Cree, 2008; Cannon et al., 2014; Cross et al., 2012; Proverbio, 2012; Ruther et al., 2014; Schubotz, Wurm, Wittmann, Cramon, & Watson, 2014). In other words, as soon as we recognise an object we might automatically retrieve knowledge on how we could manipulate it. These manipulations can be afforded by the geometry of an object (i.e. structural affordance) or a learnt property of that object (i.e. functional affordance, such as tool use). For some objects and tools, we use the same manipulation or grip whether we intend to use or simply move them. For example, when moving a hammer to a different location we would habitually have a similar grip of the handle as we would in order to use it as a tool. Others, so-called 'conflictuals' (Jax & Buxbaum, 2010; Kalénine et al., 2016; Wamain et al., 2018), require very distinct grips and manipulations for the two actions. For example, when picking up a pen we would employ very specific digit postures if intending to write with it that would be superfluous if we simply intend to move it.

A recent study have shown that we take more time to grasp conflictual objects than those with only a single habitual manipulation, even when we only intend to move them (Jax & Buxbaum, 2010). The authors propose that an intention to act triggers a competition between responses relevant to both the structural and functional properties of an object. As structural responses can be constructed 'on the fly' from visual experience they tend to be activated in advance of functional responses, which require the activation of long-term conceptual representations. Thus, the residual activation of early structural responses can interfere with the later activation of functional responses if those responses are different, as in the case of conflictual objects. Manipulating these conflictual

objects also appears particularly difficult for patients with apraxia (Jax & Buxbaum, 2013; Watson & Buxbaum, 2015), which led authors to conclude that a subtype of apraxia could rely on a deficit of action selection (see also Rounis & Humphreys, 2015).

An important aspect of previous studies on conflictual objects is that the conflict is borne from responses originating from fundamentally different cognitive systems. Many would consider the systems involved in moving or using an object to be cognitively distinct (Binkofski & Buxbaum, 2013; Brandi et al., 2014; Buxbaum et al., 2006; Watson & Buxbaum, 2015) with different planning (Valyear et al., 2011) and timing (Jax & Buxbaum, 2010). In this study, we sought to examine the locus of conflictual interference (Jax & Buxbaum, 2010, 2013). That is, whether this effect is due to competition between cognitive systems involved in moving or using an object, or whether it is simply the result of the activation of competing motoric representations, irrelevant of our intentions to move or use that object.

Our study used a category of hereto-unexamined conflictuals: objects with more than one functional representation. For example, while a conventional hammer is non-conflictual, as the structural and functional responses are similar, a claw hammer has two distinct functional representations, one to drive in a nail, the other to remove it (i.e. a dual use). If we were to find interference effects in these 'functional conflictual' objects, when compared to single use objects, this would indicate that previous conflictual findings were due to motoric interference, rather than systemic cognitive interference. In addition, evidence for interference in functional conflictuals would provide evidence for an extension of the ACH theory (Cisek, 2007; Cisek & Kalaska, 2010). The ACH proposes that actions extracted from structural affordances available in the physical environment are processed in parallel and compete for motor execution. The model suggests that information from external (i.e. sensory inputs) and internal (i.e. knowledge about the environment)

sources are gathered to facilitate the selection of an affordance (see the 2AS+ model for a similar proposal; Buxbaum, 2017). If the two potential responses of the functional conflictual objects were found to interfere with each other, this would suggest that the tenets of the ACH could be extended from structural to functional affordances.

Using an interactive virtual reality environment, we were able to conduct a direct comparison between functional conflictual and non-conflictual objects by creating novel tools that either had single (e.g. a tool that can be used to light a candle) or dual functionality (e.g. a tool that can be used to light a candle or open a box). These single or dual-use virtual tools were mapped onto a physical manipulator device that participants picked up and used on a nearby virtual object by performing a specific sequence of manipulations (e.g. open a box by inserting the tool into a hole and rotating it to the left and right – as with a key). These manipulations were framed in a two-stage behavioural task; where participants were required to withhold action selection and execution upon visual presentation of the tool until they heard an auditory tone. This tone provided both a go-signal to use the tool and, in the case of dual-use tools, the frequency of the tone indicated which of the two tool uses they should execute. This two-stage procedure was adopted in an attempt to separate the continuous processes of motor planning (Cisek, 2007; Cisek & Kalaska, 2010), specifically those involved in the retrieval of object representations from those related to the action selection and execution. Behavioural measures captured reaction-time latencies from the onset of the tone until the initiation of the grasping movement towards the tool, as well as the time taken to grasp the tool and execute the action. Based upon our re-evaluation of Jax and Buxbaum's (2010) conclusions, we hypothesised (H1) that reaction-time latencies for the initiation and execution of object use would be slower for functional conflictual dual-use tools than non-conflictual single use tools. In addition, we recorded electrophysiological signals throughout the procedure, with separate Event-Related

Potentials (ERPs) time-locked to both the onset of the tool and go-tone. General and specific frequency-band analyses of this ERP data provide further insight on the potential competition between functional representations of tools, both during the retrieval of object representation (tool onset) and action selection and execution (tone onset).

Rolandic mu rhythms (8~14 Hz) found in EEG are thought to represent perceptual and motor information (Llanos, Rodriguez, Rodriguez-Sabate, Morales, & Sabate, 2013; Pineda, 2005; Sabate, Llanos, Enriquez, & Rodriguez, 2012) reflected from sensorimotor bindings. The idling of these rhythms becomes desynchronised by movement execution or motor imagery and has also been found to be modulated by an object's affordances (Proverbio, 2012), specifically when objects are within our reachable space (Wamain et al., 2016). These rhythms are also sensitive to the activation of functional representations, a pre-requisite to the use of tools (Binkofski & Buxbaum, 2013; Buxbaum, 2017; van Elk, van Schie, & Bekkering, 2009; van Elk et al., 2014; van Elk, van Schie, & Bekkering, 2010). Proverbio (2012) found the functional affordances provided by tools increase the mu desynchronisation during the first 200 ms of viewing when compared to non-functional objects, while Ruther et al. (2014) found that associating an object with a meaningful function also led increased mu desynchronisation. These findings have been typically observed over central sites, supporting the sensory-motor account of object knowledge which proposes that motor-related brain regions represent both our knowledge about object manipulation and their associated motor processes (Beauchamp & Martin, 2007). Importantly, Wamain et al. (2018) also found that the processing of conflictual objects led to early increases of the mu rhythm power compared to non-conflictual objects. This suggests that the structural motor representation reflected in EEG mu rhythms is modulated by the competition with functional affordances.

EEG beta rhythms (14~30 Hz) have also been associated with the activation of learnt information associated with an object or tool, such as the object's weight (Quandt & Marshall, 2014; Quandt et al., 2012). Reflecting communications intra- and inter-cortical areas (Kilavik et al., 2013), fast beta rhythms can be generated in the hand areas of the primary sensorimotor cortex (Jensen et al., 2005). These rhythms, and in particular their desynchronisations, are sensitive to the motoric and semantic properties of the effector-object interaction, such as the meaningfulness of tool manipulations (van Elk, van Schie, van den Heuvel, et al., 2010), action semantics and memory processing (Weiss & Mueller, 2012). They are thought to represent top-down signals and the activation of representations relative to task demands (Spitzer & Haegens, 2017; Wang, 2010) within both dorsal and ventral streams (Turella et al., 2016). This means an examination of beta rhythm desynchronization (i.e. a decrease of the signal amplitude/power) provides a privileged insight into the role of motor and semantic representation associated with functional objects.

Given that functional affordances are derived from learnt associations between objects and motor plans, the present study seeks to investigate whether the competition between affordances is due to the extraction of multiple visual properties, most likely reflected in mu rhythms, and/or the competition between retrieval of learnt manipulations reflected in beta rhythms. We posit that beta desynchronisation represents a mechanistic role for the re-activation of learnt properties of tools derived from memory, in agreement with the NSOM theory. Hence, the competition between functional affordances should influence both early mu synchronisation but also beta desynchronisation during tool recognition. Our second hypothesis (H2) is that our functional conflictual dual-use tool would lead to an early increase of the early mu synchronisation (Wamain et al., 2018) and an increase of beta desynchronisation in comparison with our single-use tool at the onset of presentation, indicating the activation of multiple functional action representations. The

absence of a mu effect would exclude perceptual processes from tool use retrieval whereas the absence of a beta effect would exclude a mechanistic role of beta rhythms in the retrieval of such tool use. We also explored the N1 ERP component during the tool visualization, possibly indexing the processing of visual affordance at visual (Goslin et al. 2012) and motor (Proverbio et al., 2013) cortical levels.

ERPs related to the onset of the cueing tone, representing action selection and activation, also allow further evaluation of the predictions of theoretical models. In the continuation of the ACH model (Cisek, 2007; Cisek & Kalaska, 2010), the 2AS+ model (Buxbaum, 2017) proposes that the inferior frontal gyrus (IFG) sends goal-relevant signals biasing the competition between conflicting manipulations available and accumulated in the supramarginal gyrus (SMG). Could these biasing signals re-activate the desired functional manipulation upon presentation of the cuing tone? A previous study demonstrated that both activation and inhibition processes are involved in the selection of a reach in non-human primates (Cisek & Kalaska, 2005). Hence, mu and beta modulations would suggest a re-activation of motoric representation related tool function. This means that, when an affordance has to be selected, our conflictual dual-use tool could induce greater mu and beta perturbations than our non-conflictual single tool-use. Thus, our third hypothesis (H3) states that the selection of specific tool use would require the re-activation of the functional action representation. This would be reflected in greater synchronisation of the mu rhythms and desynchronisation of the beta rhythms when performing an action with a dual-use tool than with a single-use tool. Exploratory analysis investigated the P3 and N400 ERP component at the tone onset, known to reflect motor decision (Jackson et al., 1999) and grasp planning (De Sanctis, Tarantino, Straulino, Begliomini, & Castiello, 2013), respectively.

4.3. Method

4.3.1. Participants

Forty adult volunteers (including 17 males, mean age = 20.8, years old, SD = 2.3) from the University of Plymouth participated in our study in exchange of course credit. All participants reported being right-handed or ambidextrous and having normal vision. Data from three participants were removed from analysis due to excessive EEG artifacts. The experiment and consent form were approved by the ethics committee of the University of Plymouth and conform with the 2008 Helsinki Declaration.

4.3.2. Experimental design and procedure

During the experiment, participants were seated at a desk with a press button placed adjacent to the resting place of their right hand. Throughout the procedure, they interacted in a virtual environment that provided an approximate facsimile of their physical environment, with virtual representations of the room, desk, and physical push button. In addition, the participants also saw virtual representations of a box and candle, presented side by side in front of them on the virtual table within comfortable reaching distance. An area of the virtual table immediately in front of the participants was marked out using a dashed rectangle. A representation of this virtual environment is shown in Fig. 11A. These and other virtual representations were developed using Unity software (Unity technologies, version 7.1.0f3), and displayed using an HTC Vive hardware (HTC Corp.).

To initiate each trial participants were required to press the button with their right hand. When the button was pressed a white fixation cross would appear directly over the white dashed rectangle on the virtual table for 1000 ms (Fig. 11B). 1000-1400 ms after the offset of the fixation a

virtual representation of one of two novel tools (one predominantly green, the other red) would appear in the rectangle, projected over a physical manipulation device. Between 800-1200 ms after the visual onset of the novel tool, the participant would hear either a high- or low-pitched audible go-signal. This was the cue for participants to potentially release their hand from the button and to reach out, grasp, and use the tool. After they used the tool they would replace it in the dashed rectangular area.
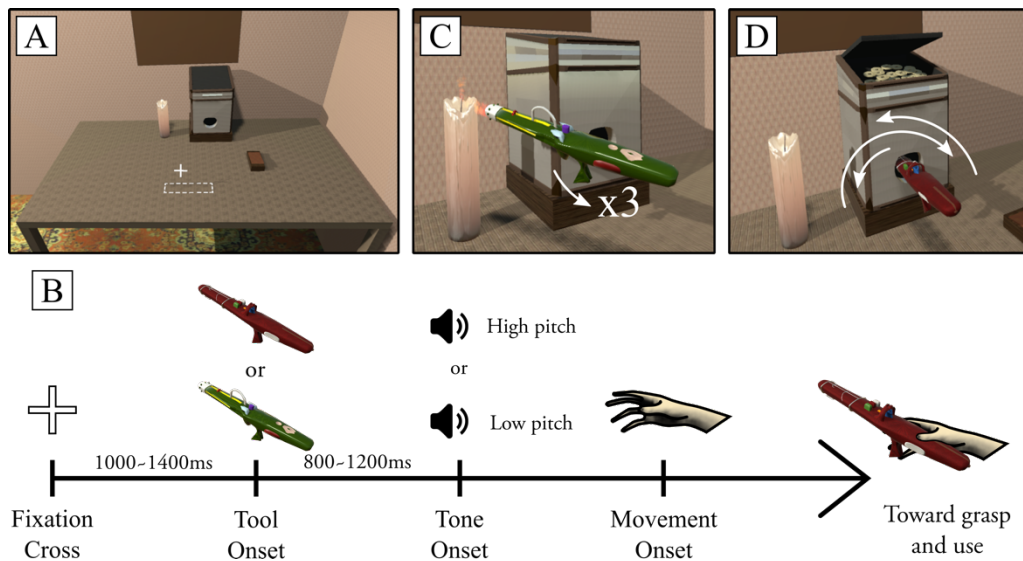
Fig. 11 Experimental design. (A) The immersive 3D virtual environment perceived by the participants. (B) After viewing a fixation cross appeared the single tool or the dual tool. Then, a tone instructed the participants which tool use to perform. (C) To light the candle, participants pressed three times to trigger at the back of the controller. (D) To open the box, participants inserted the controller in the hole of the box then performed three rotations: turning 90o anti-clockwise, then to 90o to the clockwise and finally back to 0o.

In the experiment, participants were trained to associate both the tools and go-tones with one of two particular actions. In the 'light' action the participant would be required to grasp and move the tool such that the nose of the tool was adjacent to the candle. After pressing the trigger button on the back of the controller three times a flame would be produced from the nose of the tool and light the candle (Fig. 11C). In the 'open' action the participant would grasp the tool and insert the nose of the tool into the hole in front of the box. They would then be required to rotate the tool to position 90° anti-clockwise of vertical, then 90° clockwise of vertical, and then back to 0°. When this was completed the box would open, revealing a trove of gold coins (Fig. 11D).

In an initial phase of training, participants associated either the low or high go-tone with one of these actions (e.g. low tone with 'light'). After hearing the go-tone they were be required to perform the requisite action with one of the two novel tools (e.g. red tool as a 'lighter'). In all of the 10 training trials in this phase, the participants would hear only one of the tones, and be presented with only one of the novel tools. Thus, the novel tool trained in this phase would be associated with only one of the two actions (e.g. red tool used to light the candle when hearing the low go-tone).

In the second phase of training, participants would be instructed to associate the other tone with the remaining action (e.g. high tone with 'open'). However, in this phase the participants could hear either the low or high go-tones, instructing them to perform either the 'light' or 'open' actions. They would perform either of these actions with the novel tool that was not used in the initial phase of training (e.g. green tool). Thus, the tool trained in this phase had dual functionality; and could be used to perform both actions. The associations of go-tones (high or low) to actions (light or open), tool type to action and mapping of dual/single use were randomised for each participant.

In the test phase of the experiment 250 trials were presented in five blocks of 50 trials each, with a total duration of around 25 minutes. Between each trial block participants could take a break

and remove the VR headset. In each of the test trials participants were presented with one of the two novel tools, selected at random, and asked to perform or withhold an action upon hearing the low and high go-tones, also presented at random. For the dual-functionality tool either of the tones would be associated with a valid action (as it could be used as both a key or a lighter). However, for the single-function tool the participant could only perform the action associated with one of the tones (e.g. red tool used to light the candle when hearing the low go-tone), whereas hearing the other tone they would have to withhold their action. In this last case, the participant had to inhibit the release of the button (i.e. no-go trial) until the tool disappeared and the next trial started. No-go trials were used to motivate participants to decide which tool use to perform before the release of the button. Errors in no-go trials or inappropriate tool use (lighting the candle instead of opening the box) triggered an audible and visible feedback about the participant's performance to the task in order to correct him/herself in the subsequent trials.

4.3.3. Behavioural analyses.

Behavioural reaction times were recorded at three points in the motor sequence: a) Initiation time, the duration between tone onset and button release; b) Grasping time, the duration between button release and the grasp of the tool; c) Execution time, the duration between grasp onset and action onset. RStudio (v. 0.99.489) and the lme4 (v. 1.1-12) were used to calculate separate linear mixed-effect models analyses for each of the three reaction times. The strategy used for the following modelling was to maximize the complexity of the structure to control for a maximum of variance while keeping converging models given the size of our dataset. In each model, the tool functionality (single or dual use) was entered as a fixed effect, with the participant as a random effect with by-participant random slopes for the effect of the tools, the tool use (lighter or key actions) and the trial block (1-5 blocks; formula: lmer(ReactionTime ~ Functionality + TrialBlock + (1|Subject)

+ (0+ Functionality|Subject) + (0+ToolUse|Subject) + (0+TrialBlock|Subject)). Visual inspection of residuals plots did not reveal any violation of the assumptions of application. P-values were obtained by likelihood ratio tests of the full model against the null model, with and without the effect of the tool functionality, respectively. Pseudo-R-squared effect sizes were estimated with the r.squaredLR function of the MuMIn (v. 1.15.6) packages.

4.3.4. Electrophysiological recording and analyses

During the experiment, EEG was recorded from 61 actively amplified Ag/AgCl electrodes (actiCAP, Brain Products, Gilching, Germany) mounted on an elastic cap and following an extended international 10-20 montage. Electrodes were referenced to the left mastoid electrode at recording, amplified using a BrainAmp MR Plus amplifier (Brain Products), and continuously sampled at 500 Hz, with electrode impedance maintained below 20 kΩ. EEG from 16 of the 61 electrodes in immediate contact with the VR headset were excluded from analyses (Fp1, Fp2, Fpz, AF7, AF8, AF3, AF4, FT7, FT8, F5, F6, F3, F4, F1, F2, and Fz).

EEGs recordings were analysed with Brain Vision Analyzer (Brain Products, Munich, Germany, v. 2.1) and filtered on-line with a 0.1 Hz high pass filter, a 50 Hz low pass filter and a 50 Hz notch filter. Electrodes were re-referenced off-line to the average of left and right mastoids activity and the fronto-central electrode AFz was used as the ground. Separate ERPs were time-locked on a) the visual onset of the presentation of the tool, and b) the onset of the audible go-tone, each with a 1800 ms time window spanning from -600 to 1200 ms before and after the time-lock. Baseline correction was performed with the 200 ms of ERP immediately before each time-lock. ERP segments were rejected if they met any of the following criteria: a voltage step greater than $\pm$50 μV/ms, a total voltage difference of greater than 150 μV within a 200 ms interval, or a voltage exceeding $\pm$ 100 μV/ms or less than 0.5 μV within a 100 ms interval. These criteria led to the

rejection of a total of 14% of segments at the tool onset, and 3% of segments at tone onsets. In addition, individual electrodes having greater than ~10% of rejected segments were removed from analyses and substituted with topographically interpolated replacements (Perrin et al., 1989), with 1.8% of electrodes replaced over the cohort of participants.

Time-frequency representations (TFRs) were calculated for each segment of the ERPs by convolving Morlet wavelets with a width of seven cycles and a frequency range of 0.1 to 50 Hz. TFRs were then re-segmented to a period 200 ms before the time-lock and 800 ms to remove edge effects inherent in wavelet analyses of segmented data and focus analyses on the temporal period of interest. TFRs were represented in terms of the percent of power change relative to the average power calculated over the initial 200 ms baseline. Average relative power TFRs were calculated separately for each tool and subject, and analysed across 11 electrodes of interest (FC1, FC2, FCz, C1, C2, C3, C4, Cz, CP1, CP2 and CPz) located around the sensorimotor areas to test the predicted mu and beta rhythm modulation (Brinkman et al., 2014, 2016; Proverbio, 2012; van Elk, van Schie, van den Heuvel, et al., 2010; Wamain et al., 2016, 2018).

Further ERD/ERS analyses were conducted to test the power of the oscillatory activities of mu and beta rhythms, as described in the literature (Pfurtscheller, 1992; Pfurtscheller & Lopes, 1999). After artifact rejection, each trial was band-pass filtered for the mu band and the beta frequency band and then squared to produce power values (μV^2). These squared values were them converted to represent the percentage of power change (similar to van Elk, van Schie, van den Heuvel, et al., 2010) relative to the average power calculated over the baseline period. These ERD/ERS traces were smoothed using a running average time-window of 45 ms (as in Hanslmayr, Spitzer, & Bäuml, 2009; Ruther et al., 2014). In this representation power values inferior to zero indicate desynchronisation (ERD) and values superior to zero indicate synchronisation (ERS).

Statistical analysis of the ERPs, TFRs and ERD/ERS opposing the single tool with the dual tool was conducted using a pairwise comparison based on the cluster randomisation technique of Maris and Oostenveld (2007) in order to avoid multiple comparisons. Two-tailed *t*-tests were performed across all electrodes and data points comprised in the first 800 ms following the tool and tone onsets comparing the two tools. Concerning the analyses of the TFRs, the two-tailed *t*-tests also included the 0.1 to 50 Hz frequency range. Those samples with *t* statistic above the significance threshold of $P < .05$ were clustered together in spatial, temporal, frequency terms. Each cluster was based on a minimum of eight samples and used for the subsequent cluster analysis. The cluster-level *t* statistic was calculated as the sum of the *t* statistic of all electrode-time and electrodes-frequency samples of a given cluster. For the cluster analysis, the cluster with the largest *t* statistic was selected for a Monte-Carlo simulation. Thus, each of the original pairs of *t*-tests sample that compose the cluster was repeated 1000 times, with permutations of each paired samples randomly assigned to the dual or single tool. It generated a Monte-Carlo distribution of summed *t* statistic corresponding to the null hypothesis. A Monte-Carlo *p*-value was calculated as the ratio of the 1000 summed *t* statistics in the random distribution that was above the cluster-level *t* statistic. This *p*-value was considered significant above $P < .025$. Averaged TFRs were re-plotted as *t*-values in the time-frequency domain, derived from *t*-tests against baselines of zero, for a comprehensive understanding of the effects. Concerning the ERPs, *t*-values of the cluster had been used to create topographic maps in Brain Vision Analyzer (Brain Products, Munich, Germany, v. 2.1), using spherical spline interpolation with an order of splines of 4 and a maximum degree of Legendre polynomials of 10 (default parameters).

4.4. Results

4.4.1. Behavioural results

Only the successful trials from the test phase of the experiment were included in the analyses. Successful trials were defined as those in which the appropriate action was initiated at least 200 ms after the onset of the go-tone and completed using the correct motor sequence. In addition trials with reaction time values inferior or superior to three standard deviations from each participant's mean for each individual block of 50 trials (as used in Chainay, Bruers, Martin, & Osiurak, 2014; Osiurak, Roche, Ramone, & Chainay, 2013) were also excluded, representing a total of 2.86% of the trials.

Mixed-effect models of reaction time data did not reveal did not reveal any significant effects in initiation or (Fig. 12; Chi^2 (2) = 0.545, R^2 < .001, P = .46; M $_{dual\ tool}$ = 792 ms, SD = 276 ms; M $_{simple\ tool}$ = 791 ms; SD = 270 ms) execution latencies (Chi^2 (2) = 0.111, R^2 < .001, P = .739; M $_{dual\ tool}$ = 348 ms, SD = 286 ms; M $_{simple\ tool}$ = 347 ms; SD = 281 ms). However, grasping latencies were found to be significantly longer with the dual tool (M = 906 ms; SD = 242 ms) than with the single tool (M = 883 ms; SD = 238 ms; Chi^2 (2) = 5.068, R^2 = .001, P = .024).
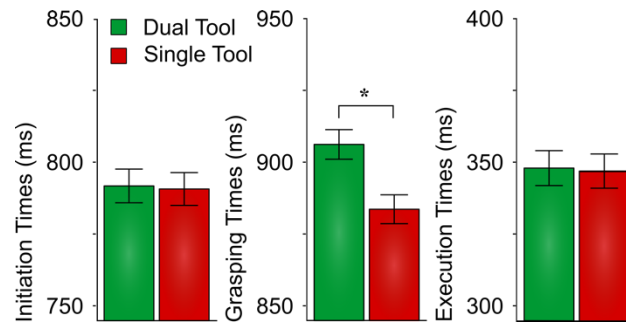
Fig. 12 Behavioural results. Reaction latencies for Initiation Times, Grasping Times and Execution Times. Standard errors of the mean are represented into brackets. * P < 0.05

4.4.2. ERP analyses from tool onset

The cluster-randomization technique revealed that the perception of the dual tool reduced the ERP N1 component recorded over the left fronto-central areas (Fig. 13) compared to the perception of the single tool (maximum time-interval 118 to 186 ms, $P = .001$).
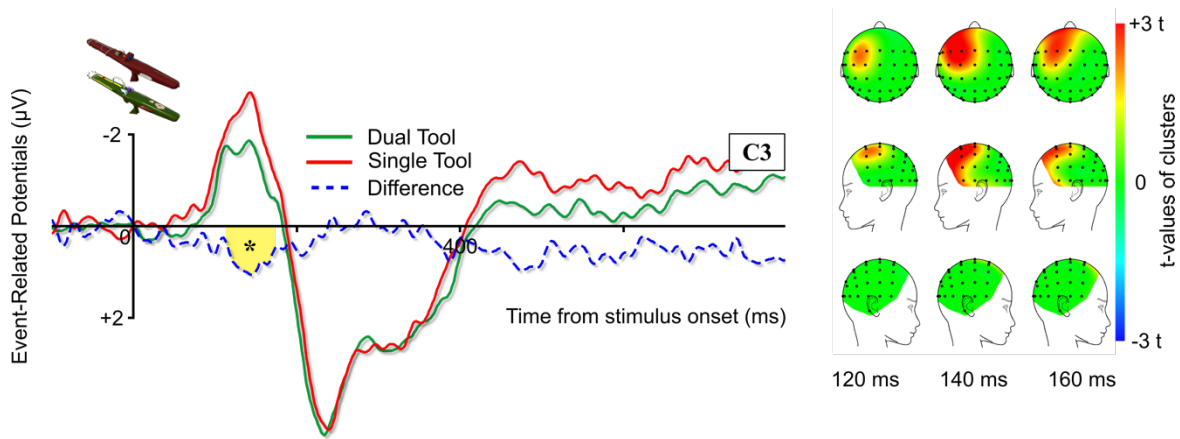
Fig. 13 ERPs at tool onset. Grand average ERPs at electrode C3 for dual and single use tools, with the difference wave representing dual tool – single tool conditions (* = significant difference between tools, $P < 0.001$). Scalp maps show the topographic distribution t-values representing the difference between the use of the two types of tool.

TFRs showed that the onset of both dual and single use tools led to early mu synchronisation, represented by a positive power change relative to baseline, followed by a late mu and beta desynchronisation (Fig. 14), with a negative power change relative to baseline. Statistical comparisons revealed four clusters of significantly different activity between single and dual tools. First, the early mu synchronisation was reduced for the dual tool compared to the single tool (maximal from 0 to 310 ms between 11 to 14 Hz, $P = .007$). Second, the late mu desynchronisation

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was reduced for the dual tool in comparison with the single tool (maximal from 340 to 800 ms at around 9 Hz, $P = .006$). Third, the dual tool reduced the late beta desynchronisation compared to the single tool (maximal from 470 to 565 ms between 21 to 28 Hz, $P = .02$). Finally, the dual tool increased the late gamma (30-50 Hz) desynchronisation in comparison with the single tool (maximal 400 to 480 ms between 28 to 40 Hz, $P < .001$).

Fig. 14 TFRs at tool onset. Each quadrant represents an electrode located over the sensorimotor areas displaying the power change of the signal in comparison with the baseline period in frequency bands from 0.1 to 50 Hz over a time-window from 0 to 800 ms post-tool onset. TFRs are represented for dual tools, single tools, and the difference between dual and single use tools (dual tool minus single tool). Significant clusters resulting from the cluster-randomization technique are

represented in terms of summed t-values, displaying the modulations of the mu, beta and low-gamma bands.

The ERD/ERS analysis (Fig. 15) were congruent with the TFRs analysis, where both late mu desynchronisation (350 to 645 ms, $P = .001$) and late beta desynchronisation (495 to 555 ms, $P = .001$) were reduced for the dual use tool in comparison with the single use tool.
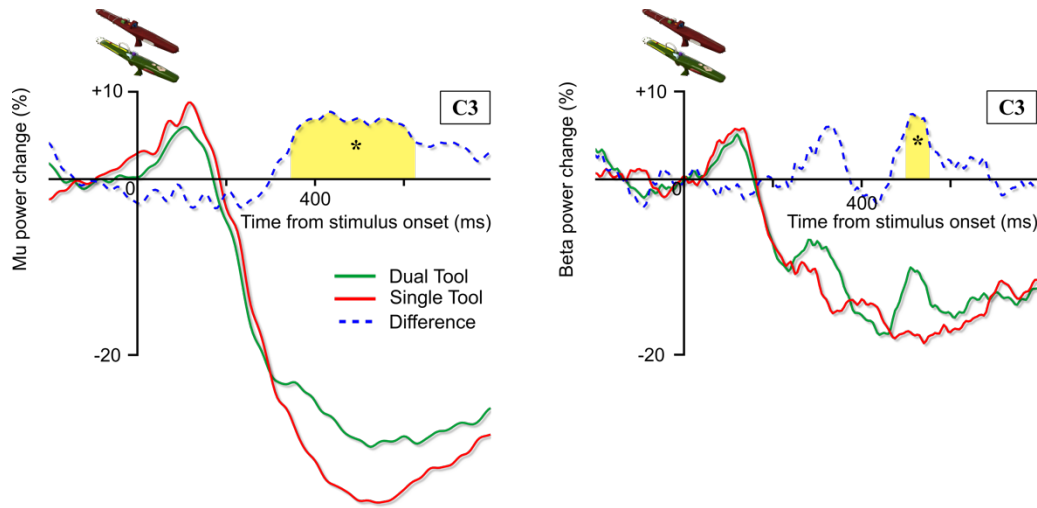
Fig. 15 ERD/ERS at tool onset. Grand averages of ERD/ERS for dual and single use tools time-locked at the tool onset for electrode C3 in mu (left) and beta (right) frequency bands. Difference waves signify activity from dual tools – single tools, with indicated areas of significant difference (* $P = 0.001$).

4.4.3. ERP analyses from tone onset

Analysis of the ERPs time-locked to tone onset revealed that the selection of an action using a dual versus a single use tool resulted in more negative voltages between ~ 300-700 ms after the onset of the go-tone (Fig. 16; $P < .001$).
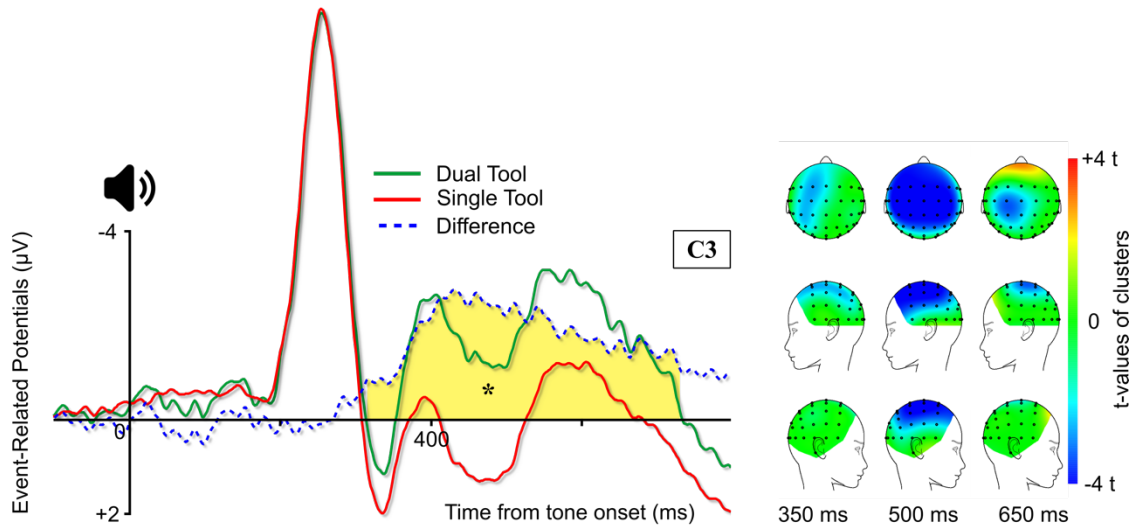
Fig. 16 ERPs at tone onset. Grand average ERPs for dual and single use tools time-locked at the onset of the go-tone. Difference waves signify activity from dual tools – single tools, with indicated areas of significant difference (* = significant differences with $P < 0.001$). Scalp maps show the topographic distribution t-values representing the difference between the use of the two types of tool.

At the onset of the go-tone onset TRFs revealed synchronisation of the slow delta and theta rhythms for action selection (Fig. 17). Comparisons between dual and single use objects using the cluster-randomization technique revealed a single cluster of significant differences, where synchronisation was reduced for the dual use tool compared to the single use tool (maximal from 0 to 800 ms between 2 to 5 Hz, $P < .001$). This cluster represents a transient modulation in the theta frequency band, prominent between 0-100 ms, as well as modulation in delta throughout the duration of the cluster.

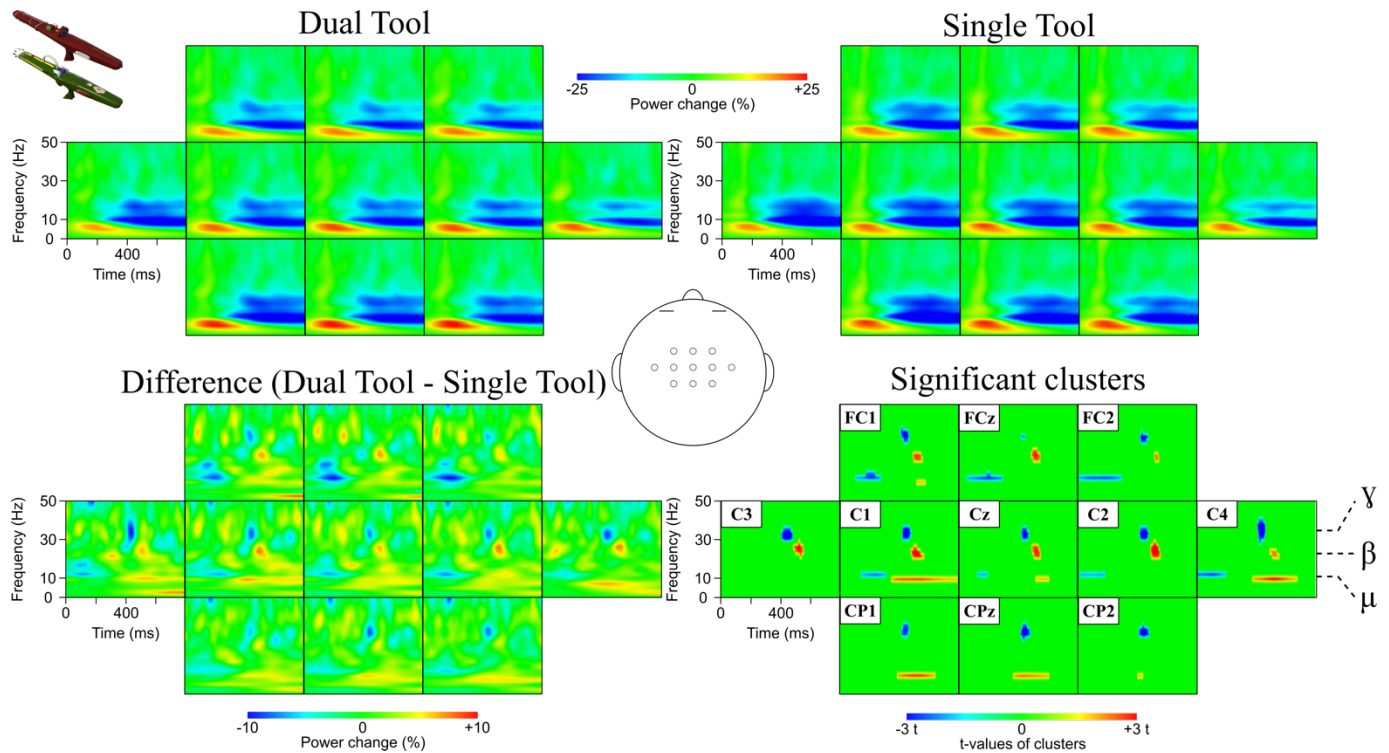Brain Rhythms in Object Recognition and Manipulation
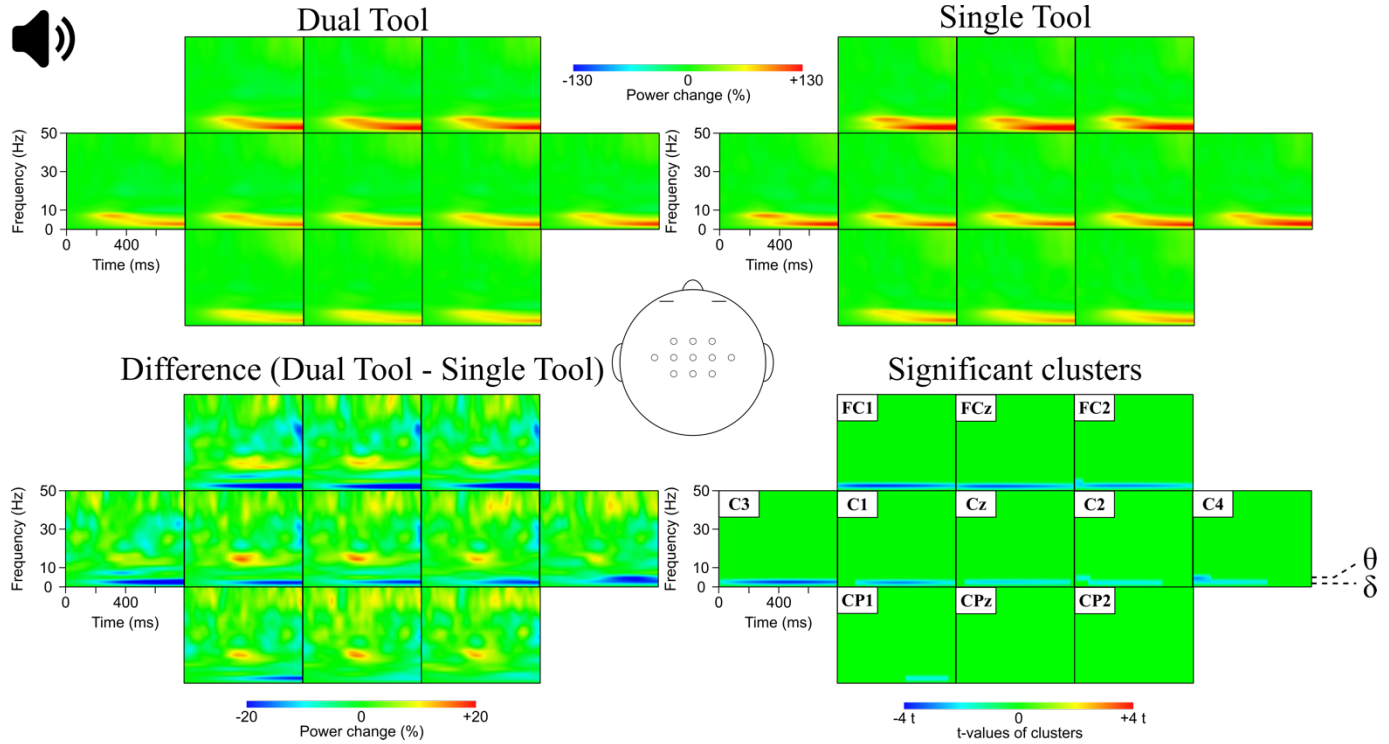
Fig. 17 TFRs at tone onset. Each quadrant represents an electrode located over the sensorimotor areas displaying the power change of the signal in comparison with the baseline period in frequency bands from 0.1 to 50 Hz over a time-window from 0 to 800 ms post-tone onset. TFRs are represented for dual tools, single tools, and the difference between dual and single use tools (dual tool minus single tool). Significant clusters resulting from the cluster-randomization technique are represented in terms of summed t-values, displaying the modulations of the mu, beta and gamma bands.

Analysis of the ERD/ERS revealed only a brief period of significant difference between the use of single and dual use tools between 730-800 ms (Fig. 18; $P < 0.01$) in the beta frequency band, where dual use tool led to increased desynchronisation compared to the single use tool.

Brain Rhythms in Object Recognition and Manipulation
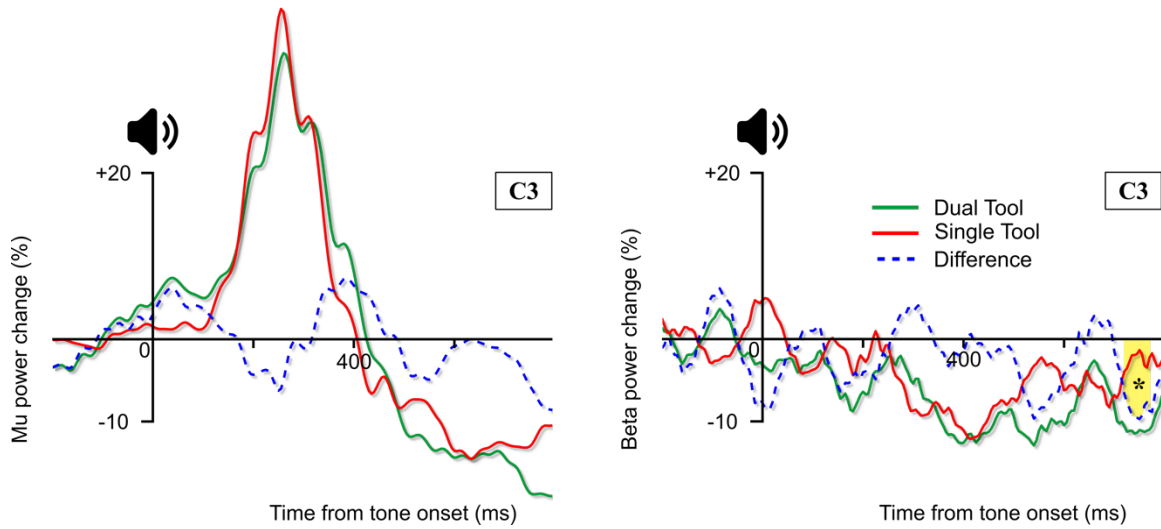
Fig. 18 ERD/ERS at tone onset. Grand averages of ERD/ERS traces for dual and single use tools time-locked at the tone onset recorded on electrode C3, showing the mu (left) and beta (right) frequency bands, Difference waves signify activity from dual tools – single tools, with indicated areas of significant difference (* = significant difference at $P < 0.01$).

4.5. Discussion

In this Experiment 4, we sought to evaluate whether the locus of conflictual interference (Jax & Buxbaum, 2010, 2013; Wamain et al. 2018) originating from tools with differing functional and structural affordances was due to competition between cognitive systems involved in moving or using objects. To do this we examined whether competitive interference could also be seen in 'functional conflictual' tools, those with two functional representations. We hypothesised that if our functional conflictuals produced similar behavioural interference (H1) and modulation of EEG mu (8-13 Hz) desynchronization (H2) as the previously investigated conflictuals, they were more likely due to competition between competing motoric representation, rather than specific competition between cognitive systems involved in moving and using objects. We also hypothesised that, in

addition to modulation of the mu power, functional conflictuals would also lead to increased beta (14-30 Hz) desynchronization (Quandt et al., 2012; Spitzer & Haegens, 2017; Supp et al., 2005; van Elk, van Schie, van den Heuvel, et al., 2010; Wang, 2010), suggesting a role of beta rhythms in the retrieval of functional tool representation. Finally, we sought to investigate the processes behind the competition between functional affordances, predicted the re-activation of tool use representations at the cuing tone of the task would be reflected in greater synchronisation of the mu rhythms and desynchronisation of the beta rhythms (H3).

4.5.1. Tool use competitors interfere during reach and grasp control

Jax and Buxbaum (2010) showed that when we interact with conflictual objects the competition of affordances between Grasp (i.e. dorsal) and Use (i.e. ventral) systems delay response times. We investigated whether a similar delay could also be found when the competition was limited to the ventral system by examining interactions with tools that had multiple functions. To test this hypothesis, we used an experimental task that allowed us to differentiate motor planning steps, in separating the retrieval of object representation from the processes of action selection and execution. Our study did not reveal the difference in motor preparation times reported in Jax and Buxbaum between conflictual and non-conflictual tools. No significant differences were seen in latencies required to initiate hand movement towards the manipulators that represented these two categories of tools. It should be noted that Jax and Buxbaum used a single stage task, where participants initiated their reactions immediately upon the visual presentation of the object. In our study, the onset of the go-tone would trigger the activation and/or inhibition of already retrieved representations, as the tool was presented prior to the onset of the tone. Thus, our behavioural measures do not necessarily reflect processes involved in the retrieval of tool representation, which would have been captured in the task used by Jax and Buxbaum. We did find latency differences in

the second component of hand movement sequence, that is the time required to grasp the manipulator. Here we found significantly longer reaction times for dual than single-use tools, showing that competition between functional affordances can cause similar interference to that seen between structural and functional affordance. This effect cannot be due to motoric complexity of actions, or differences in the geometric affordances of the tools, as these factors were fully counterbalanced in our study. Finally, we did not find latency difference during the execution of the tool use. This suggests that functional motoric representations mainly interfere prior tool use control, that is the tool use selection instantiated during the reach-and-grasp movement. This result extends the ACH model (Cisek & Kalaska, 2005, 2010; Pezzulo & Cisek, 2016) to a broader domain of object manipulation. That is, not only there are competition and interference between the intrinsic features of objects (e.g. multiple graspable parts), but also competition between functional representations that are learnt, and so can be independent of perceptual processes. It also suggests that motor interference found from multiple available actions rely on specific motor selection processes rather than competition between multiple action systems (Binkofski & Buxbaum, 2013; Jax & Buxbaum, 2010, 2013).

4.5.2. Fast mu and beta rhythms reflect the retrieval of multiple tool use

It has previously been shown that competition between structural and functional action representation lead to increased mu synchronisation (Wamain et al., 2018), a marker of sensorimotor processing. Wamain et al. (2016) found an increase of the late mu desynchronisation starting 300 ms after presentation of a manipulable object in the peripersonal space, in comparison with non-manipulable objects or objects in an unreachable radius. In our study, we found that the use of functional conflictual tools led to decreases in early mu synchronisation followed by decreases desynchronization in mu and beta frequency bands in later time periods. These data suggest that

competition between conflicting motor responses within the ventral system produce a similar modulation of mu than competition between motor representations separated by ventral and dorsal streams. They also support Wamain et al.'s suggestions that mu rhythms reflect the motor resonance phenomenon, that is, the automatic activation of the action system due to the perception of object affordance. However, our own study suggests that this phenomenon is not limited to structural affordance, inherent in the perceptual geometries of an object, but also in functional affordances learnt through extrinsic experience. Furthermore, our extension of EEG frequency analyses to the beta range also indicates that these rhythms could provide a specific marker related to the retrieval of object-based functional representation.

Beta rhythms have predominantly been associated with sensorimotor processing, but have also associated with object knowledge (Quandt et al., 2012; Supp et al., 2005), memory retrieval (Muller, Gruber, & Keil, 2000) and action semantics (Weiss & Mueller, 2012). Of particular relevance to our study, Cannon et al. (2014) showed that beta desynchronisation is enhanced when we see a tool associated with a specific use. In our study we found that dual-use tools produced weaker beta desynchronisation than single-use tools, potentially reflecting the competition between functional roles. Under the 2AS+ model (Buxbaum, 2017) it is expected that mu rhythms would reflect an accumulation of perceptually extracted actions based on the structural properties of an object. We propose that beta rhythms could reflect the accumulation of potential functional actions retrieved from memory that are necessary to formulate grasp planning to use functional objects such as tools.

In addition to the analyses of mu and beta rhythms, we also noted that the use of dual tools also increased desynchronization of low gamma/high-beta (28-40 Hz) frequency bands when compared to the single-use tools. The role of the gamma rhythms in cognitive processing has yet to

be thoroughly explored, but these frequencies have been shown to be sensitive to visual attention (Muller et al., 2000), tactile spatial attention (Bauer, Oostenveld, Peeters, & Fries, 2006) and vigilance states (Wang, 2010). On balance, the closest parallel between our findings and those previously associated with low gamma would relate to dual-tools attracting increased attention when compared with single-use tools. This would be similar to the findings of Handy, Grafton, Shroff, Ketay, & Gazzaniga (2003), who compared tools with non-functional objects, but would bear further examination. As discussed in previous chapters, this modulation of ~30 Hz EEG activity could also reflect the access to multiple tool use information from memory, in accordance with the NSOM theory.

We also found that dual-use tools increased the amplitude of the N1 component. This might suggest early retrieval of the functional properties of objects, beginning only 120 ms after the visual presentation, a finding also supported by the temporal pattern of early mu modulation. Both Proverbio et al. (2013) and Goslin et al. (2012) have previously shown that the congruency of the lateral orientation of a tool (handle on the left/right side) with respect to response hand modulated the N1 component. Our study suggests that functional affordances can be extracted within a similar time-frame as found in prior studies of structural affordance, providing additional support to embodied perspectives of cognition (Borghi et al., 2007; Clark, 1999; Wilson, 2002).

4.5.3. Slow delta and theta synchronisations for tool use selection

We tested the possibility that the selection of specific tool use would rely on the re-activation of the perceptual and semantic representations of the tool through mu and beta rhythms. When the tone instructed participants about which tool use to select, an early burst of theta synchronisation accompanying a long-lasting delta synchronisation appeared reduced with the dual tool in comparison with the single tool. However, there was no modulation of the mu and beta rhythms

that would potentially reflect action selection (Brinkman et al., 2016; Wamain et al., 2018), as postulated in our hypotheses (H3). Why no mu or beta rhythms involved in the selection of tool use? First, the re-activation of functional conflictual representations from memory indexed by beta responses may not occur during initial action selection, as the grasp of objects with functional rather than structural posture has been shown to modulate beta rhythms during the reach towards objects (van Elk, van Schie, van den Heuvel, et al., 2010). Thus, functional representations of tools may not be re-activated during motor preparation, but during the reach of the tool when they are necessary to the formation of a handgrip corresponding to the functional manipulation. Our behavioural data support this interpretation. Another possibility is that the activation of functional representation is only reflected in mu and beta rhythms when driven by perceptual sources. It is known that mu oscillations reflect the transformation of visual percepts to motor information (Pineda, 2005), the basis of visual affordance (Proverbio, 2012; Wamain et al., 2016, 2018). As our procedure separated the visual presentation of the tool from action selection, no new visual information is provided during the latter process. This means that the selection of functional representations following the cue would have to be delivered by a non-visual process, reflected in theta and delta frequencies rather than mu and beta. The role of cortical theta and delta rhythms, possibly related to working memory, is still a matter of debate (Gulbinaite, van Rijn, & Cohen, 2014; Harmony, 2013; Prada, Barceló, Herrmann, & Escera, 2014), but have been linked to the implementation of adaptive control during situations of uncertainty related to actions and outcomes (Cavanagh & Frank, 2014). Using a go/no-go task, Schmiedt-Fehr & Basar-Eroglu (2011) found increases of theta and delta power in no-go trials compared with go trials and proposed that early theta activities might reflect response inhibition whereas delta activities could reflect motor inhibition (see also Harper et al., 2014, for similar data reported). In a reaching task, Töllner et al. (2017) showed the theta power

recorded from a middle frontal electrode increases with the amount of conflicting task information. These findings have similarities to those seen in our own study, where the reach-and-grasp sequence had to be inhibited in half of the trials with the single-use tool, which had stronger theta and delta synchronization compared to the dual-use tools, where both actions were executed.

4.5.4. Conclusion

The ACH theory (Cisek, 2007; Cisek & Kalaska, 2010) proposes that structural affordances are processed in parallel and compete for action selection. The 2AS+ model (Buxbaum, 2017) suggest that such selection is enabled through the IFG signal influencing the competition between the different available actions accumulated in the left SMG. This study indicates that these theories should be extended to include functional affordance, with behavioural and electrophysiological evidence for interference between competing functional representations inherent in functional conflictual objects. These data also show that the locus of conflictual interference shown in prior studies (Jax & Buxbaum, 2010, 2013) is not specific to conflict between cognitive systems involved in moving and using objects, related to dorsal and ventral streams. Rather, it would appear to be borne from generic interference between competing motoric representations, whether they originate from the same (functional conflictual) or different (conflictual) cognitive systems. This study also established that competition between conflicting functional motor representations occurs within 120 ms of viewing an object, reflected in the modulation of N1 amplitudes and fast mu and beta sensorimotor rhythms. However, the selection of competing sensorimotor representations does not appear to be represented in mu and beta, but rather in slow delta and theta rhythms. Our findings indicate that beta rhythms provide a marker for the retrieval of an object's functional representation(s) during visual processing.
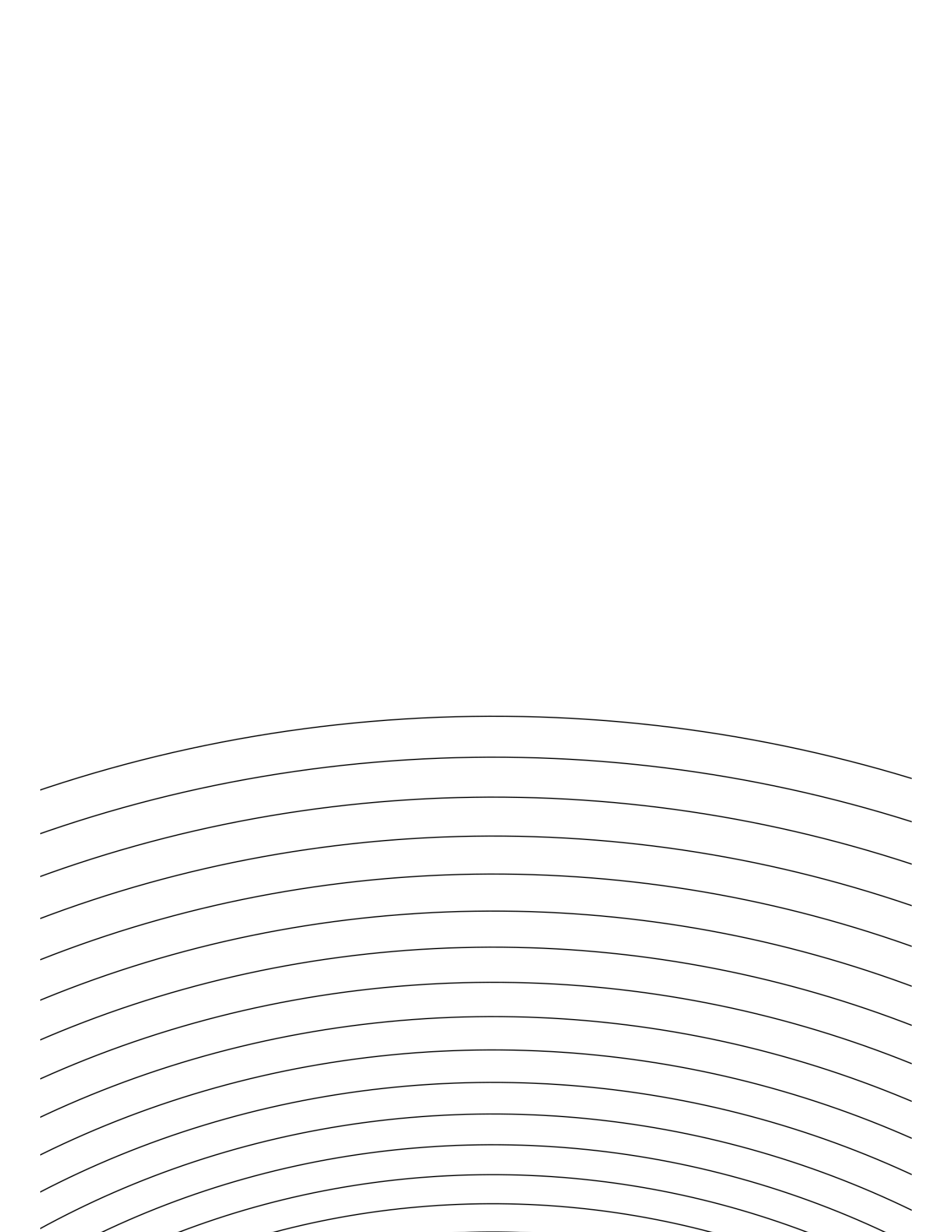
5. Label-augmented learning and performance of tool use

The work presented in this chapter is based on a paper in preparation for PNAS, realized in collaboration with Dr. Anna Borghi. For a better comprehension of the chapter, we invite the reader to watch a video describing the experiment via the QR code at the bottom of the page or the following link: https://www.youtube.com/watch?v=YGHpUoIQ3_0

5.1. Chapter Abstract

Recent works in psychology and cognitive neuroscience showed that language affects our perception of the world. An outstanding question is whether language influences the way we physically interact with that world. Complex tool use and language are endowments of human nature. This study explores how learning the label of a tool affects the encoding and selection of complex tool use. It reveals that associating a novel label to a novel tool facilitates the execution of its use while impedes its transportation. This enhancement is reflected in the beta-band power, reflecting augmented sensorimotor processing induced by the label. The results explain why humans attribute labels to tools: labels not only allow us to communicate about tools and help us to identify their referents, they also enhance their usage. This finding extends the Sapir-Whorf hypothesis that language influences the way we think, to the way we act and blurs the distinction between linguistic and motor processing.

5.2. Introduction

Language and tool use are endowments of our species. Notable, they share evolutionary origins (Arbib, 2011) and neuroanatomical implementations (Frey, 2008). Recent empirical studies

(Boutonnet, Dering, Viñas-Guasch, & Thierry, 2013; Boutonnet & Lupyan, 2015; Cibelli, Xu, Austerweil, Griffiths, & Regier, 2016; Lupyan, Rakison, & Mcclelland, 2007; Lupyan & Ward, 2013; Thierry, Athanasopoulos, Wiggett, Dering, & Kuipers, 2009; Winawer et al., 2007) support the Sapir-Whorf hypothesis (Sapir, 1929; Whorf, 1956) that the way we speak shapes the way we think, in opposition with the idea that our 'thoughts' are of common ground between human being. Here we test and demonstrate that language influences also the way we act, and in particular our tool use ability.

The Sapir-Whorf hypothesis has been recently formulated in terms of predictive processing (Lupyan & Clark, 2015) and probabilistic inference (Cibelli et al., 2016; Regier & Xu, 2017). It has been proposed that language guides cognitive processing, especially when facing situations of high uncertainty. Such a situation occurs when we learn to manipulate a novel tool: at first, the manipulation is approximate; only later experience leads to motor expertise. The label-feedback hypothesis (LFH) proposes that object labels play a role of transient top-down modulators on perception and cognition (Lupyan, 2012), facilitating the identification of objects (Boutonnet et al., 2013; Boutonnet & Lupyan, 2015; Lupyan et al., 2007; Lupyan & Ward, 2013). Beyond this claim, we propose and demonstrate that labeling tools increase the saliency of sensorimotor features relevant for motor learning, such as placing the thumb in a specific location on the pencil when learning to write (Cibelli et al., 2016).

Related suggestions have been made in the literature on affordances, the invitations to act tools offer to us. Tools evoke variable (e.g. orientation) and stable affordances (e.g. size; Borghi & Riggio, 2015). For example, it is useful for us to keep in memory information on a tool function, as it is common to each exemplar of the tool category (we cut with any knife), but not on its orientation because it may vary depending on the context. Perceiving tools activates the motor

representations congruent with both variable and stable affordances, whereas reading the label of a tool evokes more specifically stable affordances (Borghi, Flumini, Natraj, & Wheaton, 2012; Borghi & Riggio, 2009; Bub et al., 2008; Ferri, Riggio, Gallese, & Costantini, 2011; Myachykov, Ellis, Cangelosi, & Fischer, 2013). This suggests that tool labels carry function-based rather than structure-based action information (Binkofski & Buxbaum, 2013). Our rationale is that language helps to learn the invariant properties of tools. For instance, during tool use learning, using a label could strengthen the association of a functional grip with the tool in working memory. In contrast, information on variable affordances, such as the orientation of the tool, doesn't need to be learnt but simply extracted from perceptual inputs to guide on-line motor computations. In the present study, we bring behavioural and neurophysiological evidence that linguistic labels help us to learn and remember novel tool use, and propose a new perspective according to which language not only helps to ground conceptual information but also plays a key role in motor learning.

Research in cognitive neuroscience revealed neuronal markers of language and motor processing, through event-related synchronization/desynchronization (ERD/ERS) techniques applied to EEG recordings. These techniques allow dissociating information processing in terms of oscillatory activities in specific frequency bands. Beta-band (14-30 Hz) power reflect not only motor processing, as well-known for decades (Kilavik et al., 2013; McFarland et al., 2000; Pfurtscheller, 1992; Pfurtscheller & Lopes, 1999; Turella et al., 2016) but also action semantics (van Elk, van Schie, van den Heuvel, et al., 2010; van Elk, van Schie, Zwaan, et al., 2010), semantic memory (Slotnick et al., 2002) and language processing (Weiss & Mueller, 2012). Beta-band power index the activation of motor knowledge via language (Bechtold et al., 2018). The NSOM model proposes that ~30 Hz thalamocortical activities reflect the retrieval of semantic information about objects (Hart & Kraut,

2007; Kraut et al., 2003; Slotnick et al., 2002), such as colors or shapes. Therefore, this ~30 Hz beta-band would indicate whether labels play a role in accessing tool use information from memory.

We used immersive virtual reality to test the hypothesis that labeling novel tools facilitate the use of tools. To do so, forty participants were trained with six novel tools (Fig. 19*A*). The first phase consisted of learning the specific label ('Lum', 'Sni' or 'Unt') of three of these tools (categorization task; Fig. 19*B*). Then, they learnt a unique and novel tool use for each of them (training task; Fig. 19*C*). Finally, participants were asked to move or use these labeled- vs unlabeled-tools (move-use task; Fig. 19*D*). The move-use task allowed us to disentangle the effect of labels in perceptual and/or actions systems. Previous results have shown that labels promote tool identification. If this is the case, labels should lead to faster initiation times independently of the motor task. If instead, labels especially contribute to learn and retrieve tool use, participants would be quicker to execute the use but not the move of tools. A decrease (Hanslmayr et al., 2012) of beta-band power would testify for this sensorimotor facilitation during tool use retrieval only. Behavioural timings and EEGs were simultaneously recorded during the move-use task.

5.3. Method

5.3.1. Participants

Forty adult volunteers (including seven males, mean age = 21.2, years old, SD = 6.2) from the University of Plymouth participated in our study in exchange of course credit. All participants reported being right-handed and having normal or corrected-to-normal vision. Data from one participant was removed from the analysis due to a technical problem. Protocols were approved by the ethics committee of the University of Plymouth and conform to the 2008 Helsinki Declaration.

5.3.2. Experimental Protocol

Participants interacted with this experiment in a virtual environment using a virtual reality headset (HTC Corp.). This environment provided an approximation of their physical environment; seated at a desk with a physical push button and white dashed rectangle, representing the 'home' location for the manipulator, immediately in front of them.
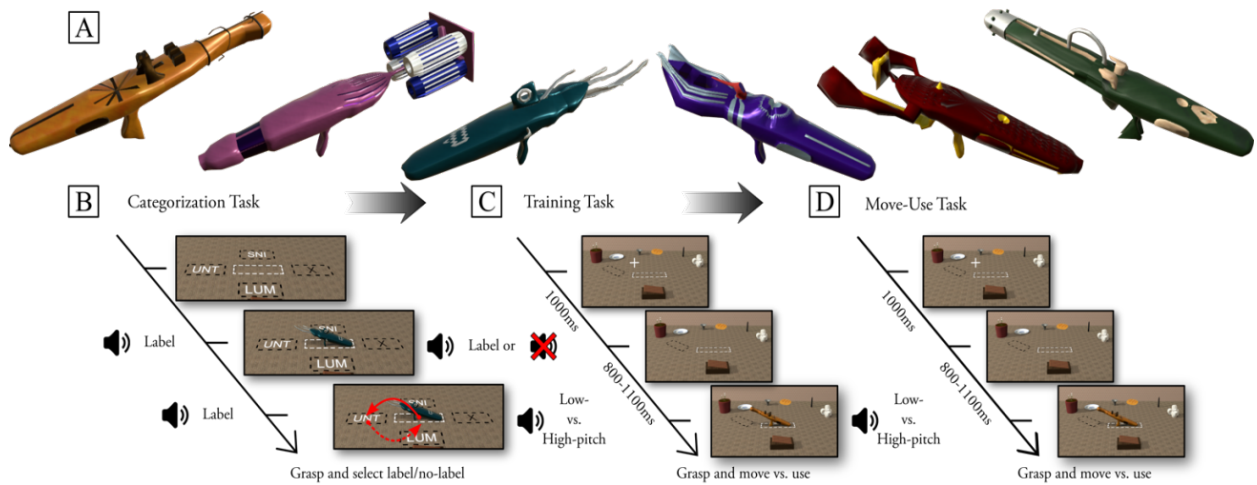
Fig. 19 Experimental design. (A) Visual representations of the six novel tools manipulable in VR. (B) Participants learnt the labels ('Sni', 'Unt' or 'Lum') of three of the six novel tools in a categorization task. (C) Participants learnt a specific tool use. (D) EEG and behavioural timings were recorded while participants were instructed to move or use the labeled and unlabeled tools, depending on a high- or low-pitched tone triggered at tool appearance.

5.3.2.1.   Categorization task

The instructions to the task were displayed on the TV screen located in front of the participant in VR. On the left, right, upper and lower sides of the central white dashed rectangle were placed four black dashed rectangles with the labels 'Sni', 'Unt', 'Lum' and 'X'. At the beginning of each trial, the locations of the four black rectangles were randomly permuted and one of the six

tools (Fig. 19A) appeared at the location of the physical VR controller over the central white rectangle. In one possible case, when the tool appeared the participant heard a voice from a speaker in the room, labeling the tool with one of the three possible names. The task of the participant was to grasp and transport the tool on the black rectangle associated with its label. If the tool was placed on the correct rectangle, the same voice was triggered again to reinforce the learning. If the tool was placed on a wrong rectangle, a buzzing sound followed by the voice was triggered, informing the participant of the wrong name categorization of the tool. Importantly, at the appearance of the tool, the voice was triggered only for the first exposure, forcing the participant to actively remember the name of the tool during the following trials. In the other possible case, no voice was triggered at the appearance of the tool, suggesting the tool doesn't have a name. In this situation, the participant had to grasp and transport the tool to the black rectangle marked with the 'X'. If the tool was not placed on the 'X' rectangle, the buzzing sound was triggered. In both cases, once the tool was transported on a black rectangle the participant had to put the VR controller back on the central white rectangle, which initialized the next trial. As a result of the categorization task, a first tool was associated with the voice and label 'Sni', a second with 'Unt', a third with 'Lum' (forming the tool category Labeled) and the three other tools were associated with the 'X' (forming the tool category Unlabeled). Three sets of voices (two men and one female) for each name were recorded and randomly assigned to each trial. We used multiple voices to strengthen the semantic processing of the voices (i.e. the label) while minimizing the processing of their perceptual properties (e.g. pitch). The participants performed the categorization task until they reach the following requirements: 1) minimum of five trials to each tool, and 2) four correct categorizations over the last five attempts for each tool. These requirements were implemented to assure the learning of the name of each tool before initiating the training task. This categorization task lasted approximately 8-10 minutes for each participant.

5.3.2.2. *Training task*

In the training task, participants learnt to perform a unique tool use with each tool and to associate each tone (low- or high-pitch go-signal) to a type of action (move or use). At the beginning of the training task, the black rectangles of the categorization task disappeared and six other target-tools plus a single black rectangle appeared on the table. These target-tools were a red pot with a plant, a white and blue small plate, a grey cup-like shape, a yellow waffle, a black spike, and four ice cubes. At the beginning of each trial, the locations of these six target-tools were randomly permuted and the location of the black rectangle was randomly assigned in the front of one of these target-tools. Each tool was manipulated seven times in a row, including six trials to use the tool followed by another single trial to move the tool. In total, the training task resulted in 42 trials. For each tool use, on the TV screen were displayed a video of the physical manipulation of the controller (recorded off-line and performed by the experimenter) and a schematic representation of the controller with the different buttons to press. These buttons were a big 'pad' button located on the top of the controller, a small 'top' button on the top, two 'grip' buttons on the sides and a 'trigger' button on the back. Instructions were given orally by the experimenter rather than written for a maximum of clarity. During this training task, each tool was associated with a novel function, unique manipulation and paired with one of the six target-tools on the table. We designed novel functions in order to control for the inference of a function, manipulation or target-tool pair from the structural properties the tool (e.g. the red tool could be a weird claw to lift the plant's pot). Each tool was associated with one of the six following tool use: 1) pressing three times a grip button to grow the plant, 2) swinging successively the tool to the right, left and right side to dissolve the plate in dust, 3) holding down the top button for 2 sec to create a rock on the top of the grey cup, 4) pressing the trigger button then rotating the wrist 45° to the left to remove the gravity of the waffle (resulting in

a floating effect), 5) pressing successively the trigger, pad and trigger buttons to generate a black hole on the tip of the black spike, and 6) swinging vertically the tool up, down and up again to produce a grey cloud and falling snowflakes on the top of the ice cubes. Importantly, the tool needed to be in close distance from and pointing at the correct target-tool to trigger the different audiovisual effects associated with each tool use. During this training task, black panels located over the target-tools instructed the different manipulations to perform with each tool (Fig. 20). To initiate a trial, the participant was required to press and hold down the physical button on the table. Pressing the button resulted in the appearance of a white fixation cross over the white rectangle for 1000 ms before disappearing. If the tool assigned to the trial was associated with a label, this label was spoken by one of the three possible voices. Between 800 ms and 1100 ms after the offset of the fixation cross, one of the two tones was triggered and the virtual representation of the tool appeared. At this moment, the participant had to release the press button, grasp and use the tool with the correct target-tool or move the tool to the black dashed rectangle. Once the action was executed, placing the controller back on the white dashed rectangle initiated the next trial and the visual representation of the tool disappeared.

The pairing of the tones to the move-use actions and visual representation of tools to the tool use was completely counterbalanced for each participant. This training task lasted approximately 20 minutes for each participant.

Fig. 20 Visual representation of the virtual environment at the end of the training task. Black panels with the manipulation instructions were displayed along with the tools, the labels were displayed on red panels. Before to start the move-use task, tools and black and red panels disappeared.

5.3.2.3. *Move-Use task*

The Move-Use task was very similar to the training task. However, no voices were spoken and the tool and the tone (instructing to move or use the tool) were randomly assigned at the beginning of each trial. Also, black panels and representative tools disappeared from the table. The task of the participant was to perform the use or move manipulation of the tools depending on the tone at tool appearance. If the press button was released before the tool onset or below 200 ms after tool onset, a panel appeared reminding the participant to hold the press button down until she/he decided of the tool manipulation to do. Also, if the participants were not able to perform the move or tool use manipulation in the coming 4 sec following the tool onset, a panel displaying the

manipulation to do appeared and lasted until the end of the trial in order to provide feedback about their participant's performance. In both these cases, the trial was considered as failed. At first, participants practiced 20 trials in the presence of the experimenter. During these 20 trials, the chance of the tone representing the tool use actions to appear was of 80% and the tone representing the tool move actions of 20%. We used this bias to train particularly the participants to the most difficult task of remembering how to use the tools. Once the first 20 trials were executed, the participants performed three blocks of 100 trials each. During these blocks, each type of move-use trials had a 50% chance of occurrence and we recorded participants' EEG. At the beginning of the first block and between each block, break times were proposed to the participants in order to remove the VR headset. This move-use task lasted approximately 40 minutes for each participant.

5.3.2.4.   *Recall task*

Before to finish the experiment, we asked participants to perform a recall task in order to evaluate the long-term association of the tool with its name (or no-name). To do so, the procedure was the same as the categorization task, except the following points: 1) no voice or buzz sound was triggered (i.e. no feedback about the correctness or incorrectness of the categorization), and 2) each tool was presented a single time. Hence, the recall task consisted of 6 trials. Data recording and processing

5.3.2.5.   *Behavioural data*

Analyses were conducted on behavioural measures taken during the Move-Use phase of the experiment. Measures of accuracy were based upon the participant's ability to apply the presented tool using the correct motor sequence on the appropriate target tool (Use condition) or moving the tool to the location next to the appropriate tool (Move condition). Reaction times were also measured at three points during this process: a) Initiation time, the duration between tool

presentation onset and button release; b) Grasping time, the duration between button release and the grasp of the tool; c) Execution time, the duration between grasp onset and completion of the move/use action.

5.3.2.6.   *EEG data*

EEG was recorded and sampled at 500Hz during the move-use task of the experiment from 62 actively amplified Ag/AgCl electrodes (actiCAP, Brain Products, Gilching, Germany) using a BrainAmp MR Plus amplifier (Brain Products). The data were analysed with Brain Vision Analyzer (Brain Products, Munich, Germany, v. 2.1) and filtered on-line with a 0.1 Hz high pass filter, a 50 Hz low pass filter and a 50 Hz notch filter. Electrodes were re-referenced off-line to the average of left and right mastoids activity (TP9 & TP10) and the fronto-central electrode AFz was used as the ground. ERPs were time-locked on the visual onset of the presentation of the tool with 1800 ms time window spanning from -600 to 1200 ms before and after the time-lock. Trials with the press button released before the tool onset or within the first 200 ms following the tool onset were discarded. Baseline correction was performed with the 200 ms of ERP immediately before the time-lock. A semi-automatic artefact rejection procedure was run on these ERPs to exclude segments violating the following parameters: maximal allowed voltage step of 50 µV/ms, maximal voltage differences allowed of 150 µV within 100 ms intervals, maximal/minimal allowed amplitude of ± 120 µV/ms, and minimum amplitude of 0.5µV within 100 ms intervals. These parameters were slightly adapted manually for each participant to maximize the signal/noise ratio and resulted in a total of 15% of segments rejected. Individual electrodes having greater than ~8% of rejected segments were removed from analyses and substituted with topographically interpolated replacements (Perrin et al. 1989), representing a total of ~1% of electrodes replaced over the cohort of participants.

Event-Related Desynchronization/Synchronization (ERD/ERS) were calculated for each segment of the ERPs using a pass-band filter ranging from 20 to 40 Hz. Resulting ERD/ERS amplitude values were then squared and traces were smoothed using a running average time-window of 45 msec (as in Ruther et al. (2014) for instance). Each power value was converted in a percentage of power change relative to the average power calculated over the baseline period.

Finally, each trial was re-segmented to a period 200 ms before the time-lock and 500 ms to remove edge effects inherent in decomposition analyses of segmented data and focus analyses on the temporal period of interest (~400 ms) and prior participants' motor response (~530 ms). Averaged ERD/ERS traces were calculated separately for each subject and each tool and task (i.e. labeled and move, labeled and use, unlabeled and move, unlabeled and use), then analysed across the whole scalp.

5.3.3. Statistical Analysis

5.3.3.1. *Behavioural data*

RStudio (v. 1.1.456) and the lme4 (v. 1.1-12) were used to calculate separate linear mixed-effect models analyses for accuracy and each of the three reaction times. Visual inspection of the residuals' plots did not reveal any violation of the assumptions of application. Pseudo-R-squared effect sizes were estimated with the r.squaredLR function of the MuMIn (v. 1.15.6) packages. We calculated the percentage of success to perform the tool use for each participant and each trial block, depending on the tool (labeled vs unlabeled). The strategy used for the following modelling was to maximize the complexity of the structure to control for a maximum of variance while keeping converging models given the size of our dataset. In each model the tool (labeled or unlabeled), the trial block (first, second or third) were entered as fixed effects, with the participant as a random effect and by-participant random slopes for the effect of the trial block. *P*-values were obtained by

likelihood ratio tests of the full model against the null model, with and without the interaction term for the tool and the trial block, respectively (formula of the full model: lmer(PercentOfSuccess ~ Tool + TrialBlock + Tool*TrialBlock + (1|Subject) + (0+TrialBlock|Subject)). Subsequent contrasts evaluated the influence of the tool (labeled vs unlabeled) within each trial block, without the interaction and random effect term, and by dropping the tool term for the null model (formula of the full model: lmer(ReactionTime ~ Tool + TrialBlock + (1|Subject)). Concerning the analysis of the reaction times, in each model the tool (labeled or unlabeled), the task (move or use) and the trial block (first, second or third) were entered as fixed effects, with the participant as a random effect and by-participant random slopes for the effect of the trial block. *P*-values were obtained by likelihood ratio tests of the full model against the null model, with and without the interaction term for the tool and the task, respectively (formula of the full model: lmer(ReactionTime ~ Tool + Task + Tool*Task + TrialBlock + (1|Subject) + (0+TrialBlock|Subject)). Subsequent contrasts evaluated the influence of the tool (labeled or unlabeled) for each reaction time and individual task, without the interaction term and by dropping the tool term for the null model (formula of the full model: lmer(ReactionTime ~ Tool + Task + TrialBlock + (1|Subject) + (0+TrialBlock|Subject)).

5.3.3.2.   *EEG Data*

Statistical analysis of the ERD/ERS traces opposing the labeled and unlabeled tools within each type of action (move or use) was conducted using a pairwise comparison based on a cluster randomisation technique (Maris and Oostenveld, 2007) in order to avoid multiple comparisons. Two-tailed t-tests were performed across all electrodes and data points comprised in the first 500 ms following the tool onset in order to compare the labeled and unlabeled tools, separately for the action move and use actions. Those samples with t statistic above the significance threshold of *P* < 0.05 were clustered together in spatial and temporal terms. Each cluster was based on a minimum of

eight samples and used for the subsequent cluster analysis. The cluster-level t statistic was calculated as the sum of the t statistic of all electrode-time samples of a given cluster. For the cluster analysis, the cluster with the largest t statistic was selected for a Monte-Carlo simulation. Thus, each of the original pairs of t-tests sample that compose the cluster was repeated 1000 times, with permutations of each paired samples randomly assigned to the labeled or unlabeled tools for a given type of action. It generated a Monte-Carlo distribution of summed t statistic corresponding to the null hypothesis. A Monte-Carlo p-value was calculated as the ratio of the 1000 summed t statistics in the random distribution that was above the cluster-level t statistic. This p-value was considered significant above $P < 0.025$. Averaged ERD/ERS traces were re-plotted as t-values in the time domain, derived from t-tests against baselines of zero. For a good visualization of the effect, these t-values of the significant cluster had been used to create topographic maps in Brain Vision Analyzer (Brain Products, Munich, Germany, v. 2.1), using spherical spline interpolation with an order of splines of 5 and a maximum degree of Legendre polynomials of 10.

5.4. Results

5.4.1. Behavioural Results

Our behavioural analysis relied on the participants' accuracy to remember how to use the tools and three type of reactions times: the initiation times indicating the time necessary to initiate the reach of the tools, the grasping times representing the time between the initiation of the reach and the actual grasp of the tools, and the execution times reflecting the time necessary to move or use the tools once handle. Firstly, we looked at the participants' accuracy, defined as the percentage of tool use performed within the 4 s following tool and tone onset (i.e. before the black panel instructed how to perform the action) over the total of trials. Hence, the success tool use rate indicates how

well participants were able to fully remember how to perform the tool use within each of the three blocks of trials. Trials with initiation times below 200 ms were discarded, as they most likely reflected a failure to press the button correctly or to process the stimuli (2.99% of the trials). Mixed-effects models of the tool use performance did not reveal main effect of the label in the comparison between labeled (Fig. 21A; $M_{labeled}$ = 85.7%, SD = 14.4%) and unlabeled tools ($M_{unlabeled}$ = 84.4%, SD = 12.6%; Chi^2 (3) = 0.89, R^2 = 0.003, P = 0.343). However, the models revealed an interaction effect between the labelling of tools and the trial block (Chi^2 (2) = 7.18, R^2 = 0.031, P = 0.028). Analysis of the contrasts revealed the effect of labelling was not significant in the first block ($M_{labeled}$ = 72.8%, SD = 15.9%; $M_{unlabeled}$ = 76.5%, SD = 13.7%; Chi^2 (2) = 1.21, R^2 = 0.016, P = 0.270), marginal in the second block ($M_{labeled}$ = 91.9%, SD = 8.12%; $M_{unlabeled}$ = 88.1%, SD = 9.81%; Chi^2 (2) = 3.55, R^2 = 0.046, P = 0.059) and significant in the third block ($M_{labeled}$ = 92.2%, SD = 7.75%; $M_{unlabeled}$ = 88.6%, SD = 10.2%; Chi^2 (2) = 3.86, R^2 = 0.049, P = 0.049). Thus, labeling the tools reinforced in memory the tool use over experience.
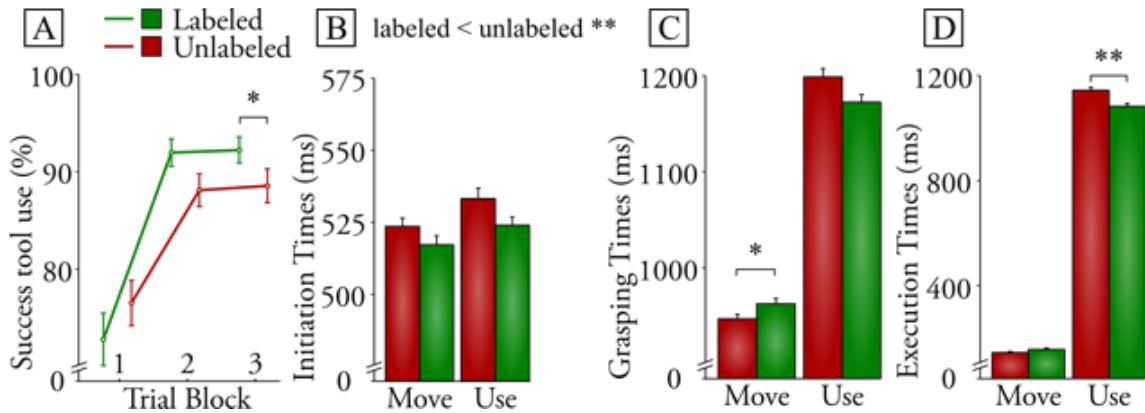

Fig. 21 Behavioural results. (A) Tool use performance, reflecting the participants' accuracy to remember how to use the tools. (B) Initiation Times. The time necessary to initiate the reach of the tools. (C) Grasping Times. The time between the initiation of the reach and the actual grasp of the

tools. (D) Execution Times. The time necessary to move or use the tools once handled. Error bars show ±1 stand error of the mean (*$P < 0.05$; **$P < 0.01$).

Concerning the following analysis, failed trials were discarded and defined as trials were participants did not perform the appropriate actions (move or use) within the 4 s following tool and tone onset (5.75% of the trials). Then, trials with reaction time values inferior or superior to three standard deviations from each participant's mean for each individual trial block were also excluded (Chainay et al., 2014; Osiurak et al., 2013), representing a total of 5.01% of the trials. Mixed-effect models evaluated the three different reaction times from the lasting 10392 trial. The models revealed a main effect of the label on initiation times, such as labeled tools induced shorter initiation times (Fig. 21B; $M_{labeled}$ = 521 ms, SD = 155 ms; $M_{unlabeled}$ = 528 ms, SD = 175 ms; Chi^2 (2) = 7.47, $R^2 <$ 0.001, P = 0.006), reflecting a general identification advantage. Interaction effects revealed that the label improves the recall of learnt motor sequence during the grasping (Fig. 21C; Chi^2 (2) = 5.26, $R^2 <$ 0.001, P = 0.022) and execution (Chi^2 (2) = 10.38, R^2 = 0.005, P = 0.001) times. As a consequence, when required to move the tools, labels increased the grasping times ($M_{labeled-move}$ = 962 ms, SD = 324 ms; $M_{unlabeled-move}$ = 947 ms, SD = 289 ms; Chi^2 (2) = 4.15, R^2 = 0.001, P = 0.042) but reduced the execution times when required to use (Fig. 21D; $M_{labeled-use}$ = 1083 ms, SD = 649 ms; $M_{unlabeled-use}$ = 1144 ms, SD = 702 ms; Chi^2 (2) = 7.06, R^2 = 0.003, P = 0.007).

5.4.2. EEG Results

We computed the relative baseline-corrected ERD/ERS from the simultaneous appearance of tools and tone cues, comparing the labeled vs. unlabeled tools within the tool use and move actions. The analysis included a time-window limited to 500 ms post-onset, preventing a maximum of movement-related artefacts. When required to use the tools, a single significant cluster has been

revealed by the cluster randomization technique, indicating that labeled tools decreased the beta-band power recorded over the somatosensory and motor areas compared to the unlabeled tools (Fig. 21; single cluster ranging from 230 to 500 ms, $P < 0.002$). The beta-band modulation revealed by the analysis concerned the electrodes Fz, F1, F2, FCz, FC1, FC2, FC3, Cz, C1, C2, C3, C5, CPz, CP1, CP2, CP3, CP4, Pz, P1, P3, P5, P7, POz, PO3, PO4, PO8, Oz, O1, and O2, with a peak of t-values around medial and left-lateralized centro-parietal electrodes at 400 ms post-onset.

The effect of the labels was absent when participants intended to move the tools, suggesting that the sensorimotor ~30 Hz power decrease rely on tool use retrieval rather than tool identification. Visual inspection of the probability distributions of initiation times did not reveal differences prior to 500 ms between tasks and labels conditions, excluding the possibility that the beta-band effects relate to movement artefacts.

To test the robustness of the effect, we also statistically compared the difference of signal induced by the labels within tool use and move, using the following comparison: (Use Labeled - Use Unlabeled) vs (Move Labeled – Move Unlabeled). This comparison allowed to verify the presence of an interaction effect in the time-window revealed specifically in the use task. Given the timing of the interaction effect to test, the analysis only concerned the signal between the a priori time-window of 200 to 500 ms. The single significant cluster (Fig. 23; single cluster ranging from 304 to 360 ms, $P = 0.013$) revealed a decrease of beta-band power only when intended to use the tool. The significant modulation concerned the electrodes C1, Pz, P2, CPz, CP1, POz, Oz, and O2.

Finally, we performed an additional analysis of the main effect on the same time-window to compare the implication of the beta-band power in both the types of action (independently of the labelling) and the labelling of the tools (independently of the types of action). Concerning the type of action, the analysis revealed that tool use significantly decreased the beta-band power (single

cluster ranging from 384 to 500 ms, $P = 0.001$) recorded at electrodes sites T7, FT7, and FT9, located in left fronto-temporal areas. About the labelling, the beta-band power of labeled tools was significantly reduced compared to unlabeled tools (single cluster ranging from 360 to 470 ms, $P = .005$). This modulation concerned the signal recorded at electrodes sites FC5, C3, CP1, CP2, P3, C5, C1, C2, CP3, CPz, P5, and P1, located over parieto-central areas and in particular in the left hemisphere (results not shown).
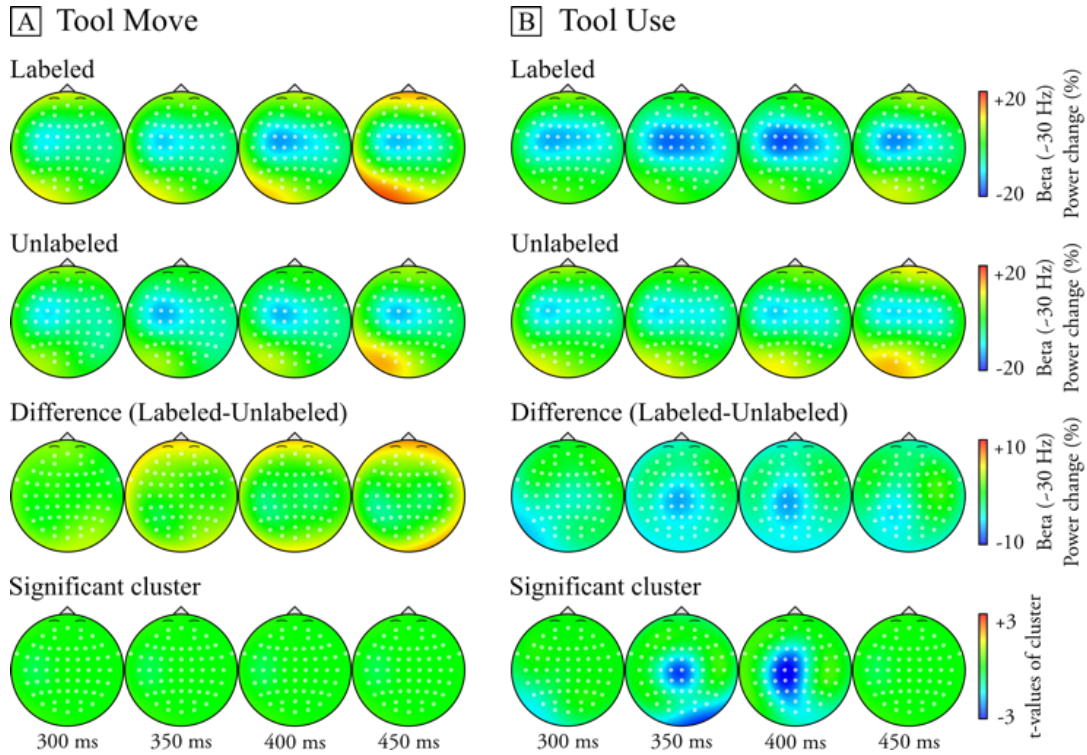
Fig. 22 EEG results. (A) Topographic maps of beta (~30 Hz) power, comparing labeled and unlabeled tools when required to move (A) or use (B). Statistical analysis revealed that labeled tools induced beta decrease during the preparation of tool use only. This decrease appears over left sensorimotor and parietal areas at around 350-400 ms from tool perception.
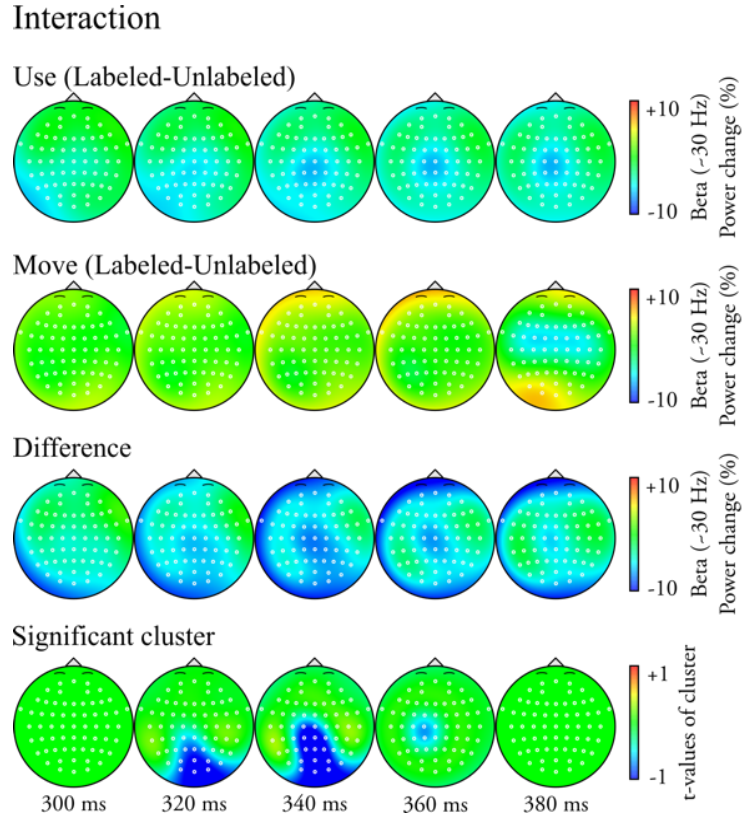
Fig. 23 EEG results. Difference of topographic maps of beta (~30 Hz) power, comparing labeled and unlabeled tools when required to move or use. Statistical analysis revealed that labeled tools induced beta decrease during the preparation of tool use only. This decrease appears over centro-parieto-occipital areas at around 340 ms from tool perception.

5.5. Discussion

Which are the consequences of knowing that our pen and screwdriver are called 'pen' and 'screwdriver'? Humans constantly associate labels to objects and tools to be able to talk about them. Beyond social and communicative reasons, data of this Experiment 5 suggest that linguistic labels play an important role in tool use learning and performance, which extends the general idea of Sapir

(Sapir, 1929) and Whorf (Whorf, 1956) that our language influences the way we think, to the way we act.

Labeling the tools led to faster grasp initiation to move and use the tools. This could simply reflect a better identification of the tools and provide further support to the LFH (Lupyan, 2012; Lupyan & Clark, 2015; Lupyan & Ward, 2013) that labels can guide our perceptual experience as they sharpen the processing of visual details relevant for object recognition. Crucially, however, adopting the move-use task allowed us to distinguish the effect of the labels on perceptual and/or action systems. We hypothesized that tool use would rely more on motor learning and would benefit more from top-down sensorimotor beta-band signals. In keeping with our hypothesis, we found that knowledge of labels helped the participants to remember how to use the tools. This suggests that labels strengthen the association of stable properties (e.g. functional grip to use the tools) with their referent during learning. In accordance, our EEG data revealed that the benefit of the labels is at least partially action-goal specific. When intended to use the tools – but not to move them, labels induced a decrease of ~30 Hz beta-band power over somatosensory and motor areas. The location of the modulation suggests that adding a lexical representation to a novel tool guides its grounding in action systems. Here, the beta-band modulation reflects not only an identification benefit but an enhancement of tool use retrieval, so that the functional manipulation could be remembered better during tool recognition. Both the timing and topography of the beta-band effect support this interpretation, as perceptual facilitation would rather be reflected in the first 100 ms of object recognition in occipital areas (Boutonnet & Lupyan, 2015). In accordance with our interpretation, an fMRI study reported that associating novel names with novel knots affects the ability to discriminate these knots and increases parietal activities (Cross et al., 2012), highlighting that labels are integral

parts of embodied object representations. Here we provide a demonstration that labels facilitate tool recognition, but furthermore, they contribute to our skilled tool use abilities.

Why learning the label of a tool would influence our ability to manipulate it? In the perceptual domain, labels help to generate predictions on noisy visual inputs and render visual discrimination more effective (Lupyan & Ward, 2013). A recent study reported a label-augmented discrimination skill of vibrotactile stimuli (Miller, Schmidt, Pulvermüller, & Blankenburg, 2018), where learning the label of Braille-like stimuli increased the connectivity strength between hippocampi, auditory and somatosensory cortical regions (Schmidt, Miller, Blankenburg, & Pulvermüller, 2019). Beyond these effects of language on perception, multiple proposals already support our claim that labels influence tool manipulation.

For instance, the ACH (Cisek, 2007; Cisek & Kalaska, 2010) proposes that action selection and specification are parallel neural computations, such as grasping, moving or using a tool would be continuously (re-)elaborated during the action. A role played by non-motoric information, stored in semantic memory, for example, is to bias the competition between the multiple actions available and choose the most appropriate behaviour. The model explains why task-irrelevant motor responses interfere with action selection (Jax & Buxbaum, 2010, 2013), which is what happens with tools like calculators that require to poke for their use but needs a clenched grip for their transportation. In the same way, the model elucidates our pattern of behavioural timings. The label brings a computational advantage in remembering the complex tool use manipulation, speeding up the actual use – but not the move, once the tool is handled. In other terms, the label would reduce the uncertainty in the decision to use the tool. This benefit is minimized during the reach, as only the functional grip needs to be specified and not yet the whole tool use sequence, more complex. When intended to move the tools, the reinforced retrieval of the tool use by the label would disfavor the

selection of structural grasp-to-move parameters, slowing down the grasping. In this case, the label would decrease the certainty about which structural handgrip to select. Once the grasp-to-move parameters are specified and the tool is handled, no complex manual manipulations but only arm movements are required, which extinguish the influence of the linguistic label. In support with the influent ACH theory (Cisek, 2007; Cisek & Kalaska, 2010), we report an influence of linguistic information in motor experience, such as lexical representations associated with tools affect the selection of handgrips and could even foster skilled tool use.

A recent proposal on the role of language in processing stable/variable affordances (Borghi, 2012; Borghi & Riggio, 2009, 2015) suggest that language filters and encodes specifically stable tool properties. Given that functional actions are particularly frequent when interacting with tools – but not natural objects, language would build motor prototypes around tool use information. Stable tool properties would be represented in parietal ventro-dorsal circuits (involving the anterior supramarginal gyrus and human putative anterior intraparietal area; Orban & Caruana, 2014) rather than bilaterally. This suggests that learning the label of a tool would favorize the encoding and retrieval of stable tool use information rather than variable ones, e.g. the locations and kinematics parameters to move a tool, and reactivate left-lateralized representations, as the present study demonstrates.

Interestingly, our results also support recent theories of neural reuse (Anderson, 2010; Gallese, 2008), proposing the human evolution led to the overlapping of functional neural networks, from which emerged novel cognitive functions such as language and complex tool use. Hence, language would be partially grounded in our perceptual and motor systems. In accordance, we see here that learning novel words and tool manipulation reflect some, but not complete overlap: our skilled tool use but not structural grasp is augmented by labels. Bearing in mind the idea of

neural reuse, we believe it is important to note that the NSOM theory (Hart & Kraut, 2007; Kraut et al., 2003) proposing that the retrieval of object properties rely on thalamocortical connections processing information paced at ~30 Hz rhythms also shares overlapping with the circuitry involved in action selection (Buxbaum, 2017; Cisek, 2007; Cisek & Kalaska, 2010; Humphries, Stewart, & Gurney, 2006).

On the neural architecture devoted to action, the 2AS model (Buxbaum & Kalenine, 2010) and its updated version (Buxbaum, 2017), proposed that grasping tools rely on a bilateral Structure system, whereas using tools requires a left-lateralized Function system. During the preparation of tool manipulation, the two systems are activated and may interfere with each other. Our reported data indicate that learning labels enhance this interference, especially in the left hemisphere – the Function system. Authors proposed our manipulation knowledge generates motor predictions about desired body states, while sensory predictions are used to minimize the error in motor commands. Performing a tool use would involve the retrieval and online refining of stored body states predictions (what to expect to see and feel about using the tool). Hence, our beta-band effect could reflect an augmented retrieval of these tool use states and/or predictions of action consequences. Following these lines, we suggest that the perceptual gain offered by linguistic labels is expanded to the motor domain, such as labels would facilitate the acquisition of key body states (e.g. fingers position on the handle of a tool) and remembering tool use parameters would be more precise and less noisy. Future kinematic investigations could examine jerks and movement variability to verify this assumption.

If language carves up one's reality, why would it be restricted to the perceptual experience? Here, we evidenced that labeling tools help to learn novel tool use. These labels appear to support action selection, such as choosing handgrips and tool use. Thus, our lexicon helps us to learn motor

information in our everyday interactions with tools. Hence, labels are "neuroenhancements" (Dove,

2018) linking lexical, semantic and motor brain representations.
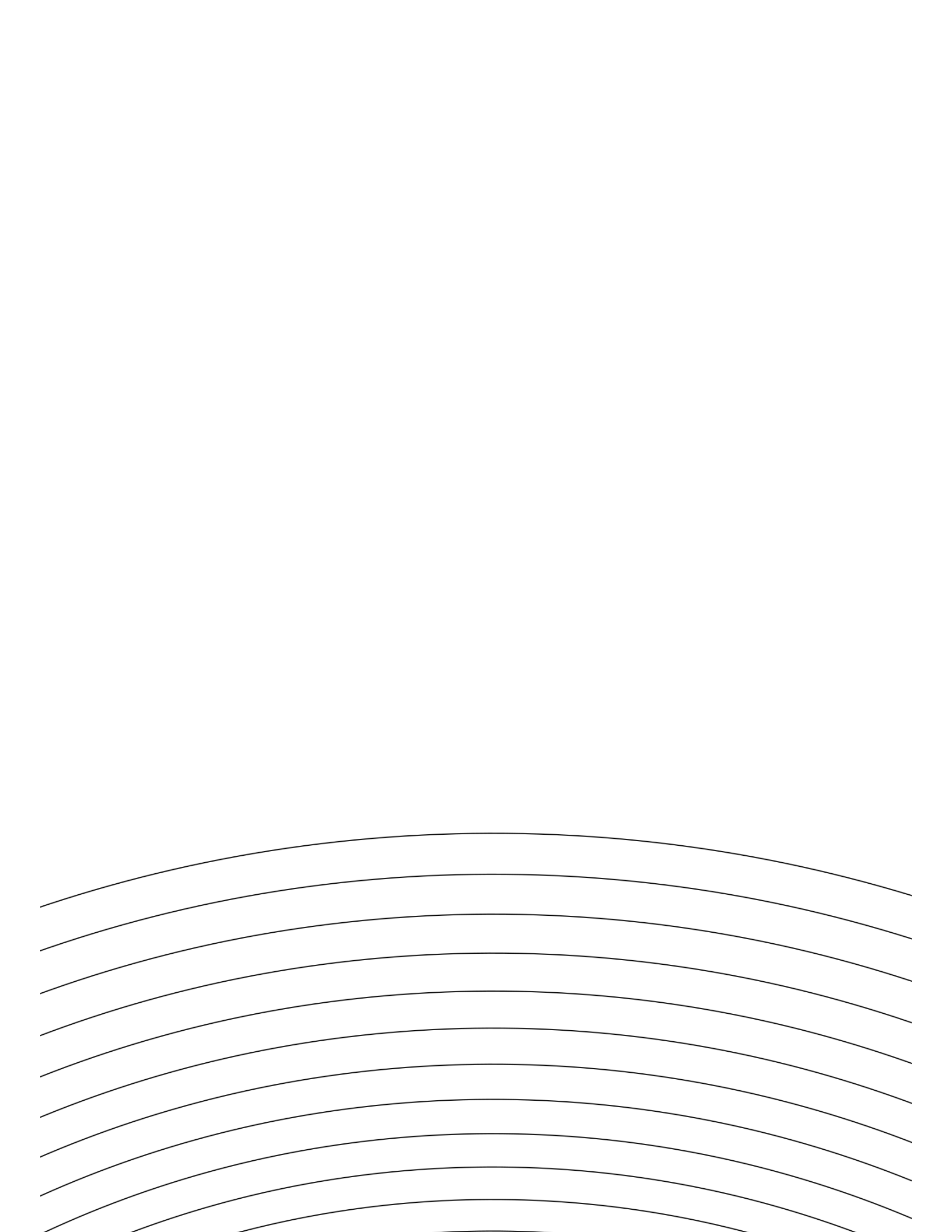
6. General Discussion

In this thesis, we have investigated how and when the retrieval of object knowledge takes place in the brain. Fundamental questions have been raised in the introduction. In the following sections, we will summarize the EEG results reported in the five experiments presented above, then examine these questions in light of the findings. From these discussions, we will propose three testable and closely related hypotheses coined as H_1, H_2 and H_3.

6.1. Summary of beta-band power modulations

In this series of investigations, multiple modulations of beta rhythms have been revealed. All the comparisons made in these studies were paired, which allows expressing all the results in terms of power decrease, which represents neuronal information processing, according to Hanslmayr et al. (2012). For instance, in Experiment 1 we found a more important beta power decrease in the early time-window for the preparation of functional action (tool use *versus* tool move) and the late time-window for the structural action (tool move *versus* tool use). Table 1 summarizes these significant decreases in the beta-band power found in the experiments.

The most striking differences of beta responses concerned the scenarios when the tool appeared at the participant's sight (Experiments 2, 3, 4 and 5) compared with the scenario that did not (Experiment 1). During action selection and preparation (without object recognition), we found an early decrease, followed by an increase of beta-band power (Experiment 1). The laterality and the frequency range of these two modulations are distinct, which suggests that different information processing happened. During object recognition (without action selection), we found a beta power increase (Experiment 2) and decrease (Experiments 3 and 4) at around ~30 Hz. This beta decrease

also occurred when object recognition and action selection were confounded (Experiment 5). During object recognition (Experiments 2, 3, 4 & 5), the high beta-band power modulations started 350 ms after the appearance of the object, which may indicate that the activation of object knowledge (function, manipulation or label) takes a relatively longer time compared to earlier visual processes.

In the studies employing a delayed-response paradigm, the duration of the beta-power modulations was extended when participants prepared grasp-to-move (Experiments 2 & 3) compared to grasp-to-use (Experiment 4) actions. The onsets of beta-power decrease were visibly different in the investigations based on an immediate-response paradigm (Experiments 1 & 5). Finally, the spatial localization of these beta-band perturbations is heterogeneous, but beta power decreases seem especially present within the left hemisphere at posterior sites (Experiments 1, 3 & 5) whereas the beta increases appear mainly within the right hemisphere (Experiments 1 & 2).

Brain Rhythms in Object Recognition and Manipulation

	Comparison	Processing	Beta-range	Timing	Topography	Polarity
Experiment 1 (Chapter 2)	Tool use vs. move preparation	Action selection	25-30 Hz	0-155 ms	Left dorsal	Decrease for tool use
			15-25 Hz	150-500 ms	Bilateral dorsal	Decrease for tool move
Experiment 2 (Chapter 3)	Learning vs non-learning of function knowledge	Object recognition	25-35 Hz	400-740 ms	Right frontal	Decrease when non-learnt
Experiment 3 (Chapter 3)	Learning vs non-learning of function and manipulation knowledge	Object recognition	25-35 Hz	340-640 ms	Left lateral parieto-occipital	Decrease when learnt
Experiment 4 (Chapter 4)	Single vs. dual tool use knowledge	Object recognition	28-40 Hz	400-480 ms	Central	Decrease for dual use
			21-28 Hz	470-565 ms	Central	Decrease for single use
Experiment 5 (Chapter 5)	Interaction effect	Object recognition & Action selection	20-40 Hz	304-360 ms	Left parieto-central	Decrease for labeled tools to use
	Tool use vs. move		20-40 Hz	384-500 ms	Left fronto-temporal	Decrease for tool use
	Labeled vs. Unlabeled tools		20-40 Hz	360-470 ms	Left parieto-central	Decrease for labeled tools

Table 1. Summary of the beta-band power modulations reported in the five experiments constituting the dissertation. Following the concept that beta desynchronization reflects neuronal information processing (Hanslmayr et al., 2012), all experimental pairwise comparisons are expressed as power decreases.

6.2. Beta rhythms in the preparation of structural and functional tool manipulations

How does the brain access the tool use information during action preparation? This question is crucial as it is still unclear why the preparation of tool use, but not structural actions, is impaired in apraxic patients. A first hypothesis is that patients have difficulties in selecting stored manipulation over perceptually afforded (structural) manipulations, thus relates on decision-making computations (Jax & Buxbaum, 2013; Rounis & Humphreys, 2015) and possibly interferences between and within action systems. Could beta oscillations play a role in this selection and preparation of complex tool use?

A decade ago, a study investigated the involvement of the beta band (18–22 Hz) rhythms recorded over parietal areas in the preparation of tool use pantomimes (Wheaton, Fridman, Bohlhalter, Vorbach, & Hallett, 2009). The authors showed that the signal power drops in comparison with no motor preparation at all, which may indicate that decreases of beta power in the 18-22 Hz range reflects the motor preparation to pantomime tool use. Within the same frequency band, Zaepffel et al. (2013) showed that the signal power reduced in centro-parietal sites with the increase of the amount of information provided to the participant about a structural grasp (e.g. type of grip, force) to prepare. So, increasing the motor information to process seems reflected in the drop of beta power. However, these studies did not involve real manipulations of tools.

In Experiments 1 and 5, we employed the move-use paradigm to test the hypothesis that the preparation of tool use involves more important beta power decrease than the preparation of visually afforded structural actions. In Experiment 1, we found a large range of beta oscillations (15-40 Hz) involved in the preparation of manipulations. However, the dynamics of these beta rhythms were largely widespread in time and around the posterior areas of the scalp. On one side, the

preparation of a tool use involved an early (0-150 ms) decrease of beta power. On the other side, the preparation of the tool transportation induced a later (150-500 ms) power decrease on frequencies below 25 Hz. Hence, different manipulations may rely on different dynamics of beta oscillations.

In Experiment 5, we found that a tone indicating to use tools rather than transporting them induced a decrease of high-beta power (20-40 Hz) recorded over the left lateral fronto-temporal areas, a modulation that started 380 ms after the tone. This temporal activation could reflect the activation of the ventral stream for the extraction of the meaning (i.e. the 'What') of the action (Ungerleider & Mishkin, 1982), a prerequisite for the preparation of meaningful object manipulations.

Thus, the two experiments revealed that beta oscillations are involved in the preparation of structural and functional tool manipulation. The EEG responses were very distinct in their timing and topography, but the frequency ranges were clearly overlapping. Therefore, it is possible that the beta oscillations (especially at around 30 Hz) have a mechanistic role in the preparation of tool use, but they are greatly dependent on the task settings. For instance, the co-occurrence of object recognition in Experiment 5 could interfere and delay these beta oscillations in comparison with Experiment 1, where beta responses appear earlier for the preparation of tool use.

To my knowledge, these experiments provide the first evidence of the involvement of beta oscillations in the selection and preparation of real tool manipulations. Unfortunately, it remains difficult to interpret whether beta rhythms have a functional role in the manipulation selection, preparation, or both, often confused in the literature. The next challenge would be to demonstrate whether these beta oscillations for the preparation of tool use are present in patients with apraxia.

6.3. Beta rhythms in the access to functional and manipulative object knowledge during tool recognition

A second hypothesis explaining why patients with apraxia have tool use impairments relies on the difficulties in accessing stored object manipulations, necessary to most of the functional manipulations. Hence, the impairment would relate to semantic memory processing. In that case, how does the brain access the tool use information during object processing?

Proverbio (2012) showed that perceiving tools, compared to non-tool objects, induce a decrease of the mu-band (especially in the 10-12 Hz) power recorded over centroparietal sites at around 140-175 ms. Thus, mu-band rhythms may play a role in the early processing of tools. However, the study does not allow to clearly distinguish structural from learnt tool affordances, in comparison with the present Experiments 1–5. Still, it is congruent with the idea that an increase in cognitive processing can be seen as a decrease of oscillatory activities in the brain (Hanslmayr et al., 2012).

Another study reported a more important decrease of the mu-band power recorded over central electrodes sites for the processing of conflictual tools (i.e. affording multiple actions) presented in peripersonal rather than extrapersonal space (Wamain et al., 2018). Similar results have been reported in Experiment 4, when teaching a novel tool manipulation to participants modulated the early decrease of mu-band (11-14 Hz) power during the recognition of this tool. Hence, it is possible that the reduction of mu-band power (especially at around 12 Hz) recorded over central electrodes sites could reflect a motor resonance phenomenon induced by the processing of the affordances during object recognition (as suggested in Wamain et al., 2018). In other words, visually afforded actions could be indexed by the perturbation of mu oscillations within these cortical areas.

However, the experiments presented above clearly suggest that beta rhythms are somehow involved in, and possibly specific to, the processing of learnt affordances and tool use. To my knowledge, there is no clear evidence that brain rhythms outside the alpha/mu-band range play a role in the processing of structural affordances. For instance, Proverbio (2012) and Wamain et al. (2016, 2018) did not report any beta-band power analysis. The shreds of evidence converged toward a structural affordance processing reflected in the early mu rhythms recorded over the dorsal stream during object processing. Nevertheless, we provide seminal evidence that, when the affordances are learnt, additional beta oscillations come into play. These beta oscillations could, therefore, testify that the brain processes differently perceptually- and memory-based affordances.

In Experiments 2–5 we found that beta rhythms were involved in the retrieval of novel object knowledge during tool recognition. More investigations are required to interpret why learning a tool function induced an increase of beta power in frontal sites (Experiment 2). Yet, learning a novel or additional tool use induced decreases of high beta-band power at around 30 Hz during object processing in Experiments 3 and 4. Both signal perturbations were initiated relatively close to each other, at around 350-400 ms following the object appearance. So, it is possible that beta oscillations recorded over central and posterior electrodes sites indicate the retrieval of functional and manipulative information about tool use during object processing. Variations in the topography of the beta oscillations during object recognition could depend on the task settings – tool recognition followed by an execution of structural (Experiment 3) or functional (Experiment 4) actions. More precise conclusions remain to be investigated in further studies.

6.4. Beta rhythms indexing the grounding of functional action information in embodied systems through language

Naming objects in the environment is a fundamental activity on a daily basis. After all, we learn manipulative and functional information about novel objects and tools along their linguistic referents: the name of a new technology helps to remember what it does. Therefore, we tested the exquisite hypothesis that this linguistic property has an impact on the cognitive processing involved in object recognition and the execution of manipulations.

In the framework of this dissertation, an additional analysis in Experiment 5 reported that processing labeled tools induced a drop of the high-beta power in the 360-470 ms time-range compared to unlabeled tools. Hence, not only associating a tool use with an object name induces beta-band power decrease during the processing of that name (Bechtold et al., 2018) but also during the processing of that object. The main analysis revealed that this power decrease was particularly present at a slightly earlier time during the preparation of complex tool use. Both modulations were recorded over the left parietal lobe. As found in Cross et al. (2012), language seems to assist the grounding of novel action information in the embodied systems. Our data suggest this augmented embodiment is indexed by EEG beta rhythms. Congruently, Experiment 3 showed that beta rhythms could reflect the embodiment of an object through the learning of manipulation knowledge. All of these onsets of modulations were closely related in time and space.

All in all, we have multiple evidence suggesting that beta oscillations reflect the activation of the 'Function' action system. Also, both linguistic and manipulative information helps the grounding of novel object representations in embodied brain systems. Our rationale is that linguistic information helps in storing the invariant properties of tools. In this context, language favorises

embodied information processing such as the retrieval of tool use information from memory. This point joints the conceptions that 1) language incorporates stable – but not variables object affordances (Borghi & Riggio, 2015) and 2) both linguistic and manipulation knowledge could share brain mechanisms involving beta oscillations (Weiss & Mueller, 2012).

6.5. Discussing the Two Action Systems theory

The present investigation provides rich information about concerns developed in the 2AS theory (Buxbaum, 2017; Buxbaum & Kalenine, 2010), a neurocognitive model of structural and functional interactions with objects.

Firstly, the authors commented that an "… open question is whether passive viewing of objects may under any circumstance induce motor resonance phenomena without a prior intention to act in object-compatible ways" (p. 214). Wamain et al. (2016) asked participants to estimate whether they could reach appearing objects (reachability judgement task) or discriminate their visual representation (perceptual judgement task) that had either a prototypical or distorted shape. Only in the reachability judgment task, the authors reported a decrease of mu-band power recorded over central sites when the prototypically shaped objects were located in the peripersonal rather than extrapersonal space. This means that mu-band rhythms were sensitive to 1) the task (or the context of the perception) and 2) the intrinsic value of the structural affordance for the participant, which is its graspability given its shape and location in the space. Thus, this result provides a partial answer to the question. To step forward, Experiment 3 tested whether functional action information would also be automatically re-activated during object processing, without any intention to execute functional manipulations. After all, the usage of a tool is what defines its category, and therefore might be accessed during object recognition. Indeed, the EEG results supported this exquisite

proposal, where tool use information seemed automatically retrieved during object processing, even when intended to perform a structural action (tool transportation). In other words, manipulation knowledge could be activated independently of the action goal. This fits in the ACH model, but disagrees with the 2AS theory claiming that the 'Function' system is activated only when it is relevant to the intention or goal of the action.

Secondly, the authors mentioned that an "… area of inquiry concerns fleshing out the details of the competition that may occur between transient and more stable action representations" (p. 214). We have now multiple information concerning the neuronal dynamics induced by the competition of action systems. Wamain et al. (2018) revealed that mu rhythms reflect between-systems interference (structural *versus* functional) during the processing of conflictual tools. Experiment 4 evidenced that 1) within-system interference (functional *versus* functional) also exists and impedes grasping and 2) both mu and beta rhythms are involved in this tool use competition during object processing. Plus, Experiment 5 provided evidence that the competition between actions is influenced by task-irrelevant information outside the action domain, that is linguistic. We showed that associating a name to a novel object slows down structural grasp but speeds up functional manipulations. Consequently, the delayed structural grasp could reflect an inhibition of the 'Structure' system competing against the 'Function' system. Then, the speeded-up tool use manipulation could be explained by a computational advantage of the 'Function' system by the presence of a label gluing multimodal action and object representations altogether, as proposed in Dove (2018). Therefore, stable action representations seem to affect the selection and implementation of structural actions.

Thirdly, we reported here initial evidence that the competition between- and within-action systems could be mirrored by distinct neuronal oscillatory activities recorded via EEG. Experiment

4 indicated that the recognition of a tool associated with multiple tool use representations activated both mu and beta rhythms. The extraction of geometrical affordances seems to be an automatic process – at least in the peripersonal space (Ambrosini & Costantini, 2013; Costantini, Ambrosini, Scorolli, & Borghi, 2011; Goslin, Dixon, Fischer, Cangelosi, & Ellis, 2012; Kalénine et al., 2016; Tucker & Ellis, 1998; Wamain et al., 2016), translating visual inputs into potential actions. Bearing in mind that alpha/mu oscillations could reflect the extraction of these visual affordances (Pineda, 2005) from inputs, it is possible that associating multiple functional manipulations to an object reduces the subsequent activation of the 'Structure' system. In support with this idea, Experiment 4 indicated that the mu-band power decrease is maximal for the tool associated with unique tool use.

However, for the first time, we described here an involvement of beta oscillations in the competition between multiple functional actions. Importantly, we can consider that the learnt object in Experiment 3 represents a conflictual tool, as previously defined in the literature (Jax & Buxbaum, 2010, 2013; Kalénine et al., 2016; Wamain et al., 2018). Hence, the beta modulation reported in Experiment 3 would also point toward the involvement of beta oscillations in the competition between structural and functional action systems.

So far, we have evidenced that beta rhythms play a role in the processing of affordances. I propose a first hypothesis (H_1) extending the two action systems models (Binkofski & Buxbaum, 2013; Buxbaum, 2017; Buxbaum & Kalenine, 2010; Daprati & Sirigu, 2006) based in the framework of variable/stable affordances of Borghi and Riggio (2015). There could be a functional dissociation between the beta rhythms and alpha/mu rhythms in the activation of action representations. The power of these rhythms could reflect the balanced activation of the 'Function-Stable' and 'Structure-Variable' action systems. More precisely, on one hand, increasing the manipulation knowledge (e.g. learning a tool use) about an object would induce a decrease of the beta-band power

(Experiments 3 & 4) and increase the power of the alpha/mu-bands power (Experiment 4; Wamain et al., 2018) during object recognition. On the other hand, recognizing objects associated with very little manipulation knowledge (e.g. non-conflictual tools, non-tool objects) would provoke the opposite pattern of EEG responses, with an increase of the beta-band power and decrease of the alpha/mu-bands power. In other words, the desynchronization of alpha/mu-bands power would index the strength of the perceptual processing of the object (variable information), whereas the desynchronization of beta-band power would mirror a reinforced retrieval of stable information about the object. The absence of mu power increase for tools reported in Proverbio (2012) could be explained by the task employed (responding to pictures of plants while ignoring the objects) or the distance (120 cm) separating the participants from the pictured objects. Our hypothesis is already supported by broader theoretic functions of mu and beta oscillations in the brain (Hanslmayr et al., 2009; Pineda, 2005; Spitzer & Haegens, 2017).

6.6. Extending the Affordance Competition Hypothesis

The ACH theory (Cisek, 2007; Cisek & Kalaska, 2010) proposed a common ground for motor and cognitive processing in the animal brain: how it selects and implements behaviours. It led to interesting progression in the field of motor control (Gallivan et al., 2015; Gallivan, Chapman, Wolpert, & Flanagan, 2018; Gallivan et al., 2016) but it is still quite unused to explain the cognitive aspects of complex actions, such as the everyday manipulations of diverse objects and tools.

Even though action intentions would play a major role in the preparation of movements, selecting a goal does not mean selecting all action parameters to reach that goal. As proposed in the ACH theory, it is most likely that the selection of action parameters unfolds during the action execution. For instance, when a task is to decide how to manipulate an object and with which hand

(Experiment 1), it is likely that at first the hand is selected, as it is the decision necessary to initiate the reach of the object with a single effector. Following the hand decision, the question of how to manipulate the object needs to be answered prior the actual manipulation. This means that the selection of a manipulation partially happens during the reach of the object, as reported in Experiments 1, 4 and 5. When there are multiple possibilities of manipulation, for instance, multiple tool use, the selection of an action might occur during the reach of the object (Experiment 4) or once it is handled (Experiment 5). This is what happens when we manipulate a swiss-knife: we first decide the goal of the manipulation (e.g. cutting with a blade), but most of the motor decisions occur when the tool is already handled (such as finding the blade among the other functional-ends of the swiss knife).

Unfortunately, the interpretation of the behavioural data in Experiment 1 was laborious, as we did not know what parts of the behaviours were due to the action selection or to the consideration of physical constraints (i.e. interaction with the table). However, Experiment 5 provided evidence in favor of the ACH theory. The linguistic object knowledge induced two antithetical effects on behaviours, namely an interference during the object grasp and facilitation during the object use. This highlights that, indeed, a competition between structural and functional action representations occurs during these two motor sequences. The proposal of the ACH is that actions visually afforded by the environment are in constant competition. In Experiment 4, we found that learning an additional functional action knowledge about an object significantly delayed its grasp (by approximatively 2,6 % of the total grasping time). Again, this reveals that the competition between multiple actions happens simultaneously to the implementation of behavior, that is the reach of an object. Furthermore, we interpret this result as an extension of the ACH theory and propose the hypothesis (H_2) that not only actions extrinsic to the environment but also

intrinsic to the actor are competing for execution. In this case, the affordance competition relies on memory components of the actor rather than on a property of the environment itself, therefore opening the theory to domains outside the visual perception.

Compared to the 2AS theory, the ACH does not dissociate activation of object knowledge depending on the action goal (e.g. move or use), because the selection of an action would automatically rely on multiple sources of information from disparate cortical systems. This accommodates well the role played by the label found in Experiment 5, where the linguistic inhibited the selection of visually afforded actions. Previous studies did not consider the competitions based on multiple functional action knowledge (Jax & Buxbaum, 2010, 2013; Kalénine et al., 2016; Wamain et al., 2018; Watson & Buxbaum, 2015). However, we found an interference effect during the grasp of a functional conflictual tool in Experiment 4, supporting the idea that action knowledge interferes during motor control. We hope that future work on action selection will lead to a better understanding of how action competitions occur and how the brain solves them. It would constrain contemporary hypotheses about praxic skills (Botvinick, Buxbaum, Bylsma, & Jax, 2009; Buxbaum, 2001; Goldenberg & Spatt, 2009; Watson & Buxbaum, 2015) and help to target the impairments found in clinical populations.

6.7. Upholding the Neural hybrid Semantic Object Memory theory

The NSOM theory (Hart & Kraut, 2007) describes a mechanism for the storage and retrieval of semantic knowledge at a neurophysiological level. The authors proposed that components of object memory are stored within specific systems. The retrieval of object knowledge would occur via thalamocortical synchronization mechanisms. More precisely, the low-frequency synchronization reflects a tonic state of cortical inhibition, whereas the bursts of ~30 Hz synchronization of

thalamocortical connections mediates features binding during memory recall (Pulvermüller et al., 1999; Slotnick et al., 2002).

Data reported in Experiments 3-5 bring three observations to its phenomenon. First, the present experiments suggest that ~30 Hz oscillations elicited during object processing appear mainly located in left-lateralized motor, parietal and occipital areas. Second, these oscillations do not occur during the first 350 ms of tool recognition. Third, the retrieval of object knowledge seems expressed as a decrease in signal power. However, this decrease of the power for the retrieval of stored information contrasts with the seminar data (Slotnick et al., 2002) that led to the formulation of the NSOM theory. Yet, our data are coherent with a more recent view suggesting that neural desynchronizations of beta rhythms play an active role in memory retrieval (Hanslmayr et al., 2012). In this sense, we report data suggesting that the NSOM theory could be valid on the mechanistic roles played by high-frequency oscillations on the retrieval of object knowledge, but not on the polarity of the signal expressing such information processing.

Lately, Spitzer and Haegens (2017) proposed that beta oscillations reflect the reactivation of the content encoded in local neuronal assemblies. Rather than long-lasting over time, these reactivations could be characterized by 'burst-like' temporal shape (Jones, 2016). Our results from Experiments 4 and 5 are congruent with this idea of bursts of beta oscillations, lasting no longer than 100 ms. Consequently, we propose the hypothesis (H_3) that the retrieval of semantic object knowledge during object recognition could be indexed in bursts of high-beta decrease responses. I hope that further studies will investigate deeper the possible functions these oscillations can have in our everyday recognition and manipulation of objects.

6.8. Conclusion

How the brain accesses learnt information remains an outstanding question unsolved throughout centuries. Seeking answers, neuroscientists and psychologists need creativity to rethink the way the brain could work and develop novel paradigms and techniques. As remarked in Brandi et al. (2014), to understand the neural principles of real tool use preparation, we need investigations involving tool use execution rather than pantomime (Goldenberg et al., 2007; Moll et al., 2000) or imagined (Boronat et al., 2005) tool use. To do so, we exploited immersive virtual reality as a means to create novel tools affording different actions to prepare, coupled with EEG recording to assess the brain dynamics during this preparation.

In this investigation, we provided multiple evidences that the retrieval of object knowledge upon object processing occurs during the first 300-400 ms. Furthermore, accessing object knowledge during perception and action preparation involved reductions of beta-band oscillations in disparate cortical areas. The original data reported here and the existing literature led us to formulate novel hypotheses to investigate in further investigations.

First, during object processing, the extraction of structural affordance could rely on alpha/mu rhythms whereas retrieving learnt affordances would involve beta oscillations, both mechanisms expressed in terms of desynchronizations. Second, as much as visually extracted affordances, learnt affordances compete for action execution during motor control. Third, we proposed that retrieving semantic object knowledge is based on bursts of desynchronization of high-beta band rhythms at a cortical level.

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