Title: Conflict between gesture representations extinguishes μ rhythm desynchronization during manipulable object perception: an EEG study

Author names : Yannick Wamain, Aïsha Sahaï, Jérémy Decroix, Yann Coello & Solène Kalénine

Affiliations: Univ. Lille, CNRS, CHU Lille, UMR 9193 - SCALab - Sciences Cognitives et Sciences Affectives, F-59000 Lille, France

Corresponding author:
Yannick WAMAIN
Mail : yannick.wamain@univ-lille3.fr
Phone : +33 3 20 41 69 89

Laboratoire SCALab UMR CNRS 9193
Université Lille 3
Batiment A2 - Niveau forum +2
Domaine universitaire du Pont de Bois, BP 149
59653 Villeneuve d'Ascq Cedex, France

Conflict between gesture representations extinguishes μ rhythm desynchronization during manipulable object perception: an EEG study

Wamain Yannick, Sahaï Aïsha, Decroix Jérémy, Coello Yann & Kalénine Solène

Abstract:

Recent findings showed that the competition between object structural and functional gestures slows down the initiation of object-directed actions but also object visual processing. The present study investigates the neurophysiological correlates of the competition between gesture representations during object perception. 3D conflictual objects (distinct structural and functional gestures) and non-conflictual objects (similar structural and functional gestures) were presented in three different spaces (peripersonal, boundary of peripersonal and extrapersonal) in a virtual environment. Participants performed reach-to-grasp judgments and semantic judgments on objects while EEG was recorded. Results revealed that the conflict between evoked gestures impacts 8-12 Hz desynchronization at both central (μ rhythm) and posterior (α rhythm) sites. Critically, μ rhythm desynchronization was suppressed when conflictual objects were presented in peripersonal space. Findings indicate that μ rhythm desynchronization is reduced by the competition between evoked gestures and suggest that neural motor resonance may also reflect action selection processes during object perception.

Keywords:

Manipulable object; Visual perception; Action selection; μ rhythm; Virtual reality

1. **Introduction**

The mere perception of a mug on your desk may evoke in your mind multiple action representations, as many objects are associated with several possible actions. Yet, only a subset of actions will be relevant depending on your precise intentions. For instance, if you are thirsty, you will consider grasping the mug with the most suitable gesture for drinking. However, different gestures would be appropriate if you want to wash the mug or use it to store your pencils. In the case of overt execution of object-directed actions, the selection of the correct object action representation, among several alternatives, has to be achieved by the cognitive system (Cisek, 2007) based on the situational and/or individual context. Recent findings have demonstrated that when distinct action representations are equally good candidates in a given context, they may interfere with one another. In particular, the co-activation of distinct functional ("grasp-to-use") and structural ("grasp-to-move") gestures when preparing to act on an object induces a processing cost and increases the time needed to initiate the action (Jax & Buxbaum, 2010, 2013).

In a recent behavioural study, we showed that this cost is not restricted to action planning but also affects the field of object perception (Kalénine et al., 2016). Participants were immerged in a 3D virtual environment where objects associated with distinct structural and functional gestures (hereafter conflictual objects, e.g. a calculator associated with poke and clench gestures) and objects associated with similar structural and functional gestures (hereafter non-conflictual objects, e.g. a bottle associated with clench gesture only) were presented at different distances from the participant. They performed different perceptual judgments on the objects, reach-and-grasp judgments ("could the object be reached and grasp with the right hand?") and semantic judgments ("could the object be found in the kitchen?“). The rationale was that conflictual objects were assumed to slow down perceptual judgments, as compared to non-conflictual objects, due to the co-activation of different structural and functional gestures during perception. Indeed, several empirical findings now indicate that visual objects may evoke both structural and functional gestures (Bub, Masson, & Cree, 2008; Lee, Middleton, Mirman, & Buxbaum, 2013). Moreover, evocation of structural and functional gestures was expected to be context-dependent (Borghi, 2004; Borghi, Flumini, Natraj, & Wheaton, 2012; Kalénine, Shapiro, Flumini, Borghi, & Buxbaum, 2014; Lee, Middleton, Mirman, Kalénine, & Buxbaum, 2013; Marino, Borghi, Buccino, & Riggio, 2017; Natraj et al., 2013; Natraj, Pella, Borghi, & Wheaton, 2015) and in particular sensitive to object position in space (Costantini, Ambrosini, Scorolli, & Borghi, 2011; Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010; Wamain, Gabrielli, & Coello, 2016; Yang & Beilock, 2011). Structural gesture evocation was assumed to be stronger when objects were presented within reach. In contrast, functional gesture evocation was hypothesized to be less sensitive to space, as functional gestures would be more closely related to object semantics regardless of object location. Thus, the cost associated with conflictual object processing was anticipated only when perceptual judgments were performed on conflictual objects presented in peripersonal space, which was exactly the pattern of results found. Furthermore, the conflict effect modulation as a function of space was observed independently of the type of perceptual judgment (reach-and-grasp judgments and semantic judgments). However, an interaction between task requirement and object type was also observed suggesting that structural and functional gestures were not equally relevant in both perceptual judgment tasks. Indeed, structural gestures appeared more relevant for reach-and-grasp judgments than semantic judgments.

This behavioural study reported for the first time a space-dependent perceptual cost during object visual processing when objects afforded distinct structural and functional gestures. Findings support the existence of strong interrelations between action, perception, and object knowledge, in accordance with grounded and embodied views of cognition (Barsalou, 2008; Coello & Fischer, 2016). In particular, they strongly suggest to extend cognitive and cerebral mechanisms of action activation and selection to the perceptual domain. To this aim, we conducted an EEG experiment in order to identify the neurophysiological correlates of the space-dependent perceptual cost induced by gesture co-evocation, as reported in Kalénine et al. (2016).

Classically, the perception of manipulable objects entails a phenomenon of motor resonance, which is visible in the reactivation of a broad fronto-parietal network typically involved in the execution of object-directed actions, in addition to the recruitment of visual areas devoted to visual processing. Thus, several areas including ventral and dorsal premotor cortices, inferior frontal cortex, posterior parietal and posterior temporal areas have been reported in neuroimaging and patient studies on manipulable object perception (Bartolo et al., 2014; Chao & Martin, 2000; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003; Schubotz, Wurm, Wittmann, & von Cramon, 2014; Watson & Buxbaum, 2015) that could be activated within the first hundred milliseconds of object processing (Proverbio, 2012). However, the mechanisms underlying this phenomenon of motor resonance remain a matter of debate. On the one hand, activity of the motor neural network during object perception could reflect the activation of related motor content. According to this view, the involvement of fronto-parietal regions in object perception would be a marker of affordance evocation (e.g., Grèzes et al., 2003), i.e. the activation of gesture representations associated with the object (e.g. Buxbaum &

Kalenine, 2010; Watson & Buxbaum, 2015). On the other hand, recruitment of fronto-parietal areas during object perception may reflect the exploitation of this motor content, possibly corresponding to action selection processes (Schubotz et al., 2014; Watson & Buxbaum, 2015; Wurm, Cramon, & Schubotz, 2012) and/or technical reasoning (Osiurak & Badets, 2016). Thus, when visual objects activate distinct structural and functional gestures, as during the perception of conflictual objects presented in peripersonal space, the activity of the fronto-parietal motor network should be modulated. This modulation would reflect the evocation of multiple gestures (motor content) or the cost of the competition between them (exploitation of this content).

The specific goal of the present EEG study was to examine the sensitivity of the fronto-parietal motor network to the co-evocation of distinct gestures during object perception. To this aim, we focused on the 8-12 Hz rhythm desynchronization recorded over the central region (referred to as μ rhythm) known to reflect the activation of the motor neural network (Cochin, Barthelemy, Roux, & Martineau, 1999; Muthukumaraswamy & Johnson, 2004; Pfurtscheller & Neuper, 1994). Several studies have evidenced that μ rhythm is sensitive to gestures evoked by manipulable objects during mere object observation (Proverbio et al., 2012; Wamain et al., 2016). In Proverbio et al. (2012), the level of manipulability of the object affected the amplitude of μ desynchonization. In Wamain et al. (2016), manipulable objects induced a stronger μ desynchronization when they were presented in peripersonal space in comparison to extrapersonal space. For these reasons, μ rhythm desynchronization was a good candidate to evaluate the neural correlates of conflict effects in objects perception. Critically, we expected 8-12 Hz rhythm desynchronization to differ between conflictual and non-conflictual objects, but only when objects were presented in peripersonal space. Moreover, the direction of the difference (increase or reduction of the activity of the motor neural network for conflictual objects) may further inform about the mechanisms involved in motor resonance effects.

2. Methods

2.1. Participants

Twenty adults took part in the experiment. Data from five participants with excessive noise in the EEG signal recorded were excluded from the analysis. The fifteen remaining participants (mean age = 22,3; age range 19-33; 11 women) were right-handed (handedness quotients 42-100 %; mean 89,5 %; Oldfield, 1971), and had normal or corrected-to-normal visual acuity. All participants gave written informed consent and were not paid for their participation. The protocol was approved by the Ethical Committee of the University and was in accordance with the declaration of Helsinki.

2.2. Stimuli

The stimuli were the same as the ones used in a previous behavioral experiment (Kalénine et al., 2016). Three-dimensional pictures of 40 unimanual manipulable objects displayed in virtual scenes were generated with MatLab 6.5 (MathWorks, Natiek, MA, USA) and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Based on a pretest, half of the objects were identified as "conflictual" while the other half was "non-conflictual" (see Kalénine et al., 2016 for more details). Non-conflictual objects could only elicit one given hand posture (i.e. the hand posture for the structural gesture and the hand posture for the functional gesture were the same; e.g. paper cup, Figure 1). Conflictual objects could elicit two distinct hand postures (i.e. the hand posture for the structural gesture and the hand posture for the functional gesture were different; e.g. soap dispenser). In addition, half of the objects of the total set could be found in the kitchen. Using the virtual reality system (described below), objects were presented on a wooden table at different distances from the participant depending on their reachable capacity. The extent of the peripersonal space was initially measured for each participant (see section 2.4 below), and objects were displayed at a distance of -50%, -60%, -70% (peripersonal space), -10%, 0%, +10% (boundary of peripersonal space) and +50%, +60%, +70% (extrapersonal space) of individual maximum reachable distance.

2.3. Perception in 3D immersive virtual reality system

A 2 m x 4 m rear projection screen using a 3D stereoscopic projector (Christie Mirage 4K35) coupled with active 3D eyewear (Christie) was used for producing 3D images perception with a 4 K spatial resolution (3840 x 2060 pixels at 120 Hz, Figure 1). For each stimulus, two different pictures of the same scene (with different viewpoint) were computed according to the participant and displayed 8.33 ms to each eye alternatively so that normal fusion would create the illusion of viewing a single object. Eye-floor distance was measured and used to generate realistic 3D images for each participant. The relative size of 3D objects and perspective cues in the visual scene induced an immersive perception of the objects at different distances from the observer. Participants were seated approximately 100 cm from the 2 x 4 m rear projection screen. They wore Active 3D eyewear and a EEG cap. A two pedals device was positioned in front of the screen to collect the participants' responses provided with the feet. They were instructed to respond to different tasks with their feet by clicking on the pedals. After determining the individual boundary of peripersonal space, two different tasks were administrated to the participant in two separate blocks: a Reach-and-grasp judgment task and semantic judgment task. The order of the two tasks was counterbalanced between subjects.

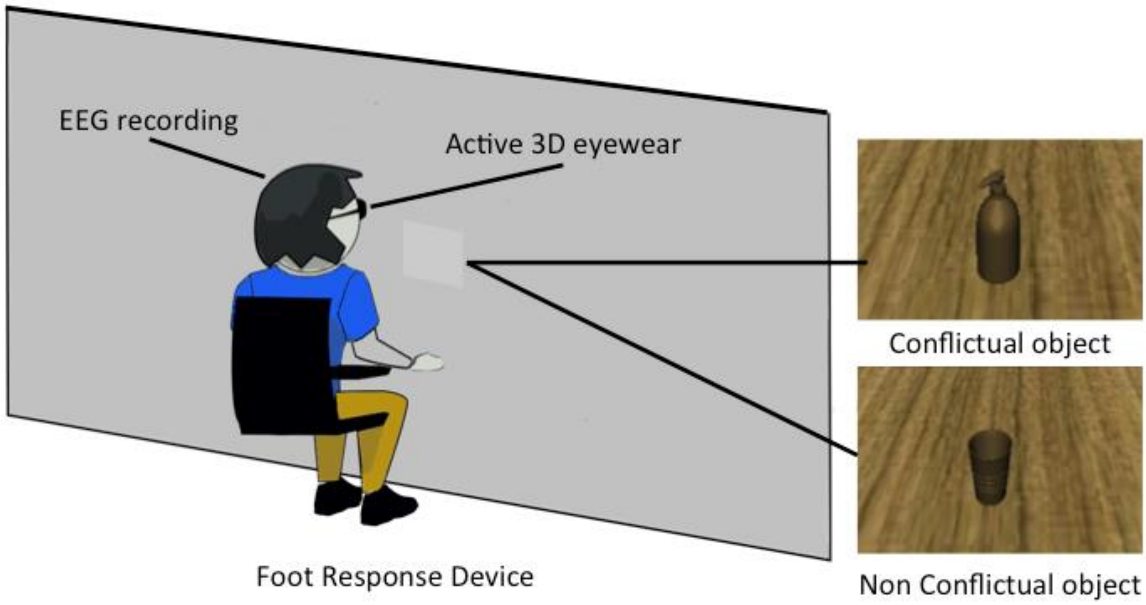

Figure 1: Schematic representation of experimental protocol using immersive virtual reality system for the presentation of conflictual and non-conflictual objects.

2.4. Perceptual tasks

Preliminary evaluation of peripersonal space

Individual peripersonal space was evaluated using a 7 x 7.5 cm cylinder presented in the virtual environment previously described. The cylinder was placed on the wooden table at different distances from the participant. Distances varied randomly between 20 cm and 160 cm by steps of 5 cm. Each of the 29 distances was repeated 4 times (116 trials). At each trial and without moving, participants was requested to judge whether or not the cylinder could be reached and grasped with the right hand. Yes/no responses were given by clicking on the left/right pedals. Mapping between yes/no responses and pedal side was counterbalanced between participants. The stimulus was visible on the screen until the participants' response. The boundary of peripersonal space was determined using a maximum likelihood fit procedure based on second-order derivatives (quasi-newton method). The procedure allows the identification of the logit regression model that best fitted the reachable / unreachable responses of the participants. The nine object distances used in the experimental session were then computed using the individual boundaries previously identified.

Reach-and-grasp and semantic judgment tasks

After ensuring that participants correctly perceived the 3D stimuli and were able to accurately recognize the 40 different objects, instructions for reach-and-grasp and semantic judgment tasks were presented. For the two tasks, all 40 objects were presented during 1000ms at nine distances in the virtual environment (three per space). Inter-stimuli intervals randomly varied between 1500 and 1900 ms. The virtual visual scene remained visible on the screen between the trials. In the reach-and-grasp judgment task, participants judged whether they would be able to grasp the objects stretching their right arm with no movement of the torso. However, participants were instructed to answer only when the object was immediately followed by a question mark (10% of the trials corresponding to additional trials not analyzed). This procedure was used in order to prevent the EEG signal to be contaminated by the actual foot motor response on critical trials, while ensuring that participants performed the task on all trials. In the presence of the question mark, participants had to determine whether the object is reachable by clicking on the left or right pedal of the response device. The same stimulus-response mapping as in the determination of individual space boundary was used. The design was 2 Objects Types (conflictual, non-conflictual) x 9 distances (3 for each space: peripersonal, boundary, extrapersonal) x 20 objects + 36 extra trials with motor response, leading thus to a total of 396 trials in the Reach-and-grasp judgment task. In the semantic judgment task, the exact same procedure was used except that participants were asked to determine whether the presented object was typically found in the kitchen, or not.

2.5. EEG recording and analysis

EEG data were continuously collected from 128-channel Biosemi ActiveTwo (Biosemi B.V., Amsterdam, Netherlands) at a sampling rate of 1024 Hz thanks to ActiView software. Electrode caps covering the whole head with equidistant-layout were used. Electrode offset was kept below 20 mV. The offset values were the voltage difference between each electrode and the CMS-DRL reference. Two additional electrodes were placed at lateral canthi and below the eyes in order to monitor eye movements and blinks. For offline analysis performed with EEGLAB software, the continuous EEG signal was re-referenced based on average reference (Delorme & Makeig, 2004). This procedure was required after using the free reference recording method allowed by the Biosemi system. Signal was filtered (1-100 Hz), using two successive Basic FIR filter: a high pass filter (order: 3381 points, transition band width: 1Hz) followed by a low pass filter (order: 137 points, transition band width: 25Hz). The choice of a relatively restrictive high pass filter of 1 Hz was constrained by the ICA procedure used to correct for blink artifacts (see below). After the filtering procedure, visual inspection of the signal allowed us to remove periods with excessive noise artifacts. Then, ICA-based artifact correction (runICA algorithm) was used in order to correct for blink artifacts (Delorme, Sejnowski, & Makeig, 2007). The signal was then segmented into periods of 4000 ms around the onset of the target object (1000 ms pre-target and 3000 ms post target onset). Epochs still contaminated by muscular contractions or excessive deflection (± 75 µV) were detected and excluded (*total rejection rate was about 5%*). Finally, a Laplacian filter was used in order to increase the spatial and temporal resolution of the signal. This was done following Perrin et al.'s (1997) method, and implemented in custom Matlab code. The order of the spline used was set to 3, and the smoothing constant was set to 10^{-5} (λparameter). Event-related changes in the oscillatory activity were quantified using a time-frequency wavelet decomposition of the continuous EEG signals between 1 and 45 Hz by step of 1 Hz (complex Morlet's wavelets, ratio fo/σf=7) implemented in Matlab toolbox (Fieldtrip software; for a complete description of the method see Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). Following the recommendations of Hobson and Bishop (2016), mean spectral power was computed on the entire time window and transformed with a base 10-logarithm function. This transformation was applied to make electrodes with various maximum power and frequency bands comparable. Then, in order to evaluate power modulation induced by object presentation, the pre-event period (from -500 ms to 0 ms) of each trial was considered as a baseline and was subtracted from each time point for a given frequency and participant for the next 1000 ms of the trial (for more details about the procedure, see Hobson & Bishop, 2016). For each participant, mean spectral power of 8-12 Hz was quantified on each electrode of the centro-parietal site corresponding to channels A1, A2, A3, B1, B2, D15, D16 (see Figure 2, Behmer & Jantzen, 2011; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Perry & Bentin, 2009; Perry, Stein, & Bentin, 2011; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; Pineda, Giromini, Porcelli, Parolin, & Viglione, 2011; Proverbio, 2012; Wamain et al., 2016). An electrode of the posterior site (A23, see Figure 3) was added as a control since activity in the 8-12 Hz frequency band recorded over posterior electrodes would not be related to the activity of the motor neural network. Finally, the change in power in the 8-12 Hz frequency band was averaged across the entire stimulus presentation period (time-window 0-1000 ms).

2.6. Statistical Analysis

We predicted that object structural and functional gestures should be activated differently depending on object position in space. While functional gestures should be activated irrespective of object reachability, structural gestures should be evoked only when objects are presented in peripersonal space. At the behavioral level, differences in response times between conflictual and non-conflictual objects were only visible in peripersonal space (Kalénine et al., 2016). Based on these results, we predicted that the 8-12 Hz desynchronization observed in the central region (μ rhythm) would vary between conflictual and non-conflictual objects when presented in peripersonal space, but not when presented out of reach. If 8-12 Hz desynchronization corresponds to the activation of motor affordances, conflictual objects evoking two distinct gestures should show greater desynchronization than non-conflictual objects evoking only one gesture. Alternatively, if 8-12 Hz desynchronization reflects the exploitation of object affordances, the competition between gestures activated by conflictual objects should entail a reduction of this desynchronization for this type of objects. Moreover, behavioral results also evidenced that task demands influenced the number of possible gestures afforded by the object. While structural gestures were more activated than functional gestures for reach-and-grasp judgments, both gesture types appeared to be equally evoked during semantic judgments (Kalénine et al., 2016). We thus predicted that the difference in 8-12 Hz power change between conflictual and non-conflictual objects should be modulated by the task. Accordingly, we focused our statistical analysis on two interactions of interest: the Space x Object interaction and the Task x Object interaction, after verifying the possible presence of a 3-way interaction between Space, Object, and Task.

In order to model the time course of 8-12 Hz power change over the 1000 ms window of object presentation, we conducted growth curve analyses (GCA) of the event-related desynchronization observed on the 8 different electrodes. GCA is a method of multilevel regression well suited for analysis of time course data (see for example Mirman, 2014). Moreover, as growth models are mixed-effect models, GCA captures both condition-level and individual-level changes in 8-12 Hz desynchronization curves. Concretely, data were decomposed in time bins of 100 ms. Then the effect of time on 8-12 Hz power change was modeled using third order orthogonal polynomials (Level-1 model). Each term of the polynomial captures one aspect of the fixation curve: the intercept term reflects the average height of the curve (i.e. overall effect over the whole time window), the linear term reflects the angle of the curve (i.e. the slope), the quadratic term reflects the central inflexion of the curve, and the cubic term reflects inflexions at the extremities of the curve. Thus, amplitude differences in 8-12 Hz desynchronization would be captured by differences on the intercept whereas timing differences would be captured by differences on the other terms. Then Level-2 models incorporated the effects of interest as fixed-effect factors, namely Task (Reach and grasp, Semantic), Object (Conflictual, Non-Conflictual) and Space (Peripersonal, Boundary of peripersonal, Extrapersonal). In addition, Level-2 models also included random intercepts for subjects. Random slopes were excluded after verifying that they did not capture important additional variance (Bates, Kliegl, Vasishth, & Baayen, 2015). Augmented and reduced models (i.e., with and without the fixed effect of interest) were compared using -2 LogLikelihood Ratio (distributed as X2 with degrees of freedom equal to the number of parameters added). Tests on parameter estimates, which correspond to t-tests assessing the different contrasts of the effect on the different polynomial terms, were performed for significant models. Only effects of interest ($p < .006$, corresponding to $p < .05$ Bonferroni corrected for the 8 separate analyses conducted under the 8 electrodes considered) are presented in the text, but the full results are reported in Table 1. Analyses were conducted using lme4 package version 1.1-12 in R software version 3.3.2, (Bates, Mächler, Bolker, & Walker, 2014).

3. Results

3.1. Preliminary evaluation of peripersonal space

On average, participants perceived the cylinder as reachable when positioned at a maximum distance of 80 cm (SD = 23 cm), which corresponded to an overestimation of about 6% of their actual capacities (mean arm length = 75 cm, SD = 4 cm).

Table 1: Full results of the model comparisons performed on the 8-12 Hz power change computed under the D16, B1, A2 and A23 electrodes. Significant models (Bonferroni corrected) appear in boldface. Those highlighting differences in the amplitude of the 8-12 Hz desynchronization for conflictual and non-conflictual objects between peripersonal and extrapersonal space are marked with an asterisk.

Electrode	**D16**	**B1**	**A2**	**A23**
Task	$X^2(7) = 6.42$, $p = 0.49$	$X^2(7) = 14.70$, $p = 0.05$	$X^2(7) = 32.25$, **$p < 0.001$**	$X^2(7) = 17.72$, $p = 0.01$
Object	$X^2(7) = 4.78$, $p = 0.69$	**$X^2(7) = 24.44$ $p < 0.001$**	$X^2(7) = 11.33$ $p = 0.12$	$X^2(7) = 13.12$, $p = 0.07$
Space	$X^2(11) = 19.99$, $p = 0.045$	**$X^2(11) = 38.20$, $p < 0.001$**	$X^2(11) = 18.02$, $p = 0.08$	**$X^2(11) = 49.33$, $p <0.001$**
Task x Object	$X^2(4) = 2.53$, $p = 0.64$	$X^2(4) = 7.56$, $p = 0.11$	$X^2(4) = 7.96$, $p = 0.09$	**$X^2(4) = 25.71$, $p <0.001$**
Task x Space	$X^2(8) = 20.11$, $p = 0.01$	$X^2(8) = 10.99$, $p = 0.20$	**$X^2(8) = 31.21$, $p < 0.001$**	$X^2(8) = 6.77$, $p = 0.56$
Object x Space	**$X^2(8) = 49.67$, $p < 0.001$***	$X^2(8) = 15.25$, $p = 0.05$	$X^2(8) = 18.09$, $p = 0.02$	**$X^2(8) = 23.20$, $p = 0.003$**
Task x Object x Space	$X^2(8) = 13.39$, $p = 0.10$	**$X^2(8) = 25.65$, $p = 0.002$***	**$X^2(8) = 26.83$, $p < 0.001$**	**$X^2(8) = 23.52$, $p = 0.003$**

3.2. Perceptual processing of conflictual and non-conflictual objects in space

Analyses were performed separately on each electrodes of our region of interest (A1, A2, A3, B1, B2, D15, D16, A23) in order to preserve the spatial resolution provided by the Laplacian filtering. Whereas the 3-way interaction between Object, Space and Task did not reach significance [$X^2(8) = 13.39$, $p = 0.10$], there was a significant interaction between Object and Space [$X^2(8) = 49.67$, $p < 0.001$] on the 8-12Hz power change recorded under the D16 electrode (Figure 2). Compared to non-conflictual objects, conflictual objects elicited less 8-12Hz desynchronization in peripersonal space than extrapersonal space [intercept estimate Conflictual – Non Conflictual for Peripersonal versus Extrapersonal = + 0.031, SD = 0.008, t = 3.85]. The effect of Object was significant in peripersonal space [$X^2(7) = 33.78$, $p < 0.001$] but not in extrapersonal space [$X^2(7) = 3.38$, $p = 0.84$]. Thus, the interaction was due to a reduction of 8-12 Hz desynchronization of 154% for conflictual objects in comparison to non-conflictual objects in peripersonal space [intercept estimate Conflictual – Non Conflictual = +0.031, SD = 0.005, t = 5.42]. The effect was widespread over the whole 1000ms time window, as the difference was visible on the intercept estimate but not on the linear, quadratic or cubic estimates reflecting shape differences in the desynchronization curves for the two types of object. Note that in peripersonal space, the amplitude of 8-12Hz desynchronization under D16 differed from 0 for non-conflictual objects [estimate Non Conflictual - 0 = - 0.020, SD = 0.005, t = -4.29] but not for conflictual objects [estimate Conflictual - 0 = 0.011, SD = 0.005, t = 2.34]. This was not the case in extrapersonal space, where there was no significant 8-12Hz desynchronization for both conflictual objects [estimate Conflictual - 0 = 0.007, SD = 0.005, t = 1.57] and non-conflictual objects [estimate Non Conflictual - 0 = 0.007, SD = 0.005, t = 1.56]. Moreover, the Object x Task interaction [$X^2(4) = 2.53$, $p = 0.64$] was not significant under D16. The full result of the model comparison is reported in Table 1.

In addition, the 3-way interaction between Object x Space x Task reached significance on the 8-12Hz power change recorded under B1 [$X^2(8) = 25.65$, $p = 0.002$], A2 [$X^2(8) = 26.83$, $p < 0.001$], and A23 [$X^2(8) = 23.52$, $p = 0.003$] electrodes. Under B1, this interaction reflected the presence of an Object x Space interaction in the Reach-and-Grasp judgment task [$X^2(8) = 22.94$, $p = 0.003$] but not in the Semantic task [$X^2(8) = 17.02$, $p = 0.030$]. Compared to non-conflictual objects, conflictual objects elicited less 8-12Hz desynchronization in peripersonal space than extrapersonal space during reach-and-grasp judgments [intercept estimate Conflictual – Non Conflictual for Peripersonal versus Extrapersonal = + 0.032, SD = 0.011, t = 2.78; linear, quadratic and cubic estimates non-significant]. During reach-and-grasp judgments, the effect of Object was significant in peripersonal space [$X^2(7) = 23.39$, $p = 0.001$] but not in extrapersonal space [$X^2(7) = 7.11$, $p = 0.413$], although the parameter estimates of the models did not reach significance (intercept, linear, quadratic and cubic estimates non-significant). There was no interaction between Object and Task under B1 [$X^2(4) = 7.56$, $p = 0.109$]. Under A2, the Object x Space interaction was significant for the Semantic judgment task [$X^2(8) = 25.63$, $p = 0.001$], but not for the both Reach-and-grasp [$X^2(8) = 19.36$, $p = 0.013$]. Yet the Object x Space interaction in the Semantic task did not reflect significant differences between object types between peripersonal and extra personal spaces [parameter estimates for Conflictual – Non Conflictual for Peripersonal versus Extrapersonal non-significant on all polynomial terms]. There was no interaction between Object and Task under A2 [$X^2(4) = 7.96$ $p = 0.093$]. Finally, the 3-way interaction under the posterior electrode A23 reflected the presence of an Object x Space interaction in the Semantic judgment task [$X^2(8) = 33.81$, $p < 0.001$] but not in the Reach-and-Grasp task [$X^2(8) = 13.30$, $p = 0.102$]. However, the Object x Space interaction in the Semantic Task was not related to significant differences between object types between peripersonal and extrapersonal spaces [parameter estimates for Conflictual – Non Conflictual for Peripersonal versus Extrapersonal non-significant on all polynomial terms]. The interactions of interest were not observed on other fronto-parietal electrodes D15, B2, A1, and A3.

To summarize, results showed that 8-12 Hz desynchronization under fronto-parietal electrode D16, and to a certain extent under the neighboring electrode B1, was less important for conflictual than non-conflictual objects presented in peripersonal space, as compared to extrapersonal space. For both electrodes, the difference between object types was only visible on the intercept term, indicating that the effect was widespread over the whole 0-1000 ms time window. The difference was observed irrespective of the perceptual task performed on D16 but was restricted to the reach-and-grasp judgments on B1. Other electrodes fronto-parietal electrodes D15, B2, A1, A3 and posterior electrode A23 were not sensitive to the different processing of conflictual and non-conflictual objects between peripersonal and extrapersonal space[1].

[1] Note that the critical interaction between Object and Space was still present, although less pronounced, when 8-12 Hz desynchronization was analyzed over the 7 electrodes of the fronto-parietal region [$X^2(3) = 23.67$, $p = 0.003$; intercept estimate Conflictual – Non Conflictual for Peripersonal versus Extrapersonal = + 0.012, SD = 0.003, t = 3.85]

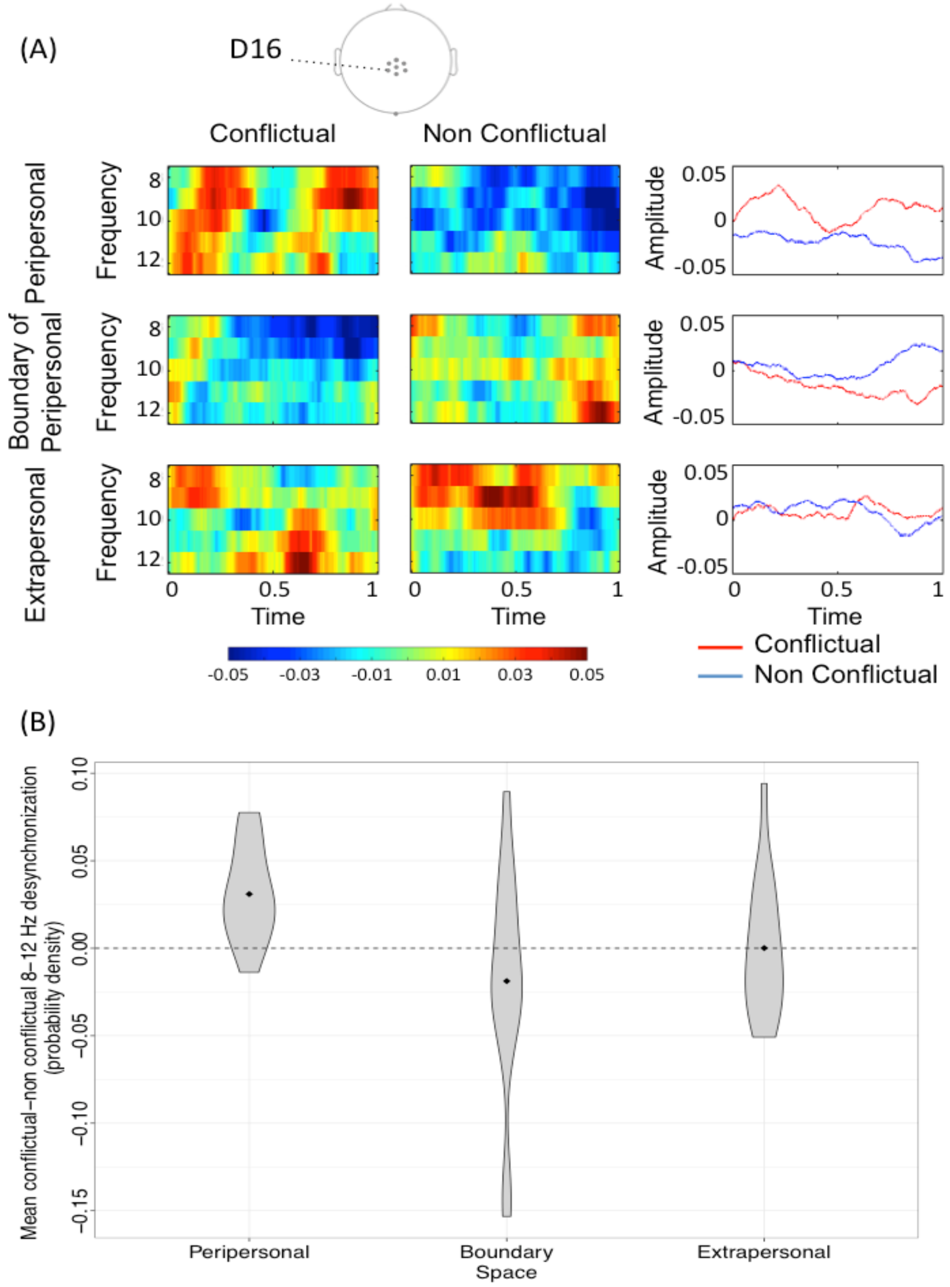

Figure 2: (A) On the left, time frequency representation of 8 Hz-12 Hz power change under the D16 electrode (central region) averaged across participants during the entire time window of object presentation (from 0 to 1000 msec), as a function of Object type (conflictual, non-conflictual) and Space (peripersonal, boundary of peripersonal space, extrapersonal). On the right, mean 8 Hz-12 Hz power change as a function of time for the three positions in space (peripersonal, boundary of peripersonal, extrapersonal) and Object type (conflictual, non-conflictual). The red curve corresponds to conflictual objects and the blue curve corresponds to non-conflictual objects. The y=0 line on the plots corresponds to the power change recorded during the baseline time-window (B) Mean conflict effect (mean of individual differences in 8 Hz-12 Hz power change between conflictual and non-conflictual objects) as a function of Space. Error bars represent 95% confidence intervals. The y = 0 line corresponds to an absence of 8 Hz-12 Hz power change difference between conflictual and non-conflictual objects.

3.3. Perceptual processing of conflictual and non-conflictual objects as a function of task demands

The Object x Task interaction was only significant on the 8-12 Hz change power recorded under the posterior control electrode A23 [$X^2(4) = 24.41$, $p <0.001$]. Reduction of 8-12Hz desynchronization for conflictual objects was more important for semantic judgments than for reach-and-grasp judgments [intercept estimate Conflictual-Non conflictual for Semantic vs. Reach-and-grasp tasks = +0.030, SD = 0.006, t = +4.69; linear, quadratic and cubic estimates non-significant]. As presented on Figure 3, the interaction was characterized by a stronger 8-12 Hz desynchronization for conflictual objects in comparison to non-conflictual objects in the Reach-to-grasp judgment task [estimate = -0.016, SD = 0.004, t = -3.49], while a complete reverse pattern of results was observed in the Semantic task [estimate = +0.014, SD = 0.004, t = 3.15].

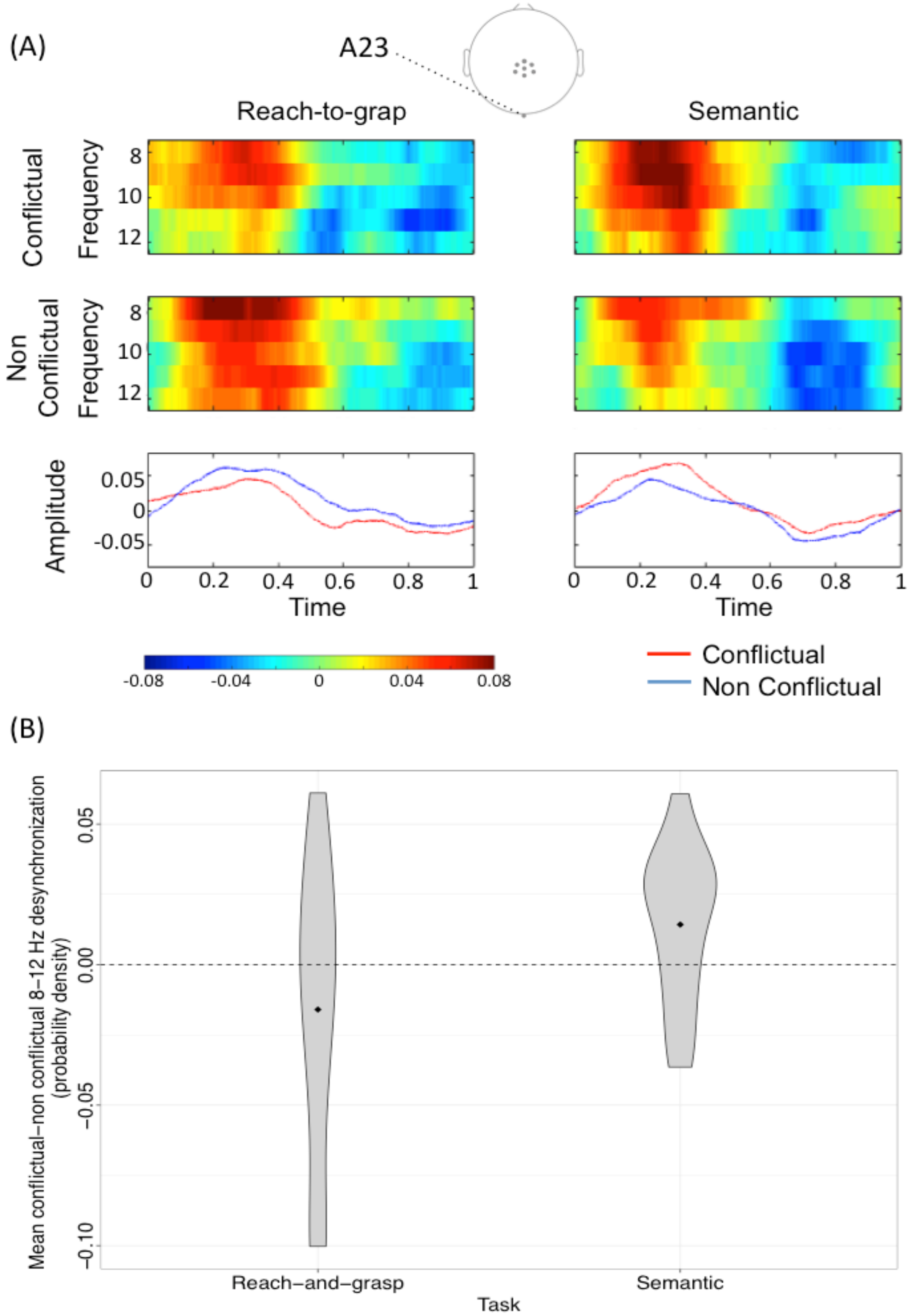

Figure 3: (A) In the upper part, time frequency representation of 8 Hz-12 Hz power change under the A23 electrode (posterior region) averaged across participants during the entire time window of object presentation (from 0 to 1000 msec), as a function of the Object type (conflictual, non-conflictual) and Task (Reach-and-grasp, Semantic). In the lower part, mean 8 Hz-12 Hz power change as a function of time for the two Object types (conflictual, non-conflictual) and the two Tasks (Reach-and-grasp, Semantic). The red curve corresponds to conflictual objects and the blue curve corresponds to non-conflictual objects. The y=0 line on the plots corresponds to the power change recorded during the baseline time-window (B) Mean conflict effect (mean of individual differences in 8 Hz-12 Hz power change between conflictual and non-conflictual objects) as a function of Task. Error bars represent 95% confidence intervals. The y = 0 line corresponds to an absence of difference in 8 Hz-12 Hz power change between conflictual and non-conflictual objects.

4. Discussion

The present study investigated the neurophysiological correlates of conflict between gesture representations during visual perception of manipulable objects using an original paradigm combining immersive virtual environment and EEG. The main result revealed that the 8-12 Hz rhythm desynchronization recorded in the central region, usually observed in the presence of manipulable objects (Proverbio, 2012; Wamain et al., 2016), was extinguished when the observed object afforded simultaneously different structural and functional gesture representations. Additional modulation was also found on the 8-12 Hz frequency band recorded at the posterior site. Furthermore, a stronger 8-12 Hz desynchronization was observed for conflictual than non-conflictual objects during reach-to-grasp judgments, whereas the opposite pattern was observed during semantic judgments. Findings indicate that processing of conflictual and non-conflictual objects depends on both visual (object position in space) and situational (task requirements) context, each contextual influence being mostly visible either in the posterior or in the central brain region considered. Thus, time-frequency analyses of EEG data suggest that at least two independent cognitive mechanisms are at play when distinct gestures are evoked by a visual object: one related to motor resonance that likely reflects action selection processes and the other relying on attentional demands. The two mechanisms are discussed below.

The neural correlates of conflict between gesture representations were identified at the level of the motor neural network, since the interaction between the type of object and its location in space was observed on the 8-12 Hz frequency band in the central region (D16 and B1 electrodes). The interaction was due to a reduction of the 8-12 Hz desynchronization for conflictual objects in comparison to non-conflictual objects that was only present in peripersonal space. In fact, 8-12 Hz desynchronization was extinguished for conflictual objects presented in peripersonal space. Desynchronization of the 8-12 Hz rhythm (ERD) has been associated to the activation of the motor neural network in many studies, with reliable effects when participants actually execute movements (Pfurtscheller & Neuper, 1994), when they observe actions performed by others (Cochin et al., 1999; Muthukumaraswamy & Johnson, 2004) or when they visually process manipulable objects (Proverbio et al., 2012; Wamain et al., 2016). Accordingly, the presentation of conflictual objects in peripersonal space showed no activation of the motor neural network whereas that of non-conflictual objects did. The effect observed on the 8-12 Hz desynchronization at the central site exactly mirrored the interaction between object type and space observed on response times, with a selective difference between conflictual and non-conflictual objects in peripersonal space (Kalénine et al. 2016). As detailed in Kalénine et al. (2016), physical differences between the two categories of object stimuli (e.g., object screen size) or subtypes of structural and functional grasps (pinch, clench, poke, palm, trigger) cannot be responsible of the modulation of the difference between object types as a function of space. Thus, we are fairly confident that the 8-12 Hz power change between conflictual and non-conflictual objects relates to the gestures associated with them. Interestingly, the absence of behavioral cost in extrapersonal space could be explained in two ways. One possibility is that object functional gestures were activated in the absence of structural gesture evocation. Another interpretation is that neither functional nor structural gestures were activated in extrapersonal space. Both scenarios are consistent with the disappearance of affordance competition in extrapersonal space. The present EEG results shed light on the behavioral data and favor the second interpretation. The absolute amplitude of the 8-12Hz desynchronization was actually not different from zero when objects were presented out of reach, suggesting that motor resonance, regardless of gesture type, was rather absent in extrapersonal space in the present study.

Interestingly, we also observed that the difference in 8-12 Hz power change between conflictual and non-conflictual objects in peripersonal space was modulated by the task demands under B1 electrode. In particular, the selective reduction of 8-12 Hz desynchronization for conflictual objects presented in peripersonal space was only present during reach-and-grasp judgments. This hint of task demand effect on the competition between affordances in peripersonal space is compatible with growing evidence indicating that affordance evocation is dependent on task demands (Griffiths & Tipper, 2009, 2012; Wamain et al., 2016; Yoon, Humphreys, & Riddoch, 2010). For example, the benefit of correctly positioning two objects for action is observed when participants perform action decisions on the objects (can they be used together?) but not when they perform semantic decisions similar to the semantic judgments proposed in our study (can they be found in the kitchen?, see Yoon et al., 2010). Modulation of motor resonance by task was visible on B1 but not on other central electrodes. The generalization of the effect over the different central sites remains to be better understood.

The pattern of results described above was observed on two electrodes (D16 and B1) of our a priori region of interest, which included 7 central electrodes based on previous studies (for instance, Proverbio, 2012; Wamain et al., 2016). The reason of the spatial selectivity of the effect partly remains unclear and probably relates to the specificities of EEG analyses, in particular the use of a Laplacian filter in the present study. The main advantage of the Laplacian filter method is to largely increase the spatial resolution of the signal by greatly reducing the effect of current diffusion (Burle et al., 2015). This may explain why the source of our effect is more circumscribed, although further research would be needed to determine the exact anatomical structures involved within the broad motor neural network. Importantly, no similar results were observed in the posterior region (A23 occipital electrode). The use of the Laplacian filter, in addition to the observation of a different pattern of results in the central and posterior regions of interest, indicates that 8-12Hz desynchronization was not the result of a simple diffusion phenomenon from occipital to central sites (Hobson & Bishop, 2016). Modulation of the activity in such frequency band at central sites is thus assumed to mainly reflect the activation of the motor neural network, as previously reported (Hobson & Bishop, 2016; Proverbio, 2012; Wamain et al., 2016). In contrast, changes in the same frequency band at posterior sites have been associated to α rhythm, which is used as an index of attentional processes (Snyder & Foxe, 2010) and should not be related to the activity of the motor system (Moore, Gale, Morris, & Forrester, 2008).

The analysis made on α rhythm (8-12 Hz) under the posterior electrode (A23) showed a unique pattern of results characterized by an interaction between object type and task. Previous studies on the α rhythm have shown that activity in the 8-12 Hz frequency band could be used as an index of attentional bias and could predict behavioral performance in several attentional tasks. Thus, the ability to correctly discriminate (Hanslmayr et al., 2007) or detect (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009) visual stimuli was found to be inversely proportional to the amplitude of the α band activity, suggesting that attentional processing was greater when α band amplitude was reduced (Snyder & Foxe, 2010). Our results on α rhythm indicated a stronger desynchronization for conflictual than non-conflictual objects during the Reach-to-grasp judgment task as compared to the Semantic judgment task. Here again, the neurophysiological data are in line with behavioral results, which showed a weaker disadvantage of conflictual objects in the reach-and-grasp judgment task than in the semantic task on reaction times (Kalénine et al., 2016). Thus, it seems that conflictual objects benefited from greater attentional resources when the task was directly relevant for action. It is possible that judging whether an object is reachable and graspable or not orients the attention towards object motor properties, which would particularly help processing the objects associated with multiple gesture representations. Although the present data do not allow determining to what extent attentional and motor resonance effects may influence one another, the different result patterns on α and μ rhythms shows that motor resonance effects are at least partially independent from attentional effects. Attentional effects were highly sensitive to task demands whereas motor resonance effects were mostly sensitive to object position in space. The influence of task demands on motor resonance effects in the present EEG study was relatively limited, and possibly related to a lack of sensitivity of our complex protocol. Task demands did not affect the conflict cost as a function of space in the previous behavioral study. Further research would be necessary to better understand the role of the type of judgment performed on objects processing, considering thus the relevance of the task for action on a larger scale

In summary, the analysis on µ rhythm demonstrates that the motor neural network is less activated when several different gestures are evoked by a single object (conflictual objects in peripersonal space). This result is difficult to reconcile with the idea that the activity of the motor neural network reflects the mere activation of object motor properties from the visual object. If that was the case, following an "additive model" of affordance evocation, conflictual objects associated with two different gestures should have entailed increased activation of the motor neural network when presented in peripersonal space. The co-evocation of distinct functional and structural gestures should have indeed resulted in stronger µ rhythm desynchronization in this particular condition. By contrast, a reduction of µ rhythm desynchronization was observed with conflictual objects. This new finding does not directly challenge representational views of motor resonance phenomena (Buxbaum & Kalénine, 2010). It does not rule out the claim that the activity of the motor neural network when processing visual objects can reflect the activation of object motor properties (Proverbio et al., 2012; Wamain et al., 2016). However, the present finding demonstrates for the first time that i) neural motor resonance is modulated by the context-dependent competition between gesture representations, and ii) µ rhythm desynchronization is a marker of the competition between affordances.

Findings support recent refinements about the role of the motor neural network in action planning and action recognition (Bub & Masson, 2012; Schubotz et al., 2014; Watson & Buxbaum, 2015). Our results provide novel neurophysiological evidence to this view. Modulation of µ rhythm is not only an index of gesture evocation but also an interesting correlate of conflict resolution between affordances. The relationship between changes in µ rhythm desynchronization and action selection processes has recently been illustrated during the perception of actions (Panasiti, Pavone, & Aglioti, 2016). When watching videos of pianists that may contain finger errors, the ability of participants to correctly identify errors in the action sequence was negatively correlated with µ rhythm desynchronization. This result suggests that the more participants were able to activate the correct representation of the gesture sequence, the greater their desynchronization. The present study reveals a similar mapping between μ desynchronization and action selection processes during the perception of manipulable objects.

In conclusion, the present study showed that competition between gesture representations during visual object perception is visible at the neurophysiological level in the modulation of brain activity in the 8-12 Hz frequency band recorded at central and posterior sites. Conflict between objet affordances impacts attentional and motor resonance processes reflected by the modulation of posterior α and central μ rhythms, respectively. Importantly, attentional effects greatly varied as a function of the task demand whereas motor resonance effects depended chiefly on object position in space. Critically, our data reveal that the modulation of μ rhythm desynchronization is not only an index of affordance activation but also a reliable marker of action selection processes during object perception. However, future research would be needed to determine the exact commonalities in action selection mechanisms across action planning, action understanding and object perception.

5. Acknowledgements

This work was funded by the French National Research Agency (ANR-11-EQPX-0023 and ANR-16-CE28-0003) and supported by European funds through the program FEDER SCV-IrDIVE. The authors thank Jean-Luc Bruyelle for his contribution to the programing of the experiment in the virtual reality system.

6. References

Barsalou, L. W. (2008). Grounded Cognition. *Annual Review of Psychology*, *59*(1), 617–645.

Bartolo, A., Coello, Y., Edwards, M. G., Delepoulle, S., Endo, S., & Wing, A. M. (2014). Contribution of the motor system to the perception of reachable space: an fMRI study. *The European Journal of Neuroscience*, *40*(12), 3807–17.

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. *ArXiv E-Print, under Revision*, 1–27.

Bates, D., Mächler, M., Bolker, B., & Walker. (2014). Fitting Linear Mixed-Effects Models using lme4. *Cran Vignette*, 1–51.

Behmer, L. P., & Jantzen, K. J. (2011). Reading sheet music facilitates sensorimotor mu-desynchronization in musicians. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *122*(7), 1342–7.

Borghi, A. M. (2004). Object concepts and action: Extracting affordances from objects parts. *Acta Psychologica*.

Borghi, A. M., Flumini, A., Natraj, N., & Wheaton, L. A. (2012). One hand, two objects: Emergence of affordance in contexts. *Brain and Cognition*, *80*(1), 64–73.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–6.

Bub, D. N., & Masson, M. E. J. (2012). On the dynamics of action representations evoked by names of manipulable objects. *Journal of Experimental Psychology: General*, *141*(3), 502–517.

Bub, D. N., Masson, M. E. J., & Cree, G. S. (2008). Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition*, *106*(1), 27–58.

Burle, B., Spieser, L., Roger, C., Casini, L., Hasbroucq, T., & Vidal, F. (2015). Spatial and temporal resolutions of EEG: Is it really black and white? A scalp current density view. *International Journal of Psychophysiology, 97*(3), 210–220.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, *12*(4), 478–84.

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1585–1599.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*, *11*(5), 1839–1842.

Coello, Y., & Fischer, M. H. (2016). *Foundations of embodied cognition, Perceptual and Emotional Embodiment (Vol.1)* (Hove: Psyc).

Costantini, M., Ambrosini, E., Scorolli, C., & Borghi, A. M. (2011). When objects are close to me : affordances in the peripersonal space Acknowledgments. *Psychonomic Bulletin & Review*, *18*(2), 302–308.

Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., & Committeri, G. (2010). Where does an object trigger an action? An investigation about affordances in space. *Experimental Brain Research*, *207*(1–2), 95–103.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21.

Delorme, A., Sejnowski, T., & Makeig, S. (2007). Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis. *NeuroImage*, *34*(4), 1443–1449.

Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: An fMRI study of implicit processing. *European Journal of Neuroscience*, *17*(12), 2735–2740.

Griffiths, D., & Tipper, S. P. (2009). Priming of reach trajectory when observing actions: Hand-centred effects. *Quarterly Journal of Experimental Psychology*, *62*(12), 2450–2470.

Griffiths, D., & Tipper, S. P. (2012). When far becomes near: Shared environments activate action simulation. *Quarterly Journal of Experimental Psychology*, *65*(7), 1241–1249.

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K. H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473.

Hobson, H. M., & Bishop, D. V. M. (2016). Mu suppression – A good measure of the human mirror neuron system? *Cortex*, *82*, 290–310.

Jax, S. A., & Buxbaum, L. J. (2010). Response interference between functional and structural actions linked to the same familiar object. *Cognition*, *115*(2), 350–5.

Jax, S. A., & Buxbaum, L. J. (2013). Response interference between functional and structural object-related actions is increased in patients with ideomotor apraxia. *Journal of Neuropsychology*, *7*(1), 12–18.

Kalénine, S., Shapiro, A. D., Flumini, A., Borghi, A. M., & Buxbaum, L. J. (2014). Visual context modulates potentiation of grasp types during semantic object categorization. *Psychonomic Bulletin & Review*, *21*(3), 645–51.

Lee, C., Middleton, E., Mirman, D., & Buxbaum, L. J. (2013). Incidental and Context-Responsive Activation of Structure- and Function-Based Action Features During Object Identification. *Journal of Experimental Psychology. Human Perception and Performance*, *39*(1), 257–270.

Lee, C., Middleton, E., Mirman, D., Kalénine, S., & Buxbaum, L. J. (2013). Incidental and context-responsive activation of structure- and function-based action features during object identification. *Journal of Experimental Psychology. Human Perception and Performance*, *39*(1), 257–70.

Marino, B. F., Borghi, A. M., Buccino, G., & Riggio, L. (2017). Chained activation of the motor system during language understanding. *Frontiers in Psychology*, *8*(FEB).

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To See or Not to See: Prestimulus   Phase Predicts Visual Awareness. *Journal of Neuroscience*, *29*(9), 2725–2732.

Mirman, D. (2014). *Growth Curve Analysis and Visualization using R* (Chapman an). CRC.

Moore, R. A., Gale, A., Morris, P. H., & Forrester, D. (2008). Alpha power and coherence primarily reflect neural activity related to stages of motor response during a continuous monitoring task. *International Journal of Psychophysiology*, *69*(2), 79–89.

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *115*(8), 1760–6.

Natraj, N., Pella, Y. M., Borghi, A. M., & Wheaton, L. A. (2015). The visual encoding of tool-object affordances. *Neuroscience*, *310*, 512–527.

Natraj, N., Poole, V., Mizelle, J. C., Flumini, A., Borghi, A. M., & Wheaton, L. A. (2013). Context and hand posture modulate the neural dynamics of tool-object perception. *Neuropsychologia*, *51*(3), 506–519.

Nyström, P., Ljunghammar, T., Rosander, K., & von Hofsten, C. (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Developmental Science*, *14*(2), 327–335.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological Review*, *123*(5), 534–568.

Panasiti, M. S., Pavone, E. F., & Aglioti, S. M. (2016). Electrocortical signatures of detecting errors in the actions of others: An EEG study in pianists, non-pianist musicians and musically naïve people. *Neuroscience*, *318*, 104–113.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*(4), 437–42.

Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: A comparison between EEG desynchronization in the μ-range and previous fMRI results. *Brain Research*, *1282*, 126–132.

Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction-Evidence from mu and alpha EEG suppression. *NeuroImage*, *58*(3), 895–904.

Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*(1), 153–9.

Pfurtscheller, G., & Neuper, C. (1994). Event-related synchronization of mu rhythm in the EEG over the cortical hand area in man. *Neuroscience Letters*, *174*(1), 93–96.

Pineda, J. A., Giromini, L., Porcelli, P., Parolin, L., & Viglione, D. J. (2011). Mu suppression and human movement responses to the Rorschach test. *Neuroreport*, *22*(5), 223–6.

Proverbio, A. M. (2012). Tool perception suppresses 10-12Hz μ rhythm of EEG over the somatosensory area. *Biological Psychology*, *91*(1), 1–7.

Schubotz, R. I., Wurm, M. F., Wittmann, M. K., & von Cramon, D. Y. (2014). Objects tell us what action we can expect: Dissociating brain areas for retrieval and exploitation of action knowledge during action observation in fMRI. *Frontiers in Psychology*, *5*(JUN).

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory Attentional Suppression of Visual Features Indexed by Oscillatory Alpha-Band Power Increases:A High-Density Electrical Mapping Study. *Journal of Neuroscience*, *30*(11), 4024–4032.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus Specificity of Phase-Locked and Non-Phase-Locked 40 Hz Visual Responses in Human. *J. Neurosci.*, *16*(13), 4240–4249.

Wamain, Y., Gabrielli, F., & Coello, Y. (2016). EEG μ rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex*, *74*, 20–30.

Watson, C. E., & Buxbaum, L. J. (2015). A distributed network critical for selecting among tool-directed actions. *Cortex*, *65*, 65–82.

Wurm, M. F., Cramon, D. Y., & Schubotz, R. I. (2012). The Context–Object–Manipulation Triad: Cross Talk during Action Perception Revealed by fMRI. *Journal of Cognitive Neuroscience*, *24*(7), 1548–1559.

Yang, S.-J., & Beilock, S. L. (2011). Seeing and doing: Ability to act moderates orientation effects in object perception. *The Quarterly Journal of Experimental Psychology*, *64*(4), 639–648.

Yoon, E. Y., Humphreys, G. W., & Riddoch, M. J. (2010). The paired-object affordance effect. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(4), 812–824.