



HAL
open science

Congruent action context releases Mu rhythm desynchronization when visual objects activate competing action representations

Yannick Wamain, Marc Godard, Anne-Sophie Puffet, Samuel Delepouille,
Solene Kalenine

► **To cite this version:**

Yannick Wamain, Marc Godard, Anne-Sophie Puffet, Samuel Delepouille, Solene Kalenine. Congruent action context releases Mu rhythm desynchronization when visual objects activate competing action representations. *Cortex*, 2023, *Cortex*, 161, pp.65-76. 10.1016/j.cortex.2023.01.009 . hal-04012419

HAL Id: hal-04012419

<https://hal.univ-lille.fr/hal-04012419>

Submitted on 2 Mar 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title: Congruent action context releases Mu rhythm desynchronization when visual objects activate competing action representations

Yannick Wamain^{1*}, Marc Godard¹, Anne-Sophie Puffet¹, Samuel Delepoulle², Solène Kalénine¹

¹ Univ. Lille, CNRS, UMR 9193 - SCALab - Sciences Cognitives et Sciences Affectives, F-59000 Lille, France

² Univ. Littoral Côte d'Opale, EA 4491 – LISIC – Informatique Signal et Image de la Côte d'Opale, F – 62228, France

***Corresponding author:**

Dr. Yannick Wamain

Cognitive and Affective Sciences Laboratory,

University of Lille - SHS

BP 60149

59653 Villeneuve d'Ascq, France.

Tel:+33 320 416 989

Fax:+33 320 416 036

Email: yannick.wamain@univ-lille.fr

Congruent action context releases Mu rhythm desynchronization when visual objects activate competing action representations

Abstract:

Recent findings demonstrated that object perception is affected by the competition between action representations. Simultaneous activation of distinct structural (“grasp-to-move”) and functional (“grasp-to-use”) action representations slows down perceptual judgements on objects. At the brain level, competition reduces motor resonance effects during manipulable object perception, reflected by an extinction of μ rhythm desynchronization. However, how this competition is solved in the absence of object-directed action remains unclear. The present study investigates the role of context in the resolution of the competition between conflicting action representations during mere object perception. To this aim, thirty-eight volunteers were instructed to perform a reachability judgment task on 3D objects presented at different distances in a virtual environment. Objects were conflictual objects associated with distinct structural and functional action representations. Verbs were used to provide a neutral or congruent action context prior or after object presentation. Neurophysiological correlates of the competition between action representation were recorded using EEG. The main result showed a release of μ rhythm desynchronization when reachable conflictual objects were presented with a congruent action context. Context influenced μ rhythm desynchronization when the action context was provided prior or after object presentation in a time-window compatible with object-context integration (around 1000 ms after the presentation of the first stimulus). These findings revealed that action context biases competition between co-activated action representations during mere object perception and demonstrated that μ rhythm desynchronization may be an index of activation but also competition between action representations in perception.

Keywords: 3D visual perception, manipulable objects, μ rhythm, action selection, verbal context.

1. Introduction

While traditional approaches of cognition postulate that perceptual processes are a prerequisite to act adequately on the environment, the embodied cognition framework proposes a non-serial view of cognitive processes and postulates interrelations between perception, action and knowledge representations (Barsalou, 2008). In this framework, the perception and identification of manipulable objects are closely bound to the activation of distributed neural representations involved in our direct interactions with them. Several lines of evidence support the involvement of action representations during manipulable object perceptual and conceptual processing. At the behavioral level, stimulus-response compatibility effects are observed with faster response times when participants categorize large or small visual objects as natural or manufactured with a response grip that is compatible with object size (Tucker & Ellis, 2001). Similarly, action priming effects have been reported with faster categorization when visual objects are preceded by a picture of hand in a congruent grasping posture (Borghetti et al., 2007; Godard, Wamain, & Kalénine, 2019). At the brain level, a stronger activation of the motor neural network has been highlighted during the perception of highly manipulable manufactured objects like tools in comparison to poorly manipulable objects (Chao & Martin, 2000; Gerlach, Law, & Paulson, 2002) suggesting that images of manipulable objects activate neural action representations. However, the content and conditions of activation of action representations during visual object processing has been largely debated (e.g. Kalénine & Buxbaum, 2015; Mahon & Caramazza, 2008; Masson, 2015).

There are multiple ways to interact with an object, suggesting that more than one action representation could be activated from a single visual object. For instance, one may grasp a calculator positioned on a desktop in a specific way if the goal is to store it in the drawer below. This gesture is different from the poke gesture that would be required to use the calculator to compute a multiplication (Kalénine, Shapiro, & Buxbaum, 2013). Structural (grasp) and functional (use) gestures may correspond to different action representations that rely on neuroanatomically and functionally distinct action systems (Buxbaum & Kalénine, 2010; Glover, 2004; Johnson-Frey, 2004; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Rizzolatti & Matelli, 2003; Vingerhoets, Acke, Vandemaele, & Achten, 2009). Currently, how these different action representations participate in the perception of manipulable objects remains unclear. Only a few studies have directly investigated the impact of the co-activation of distinct action representations on the processing of a single object (Bub, Masson, & van Mook, 2018;

Godard, Wamain, Ott, Delepouille, & Kalénine, 2022; Jax & Buxbaum, 2010, 2013; Kalénine, Wamain, Decroix, & Coello, 2016; Wamain, Sahaï, Decroix, Coello, & Kalénine, 2018). These studies highlighted a selective action production cost (Bub et al., 2018; Jax & Buxbaum, 2010, 2013) and selective perceptual cost (Kalénine et al., 2016; Wamain et al., 2018) for visual objects activating distinct action representations (i.e., conflictual objects). At the behavioral level, Kalénine et al. (2016) demonstrated that the activation of multiple action representations induces a processing cost during object perception that depends on the possibilities of the observer to interact with the perceived objects. They instructed participants to make judgements about perceptual characteristics of conflictual and non-conflictual objects (e.g., “is it reachable?”, “is it a kitchen object?”) presented at different distances in a 3D virtual environment. Longer response times were observed for conflictual objects compared to non-conflictual objects, but this effect was only evidenced when objects were presented in the peripersonal space of the participants. At the neurophysiological level, the typical Mu (μ) rhythm desynchronization associated with manipulable object perception (Proverbio, 2012; Wamain et al., 2016; Marini et al. 2019; Fairchild et al., 2021) was reduced – and even suppressed – when conflictual objects were presented within reach (Wamain et al., 2018). Together, these studies suggest that when activated, distinct structural and functional action representations associated with a single object compete with one another. This competition is detrimental to object perceptual processing and visible at the behavioral and neurophysiological levels. Wamain et al. (2018) suggested that μ rhythm desynchronization, in addition to its classical interpretation as a brain indicator of motor resonance during object perceptual processing (i.e. *activation* of action representations), may also reflect action selection processes at the neural level during object perception (i.e. *competition* between action representations). The present study further aims to evaluate whether μ rhythm desynchronization may be dynamically modulated by the degree of competition between structural and functional affordances during the perception of conflictual objects. The desynchronization of μ rhythm could therefore be used as a sensitive marker of (active) selection of action representations rather than a (passive and) unspecific motor resonance correlate.

Action representations have been shown to be activated in a context-dependent manner (Ambrosini, Scorolli, Borghi, & Costantini, 2012; Borghi, Flumini, Natraj, & Wheaton, 2012; Costantini, Ambrosini, Scorolli, & Borghi, 2011; Kalénine, Shapiro, Flumini, Borghi, & Buxbaum, 2014; Lee, Middleton, & Mirman, 2012; Matheson, Garcea, & Buxbaum, 2021; Wokke, Knot, Fouad, & Richard Ridderinkhof, 2016). For instance, Costantini et al. (2011)

demonstrated that when visual objects are perceived within reach, they activate both structural and functional action representations (Ambrosini et al., 2012; Costantini et al., 2011). Object-verb sequences were presented to their participants. Verbs could correspond to object manipulation (e.g., brush – to hold), object function (e.g., brush – to comb) or were observation verbs (e.g., brush – to gaze). Participants were asked to judge the appropriateness of the verb according to the preceding object. Response times were shorter when visual objects were presented in peripersonal space compared to extrapersonal space for both function and manipulation verbs, but there was no difference for observation verbs. Findings highlight the important role of context in the *activation* of structural and functional action representations. Yet this study does not address the role of context in the *competition* between structural and functional action representations. According to neurobiological models of action selection (Cisek, 2007; Cisek & Kalaska, 2010; Thill, Caligiore, Borghi, Ziemke, & Baldassarre, 2013), contextual information processed by the ventral stream is sent to the prefrontal cortex, which provides biasing signals to motor brain regions in order to select the appropriate action. Such models predict that when objects activate distinct structural and functional action representations (“conflictual” objects), contextual information may bias toward one of the two action representations and reduce the competition between them, but the neural correlates of this phenomenon have not been explored yet. The present study aims at evaluating whether a congruent action context influences the *competition* between action representations from visual objects at the neurophysiological level. As prior work demonstrated that the competition between action representations during perceptual processing of reachable objects has a negative impact on μ rhythm desynchronization (Wamain et al., 2018), reduced competition would therefore translate in a release of μ rhythm desynchronization. We further aim to investigate the temporal dynamics of context influence on the selection of action representations during object perception, by evaluating the influence of context prior and during object perception.

2. Methodology

2.1. Participants

The sample size was determined on the basis of previous studies (Wamain et al., 2016; Wamain et al., 2018). In these studies, 20 participants were sufficient to highlight modulations of μ rhythm desynchronization depending on the conditions of object presentation. Thirty-eight volunteers took part in the experiment (mean age = 21.75 years; SD = 3.79; 24 females).

Participants were all right-handed, assessed by handedness inventory (Oldfield, 1971). They all reported normal or corrected-to-normal visual acuity. They reported no history of psychological or neuropsychological disorders. They provided written informed consent and were paid 20 € for their participation. The protocol was approved by the Ethical Committee of the University of Lille (2019-385-S77) and was in accordance with the declaration of Helsinki (1964, revised in 2013). Due to technical reasons, two participants were discarded from further analyses. One additional participant was excluded due to misunderstanding of experimental instructions. Further analyses have thus been conducted on data from 35 participants.

2.2. Stimuli

2.2.1. Objects

Three-dimensional (3D) images of 20 common manipulable objects were created with Blender software and generated with a photorealistic rendering method. Objects were selected from an object set of “conflictual” objects used in a previous experiment (Godard et al., 2022, see complete list in Supplementary Material). Objects were considered as conflictual when they involved distinct hand postures for move and use actions (e.g., calculator). Object conflictuality was verified in an independent sample of participants who were asked to demonstrate the hand postures they would use to grasp-to move or use each object. In the present experiment, the conflictual objects were presented on a wooden table at different distances from the participant, along the vertical medial axis. Nine distances were sampled. The nine distances were separated in near (-70%, -60% and -50%), limit (-10%, mean arm length, +10%) and far (+50%, +60% and +70%) spaces. This procedure ensured that regardless of the individual perceived reachability boundary - computed offline (see Result section) - most participants would see objects both within reach and out of reach. Images were generated prior to the experiment by taking into account the distance to the screen (100 cm) and the mean reachability boundary of adults (81 cm) from a previous investigation (Kalénine et al., 2016).

2.2.2. Verbs

Two verbs were selected for each of the 20 conflictual objects: one action verb and one neutral verb. Action verbs were congruent with the typical gesture associated with the functional use of the object and neutral verbs were observation verbs (see table 1, for example). Verbs were presented in the imperative form, as it has been shown that verbal forms that induce an action in the moment cause the most motor activation (Aravena et al., 2014), such as when verbs are presented in affirmative (Aravena et al., 2012) or imperative (Tomasino, Weiss, & Fink, 2010) forms.

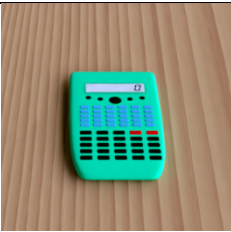

Objects	Action verb	Neutral verb
 Calculator	Compter (to count)	Regarder (to look at)
 Perfume	Vaporiser (to spray)	Observer (to observe)

Table 1. Examples of action and neutral French verbs and their English translation for two conflictual objects (see the full-list of object-verb associations in Supplementary Material).

Pretest and control of the verbal stimuli

Twelve additional right-handed young adult participants who did not participate in the main experiment were recruited to select the appropriate verbs for each object. They fulfilled a questionnaire assessing the typical use of objects. Different possible verbs (3 action verbs and 3 neutral verbs) were preselected for each object. For each object-verb association, participants had to respond to the following question: “To what extent this verb describes the typical use of the object?” by rating on a 7-point Likert scale (from 1: strongly disagree, to 7: strongly agree).

Then, one action verb and one neutral verb were chosen for each object by taking into account (1) the ratings on the survey and (2) control variables typically considered when manipulating verbal stimuli. For the ratings on the survey, we aimed to have a median rating as low as possible for neutral verbs (close to 1, strongly disagree). The action and neutral verbs differed on their degree of association with object use. Neutral verbs were weakly associated with object use (median = 1 [range = 1 – 2.5]) while action verbs were highly associated with object use (median = 6.5 [range = 4 – 7]). In addition, neutral verbs were selected so that they were paired with action verbs on frequency, letter numbers and syllable numbers overall.

2.3. Perception in 3D immersive virtual reality system

The virtual scene was presented in 3D to the participants (Figure 1a) via a 2×4m rear projection screen using a 3D stereoscopic projector (Christie Mirage 4K35) generating images at 120 Hz with a 4K spatial resolution (3840 x 2060 pixels). Participants were seated approximately 100 cm from the screen wearing the Active 3D eyewear and an EEG cap. Images of a virtual scene composed of a wooden table in a neutral room were displayed with MatLab 6.5 (MathWorks, Natick, MA, USA) and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Two different images of each stimulus were computed and presented 8.33 ms alternatively to each eye. Normal fusion created the illusion of viewing a single object. Relative size and perspective cues as well as binocular disparity were used to induce a 3D perception of the visual scene and objects.

2.4. Procedure

Before starting the experimental session, the 20 selected objects were presented in 2D and named one by one to the participant in order to make sure that each participant correctly identified the different objects. Participants were positioned so that their eyes were positioned

at 120 cm from the floor. A device with two pedals was positioned under participants' feet in order to collect the responses.

The typical trial sequence is presented in Figure 1b. Each trial started with the presentation of a blurred version of the visual scene with the wood table. Then, the verb context and the object were presented in two possible orders. On half of the trials (360 context-object trials), the verb was presented for 200 ms, followed by the empty visual scene for 300 ms, and finally by the object positioned on the table at one of the nine possible distances during 500 ms. On the other half of the trials (360 object-context trials), the object was positioned on the table at one of the nine possible distances during 500 ms, followed by a verb for 200 ms and finally the empty visual scene for 300 ms. Verbs were presented horizontally to be read as fast as possible (Byrne, 2002). Verbs were superimposed to a blurred pictured of the virtual scene, in central vision (less than 10° visual angle) at 120 cm from the floor (in front of participants' eyes) in order to reduce signal contamination by saccadic eye-movements.

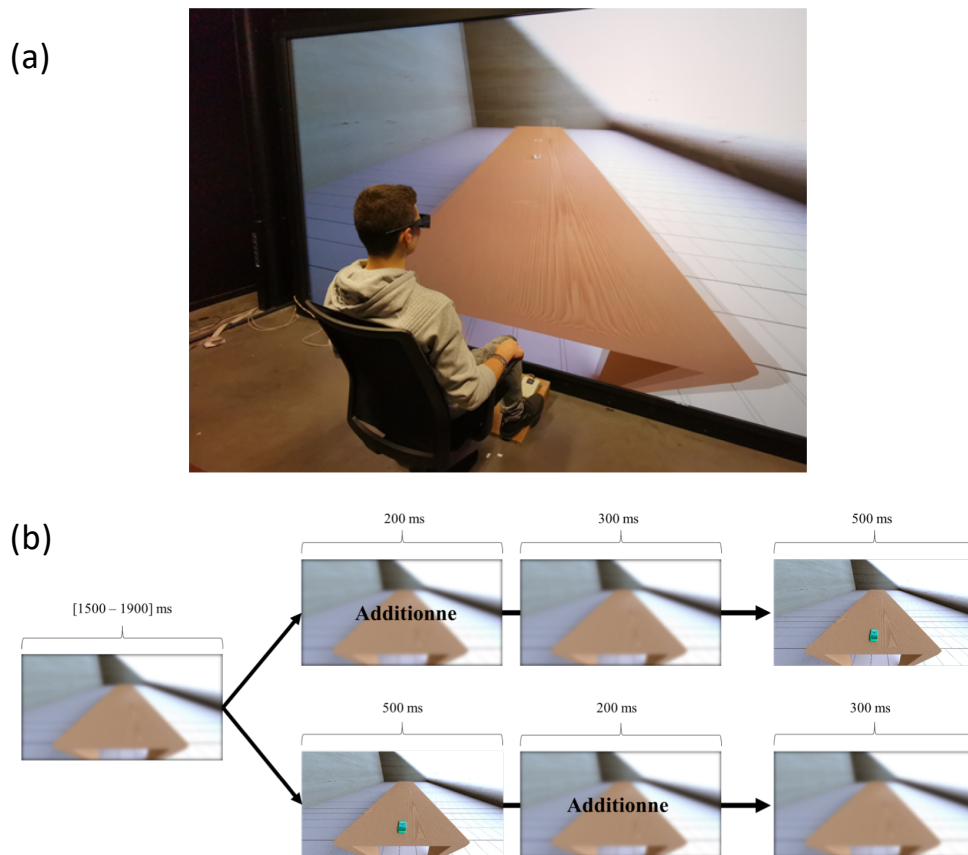


Figure 1. (a) Picture of a participant wearing the active 3D eyewear in front of the scene used during the experimental task. (b) Typical trial sequence: The upper-part corresponds to the condition with the verb preceding the object (i.e., **context-object trials**). The lower-part correspond to the condition with the verb following the object

(i.e., **object-context trials**). The blurred scene with the table alone remains on the screen, except when the object is presented.

Participants were asked to perform reachability judgements by judging whether they could reach and grasp the object with their right hand without performing the movement. Responses were given by clicking on left/right pedals with their left and right feet. The response mapping was counterbalanced between participants. To avoid any EEG signal contamination, participants were instructed to respond only when the trial presentation ended on a question mark, corresponding to 10% additional trials (72 trials) from which the associated EEG signal was not further analyzed. Inter-stimuli intervals (ITI) randomly varied between 1500 and 1900 ms. During ITI, a blurred picture of the visual scene without object was displayed (see Figure 1 for the entire procedure). The experimental session was composed of seven blocks of approximately 5 minutes each. There were 720 experimental trials (20 objects x 9 distances x 2 verbs x 2 object-context orders) randomly presented in each block, preceded by 20 practice trials.

Individual reachability boundary was evaluated with a classical cylinder reachability judgement task (Kalénine et al., 2016; Wamain et al., 2018), systematically performed after the main task. During this task, a 7×7.5 cm 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. Four repetitions of each of the 29 distances were used (116 trials). On each trial, participants had to judge without moving 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 counter-balanced between participants (and correspond to mapping used in the main task). The stimulus was visible on the screen until the participants' response.

2.5. Data Analyses

2.5.1. Determination of individual perceived reachability boundary

The nine distances were divided into reachable and unreachable spaces at the individual level according to the perceived boundary of the reachable space of each participant computed from the cylinder reachability judgement task. A maximum likelihood fitting procedure was used to obtain the logit regression model that best fit the reachable/unreachable responses of the participant with respect to the distance. Two participants were removed from the database

because their responses did not allow distinguishing between reachable and unreachable spaces. The individual perceived reachability boundary corresponds to a fifty percent chance for the participant to say “yes, it is reachable”. The mean perceived reachability boundary in the present virtual paradigm was of 83,8 cm (SD = 27 cm), which corresponded to an overestimation of about 19,7% of their actual capacities (mean arm length = 70 cm, SD = 6,4 cm).

2.5.2. EEG recording and preprocessing

EEG data were continuously collected during the reach-to-grasp judgment task from 128-channel Biosemi ActiveTwo (Biosemi B.V., Amsterdam, Netherlands) at a sampling rate of 1024 Hz with the ActiView software. Electrode caps covering the whole head with equidistant layout were used. Electrode offset was kept below 20 μ V. 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. Offline EEG preprocessing were performed with EEGLAB software (Delorme & Makeig, 2004). Continuous EEG signal was filtered (1–100 Hz) using two successive filters: a high pass filter (1 Hz) followed by a low pass filter (100 Hz). 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 identifying noisy electrodes, 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 done by the Biosemi system. Then, ICA-based artifact correction (runICA algorithm) was used in order to correct for blink artifacts (Delorme, Sejnowski, & Makeig, 2007). Electrodes with excessive electrical noise were not included (mean = 2; range: 1-6) in referencing and ICA procedure and were, when possible, interpolated after blink artefact correction. The signal was then segmented into periods of 3000 ms around the onset of the target object (1500 ms pre-target and 1500 ms post target onset). Visual inspection of the signal allowed to reject epochs with excessive noise artifacts (mean = 65 [9,1%]; range: 14 – 147). At this step, five additional participants were discarded from further analyses due to excessive rejection of trials (>20%). Therefore, reported analyses have been conducted on data from the 28 remaining participants. There were between 20 and 174 trials left (mean = 87,2) per condition for each participant after artefact rejection and before time-frequency analysis.

Event-related changes in oscillatory activity were quantified using a time-frequency wavelet decomposition of the continuous EEG signals between 1 and 30 Hz by step of 1 Hz

(complex Morlet's wavelets, ratio $f_0/\sigma_f=7$) implemented in Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). Following the recommendations of Hobson and Bishop (Hobson & 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 500 ms pre-event period of each trial type was considered as a baseline and was subtracted from each time point for a given frequency and participant for the rest of the trial. The pre-event period is a part of the inter-stimulus interval (ITI).

We focused our analysis on μ rhythm (8-13 Hz) desynchronization and thus considered power change data from the 6 frequencies between 8 and 13 Hz. We now have important evidence indicating that 8-13 Hz rhythm desynchronization reflects the activity of motor neural network (Debnath, Salo, Buzzell, Yoo, & Fox, 2019; Proverbio, 2012; Wamain et al., 2016, 2018) when assessed over centro-parietal electrodes. Based on the topography of μ rhythm desynchronization, we selected electrodes corresponding to the centro-parietal site (channels A1, A2, A3, B1, B2, D15, D16). In order to control for attentional modulation (α rhythm), we also chose a set of 7 electrodes at a posterior site A14, A15, A22, A23, A24, A27, A28). Finally, power change data were down-sampled to 102 Hz and export to R for statistical analysis. Note that trials involving the different objects were averaged at this step. The final data matrix involved 6 frequencies x 14 electrodes per time point, subject and condition.

2.5.3. Statistical analysis

Statistical effects of interest

We expected that a congruent use action verb context would orient the processing of object motor information towards the typical use of conflictual objects. Depending on when contextual information is provided, the action verb may bias the activation of use-relevant action representation and/or help resolving the competition between conflicting use and grasp representations. Both phenomena would result in a reduction of the typical effects observed when action representations compete. With similar stimuli, we demonstrated that competition between action representations during the perception of reachable conflictual objects induced an extinction of μ rhythm desynchronization (Wamain et al., 2018). Therefore, we anticipated a release of μ rhythm desynchronization for reachable conflictual objects in the congruent action context, in comparison to a neutral context. This effect should be reflected by greater μ

rhythm desynchronization in the action context than neutral context when conflictual objects are presented as reachable compared to unreachable. This advantage should be also more important (if not limited) to μ rhythm recorded at centro-parietal site in comparison to α rhythm at posterior site. Accordingly, we focused our statistical analysis on the Space X Context X Region of Interest (ROI) interaction. Since μ rhythm desynchronization is negative, we expected the difference (action- neutral in reachable) – (action-neutral in unreachable) to be negative, and this negative difference to be larger at central than posterior site, leading to an overall negative estimate for the Space x Context x ROI interaction contrast.

Selection of time windows

The presence of an interaction between Space, Context and ROI was sought on the entire time-window of stimulus presentation in the two trial types (*context-object and object-context conditions*). Nonetheless, we did not have any a priori hypothesis on the temporal location of the effect within the time window, in duration and/or latency. Thus, we chose a data-driven approach in order to select the time-points at which 8-13Hz power change was modulated by Space, Context and ROI. The *clusterperm.lmer* function from the *permutes* R package was used in order to determine the p-value associated to the Space X Context X ROI interaction for each time point while controlling for multiple comparisons (Voeten, 2021). Electrodes had to be averaged within each ROI for this time-cluster analysis. Permutation p-values were obtained from mixed-effect model comparison (5% significance likelihood ratio test) at each time point. The model included all main effects and interactions between Space, Context, and ROI as fixed effects, and the function selected the maximum random effect structure allowing convergence separately for each time point. Then, based on these permutation p-values, a cluster-mass statistic was computed to identify significant clusters (Maris & Oostenveld, 2007). In the present study, the clustering method was used as a preliminary step for time window selection in order to test the effects of interests on time windows that are the more susceptible to be sensitive to the interaction between Space, Context and ROI rather than on arbitrary time windows. In a conservative approach, we only considered significant clusters related to the 3-way-interaction in the expected direction (negative estimate) that involve at least fifteen continuous time points (about 150 ms) for future analysis.

Mixed-effect linear models on selected clusters

For each cluster identified, a mixed-effect linear model was used to analyze 8-13Hz power change as a function of Space (reachable, unreachable), Context (action, neutral) and

Region of Interest (central, posterior). This approach allows taking into account both experimental factors of interest (i.e. fixed effects) and variations in the signal related to other variables (i.e. random effects) in the model, which is particularly relevant when looking at measures with potential high variability between individuals and electrodes such as μ rhythm desynchronization. Here, the fixed effects corresponded to the effect of Space, Context, Region of Interest, and their interactions. The random effect structures included random intercepts and random slopes for participants, frequencies and electrodes (analyses were conducted with lme4 3.0-1 package of R version 3.4.4). The maximal random effect structures were sought. Models were simplified following Bates et al. (2015) using the rePCA function from lme4 package that allow removing the redundant and/or least contributing random effects from the model until it reaches converge. The final model R syntaxes will be systematically provided in footnotes. Pairwise comparisons of interest were then computed with the emmeans 1.7.2 package in R.

3. Results

3.1. Context-object trials

For Context-object trials, the evolution of 8-13 Hz power change over time at the centro-parietal (μ rhythm) and posterior sites (α rhythm) for each condition is presented on Figure 2 (left part). Two time-windows were selected from the significant clusters identified in the cluster-mass analysis: a first cluster during object presentation, Cluster 1, from 566 to 732 ms and a second cluster after both verb and object presentation, Cluster 2, from 985 to 1493 ms after verb onset.

Cluster 1. The test of the mixed-effect model¹ on 8-13 Hz power change for Cluster 1 did not show any significant Space x Context x ROI interaction (Cluster 1: $F_{1,9960} = 3.34, p = .067$), indicating similar contextual modulation of 8-13 Hz power change across space in both ROI. Accordingly, interaction effect evidenced on Cluster 1 was no further decomposed.

Cluster 2. In contrast, test of the mixed-effect model² on 8-13 Hz power change for cluster 2 revealed a significant Space x Context x ROI interaction ($F_{1,10000} = 14.10, p = .0002$). For this time-window, as expected the estimate value of the 3-way interaction contrast (difference [action- neutral in reachable] – [action-neutral in unreachable] for central versus posterior ROI) was negative (estimate = -.010, SD=.003, t-value = -3,755). The direction of the 3-way

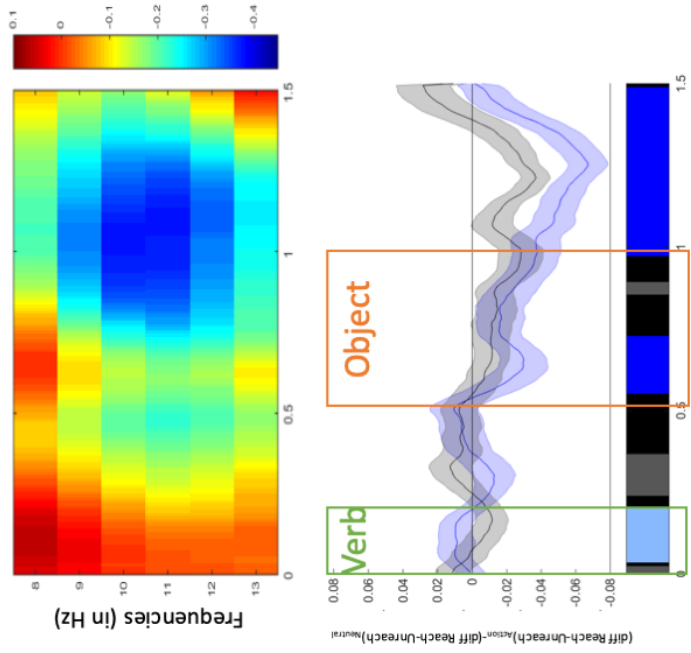
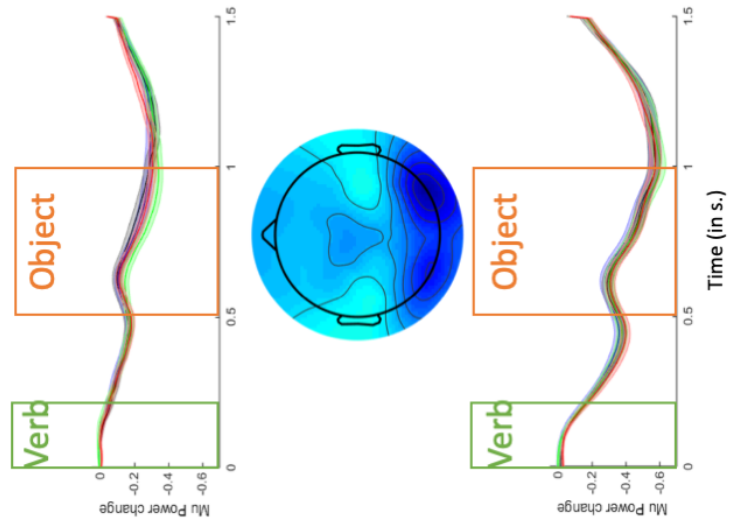
¹ R syntax cluster 1 :power change

~(Space*Context*ROI)+(1+Space+ROI|Subject)+(1|Frequency)+(1+Space|Electrode)

² R syntax cluster 2 :power change ~(Space*Context*ROI)+(1+Space|Subject)+(1|Frequency)+(1|Electrode)

interaction estimate indicates that the greater μ rhythm desynchronization in the action context (compared to neutral context) when conflictual objects are presented as reachable (compared to unreachable) was larger in magnitude at central than posterior site. Further test of the Space x Context interaction in each ROI showed that the modulation of 8-13 Hz power change as a function of space and verbal context was significant at both centro-parietal and posterior sites ($F_{1,249243} = 2389.76, p < .0001$ and $F_{1,5306} = 6.61, p = .010$ respectively, see Figure 2 right part), despite the greater magnitude of the effect at central site (as visible on Figure 2, central). Pairwise comparisons showed that at centro-parietal site, the amplitude of 8-13 Hz power change in the reachable space was increased in the action context in comparison to the neutral context (estimate = 0.009, SE= .001, $z=10.50, p < 0.0001$). Conversely, in the unreachable space, the amplitude of 8-13 Hz power change decreased in the action context compared to neutral context (estimate = -0.035, SE=.001, $z=-39.85, p < 0.0001$). At the posterior control site, the amplitude of 8-13 Hz power change decreased in the action context in comparison to the neutral context for both reachable (estimate = -0.002, SE=.001, $z=-2.69, p = 0.007$) and unreachable space (estimate = - 0.016, SE=.001, $z=-20.32, p < 0.0001$).

Context-object trials



Clusters showing significant ROI x Space x Verb interaction

Cluster1

Cluster2

Cluster 2 (between 985 and 1493ms)

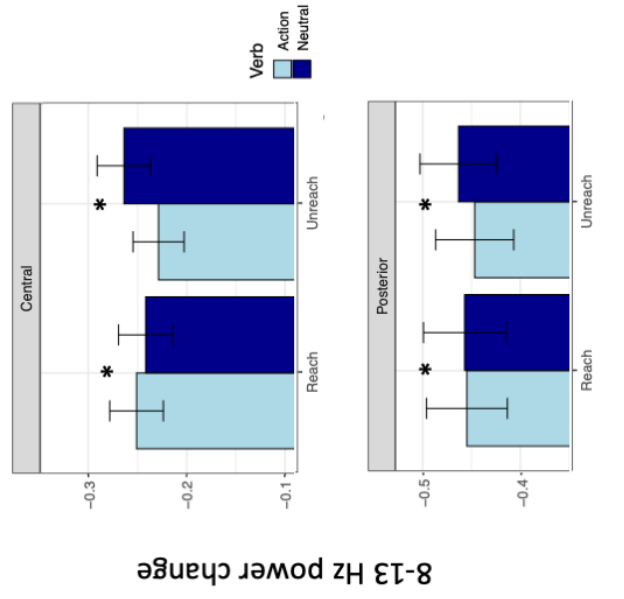


Figure 2. Evolution of 8-13 Hz power change for Context-object trials. (Left) Evolution of the 8-13 Hz power change across time for each condition of interest at centro-parietal and posterior sites (blue: Neutral verb and Reachable object, black: Action Verb and Reachable Object, green: Neutral verb and Unreachable object, red: Action Verb and Unreachable Object). Topographic map of the 8-13 Hz power change during Object Presentation. (Middle) Time frequency representation of 8-13 Hz power change at centro-parietal site on context-object trials. The data-driven approach using clusterperm identified 3 time-windows (in blue) showing significant ROI x Space x Context Interaction. Among them and according to our hypothesis, only two clusters with negative t-value (in dark blue) that evidenced a stronger effect at centro-parietal site (μ rhythm) in comparison to posterior site (α rhythm) were considered. (Right) Mean Power change observed during the time window 985-1493ms after verb onset as a function of object space (reachable vs. unreachable) and context (action vs. neutral verb) at centro-parietal and posterior sites. Errorbars show standard error between participants.

3.2. Object-context trials

For Object-context trials, the evolution of the 8-13 Hz power change over time at the centro-parietal (μ rhythm) and posterior sites for each condition is presented on Figure 3 (left part). Two time-windows were selected from the significant clusters identified in the cluster-mass analysis: a surprisingly early cluster during object presentation, Cluster 1, from 134 to 280 ms, and a later cluster after both object and verb presentation, Cluster 2, from 836 to 993 ms after object onset.

Cluster 1. The test of the mixed-effect model³ on 8-13 Hz power change for Cluster 1 revealed a significant Space x Context x ROI interaction (Cluster 1: $F_{1,9955} = 7.22, p = .007$). Although the estimate value of the 3-way interaction contrast (difference [action- neutral in reachable] – [action-neutral in unreachable] for central versus posterior ROI) was negative (estimate = -.006, SD=.002, t-value = -2.69), test of the Space x Context interaction in each ROI separately did not shown any modulation of 8-13 Hz power change as a function of context and space at centro-parietal site ($F_{1,4635} = 0.001, p = .99$), in contrast to posterior site ($F_{1,5306} = 15,05, p = .0001$). Thus, the 3-way interaction was not decomposed further.

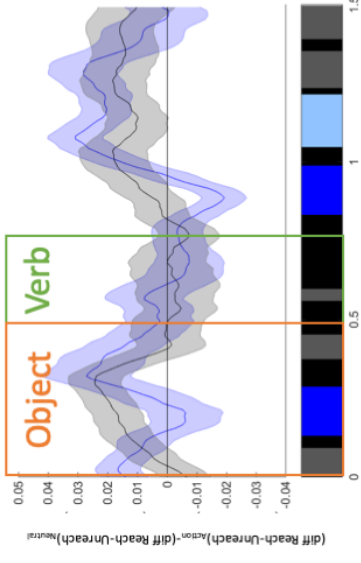
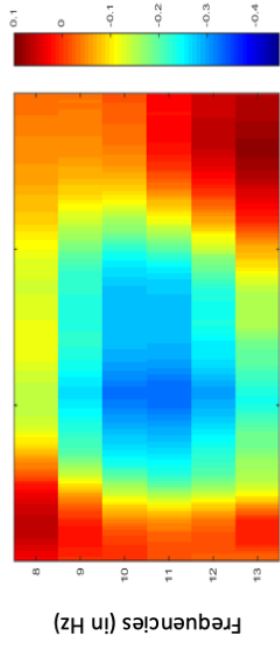
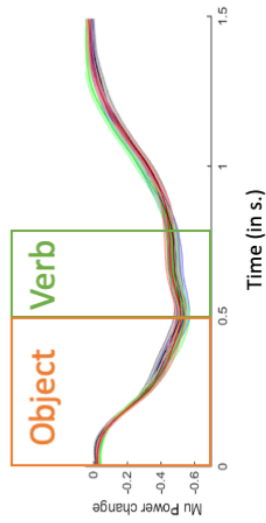
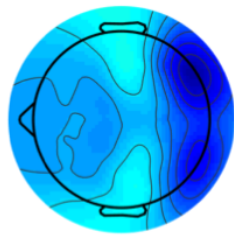
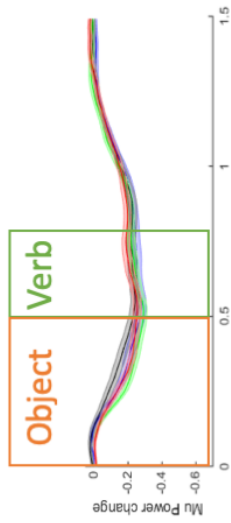
Cluster 2. In contrast, test of the mixed-effect model⁴ on 8-13 Hz power change for Cluster 2 revealed a significant Space x Context x ROI interaction ($F_{1,9960} = 5.41, p = .02$). Here again, for this time-window (836 to 993 ms after object onset), the estimate value of the interaction contrast was negative (estimate = -.006, SD=.003, t-value = -2,32). The negative estimate

³ R syntax cluster 1: power change~(Space*Context*ROI)+(1+Space+ROI|Subject)+(1+Space|Frequency)+(1+Space|Electrode)

⁴ R syntax cluster 2 :power change ~{(Space*Verb*ROI)+(1+Space+ROI|Subject)+(1|Frequency)+(1+Space|Electrode)}

reflects the fact that the greater μ rhythm desynchronization in the action context (compared to neutral context) when conflictual objects are presented as reachable (compared to unreachable) was larger in magnitude at central than posterior site. Further test of the Space x Context interaction in each ROI showed that the modulation of 8-13 Hz power change as a function of space and verbal context was significant for centro-parietal site ($F_{1,4629} = 5.25, p = .022$) but not posterior ($F_{1,5299} = 1.73, p = .19$). Pairwise comparisons at centro-parietal site demonstrated that for unreachable objects, the amplitude of 8-13 Hz power change decreased when action context was provided in comparison to neutral context (estimate = -0.016, SE=.004, $z=-4.32, p < 0.0001$). The pattern of results was not comparable for reachable objects, where action and neutral contexts induced similar 8-13 Hz power change (estimate = -0.006, SE=.004, $z=-1.64, p = 0.10$). At the posterior control site, the amplitude of 8-13 Hz power change increased for action context in comparison to neutral context for both reachable (estimate = 0.019, SE=.004, $z=5.48, p < 0.0001$) and unreachable spaces (estimate = 0.027, SE=.004, $z=7.52, p < 0.0001$).

Object-context trials



Clusters showing significant ROI x Space x Verb interaction

Cluster1 Cluster2

Cluster 2 (between 837 and 983 ms)

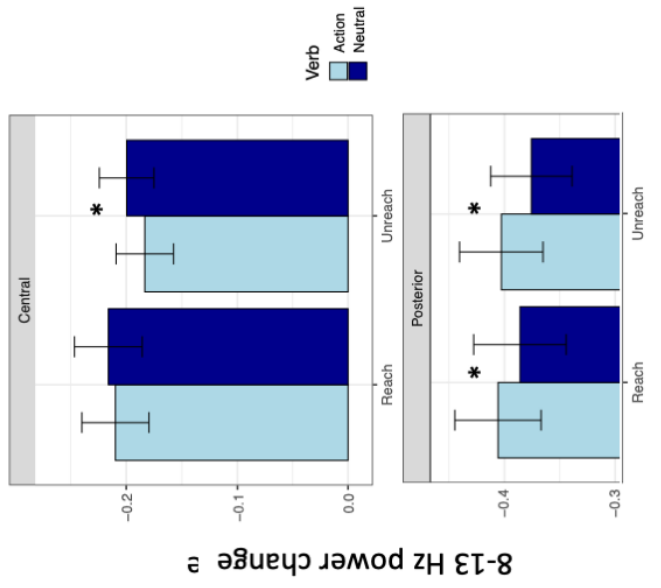


Figure 3. Evolution of 8-13 Hz power change for Object-context trials. (Left) Evolution of the 8-13 Hz power change across time for each condition of interest at centro-parietal and posterior sites (blue: Neutral verb and Reachable object, black: Action Verb and Reachable Object, green: Neutral verb and Unreachable object, red: Action Verb and Unreachable Object). Topographic map of the 8-13 Hz power change during Object Presentation. (Middle) Time frequency representation of 8-13 Hz power change at centro-parietal site on object-context trials. The data-driven approach using clusterperm identified 3 time-windows (in blue) showing significant ROI x Space x Context Interaction. Among them and according to our hypothesis, only two clusters with negative t-value (in dark blue) that evidenced a stronger effect at centro-parietal site (μ rhythm) in comparison to posterior site (α rhythm) were considered. (Right) Mean power change observed during the time window 837-983 ms after object onset as function of object space (reachable vs. unreachable) and context (action vs. neutral verb) at centro-parietal and posterior sites. Errorbars show standard error between participants.

4. Discussion

The present electrophysiological study aimed at identifying the influence of context on the competition between action representations during the perception of conflictual objects associated with distinct structural and functional gestures. Previous research indicated that the perception of reachable conflictual objects entailed the extinction of μ rhythm desynchronization usually observed during the perception of reachable manipulable objects, reflecting the impact of the competition between action representations on motor resonance effects (Wamain et al., 2018). As structural and functional action representations are known to be flexibly activated depending on the context in which they are perceived (Kalénine et al., 2014), we anticipated a reduction of the competition between action representations when conflictual objects are perceived in a verbal context triggering their typical use gesture. The main finding is consistent with this prediction. Results showed a release of μ rhythm desynchronization following the visual presentation of conflictual objects in a congruent action context in comparison to a neutral context when they were perceived as reachable compared to unreachable. This demonstrates that action context can solve the competition between action representations at play during object perception. Release of μ rhythm desynchronization for reachable conflictual objects in a congruent action context was observed when the context was provided prior or after object presentation. Moreover, we also found that the release of μ rhythm desynchronization appeared in a late time-window (around 1000 ms after the presentation of the first stimulus) for both object-context orders, although action contexts preceding object presentation led to more extended effects. As we will discuss next, the additional elements regarding the temporal dynamics of the effect will help refining our understanding of the role of context-biasing in competition reduction.

Our main result highlights a Space X Context X ROI interaction on 8-13Hz rhythm desynchronization, in the two conditions of verbal context presentation (*context-object and object-context conditions*). This interaction evaluates the effect of context on μ rhythm desynchronization (8-13 Hz, centro-parietal ROI) during the perception of reachable and unreachable conflictual objects, in comparison to α rhythm (8-13 Hz, posterior ROI) that served as a baseline. When conflictual objects were perceived as unreachable, 8-13 Hz desynchronization at centro-parietal site was smaller in a congruent action context in comparison to a neutral context. This difference may have various possible origins. When the verbal context was presented prior to the object, it may not reflect the involvement of the motor brain network but rather unspecific visuo-attentional variations, as the same pattern was also observed for 8-13 Hz desynchronization at posterior site (α rhythm). When the verbal context followed the presentation of the object, the smaller 8-13 Hz desynchronization in the action compared to neutral context was specific to 8-13 Hz desynchronization at centro-parietal site (μ rhythm) and might be a consequence of presenting verbal information conveying incongruent information (action) after an object that had already been processed as unreachable (non-action). Critically, the smaller μ rhythm desynchronization in the action than neutral context for objects perceived as unreachable disappeared or reversed when the objects were perceived as reachable. The increased μ rhythm desynchronization was visible when the verbal context oriented toward a congruent use action and this effect was limited to the centro-parietal site. This suggests that the action context can solve the competition between action representations activated during object perception.

It has been shown that the co-activation of distinct functional and structural actions induces a competition, that slows down perceptual and motor responses toward objects (Kalénine et al., 2016; Jax & Buxbaum 2010) and extinguishes μ rhythm desynchronization, an indicator of the activity of the motor neural network, during object processing (Wamain et al., 2018). This latter effect demonstrated that μ rhythm desynchronization, in addition of being a neural correlate of the *activation* of action representations (Fairchild, Marini, & Snow, 2021; Marini, Breeding, & Snow, 2019; Proverbio, 2012; Sestito, Harel, Nador, & Flach, 2018; Wamain et al., 2016) may also be a marker of the *competition* between action representations. It is important to note that competition between action representations is not an inherent property of conflictual objects, as it depends on the position of the object in space (Wamain et al., 2018). Reachable space potentiates the activation of action representations (Ambrosini et al., 2012; Costantini et al., 2011), and the potential competition between them (in the case of

conflicting representations). Thus, although evidence showing an influence of space on μ rhythm desynchronization indicates that activation and competition between action representations are context-dependent, prior studies did not inform about how competition can be reduced when distinct action representations are co-activated. Our finding clearly evidenced that information provided by the context may limit the impact of the competition at the neural level. In particular, an action verb congruent with one of the different action representations associated with conflictual objects entails a release of μ rhythm desynchronization by biasing action selection towards one specific action representation.

This finding is in line with a neurobiological model (Cisek, 2007; Cisek & Kalaska, 2010) that proposes that at least two distinct processes are at play in human-object interactions: The first corresponds to the activation of action representations from the environment while the second refers to the competition and biasing towards relevant actions. While this model is well accepted in the action domain (e.g. Jax & Buxbaum, 2010), very few studies investigated these processes in the absence of overt action. Until now it is far from clear how the competition may be solved in perceptual situations, in the absence of specific action plan toward the object. We propose that the role of context biasing in the selection of action representations may extend to the sole perception of manipulable objects. Accordingly, once the different potential action representations have been activated from the visual object, action-specific information derived from the context serves as a biasing signal and help resolving the competition by selecting the most relevant action representation for that context. Yet one may imagine an alternative scenario that does not involve selection processes. Action representations may be activated in a context-dependent manner at first. In this scenario, action context drives the activation of one of the different action representations, hence limiting the occurrence of competition. We believe that the results are rather consistent with the first interpretation and support the existence of selection processes in the context effects reported. We observed that the release of μ rhythm desynchronization appeared after the presentation of both stimuli (object and verb) irrespective of trials types (*context-object* and *object-context* conditions). One could have expected context to affect object processing as soon as the object was presented in context-object trials or as soon as the context was provided in object-context trials. Yet context effects occurred in a later time-window in both conditions. The delay observed between object presentation and the time-window where context modulation of μ desynchronization has been observed exceeds the classical timing required to activate action representation around 300-500 ms after object onset (Proverbio, 2012; Wamain et al., 2016). Therefore, it seems that action selection, reflected in

the amplitude of μ rhythm desynchronization, can be dissociated from action activation, and occurs during an integration window after activation of action representations from both visual objects and verbal context. This does not prevent μ desynchronization to be modulated by verb and/or object processing independently, a dimension that has been largely addressed in previous research (Niccolai et al., 2014; Proverbio, 2012; van Elk, van Schie, Zwaan, & Bekkering, 2010) and that was not considered here, but supports a more complex interpretation of its role in perception. It is also worth noting that despite an influence of context on object processing when presented before or right after object presentation, contextual effects were more massive and widespread when context was provided before object presentation. This suggests that although context may be able to bias action selection at any time around the presentation of the object, its impact once the object has already been processed is probably more limited, in time and magnitude.

In the present study, we highlighted that a verbal context can trigger such biasing signals and solve the competition between action representations during conflictual object perception. This finding extends influential models of action selection (Caligiore, Borghi, Parisi, & Baldassarre, 2010; Cisek, 2007) to perceptual situations. It is important to note that results support an influence of verbal context on a neurophysiological mechanism involved in action selection (Wamain et al., 2018) and not only on the consequences of action competition on behavior (Kalénine et al., 2016). Competition between action representations affects μ rhythm desynchronization and contextual information serves as a biasing signal for selection of action representations during mere object perception. Critically, μ rhythm desynchronization associated with the perceptual processing of conflictual objects increased in the presence of a congruent use action context. Thus, μ rhythm desynchronization may be considered a possible marker of action selection rather than an unspecific correlate of action activation from visual objects. However, the processes underlying context biasing in such perceptual situations remain to be clarified. In particular, the specificity of the contextual information needed to bias competition between action representations is not obvious. Can we anticipate similar context effects on μ rhythm desynchronization with verbal contexts presenting congruent structural actions? With any congruent contextual cue? In addition, the relative contribution of activation and inhibition processes also need to be clarified. Further experiments will be needed to specify the precise dynamics of activation and selection processes during the perception of conflictual objects in more naturalistic situations with diverse sources of contextual information.

5. Methodological considerations and limitations

When the verbal context was provided after object presentation, the cluster-based statistical approach identified a cluster of contextual modulation during object presentation, before the presentation of the verb (Object-Context trials, Cluster 1, from 134 to 280 ms). This effect was clearly unexpected and until now, no good explanation could be provided. There are likely some temporal fluctuations of μ rhythm desynchronization during the first 500 ms that could be manifested through higher-order interactions between conditions over a short period of time. To what extent such effect is driven by the sensitivity of the cluster-based statistical approach used remains to be clarified. As we did not have any a priori hypothesis on the temporal location of the effect, a data-driven approach based on a cluster-mass statistic was chosen to identify significant time windows for analysis. While we believe that the approach is well suited to the type of study conducted, it could be relevant to find more conservative criteria for cluster selection to select only sufficiently large significant clusters and bypass the issue of possible early fluctuations of μ rhythm desynchronization. Better understanding of spontaneous fluctuations of μ rhythm desynchronization is also needed. From a methodological point of view, further research on the development of tools and procedures to optimize temporal localization of time-frequency effects in EEG studies would be highly useful.

6. Open practices

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/ exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures and analyses was pre-registered prior to the research being conducted.

The study in this article earned Open Data and Open Materials badges for transparent practices. Materials and data for the study are available at https://osf.io/s7b9q/?view_only=fb8822ef680542b48ca8066b1fb2bb6d.

7. Acknowledgements

This work was funded by the French National Research Agency (ANR-11-EQPX-0023 and ANR-16-CE28-0003), by European funds (FEDER SCV-IrDIVE) and benefited from a regional fellowship (Hauts-de-France) to M. Godard.

8. References

- Ambrosini, E., Scorolli, C., Borghi, A. M., & Costantini, M. (2012). Which body for embodied cognition? Affordance and language within actual and perceived reaching space. *Consciousness and Cognition*, *21*(3), 1551–1557.
<https://doi.org/10.1016/j.concog.2012.06.010>
- Aravena, P., Courson, M., Frak, V., Cheylus, A., Paulignan, Y., Deprez, V., & Nazir, T. A. (2014). Action relevance in linguistic context drives word-induced motor activity. *Frontiers in Human Neuroscience*, *8*(1). <https://doi.org/10.3389/fnhum.2014.00163>
- Aravena, P., Delevoye-turrell, Y., Deprez, V., Cheylus, A., Paulignan, Y., Frak, V., & Nazir, T. (2012). Grip Force Reveals the Context Sensitivity of Language- Induced Motor Activity during ““ Action Words ”” Processing : Evidence from Sentential Negation. *PLoS ONE*, *7*(12). <https://doi.org/10.1371/journal.pone.0050287>
- Barsalou, L. W. (2008). Grounded Cognition. *Annual Review of Psychology*, *59*(1), 617–645.
<https://doi.org/10.1146/annurev.psych.59.103006.093639>
- Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. *ArXiv E-Print, under Revision*, 1–27.
- Borghi, A. M., Bonfiglioli, C., Lugli, L., Ricciardelli, P., Rubichi, S., & Nicoletti, R. (2007). Are visual stimuli sufficient to evoke motor information?. Studies with hand primes. *Neuroscience Letters*, *411*(1), 17–21. <https://doi.org/10.1016/j.neulet.2006.10.003>
- 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.
<https://doi.org/10.1016/j.bandc.2012.04.007>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Bub, D. N., Masson, M. E. J., & van Mook, H. (2018). Switching between lift and use grasp actions. *Cognition*, *174*, 28–36. <https://doi.org/10.1016/j.cognition.2018.01.013>
- Buxbaum, L. J., & Kalénine, S. (2010). Action knowledge, visuomotor activation, and embodiment in the two action systems. *Annals of the New York Academy of Sciences*, *1191*, 201–218. <https://doi.org/10.1111/j.1749-6632.2010.05447.x>
- Byrne, M. D. (2002). Reading Vertical Text: Rotated VS. marquee. *Proceedings of the*

- Human Factors and Ergonomics Society Annual Meeting*, 46(17), 1633–1635.
<https://doi.org/10.1177/154193120204601722>
- Caligiore, D., Borghi, A. M., Parisi, D., & Baldassarre, G. (2010). TRoPICALS: A Computational Embodied Neuroscience Model of Compatibility Effects. *Psychological Review*, 117(4), 1188–1228. <https://doi.org/10.1037/a0020887>
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, 12(4), 478–484. <https://doi.org/10.1006/nimg.2000.0635>
- 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. <https://doi.org/10.1098/rstb.2007.2054>
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*.
<https://doi.org/10.1146/annurev.neuro.051508.135409>
- Costantini, M., Ambrosini, E., Scroli, C., & Borghi, A. M. (2011). When objects are close to me : affordances in the peripersonal space Acknowledgments. *Psychonomic Bulletin & Review*, 18(2), 302–308.
- Debnath, R., Salo, V. C., Buzzell, G. A., Yoo, K. H., & Fox, N. A. (2019). Mu rhythm desynchronization is specific to action execution and observation: Evidence from time-frequency and connectivity analysis. *NeuroImage*, 184, 496–507.
<https://doi.org/10.1016/j.neuroimage.2018.09.053>
- 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. Retrieved from
<http://www.sciencedirect.com/science/article/pii/S0165027003003479>
- 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. Retrieved from
<http://www.sciencedirect.com/science/article/pii/S1053811906011098>
- Fairchild, G. T., Marini, F., & Snow, J. C. (2021). Graspability modulates the stronger neural signature of motor preparation for real objects vs. Pictures. *Journal of Cognitive*

- Neuroscience*, 33(12), 2477–2493. https://doi.org/10.1162/jocn_a_01771
- Gerlach, C., Law, I., & Paulson, O. B. (2002). When action turns into words. Activation of motor-based knowledge during categorization of manipulable objects. *Journal of Cognitive Neuroscience*, 14(8), 1230–1239. <https://doi.org/10.1162/089892902760807221>
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*. <https://doi.org/10.1017/s0140525x04000020>
- Godard, M., Wamain, Y., & Kalénine, S. (2019). Do manufactured and natural objects evoke similar motor information? The case of action priming. *Quarterly Journal of Experimental Psychology*, 72(12), 2801–2806. <https://doi.org/10.1177/1747021819862210>
- Godard, M., Wamain, Y., Ott, L., Delepouille, S., & Kalénine, S. (2022). How Competition between Action Representations Affects Object Perception during Development. *Journal of Cognition and Development*. <https://doi.org/10.1080/15248372.2022.2025808>
- Hobson, H. M., & Bishop, D. V. M. (2016). Mu suppression – A good measure of the human mirror neuron system? *Cortex*, 82, 290–310. <https://doi.org/10.1016/j.cortex.2016.03.019>
- Jax, S. A., & Buxbaum, L. J. (2010). Response interference between functional and structural actions linked to the same familiar object. *Cognition*, 115(2), 350–355. <https://doi.org/10.1016/j.cognition.2010.01.004>
- 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. <https://doi.org/10.1111/j.1748-6653.2012.02031.x>
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8(2), 71–78. <https://doi.org/10.1016/j.tics.2003.12.002>
- Kalénine, S., & Buxbaum, L. J. (2015). Role of action in conceptual object representation and organization. In *Conceptual and Interactive Embodiment: Foundations of Embodied Cognition* (Vol. 2, pp. 125–146). <https://doi.org/10.4324/9781315751962>
- Kalénine, S., Shapiro, A. D., & Buxbaum, L. J. (2013). Dissociations of action means and outcome processing in left-hemisphere stroke. *Neuropsychologia*, 51(7), 1224–1233. <https://doi.org/10.1016/j.neuropsychologia.2013.03.017>

- 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), 645–651. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/24186270>
- Kalénine, S., Wamain, Y., Decroix, J., & Coello, Y. (2016). Conflict between object structural and functional affordances in peripersonal space. *Cognition*, *155*. <https://doi.org/10.1016/j.cognition.2016.06.006>
- Lee, C. L., 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), 257–270.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology Paris*, *102*(1–3), 59–70. <https://doi.org/10.1016/j.jphysparis.2008.03.004>
- Marini, F., Breeding, K. A., & Snow, J. C. (2019). Distinct visuo-motor brain dynamics for real-world objects versus planar images. *NeuroImage*, *195*, 232–242. <https://doi.org/10.1016/j.neuroimage.2019.02.026>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Masson, M. E. J. (2015). Toward a Deeper Understanding of Embodiment. *Canadian Journal of Experimental Psychology*, *69*(2), 159–164. <https://doi.org/10.1037/cep0000055>
- Matheson, H. E., Garcea, F. E., & Buxbaum, L. J. (2021). Scene context shapes category representational geometry during processing of tools. *Cortex*, *141*, 1–15. <https://doi.org/10.1016/j.cortex.2021.03.021>
- Nicolai, V., Klepp, A., Weissler, H., Hoogenboom, N., Schnitzler, A., & Biermann-Ruben, K. (2014). Grasping hand verbs: Oscillatory beta and alpha correlates of action-word processing. *PLoS ONE*, *9*(9). <https://doi.org/10.1371/journal.pone.0108059>
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011. <https://doi.org/10.1155/2011/156869>
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Pisella, L., Binkofski, F., Lasek, K., Toni, I., & Rossetti, Y. (2006). No double-dissociation between optic ataxia and visual agnosia: multiple sub-streams for multiple visuo-manual integrations. *Neuropsychologia*, 44(13), 2734–2748. <https://doi.org/10.1016/j.neuropsychologia.2006.03.027>
- Proverbio, A. M. (2012). Tool perception suppresses 10-12Hz μ rhythm of EEG over the somatosensory area. *Biological Psychology*, 91(1), 1–7. <https://doi.org/10.1016/j.biopsycho.2012.04.003>
- Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: anatomy and functions. *Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale*, 153(2), 146–157. <https://doi.org/10.1007/s00221-003-1588-0>
- Sestito, M., Harel, A., Nador, J., & Flach, J. (2018). Investigating neural sensorimotor mechanisms underlying flight expertise in pilots: Preliminary data from an EEG study. *Frontiers in Human Neuroscience*, 12. <https://doi.org/10.3389/fnhum.2018.00489>
- Thill, S., Caligiore, D., Borghi, A. M., Ziemke, T., & Baldassarre, G. (2013). Theories and computational models of affordance and mirror systems: An integrative review. *Neuroscience and Biobehavioral Reviews*. <https://doi.org/10.1016/j.neubiorev.2013.01.012>
- Tomasino, B., Weiss, P. H., & Fink, G. R. (2010). To move or not to move: Imperatives modulate action-related verb processing in the motor system. *Neuroscience*, 169(1), 246–258. <https://doi.org/10.1016/j.neuroscience.2010.04.039>
- Tucker, M., & Ellis, R. (2001). The potentiation of grasp types during visual object categorization. *Visual Cognition*, 8(6), 769–800. <https://doi.org/10.1080/13506280042000144>

- van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of motor activation in language processing: Motor cortical oscillations support lexical-semantic retrieval. *NeuroImage*, *50*(2), 665–677.
<https://doi.org/10.1016/j.neuroimage.2009.12.123>
- Vingerhoets, G., Acke, F., Vandemaele, P., & Achten, E. (2009). Tool responsive regions in the posterior parietal cortex: Effect of differences in motor goal and target object during imagined transitive movements. *NeuroImage*, *47*(4), 1832–1843.
<https://doi.org/10.1016/j.neuroimage.2009.05.100>
- Voeten, C. C. (2021). Analyzing time series data using clusterperm.lmer. R package version 2.3.2. Retrieved from <https://cran.r-project.org/web/packages/permutest/vignettes/buildmer.pdf>
- 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. <https://doi.org/10.1016/j.cortex.2015.10.006>
- Wamain, Y., Sahai, A., Decroix, J., Coello, Y., & Kalénine, S. (2018). Conflict between gesture representations extinguishes μ rhythm desynchronization during manipulable object perception: An EEG study. *Biological Psychology*, *132*.
<https://doi.org/10.1016/j.biopsycho.2017.12.004>
- Wokke, M. E., Knot, S. L., Fouad, A., & Richard Ridderinkhof, K. (2016). Conflict in the kitchen: Contextual modulation of responsiveness to affordances. *Consciousness and Cognition*, *40*, 141–146. <https://doi.org/10.1016/j.concog.2016.01.007>

9. Supplementary Material

List of conflictual objects used with their corresponding level of conflictuality

			
Conflict index: 100	Conflict index: 100	Conflict index: 91.67	Conflict index: 100
			
Conflict index: 100	Conflict index: 83.33	Conflict index: 83.33	Conflict index: 100
			
Conflict index: 75	Conflict index: 100	Conflict index: 91.67	Conflict index: 100
			
Conflict index: 66.67	Conflict index: 50	Conflict index: 100	Conflict index: 100
			
Conflict index: 100	Conflict index: 58.33	Conflict index: 91.67	Conflict index: 91.67

Full list of conflictual object and verb association used in the implementation of the 3D virtual paradigm of the EEG study.

Objects	Action verbs	Neutral verbs
Gas lighter	Brûler (to burn)	Observer (to observe)
Camera	Appuyer (to press)	Inspector (to inspect)
Kitchen scale	Peser (to weight)	Contempler (to contemplate)
Tin can	Ouvrir (to open)	Observer (to observe)
Music box	Tourner (to turn)	Observer (to observe)
Spray can	Vaporiser (to spray)	Inspector (to inspect)
Calculator	Compter (to count)	Regarder (to look at)
Game die	Lancer (to throw)	Admirer (to admire)
Soap distributor	Appuyer (to press)	Admirer (to admire)
Toaster	Toaster (to toast)	Examiner (to examine)
Desk lamp	Eclairer (to light)	Evaluer (to evaluate)
Timer	Programmer (to program)	Contempler (to contemplate)
Pepper mill	Assaisonner (to season)	Regarder (to look at)
Perfume	Vaporiser (to spray)	Observer (to observe)
Cheese grater	Mouliner (to mill)	Constater (to see)
Alarm clock	Stopper (to stop)	Scruter (to scrutinize)
Salt shaker	Assaisonner (to season)	Inspector (to inspect)
Sugar bowl	Servir (to serve)	Evaluer (to evaluate)
Corkscrew	Ouvrir (to open)	Scruter (to scrutinize)
Spinning top	Tourner (to turn)	Evaluer (to evaluate)