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# Tool use and function knowledge shape visual object processing

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## ABSTRACT

Perceiving the environment automatically informs how we can interact with it through affordance mechanisms. However, it remains unknown how our knowledge about the environment shapes how it is perceived. In this training study, we evaluated whether motor and function knowledge about novel objects affects visual object processing. Forty-three participants associated a usage or function to a novel object in interactive virtual reality while their EEG was recorded. Both usage and function influenced the mu-band (8–12 Hz) rhythms, suggesting that motor and function object information influence motor processing during object recognition. Learning the usage also prevented the reduction of the theta-band (4–8 Hz) rhythms recorded over the posterior cortical areas, suggesting a predominant top-down influence of tool use information on visuo-motor pathways. The modulation being specifically induced by learning an object usage, the results support further the embodied cognition approach rather than the reasoning-based approach of object processing.

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## 1. Introduction

The perceived world through our eyes appears automatically translated as potential interaction with it (Gibson, 1979). This phenomenon called affordance rely on brain mechanisms detecting and preparing possible actions through perception. Affordances can also be learned through our everyday usage of objects and tools. In the last decade, affordance processing has been highly investigated in cognitive neuroscience using neuroimaging techniques (de Wit, de Vries, van der Kamp, & Withagen, 2017; Reynaud, Lesourd, Navarro, & Osiurak, 2016; Sakreida et al., 2016; Thill, Caligiore, Borghi, Ziemke, & Baldassarre, 2013). fMRI analysis unveiled the neuronal networks involved in the perception of and action triggered by the affordances during object recognition (Brandi, Wohlschlager, Sorg, & Hermsdorfer, 2014; Buxbaum, Kyle, Tang, & Detre, 2006; Mizelle, Kelly, & Wheaton, 2013; Sakreida et al., 2016; Tettamanti, Conca, Falini, & Perani, 2017). Some networks being well-identified, understanding their dynamics is the next milestone that cognitive and neuro-scientists have to reach (Kopell, Gritton, Whittington, & Kramer, 2014). Our focus here is that affordance processing is never naïve as perception is always relying on our pre-existing knowledge about the environment. Consequently, how such top-down knowledge influences the automatic activation of visuomotor pathways during object processing? To investigate this question, we used EEG recordings coupled with an original virtual reality (VR) setup where

participants perceived novel objects trained beforehand with novel object knowledge, which is an object usage or a function. The goal of the study was to test whether former object knowledge modulates the visual extraction of affordances during object processing.

Recent theories suggest that alpha (8–12 Hz) and theta (4–8 Hz) rhythms control the access to stored information in long-term memory via inhibition of task-irrelevant cell assemblies in visual tasks (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Klimesch, Freunberger, & Sauseng, 2010; Klimesch, Fellinger, & Freunberger, 2011). The amplitude of occipital alpha oscillations and the synchronization of their phases are increased during object recognition, reflecting the access and retrieval of semantic information (Freunberger, Klimesch, Griesmayr, Sauseng, & Gruber, 2008). Also, the visual shape of objects modulates the alpha oscillations recorded over posterior cortical areas during object recognition (Vanni, Revonsuo, & Hari, 1997). Thus, alpha-band oscillations would signal the effect of top-down object knowledge on affordance processing.

On a similar frequency-band but topographically and functionally distinct, mu-band oscillations (8–12 Hz) are understood as a processing linking perception and action (Pineda, 2005). Recorded over central areas, they have been associated with motor planning (Llanos, Rodriguez, Rodriguez-Sabate, Morales, & Sabate, 2013; Sabate, Llanos, Enriquez, & Rodriguez, 2012). Recently, Freeman, Itthipuripat, and Aron (2016) revealed that affording objects increases the central

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mu-band power desynchronization during object processing. Similarly, Proverbio (2012) showed that the perception of tools evokes less motor mu-band activity than non-tool objects, reflecting the sensitivity of the mu-band in processing object affordance. Altogether, these studies revealed markers of affordances processing. As an extension of these results, our training study investigates the causal role played by usage and functional object knowledge on the dynamics of visuo-motor processing of objects.

In this EEG study, we trained participants to manipulate two novel objects. Following the appearance of an object and a tone, the task of the participant was to transport it from a location to another. This motor task was chosen to guide the perception of the objects towards their ecological value. In the middle of the experiment, half of the participants learned how to use one of the two objects with a specific manipulation (usage condition). The other half of the participants learned the function of one of the objects (function condition), without additional manipulation. Following the additive model, one would expect that learning the object usage would strengthen the activation of the motor system during object processing, as indexed by the reduction of mu-band oscillatory activity (Freeman et al., 2016). However, previous work indicated that the processing of visual and learned affordances interfere with each other due to conflicting motor programs (Jax & Buxbaum, 2010; Kalénine, Wamain, Decroix, & Coello, 2016; Wamain, Sahaï, Decroix, Coello, & Kalénine, 2018). Hence, an alternative hypothesis is that learning an object usage reduces the activation of the motor system and be reflected as a reduction of mu-band activity. Because the reduced activation would rely on motor conflicts, such reduction would occur specifically when a manipulation is learned, and not following the learning of the function.

The question is whether uniquely embodied motor information is involved in visual object processing. Indeed, the alternative possibility is that objects and tools processing is predominantly guided by semantic information, such as the object's function, as recently suggested by the reasoning-based approach (Federico & Brandimonte, 2020; Osiurak & Badets, 2016; Osiurak, Rossetti, & Badets, 2017). Theoretically, we hypothesized that motor knowledge induced by learning an object usage would interfere with the automatic extraction of visual affordances. Practically, this would be expressed by increased reaction times (Jax & Buxbaum, 2010), and reduced early alpha-band synchronization (Wamain et al., 2018) and late motor mu-band desynchronization (Freeman et al., 2016) recorded over centro-parietal cortical areas. Training participants to learn an object function without a manipulation offered a control condition to test the specific impact of motor knowledge on visual object processing. These hypotheses were investigated on both phases and amplitudes of occipital alpha and motor mu-band (8–12 Hz) oscillations.

## 2. Methods

### 2.1. Participants

Forty-three adult volunteers (mean age = 21 years old, range 19–29, including 12 males) from the University of Plymouth participated in the study in exchange for money or course credit. All participants reported being right-handed and having normal vision. Due to the use of a VR headset, participants wearing correction glasses were not accepted. EEG data from six participants were removed due to excessive numbers of artifacts. The experimental procedure and written consent form for this study were approved by the ethics committee of the University of Plymouth and conform with the 2008 Helsinki Declaration.

### 2.2. Experimental setup and procedure

The experiment used Unity software (Unity technologies, version 7.1.0f3) to create the virtual environment and the HTC Vive (HTC Corp.) headset and controllers. Participants were wearing both the EEG and VR

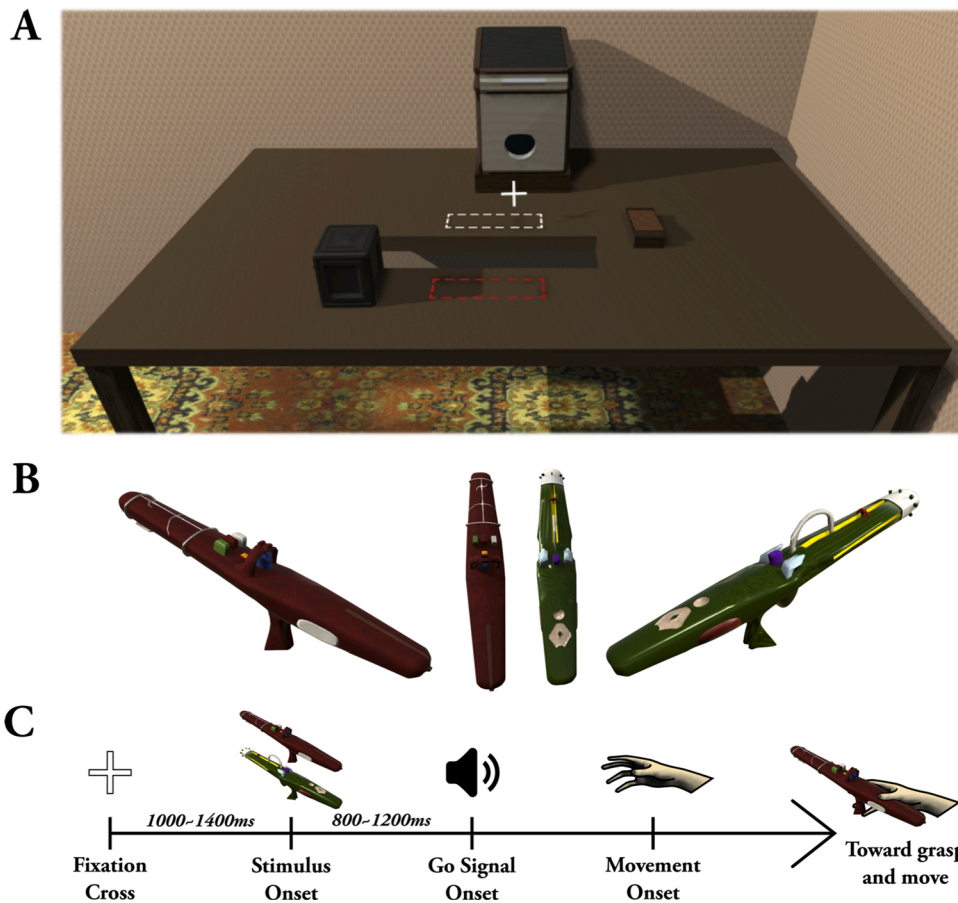
headsets and were seated in a chair next to a desk. A button box was placed on the desk situated on the right side of the participants and connected to the computer to detect movement onsets. The virtual environment was composed of a small wooden textured box, a white and a red dashed area situated on the table, a big box situated in front of the participant and, a small black cube on their left (Fig. 1A). The size and height of the room, virtual table, and the button box were fitted to the dimensions of the physical environment. For a comfortable position of the hand on the button box, the distance between the chair and the desk was adjusted for each participant. Participants were instructed to manipulate a VR controller, represented by two possible 3-D models (Fig. 1B).

The experiment was divided into three phases termed as pre-training, training, and post-training phases composed of 120 trials, 50 trials, and 120 trials, respectively. The trials for the pre-training and post-training phases were divided into four blocks of 30 trials. The training phase was divided into two blocks of 25 trials. After each block of trials, a time break was proposed to the participant and the VR headset was removed if desired. The pre-training period was used to control the possible effects of visual attention and familiarity with the two stimuli and the task on the EEG activities. The trial procedure is depicted in Fig. 1C. At the beginning of each trial, the participant had to place the right hand on the button box and look at the white fixation cross situated in the front of him/her, at the location of the invisible controller. After 1000 ms, the fixation cross disappeared. Subsequently, one of two visual representations of the controller appeared after a random time interval between 1000 ms and 1400 ms. Participants were instructed to prepare to grasp-and-move the controller from the white to the red area after hearing a tone (i.e. go-signal) triggered after a random time interval between 800 ms and 1200 ms. We used this delayed response paradigm to prevent contamination of the EEG signal from movement-related effects. Once the controller was placed on the red area, next to the black cube, the participant was instructed to return it to the white area. Then, the 3-D model of the controller disappeared. The black cube had no other importance in the experiment. The motor task had to be performed as fast as possible. If the button box was released before the onset of the go-signal, the participant received a written feedback on a virtual panel at the end of the trial, reminding him/her to move only after the tone. At the end of each trial, participants were instructed to put their right hand back on the button when ready to start a new trial. Participants were instructed to avoid movements and eye blinks during the trials, especially before the go-signal. They were able to move freely between trials. The visual representation of the controller was randomly assigned to each trial.

During both pre-training and post-training phases, participants had to grasp-and-move the two object-stimuli without distinction. The purpose of the training phase was to transform the representation of one of the two objects into a tool (i.e. a key that opens the box on the table). The object trained was randomly assigned to each participant at the beginning of the training phase. Following a mixed experimental design, two different trainings (usage vs function conditions) represented a between-subject factor.

### 2.3. Training phase in the function condition

In the training phase of the function condition, 22 participants were instructed to grasp-and-move both objects. When transported on the red area, the trained object triggered an audio-visual animation of the opening of a box located in the front of the participant. The transportation of the non-trained object did not trigger any sound or animation. Hence, in the function condition, participants associated with the trained object the novel function information "a key that opens the box", as mentioned by the experimenter. Crucially, no additional motor information was learned.



**Fig. 1.** (A) Virtual environment perceived by the participants. (B) The two possible stimuli-objects manipulated during the experiment. (C) After viewing a fixation cross, one of the two objects randomly appeared. After a time-interval between 800 ms and 1200 ms, participants heard a tone (i.e. the go-signal) and had to grasp and move the object as fast as possible. During the training phase of the object function, moving one of the two objects opened the box. During the training phase of the object usage, participants had to perform a novel tool-use to open the box with one of the two objects.

#### 2.4. Training phase in the usage condition

In the usage condition, 21 participants were trained to execute a challenging key-like movement with the trained object. At the commencement of the training, a very brief video was depicting the usage of the object to learn and perform. The participants were instructed to perform the tool use when the trained object appeared and the grasp-to-move action when the non-trained object appeared. The tool use learned by the participants was a series of three rotations (i.e. to the left, to the right, and to the left again) of the object in the hole of the wooden box to open it. The rotations were restricted by the respective angles: turn the controller 90° to the left, then turn 180° to the right, and finally turn 90° to the left back to the center, with a precision of  $\pm 10^\circ$ . Exceeding  $\pm 10^\circ$  of precision failed to open the box and consequently of the trial. After the three rotations, the trigger button of the controller must have been pressed to open the box, thus constraining the handgrip associated with the tool use. At the end of a failed trial, participants received feedback advising which rotation was performed incorrectly, assuring motor learning. Following a correct series of rotations and button press, the same audio-visual animation as in the training of the object function was triggered. Thus, in the usage condition, participants associated both novel function information “a key that opens the box”, as mentioned by the experimenter, and novel motor information (i.e. a handgrip, wrists rotations and a button press).

#### 2.5. Behavioral and electroencephalographic recording

The release of the button box was used to calculate the movement onset of the participant. Then, the lift of the grasped controller was detected and used to calculate the grasping onset. The action onset was detected when the objects were transported to the red area. The object

and movement onsets were used to time-lock EEG analysis. The action sequence was segmented and calculated as follow: a) Initiation times, as the time between go-signal onsets and movement onsets; b) Grasping times, as the time between movement onsets and grasping onsets; c) Execution times, as the time between grasping onsets and action onsets. We evaluated these time intervals depending on the stimulus-object during the and pre- and post-training phases of each condition. EEG data were collected from 61 actively amplified Ag/AgCl electrodes (easyCAP, Brain Products, Gilching, Germany) mounted on an elastic cap and following the standard International 10–20 montage. Electrode impedances were kept below 20 k $\Omega$ . The signals were amplified using a BrainAmp MR Plus amplifier (Brain Products) and continuously sampled at 500 Hz. The virtual environment and the EEG recording were run on separate computers.

#### 2.6. Data processing

The training paradigm implemented in this experiment was chosen to estimate the Training Effect (TE) of a given object, reflecting the specific consequences of learning the function and usage of the objects on reaction times and EEG activities. This TE was calculated with the following formula:  $TE = \text{object}_{\text{post-training}} - \text{object}_{\text{pre-training}}$ . This TE was calculated separately for the trained and non-trained objects in both conditions (learning usage or learning function). Hence, the comparison of the TE for the trained and non-trained objects allowed to isolate the effect of the training. Therefore, it is hypothesized that the TE values concerning the non-trained object would be minimal whereas the TE values about the trained object would be maximal.

Only successful trials during the pre- and post-training phases were used for the behavioral and EEG analyses. Successful trials were defined as trials where participants initiated the action after the go-signal onset.

EEG recordings were processed with MNE-Python (Gramfort et al., 2013, 2014). Data were filtered with a .1 Hz high pass filter and a 40 Hz low pass filter. The friction of the VR headset on the frontal and prefrontal electrodes (Fp1, Fp2, F7, F3, Fz, F4, F8, Fpz, AF7, AF3, AF4, AF8, F5, F1, F2, F6) during testing motivated us to remove these channels during data cleaning to increase the signal-noise ratio. Each trial was time-locked on the object onset and included a length of 2400 ms, starting 1200 ms before the object onset and finishing 1200 ms after the object onset. The Autoreject algorithm (Jas, Engemann, Bekhti, Raimondo, & Gramfort, 2017) was used to detect and repair artifacts. The motivation to use this algorithm was to maximize the signal-noise ratio in adapting automatically the artefact detection parameters for each participant. It implements topographic interpolations (Perrin, Pernier, Bertrand, & Echallier, 1989) to correct bad segments. The signal of each trial was then transformed using a surface Laplacian filter, resulting in a reference-free current source density (CSD) which increases the spatial resolution of the signal and reduces the artifacts due to volume conduction (Kayser & Tenke, 2015a, 2015b; Tenke & Kayser, 2012).

Time-frequency representations (TFRs) of the oscillatory activity were computed for each trial using a wavelet approach (Tallon-Baudry & Bertrand, 1999) to evaluate the specificity of the TE on the alpha and mu-band oscillations. A family of Morlet wavelets (Gaussian-windowed complex sine wave) was built to perform the convolution via fast Fourier transform over each channel. The family of wavelets was parametrized to extract frequencies from 4 Hz to 35 Hz. The number of cycles of the wavelets was linearly-adapted, from 3 cycles for the lowest frequency and 10 cycles for the highest frequency. This precaution was used to keep a well-balanced trade-off between time and frequency resolution at each frequency. Following the convolution, each trial vector was re-segmented on a time-window starting 1000 ms before the object onset and finishing 800 ms after the object onset. This re-segmentation allowed the removal of edge artifacts.

On one hand, to evaluate the TE on the amplitude of the mu-band oscillations, the CSD signals were transformed into decibels relative to a baseline, where the baseline represents the averaged signal from -1000 to 0 ms period relative to the object onset.

On the other hand, to evaluate the TE on the phase of the mu-band oscillations, the inter-trial coherence (ITC, also called inter-trial phase-coherence, phase-locking factor, or phase-locking value Lachaux, Rodriguez, Martinerie, & Varela, 1999) was calculated. The ITC corresponds to the magnitude of the amplitude-normalized complex numbers averaged across trials for each time point, frequency, condition, and electrodes of interest. Ranging from 0 to 1, a value of 0 representing an absence of synchronization of phases across trials, and a value of 1 representing a perfect synchronization of the phases over trials. Hence, the ITC coupled with amplitude analysis helped to disentangle evoked from induced oscillatory activities. For each participant, the calculation of the ITC involved an equal total number of trials within each condition.

## 2.7. Statistical analysis

RStudio (v. 0.99.489) and the rstatix (v. 0.6.0) package were used to perform analysis of variances (ANOVAs) and planned comparisons analysis with Tukey's HSD tests.

Concerning the behavioral data, repeated-measures mixed-design ANOVAs were performed, with the Stimulus (trained vs non-trained object) as a within-subjects independent variable and the Training (usage vs function conditions) as a between-subjects independent variable. The TE on Movement, Grasping and Action Times were entered as dependent variables.

Concerning the EEG data, the activation of the visual system has been evaluated through the analysis of the alpha-band (8–12 Hz) activity recorded over the midline occipital electrode Oz and the activation of the motor system through the analysis of the mu-band (8–12 Hz) activity recorded over the midline centro-parietal electrode CPz (as in Proverbio, 2012; Wamain, Gabrielli, & Coello, 2016, 2018). These two electrodes

were selected to test our hypothesis. However, electrodes C3 and C4, located over left and right motor areas, respectively, have also been found sensitive to the motor activation indexed by the mu-band oscillations (Cannon et al., 2014; Muthukumaraswamy, Johnson, & McNair, 2004). Hence, electrodes C3 and C4 were also analyzed to evaluate the broad/narrow activation of the motor network during visual object processing. Electrodes CPz, Oz, C3 and C4 represented the four regions of interest (ROIs). The EEG signals of interest were the 8–12 Hz log-transformed (decibels) amplitude and ITC. Oscillatory amplitudes were converted into decibels to facilitate statistical comparisons and interpretation. Given that 1) the possible alpha modulation would occur following a minimum of one cycle (i.e. 100 ms for an oscillation of 10 Hz), 2) last a few cycles, and 3) could be contaminated from a potential tone onset, the time window of interest concerned the 100–600 ms time interval following the object onset. To calculate the TE on the EEG data, the 8–12 Hz amplitude and ITC recorded within the 100–600 ms time interval following the object onset were averaged for each ROI. Repeated-measures mixed-design ANOVAs were performed, with the Stimulus (trained vs non-trained object) and the ROI (CPz, Oz, C3 and C4) as within-subjects independent variables and the Training (usage vs function conditions) as a between-subjects independent variable. The TE on the mu-band amplitude and ITC were entered as dependent variables.

## 2.8. Data availability statement

A public data repository containing scripts and data is available at <https://osf.io/6bjuz/>.

## 3. Results

### 3.1. Behavioral results

First, movement times below 200 ms were considered as errors (i.e. default in the button press) and were discarded, representing 3.99 % of the trials. Second, for each participant and each movement, grasping and action times above or below four standard deviations from the mean were considered as outliers and removed, representing 4.92 % of the remaining trials.

During the training phase in usage condition, participants correctly performed the challenging tool use in 40.2 % and 52.5 % of the trials in the first and second trial blocks, respectively. A Pearson correlation analysis between the trial number and the percentage of success to perform the tool use in the training phase indicated a reliable increase of the performance over time ( $r = .50, p < .0001$ ). The ANOVA evaluating the TE on Movement Times did not revealed effects of the Stimulus ( $F(1,47) < 0.01; p = .99, \eta^2 p < .001$ ), the Training ( $F(1, 47) = 0.24; p = .63, \eta^2 p < .001$ ) nor their interaction ( $F(1, 47) = 1.69; p = .20, \eta^2 p < .001$ ). Concerning the TE on Grasping Times, the ANOVA did not indicated effects of the Stimulus ( $F(1, 47) = 0.08; p = .78, \eta^2 p < .001$ ), the Training ( $F(1, 47) = 2.36; p = .13, \eta^2 p = .047$ ) nor their interaction ( $F(1, 47) = .35; p = .55, \eta^2 p < .001$ ). Similarly, the ANOVA evaluating the TE on Action Times did not revealed effects of the Stimulus ( $F(1,47) = 0.45; p = .50, \eta^2 p = .001$ ), the Training ( $F(1, 47) = 0.02; p = .89, \eta^2 p = .001$ ) nor their interaction ( $F(1, 47) = 0.76; p = .39, \eta^2 p = .002$ ).

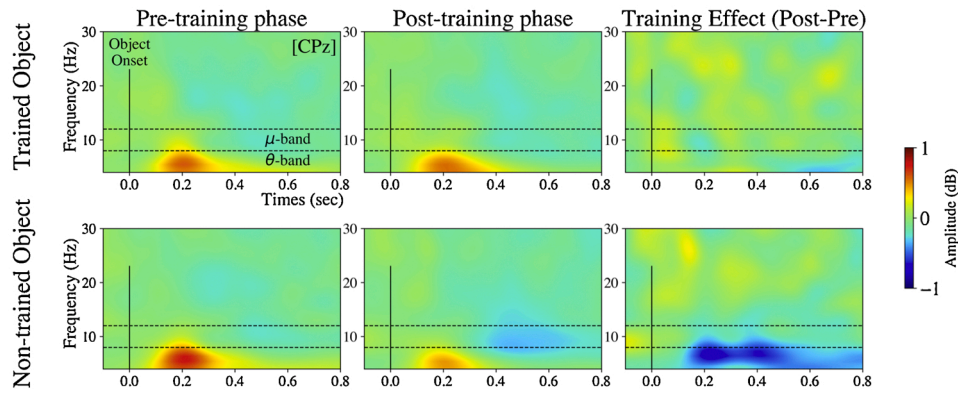
### 3.2. Electrophysiological results

The EEG analysis revealed a clear increase of amplitude in the theta-band (4–8 Hz) in the first 400 ms following the onset of all objects (Fig. 2). Then, the alpha- and beta-band (16–24 Hz) signal amplitude reduced in 200–800 ms time-window, as found in (Kourtis & Vingerhoets, 2015).

The ANOVA on the 8–12 Hz signal amplitude revealed a main effect of the Stimulus ( $F(1,156) = 7.29, p = .008, \eta^2 p = .024$ ), such as the TE were increased for non-trained objects (Mean =  $-0.11$  dB, CI = 0.04 dB) compared with the trained objects (Mean =  $-0.03$  dB, CI = 0.04 dB,



### Learning Object Usage



### Learning Object Function

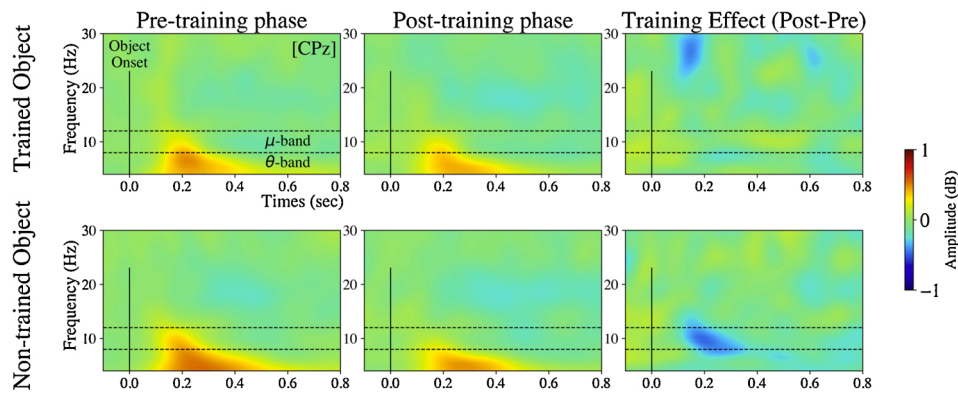


Fig. 2. Amplitude of oscillatory activity recorded at electrode CPz during the pre- and post-training phases when learning the object usage (N = 20; top) and function (N = 21; bottom). The training effect (TE) appears particularly important in the theta-band during the learning of the object usage.

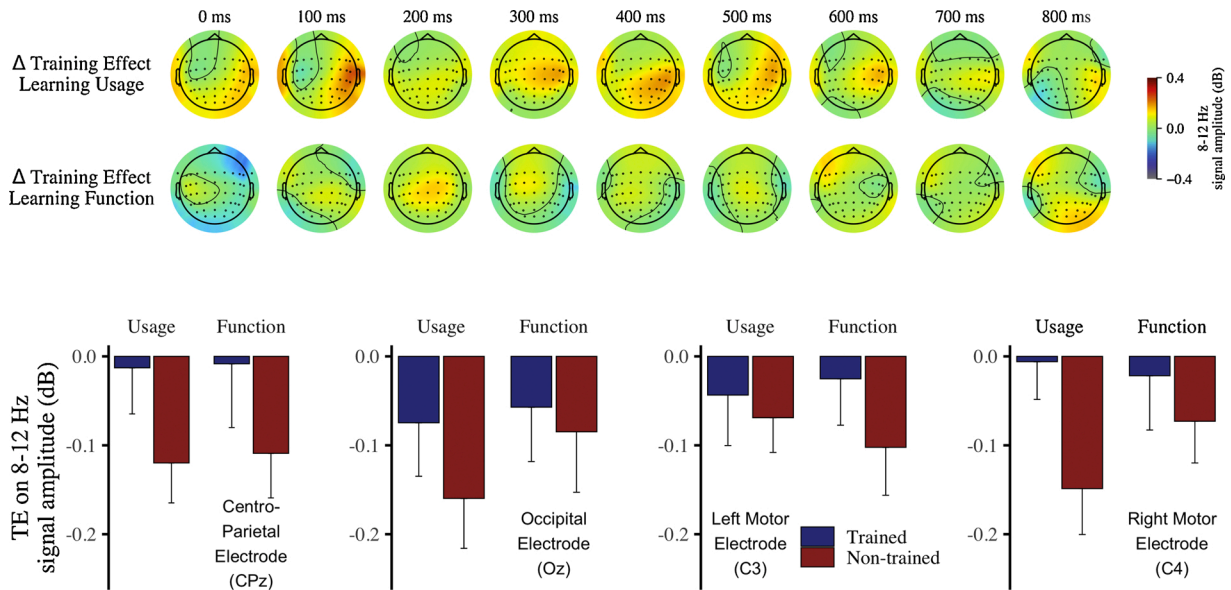


Fig. 3. Difference of training effect (TE) between the trained and the non-trained objects on the amplitude of the 8–12 Hz oscillations during visual object processing across scalp (top). Training effects depending on the regions of interest (centro-parietal, occipital, left and right motor areas), the stimulus (trained or non-trained) and the training (learning object usage or function; bottom). Training participants to associate a novel usage and functional knowledge to novel objects prevented the reduction of mu-band amplitude during visual object processing. Error bars represent one standard error of the mean.

Fig. 3). This TE reflects a reduction of the mu-band amplitude specific to non-trained objects, independently of the type of training. This also means that the trainings prevented the reduction of the mu-band amplitude during visual processing of the trained objects. No other main (all  $F < 0.52$ ; all  $p > .47$ , all  $\eta^2 p < .002$ ) or interaction effects were reported (all  $F < 0.3$ ; all  $p > .65$ , all  $\eta^2 p < .003$ ).

The ITC analysis indicated a strong synchronization in the first 200 ms following object perception, especially in the 4–10 Hz frequency range. The ANOVA revealed an effect of the Training ( $F(1,156) = 4.89$ ,  $p = .028$ ,  $\eta^2 p = .018$ ), with the TE on the 8–12 Hz ITC being generally reduced across the four ROIs when learning the object function (Mean =  $-0.01$ , CI = 0.01) compared with the learning the object usage (Mean =  $-0.03$ , CI = 0.01). The ANOVA also revealed a marginally significant interaction effect between the Training and the Stimulus ( $F(1,156) = 3.89$ ,  $p = .051$ ,  $\eta^2 p = .011$ ). The TE on the ITC seemed reduced for the trained object (Mean =  $-0.03$ , CI = 0.02) compared with the non-trained object (Mean =  $-0.01$ , CI = 0.02) when learning the function ( $p = .059$ ) but not in learning the usage ( $p = .566$ ). The ANOVA did not reveal other effect (all  $F < 1.54$ ; all  $p > .22$ , all  $\eta^2 p < .008$ ) on the TE of the 8–12 Hz ITC.

The visualization of the TFRs of the TE on the ITC did not reveal particular modulation across the frequency spectrum. However, the TFRs show that the apparent 8–12 Hz oscillatory signal originates from slower theta-band activity. The visualization of the TFRs of the TE showed that the amplitude of slow oscillations was frequency-specific and very distinct in the two learning conditions (Fig. 2). A post-hoc ANOVA has been conducted to test the TE on the theta-band (4–8 Hz) amplitude depending on the Stimulus, Training and ROIs. The analysis revealed a main effect of the Stimulus ( $F(1,156) = 15.68$ ,  $p = .0001$ ,  $\eta^2 p = .038$ ), such as the TE was increased for non-trained objects (Mean =  $-0.14$  dB, CI = 0.04 dB) compared with the trained objects (Mean =  $-0.05$  dB, CI = 0.04 dB, Fig. 4). Crucially, the analysis indicated a significant interaction effect between the Stimulus and the Training ( $F(1,117) = 6.12$ ,  $p = .014$ ,  $\eta^2 p = .015$ ), with the TE on the amplitude of theta-band oscillations being significantly reduced for the non-trained object (Mean =  $-0.19$  dB, CI = 0.06 dB) compared with the trained object (Mean =  $-0.04$  dB, CI = 0.05 dB) when learning the usage ( $p < .0001$ ) but not when learning the function only ( $p = .34$ ). This indicates a modulation of theta-band oscillations during visual object processing,

but specifically when the object is associated with motor content. The ANOVA did not reveal any other effect (all  $F < 1.51$ ; all  $p > .22$ , all  $\eta^2 p < .006$ ).

#### 4. Discussion

In this study, we assessed whether the affordance processing of objects is primarily guided by motor and/or semantic information, hence defending either the embodied cognition or reasoning-based approach of visual object processing. Using an immersive virtual reality setup coupled with EEG recording, participants were trained with novel object usage or function before and after performing a delayed grasp-and-move task. In both training conditions, the EEG training effects were particularly visible on the non-trained objects. This means that the processing of the non-trained objects, rather than the trained objects, differed in the pre- and post-training phases. Therefore, these effects suggest that training the objects prevented the reduction of the EEG signals during visual object processing that would have occurred otherwise. In this sense, both functional and motoric information modulated the motor network during visual object processing, as indexed by the mu-band oscillations. However, only the learning of tool use increased the posterior theta-band activity. This brings novel information on the mechanistic role played by theta-band rhythms and learned object information on perception, such as visual object processing appears predominantly guided by embodied motor knowledge rather than conceptual knowledge about the function.

We expected delays in reaction times with the trained compared to the non-trained object induced via the tool use training, indicating a competition between the multiple action components recruited during recognition (Cisek, 2007; Cisek & Kalaska, 2005, 2010), such as different handgrips, as found in previous studies (Jax & Buxbaum, 2010, 2013). Indeed, participants reported using a different hand grip to perform the tool use during the training phase. However, the analysis of the behavioral TE effect did not reveal such lags. The most likely reason is that, in our delayed-response paradigm, the pre-tone periods were long enough to plan robust motor decisions. Considering only our behavioral data, the study would support the literature proposing that motor knowledge about objects is selectively activated upon task requirements (Daprati & Sirigu, 2006; Lindemann, Stenneken, van Schie,

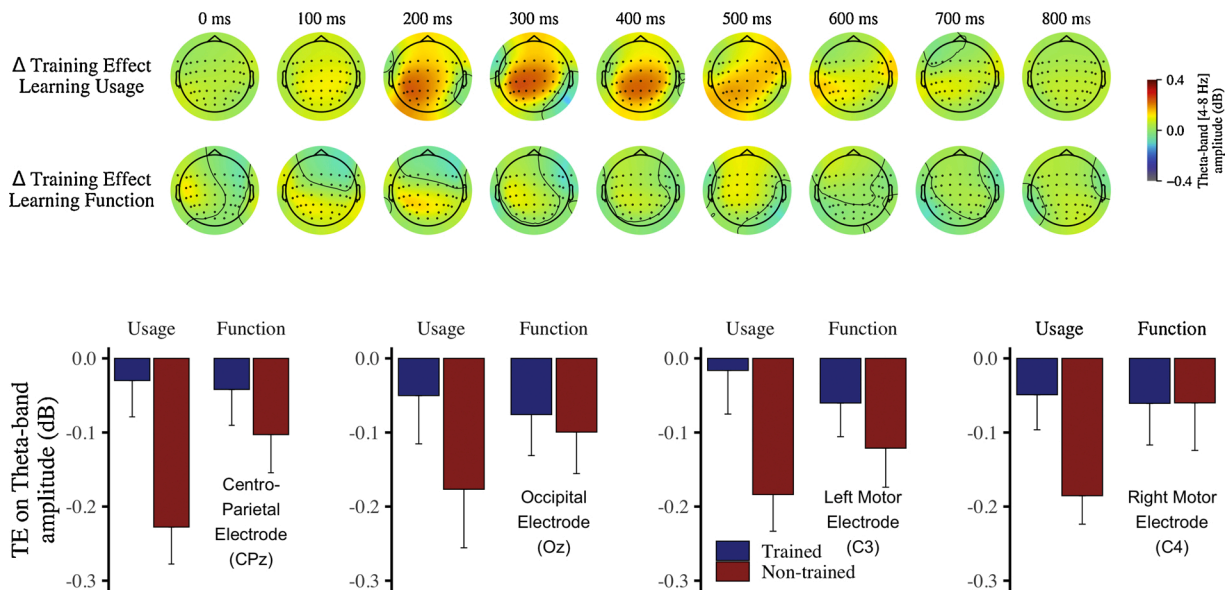


Fig. 4. Difference of training effect (TE) between the trained and the non-trained objects on the amplitude of theta-band (4–8 Hz) oscillations during object processing across scalp (top). Training effects depending on the regions of interest (centro-parietal, occipital, left and right motor areas), the stimulus (trained or non-trained) and the training (learning object usage or function; bottom). Learning the usage of a novel object prevented the desynchronization of theta-band oscillations from central to occipital cortical areas during visual object processing. Error bars represent one standard error of the mean.

& Bekkering, 2006). However, our EEG data surely challenge this claim.

In both learning conditions, the trained objects were associated with the perceptual outcome of the box opening. Thus, the theta-band modulations induced by learning the object usage might rely primarily on the manipulative information rather than the visual information associated with the novel object. This would indicate that, along with the motor mu-band oscillation, the increase of the posterior theta-band oscillatory activity directly depends on the learned object affordance (Borghi & Riggio, 2015). The present EEG analysis revealed evidence that associating function knowledge to a novel object suffices to shape motor processing involved during object recognition. Associating motor contents along with such function knowledge (i.e. the tool use) impacted the theta-band activity recorded in a broad range of posterior cortical areas during object recognition.

Theta rhythms have been associated with executive control (Cavanagh & Frank, 2014; Harper, Malone, & Bernat, 2014; Töllner et al., 2017), attention mechanisms (Clayton, Yeung, & Kadosh, 2015) and working memory (Gulbinaite, van Rijn, & Cohen, 2014; Klimesch et al., 2010). Theta rhythms play a role in large-scale network communication allowing the access to episodic and recent information from memory (see Herweg, Solomon, & Kahana, 2020; Klimesch et al., 2010 for reviews), crucial for object recognition. Using an incidental learning task, Hanslmayr, Spitzer, and Bäuml (2009) found that parietal theta-band event-related synchronization (ERS) is associated with the recollection of non-semantic information. The present training effect on theta-band activity could reflect the influence of top-down information derived from memory on the bilateral Structure system, that is the dorso-dorsal visuo-motor pathways specialized in the extraction of the geometrical features crucial for grasping actions. The results suggest that novel embodied motor representations contribute to the activation of the Structure system during object recognition. This contribution would occur even when the perception is influenced by tool use representations irrelevant to the task at hand, such as grasping to move the object. It would support the affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010) proposing that all motor representations, even irrelevant ones to the task, are gathered to feed action decision-making processing. Hence, one could question the behavioral relevance to distinguish task-relevant from task-irrelevant motor representations involved in perceptual processing such as object recognition.

A recent eye-tracking study suggested that object and tool recognition relies on the visual decoding of the functional ends (Federico & Brandimonte, 2020), indicating that semantic information, rather than motor information, is at the core of the processing. Theoretically, such a proposal question whether tools are primarily grounded on sensorimotor (embodied cognition approach) or semantic (reasoning-based approach) representations. Experimentally, the problem with known tools is that they are always associated with both sensorimotor and semantic knowledge and can be hardly isolated. The present EEG results suggest that semantics can affect motor processing during object recognition. However, tool use information remained the predominant source of top-down modulation on distributed visuo-motor pathways, hence favoring the embodied approach of object processing. Supporting this idea, a recent study showed that learning semantic invariants such as an object label influences object processing and the oscillatory activity in posterior cortical areas, but only when a novel manipulation (i.e. a tool use) is learned simultaneously (Foerster, Borghi, & Goslin, 2020).

In conclusion, tool use information, rather than function information, represent the main source of influence on visual object processing. This effect relies on theta-band oscillation, which could sign for the activation of learned affordances in action systems (Borghi & Riggio, 2015). Learning a novel tool use or a tool function affected the mu-band oscillations, which suggests that both motor and function knowledge about the surrounding objects interfere with the processing of their visual affordance.

## Declaration of Competing Interest

The authors report no declarations of interest.

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