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RESEARCH ARTICLE

Fast periodic visual stimulation to study tool-selective processing in the human brain

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Abstract

Because tools are manipulated for the purpose of action, they are often considered to be a specific object category that associates perceptual and motor properties. Their neural processing has been studied extensively by comparing the cortical activity elicited by the separate presentation of tool and non-tool objects, assuming that observed differences are solely due to activity selective for processing tools. Here, using a fast periodic visual stimulation (FPVS) paradigm, we isolated EEG activity selectively related to the processing of tool objects embedded in a stream of non-tool objects. Participants saw a continuous sequence of tool and non-tool images at a 3.7 Hz presentation rate, arranged as a repeating pattern of four non-tool images followed by one tool image. We expected the stimulation to generate an EEG response at the frequency of image presentation (3.7 Hz) and its harmonics, reflecting activity common to the processing of tool and non-tool images. Most importantly, if tool and non-tool images evoked different neural responses, we expected this differential activity to generate an additional response at the frequency of tool images (3.7 Hz/5 = 0.74 Hz). To ensure that this response was not due to unaccounted for systematic differences in low-level visual features, we also tested a phase-scrambled version of the sequence. The periodic insertion of tool stimuli within a stream of non-tool stimuli elicited a significant EEG response at the tool-selective frequency and its harmonics. This response was reduced when the images were phase-scrambled. We conclude that FPVS is a promising technique to selectively measure tool-related activity.

Keywords Electroencephalogram · Tool processing · Fast periodic visual stimulation

Introduction

Recognizing and identifying objects according to specific properties and meaning is a task the brain achieves easily and automatically (VanRullen and Thorpe 2001). Research about the visual system has identified cortical areas responsible for the categorization of objects and their semantic processing, mostly in the ventral part of the temporal cortex (Ishai et al. 2000; Peelen and Caramazza 2012). In addition to this ventral stream, a dorsal stream was described, which is involved in the spatial processing of visual information (Goodale and Milner 1992; Ungerleider and Haxby 1994). Tools are physical items that can be grasped and manipulated for the purpose of action and, therefore, represent a particular object category as they associate perceptual and motor properties. Accordingly, the image of a tool can activate both the ventral and dorsal streams (Chao and Martin 2000; Creem-Regehr and Lee 2005). Viewing tools activate the ventral stream for the identification of their specific meaningful category but also the parietal and premotor areas of the dorsal stream, related to the preparation of actions towards tools (Rizzolatti et al. 2002). Interestingly, premotor activation does not require the intention to handle—passive viewing of a tool is sufficient to generate activity in the left dorsal premotor cortex (Grafton et al. 1997; Chao and Martin 2000), as well as the parietal cortex (Johnson-Frey 2004). As such, studying how tools are processed allows investigating how perceptual inputs are translated into actions.

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How the visual system processes tool objects has been studied extensively using non-invasive neuroimaging and neurophysiological techniques, such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). An inherent drawback of the previous approaches is that they rely on assessing the differences between the brain responses elicited by the separate presentation of tool vs. non-tool objects by subtraction, assuming that the differences capture the cortical activity selective for the processing of tool objects. However, differences in the neural activity elicited by the comparison between of tools vs. non-tool objects could, at least in part, be due to differences in low-level features distinguishing at least a subset of tool objects vs. non-tool control objects. For example, Grafton et al. (1997) showed premotor activation during simple observation of tools by comparing tools and simple fractals. It is extremely delicate to determine whether the observed differential activity is due to the observation of tools, or influenced by differences in low-level visual features. Separating neural correlates of low-level visual processing from higher order processing is consequently a major obstacle in visual research (Koenig-Robert and VanRullen 2013). In addition, the tool-selective activity could also be explained by differences in the brain processes consequential to the identification of tool vs. non-tool objects.

Here, we address the issue of untangling low-level visual processes from higher order processing by directly indexing the differential response to tool objects embedded in a stream of non-tool objects, using a novel paradigm called fast periodic visual stimulation (FPVS) (Rossion et al. 2015). It relies on the fact that periodic sensory stimulation delivered at a given frequency can elicit a periodic EEG response at the frequency of stimulation and its harmonics (also called steady-state evoked potentials) (Regan 1977). The FPVS approach presents several advantages over the standard recording of event-related potentials time-locked to the onset of a transient sensory stimulus. First, FPVS often yields robust EEG responses with a high signal-to-noise ratio (Vialatte et al. 2010; Norcia et al. 2015). Second, it has the advantage of isolating and concentrating the response at well-defined frequencies. Third, responses can be obtained by periodically modulating low-level features such as visual luminance or contrast, but also by periodically modulating high-level visual features such as facial identity or facial expression (Alonso-Prieto et al. 2013; Gentile and Rossion 2014). Finally, it was recently shown that a variation of the FPVS can be used to disentangle cortical activity related to high-order visual processes from cortical activity related to the processing of low-level visual features, by concentrating both responses at distinct frequencies (Lochy et al. 2015, 2018; Dzhelyova et al. 2017; Stothart et al. 2017; Xu et al. 2017; Quek and Rossion 2017; Guillaume et al. 2018). In this specific paradigm, visual stimuli belonging to two different categories are presented as a periodic pattern of *n* base stimuli belonging to a first category, followed by one contrasting stimulus belonging to a second category. With this approach, cortical activity triggered by both types of stimuli can be expected to generate a periodic EEG signal at the base frequency of visual stimulus presentation, whereas cortical activity differentially triggered by the two categories of stimuli can be expected to generate a periodic EEG signal at the frequency of the critical stimulus. To ensure that the activity at the frequency of critical stimulation is not due to systematic unaccounted differences in low-level visual features between the two different stimulus categories, the exact same sequence can be shown, replacing each image by its phase-scrambled version. Phase scrambling is a frequently used methodology to create control images in visual research as it removes the semantic content of image while preserving low-level visual features such as spatial frequency, contrast and luminance. Using this FPVS paradigm, Liu-Shuang et al. (2014) showed that the periodic presentation of face and non-face stimuli elicits activity at the base frequency originating primarily from low-level visual areas, but also activity at the frequency isolating face-selective cortical processes (see also Retter and Rossion 2015; Quek and Rossion 2017). Using the same methods, similar studies have succeeded to dissociate EEG activities specific to words from those elicited by presentation of non-word strings of characters (Lochy et al. 2015, 2016).

As such, we hypothesised that if tools and non-tool objects are processed differently in the human brain, the presentation of tool images embedded in a periodic stream of non-tool images should lead to a periodic EEG signal at the frequency of the tool stimulus, resulting in a direct measure of the cortical activity selective to the processing of tool images.

Importantly, we hypothesised that if this activity results from high-order visual processes, this response would be absent in the EEG responses elicited by phase-scrambled versions of the same tool and non-tool images.

Materials and methods

Participants

Eleven right-handed healthy participants (6 women and 5 men, aged 22 ± 2 years, range 20–26 years) took part in the experiment. These numbers have been shown to be sufficient to show significant responses using similar FPVS paradigm (Liu-Shuang et al. 2014; Lochy et al. 2015; Rossion et al. 2015). Inclusion criteria were the absence of neurological or psychiatric disease, no regular drug use, normal or corrected-to normal vision, and having slept at least 6 h during the previous night. Approval for the experiment was obtained from the local ethical committee (Commission d'Ethique Biomédicale Hospitalo-Facultaire de l'Université catholique de Louvain) in agreement with the Declaration of Helsinki. All participants signed an informed consent form and received financial compensation for their participation.

Stimuli

We collected 285 highly variable natural photographs accessible on the internet: 98 photographs of manually handled tools (hammer, saw, pencil, cutlery, etc.) and 187 photographs of non-tool images (animals, buildings, plants, furniture etc.). Tools were broadly defined as manufactured objects that can be manipulated to perform a motor action, e.g., a pen to write, a cup to drink, a milk cartridge to pour milk from, etc. The images were transformed to grayscale and cropped/scaled to 256 × 256 pixels. Importantly, the images varied strongly in terms of background, viewpoint, size, luminance, spatial frequency and contrast, and were not equalized in terms of spatial frequency, luminance or contrast, such that the full natural image set varied widely in terms of low-level properties, as well as higher level properties such as viewpoint, background, lighting, shape, and texture (Rossion et al. 2015). While low-level properties are known to influence tool processing, the influence of high-level features, such as shape, is less clear (Sakuraba et al. 2012; Wilf et al. 2013; Bracci and Op de Beeck 2016; Proklova et al. 2016; Chen et al. 2017). However, introducing important variability in both low- and high-level properties across all images of the present study ensured that *toolness* was the only consistent difference between tool and non-tool images.

We further created a second separate image set by phase scrambling each tool and non-tool image. Phase scrambling was achieved by replacing the phases of each image by random coefficients. Both sets are available upon request (Fig. 1).

Procedure

Participants were seated 58.5 cm in front of a 32″ Display + + IPS LCD Monitor (1920 × 1080 resolution, Cambridge research System, Rochester, UK, 100 Hz refresh rate) with their head stabilized using a chinrest. The images appeared on a light grey background, subtending a visual angle of 14.7°. Each trial consisted of a central blue fixation cross (30 × 30 pixels, visual angle of 1.7°′) that appeared for 1–2 s before the start of the periodic visual stimulation, and remained visible throughout the entire trial. Participants were asked to fixate the cross throughout the trial, but were allowed to blink. Throughout the trial, images appeared at a strict periodic base rate of 3.7 Hz, that we achieved by

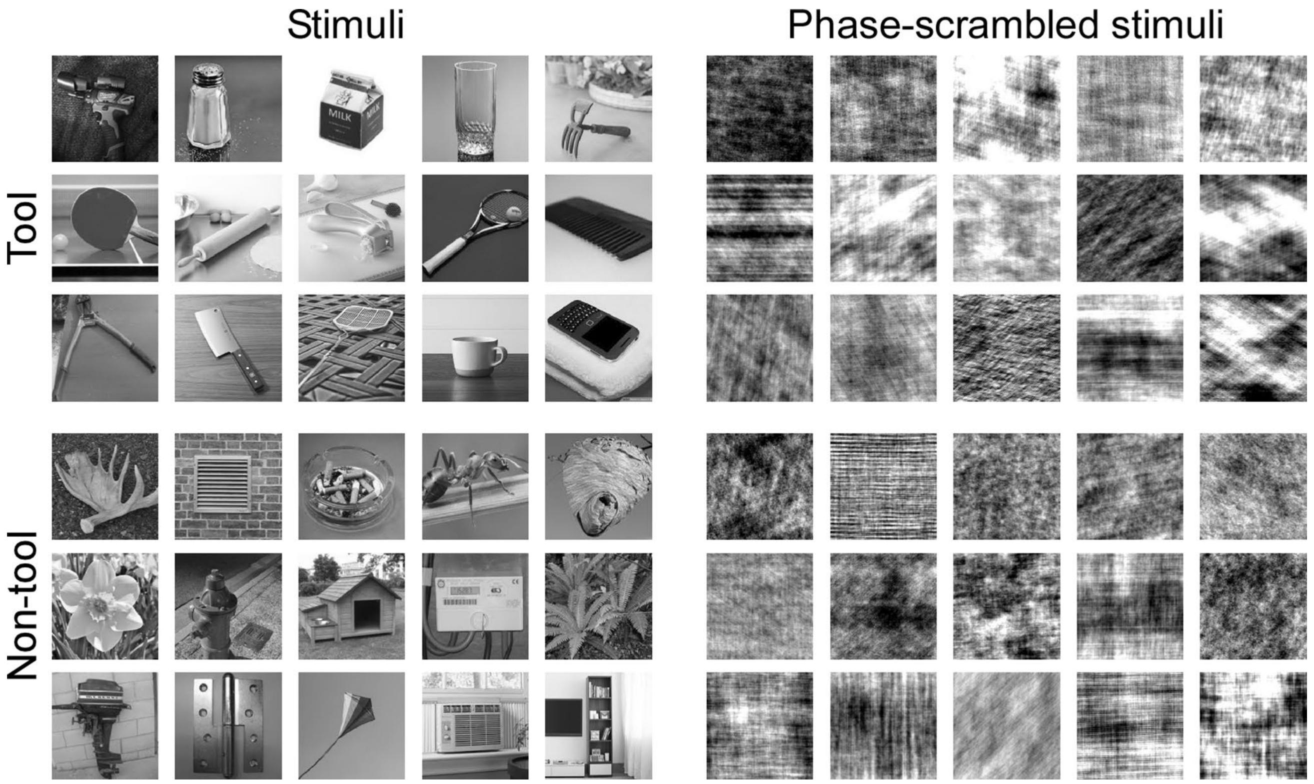

Fig. 1 Examples of stimuli (tools and non-tools, phase-scrambled and non phase-scrambled)

modulating the contrast of each image sinusoidally from 0 to 100 to 0%, creating a continuous flow of information. This periodic stimulation had a fade-in period of 5 s during which the maximal contrast was progressively increased (Fig. 2), followed by 60 s of stimulation during which maximum contrast remained constant at 100%, and then a 5 s of fade-out of contrast. Fade-in and fade-out periods were included to avoid an abrupt onset and offset of stimulation, as well as to reduce eye movements and blinks triggered by stimulation onset (Alonso-Prieto et al. 2013). A trial consisted, therefore, of a sequence of 259 images. At the end of the periodic stimulation, the fixation cross remained on the screen for 1–2 s. The onset of each trial was self-paced.

Images were presented as a pattern consisting of four non-tool images (or phase-scrambled non-tool images) followed by one tool image (or phase-scrambled tool image). Therefore, tool images (or phase-scrambled tool images) were presented at a frequency of 3.7 Hz/5 = 0.74 Hz. As such, there were two frequencies of interest: a base response at 3.7 Hz which corresponds to the presentation rate of both tool and non-tool images, and the embedded tool-selective frequency at 0.74 Hz, which corresponds to the presentation rate of the tool images. Three conditions were tested. In the first condition (TARGET IMAGE), participants were presented a target image at the beginning of each trial, and were requested to count the number of occurrences of this target image. Importantly, the target image, which changed every trial, was always a non-tool image. In the second condition (FIXATION CROSS), participants were asked how many times the fixation cross changed colour during the trial. In these trials, the fixation cross changed to red during 200 ms, 2–8 times per trial. These two conditions showing tool images embedded in a stream of non-tool objects were used to examine whether the elicited responses were modulated by attending to the content of the non-tool images. Finally, in a third condition (SCRAMBLED), each non-tool and tool image was replaced by their respective phase-scrambled versions. As in the FIXATION CROSS condition, participants were asked to count the number of colour changes of the fixation cross, and provide a verbal response at the end of each trial. This third condition showing phase-scrambled tool images embedded in a stream of phase-scrambled non-tool images was used to examine whether the tool-selective response observed in the first two conditions could be due to systematic unaccounted differences in global low-level properties of tool and non-tool images (luminance, contrast, and spatial frequency spectrum). Eight trials belonging to each condition were presented in a randomised fashion in four blocks of six trials. The presentation was programmed using SinStim, a custom-made Java program (Bruno Rossion, Face Categorization lab, Université catholique de Louvain, Belgium).

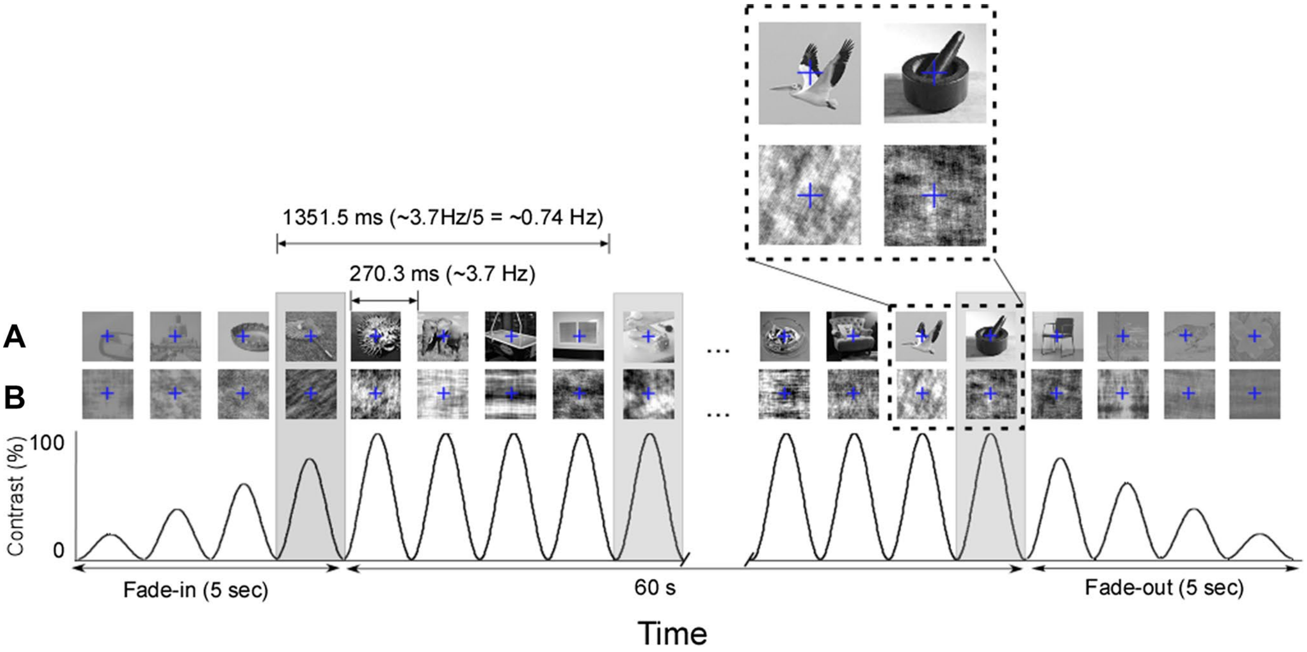

Fig. 2 Fast periodic visual stimulation using non-tool and tool images (**a**) and phase-scrambled non-tool and tool images (**b**). The periodic visual stimulation was achieved by a sinusoidal modulation of contrast at a strict periodic rate of 3.7 Hz. The stimulation sequence consisted of a pattern of four non-tool images followed by a tool image, resulting in the periodic presentation of a tool image at 0.74 Hz

Measures

The EEG was recorded using 64 Ag–AgCl electrodes placed on the scalp according to the international 10/10 system (Waveguard64 cap, Cephalon A/S, Nørresundby, Denmark). Electrode impedances were kept below 15 kΩ. Signals were amplified and recorded using a sampling rate of 1000 Hz and an average reference (64-channel high-speed amplifier, Advanced Neuro Technology, Enschede, The Netherlands). The EEG data were analysed offline using Letswave 6 (http://www.nocions.org/letswave/) running in MATLAB 2014a. The data were first segmented from 2 s before the fade-in period (with a duration of 5 s) to 2 s after fade-out period (with a duration of 5 s), resulting in 24 epochs of a total length of 74 s (2 s + 5 $s_{\text{fade-in}}$ + 60 $s_{\text{stimulation}}$ + 5 $s_{\text{fade-out}}$ + 2 s). We then applied a Butterworth 50 Hz notch filter followed by a bandpass-filter (0.1–100 Hz).

Frequency-domain analysis

All epochs were segmented to the stimulation length during which the maximum contrast was 100%, i.e., from + 5 to + 65 s relative to fade-in onset. Eye blink and movement artefacts were removed using an independent component analysis (ICA, Hyvärinen and Oja 2000; Colon et al. 2012, 2015; Nozaradan et al. 2012b). Separate 60-s average waveforms were computed for each condition and participant. Subsequently, we performed a fast Fourier transform (FFT) to transform the data into the frequency domain. Then, the contribution of background noise was removed by subtracting, at each bin of the frequency spectra, the average amplitude measured at neighbouring frequency bins [four frequency bins ranging from − 0.03 to − 0.08 Hz and four frequency bins ranging from + 0.03 to + 0.08 Hz relative to each frequency bin (Mouraux et al. 2011; Nozaradan et al. 2012a; Colon et al. 2015)]. The validity of this subtraction procedure relies on the assumption that, in the absence of a strong periodic signal, the signal amplitude at any given frequency bin should be similar to the signal amplitude of the mean of the surrounding frequency bins (Mouraux et al. 2011; Retter and Rossion 2015). Two measures were extracted from the EEG frequency spectra. The first was a measure of the amplitude of the periodic EEG signal at the base frequency (i.e., 3.7 Hz and its harmonics). The second was a measure of the amplitude of the periodic EEG signal at the tool-selective frequency (i.e., 0.74 Hz and its harmonics). To select the statistically significant harmonics to include in the estimation of response amplitude, we expressed the amplitude at each harmonic frequency as a z-score relative to the mean and standard deviation of the amplitude of the 20 neighbouring bins of the FFT, ranging from − 0.03 to − 0.18 Hz and from + 0.03 to + 0.18 Hz. A z-score greater than 1.64 (i.e., $p < 0.05$, one-tailed) was the criterion to consider the amplitude at that frequency significantly greater than the amplitude at neighbouring frequency bins (Lochy et al. 2015; Rossion et al. 2015; Dzhelyova et al. 2017; Quek and Rossion 2017). This selection of harmonics was performed on the grand average frequency spectrum, averaged over all participants, conditions, and scalp electrodes.

Activity originating from ventral and dorsal streams may be expected to contribute predominantly to the EEG signals recorded from occipito-temporal and central electrodes, respectively. Therefore, separate single-subject estimates of base and tool-selective EEG responses were computed by averaging the responses obtained at central (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, and CP2) and occipito-temporal (P7, P5, P6, P8, PO3, PO4, PO5, PO6, PO7, PO8, POz, Oz, O1, and O2) channels. We then summed the noise-subtracted amplitudes at the base frequency and its significant harmonics, and at the tool-selective frequency and its significant harmonics (excluding tool-selective frequencies overlapping with the base frequency), to obtain a single measure of the base and tool-selective response for each participant and condition (Retter and Rossion 2015; Quek and Rossion 2017).

Time-domain analysis

To assess the time course of the periodic EEG responses, the filtered signals were segmented in 1350 ms epochs, corresponding to a complete stimulation sequence (four non-tool stimuli and one tool stimulus), yielding a total of 416 epochs per participant and condition. Such as for the frequency-domain analysis, eye blink and movement artefacts were removed using an independent component analysis. Epochs containing deflections larger than 80 μV were removed. Separate averages were then computed for each participant and condition. To separate the base response from the tool-selective response, we filtered out the respective unwanted frequency components (Dzhelyova et al. 2017; Quek and Rossion 2017). Specifically, to visualize the base response in the time domain, we filtered out the tool-selective response using a series of FFT multi-notch filter at the frequencies which were significant in the frequency-domain analysis, i.e., 0.74, 1.48, 2.22, and 2.96 Hz. Similarly, to obtain the tool-selective response, we removed the base response using a series of notch filters at the frequencies which were significant in the frequency-domain analysis, i.e., 3. 7, 7.4, 11.1, 14.8, 18.5, 22.2, and 25.93 Hz.

Analysis

The sum of the amplitudes of the base and tool-selective EEG responses obtained in the different conditions were compared using a repeated-measures analysis of variance

(ANOVA) with three factors: *electrode* (OCCIPITO-TEMPORAL, CENTRAL), *condition* (TARGET IMAGE, FIXATION CROSS, SCRAMBLED), and *response type* (BASE, TOOL-SELECTIVE). Effect sizes were measured using partial Eta squared. Greenhouse–Geisser corrections of degrees of freedom were performed when necessary. Significant interactions were followed up by contrast analyses using partial ANOVA or paired-sample Student *t* tests. Significance level was set at $p \leq 0.05$ and corrected using the Bonferroni correction procedure.

Results

Frequency-domain results

In all experimental conditions, a base response at 3.7 Hz and its harmonics was observed, clearly standing out from neighbouring bins (Fig. 3). This increase was significant for the first seven harmonics (Fig. 4). The topographical distribution of this base response was maximal over occipital electrodes, and symmetrically distributed over the two hemispheres (see Fig. 5a). In both the TARGET IMAGE and the FIXATION CROSS conditions, the EEG frequency spectra revealed clear peaks at the frequency of tool presentation and its harmonics (Fig. 3). Significant peaks were present up to the fourth harmonic in the TARGET IMAGE condition, and up to the ninth harmonic in the FIXATION CROSS condition (Fig. 4). It should be noted that a different amount of harmonics does not necessarily reflect a greater response in the FIXATION CROSS condition, but a difference in the time course of the periodic signal (Zhou et al. 2016). No tool-selective responses reached significance in the SCRAMBLED condition. As compared to the occipital scalp topography of the base response, the scalp topography of tool-selective EEG response observed in the TARGET IMAGE and the FIXATION CROSS conditions extended towards occipito-temporal and central electrodes (Fig. 5b).

The repeated-measures ANOVA on the sum of the noise-subtracted amplitudes showed a main effect of *response type* [$F(1,10) = 110.9$, $p < 0.001$, $\eta^2_p = 0.67$], a main effect of *electrodes* [$F(1,10) = 131.8$, $p < 0.001$, $\eta^2_p = 0.47$], a main effect of *condition* [$F(2,20) = 4.1$, $p = 0.03$, $\eta^2_p = 0.046$], an interaction between the factors *electrodes* and *response type* [$F(1,10) = 80.6$, $p < 0.001$, $\eta^2_p = 0.27$], an interaction between the factors *response type* and *condition* [$F(2,20) = 12.0$, $p[GG] = 0.002$, $\eta^2_p = 0.14$] and a triple interaction between the factors *condition, response type*, and *electrode* [$F(2,20) = 4.46$, $p = 0.02$, $\eta^2_p = 0.02$].

We subsequently followed up this triple interaction by subjecting the base response and tool-selective response to separate repeated-measures ANOVA with two factors: *condition* (TARGET IMAGE, FIXATION CROSS, SCRAMBLED) and *electrode* (CENTRAL and OCCIPITO-TEMPORAL). The analysis of the base response showed a main effect of *electrode* [$F(1,10) = 130.56$, $p > 0.001$, $\eta^2_p = 0.57$] with larger activity at occipito-temporal electrodes as compared to

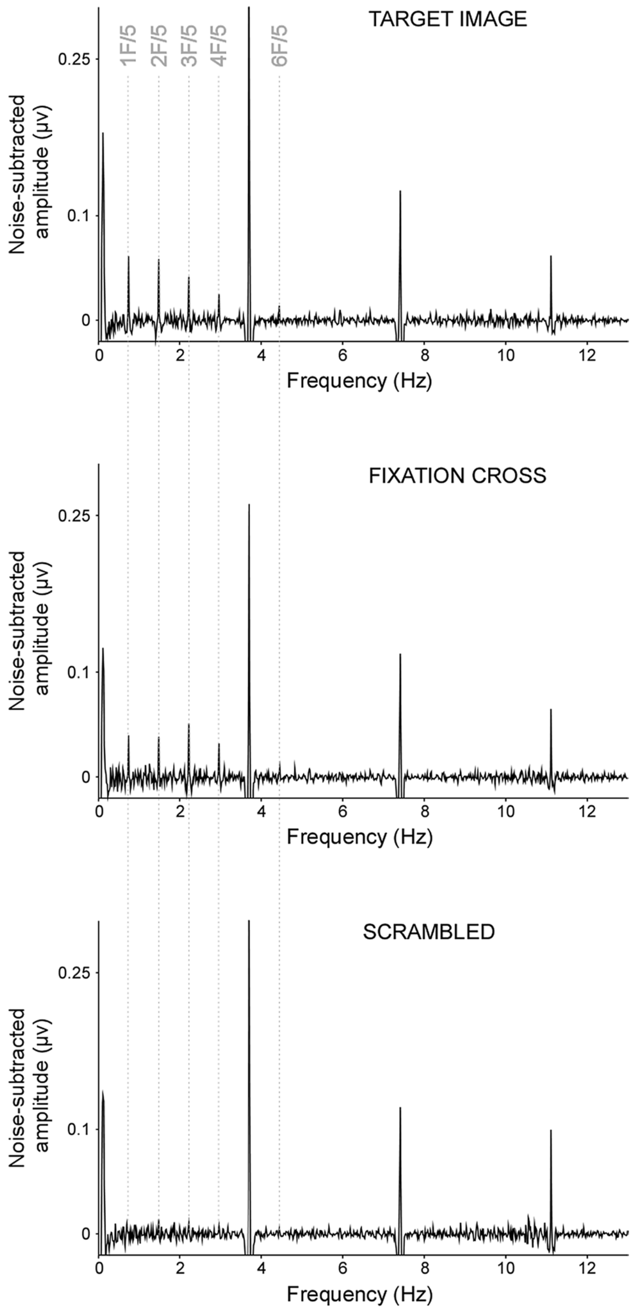

Fig. 3 Group-level average EEG frequency spectrum for each condition, averaged across all scalp channels. Tool-selective responses are indicated by the dashed vertical lines. Clear tool-selective responses are evident in the TARGET IMAGE and the FIXATION CROSS conditions. In contrast, no tool-selective response is observed in the SCRAMBLED condition. The base response is present at 3.7 Hz and harmonics in all three conditions

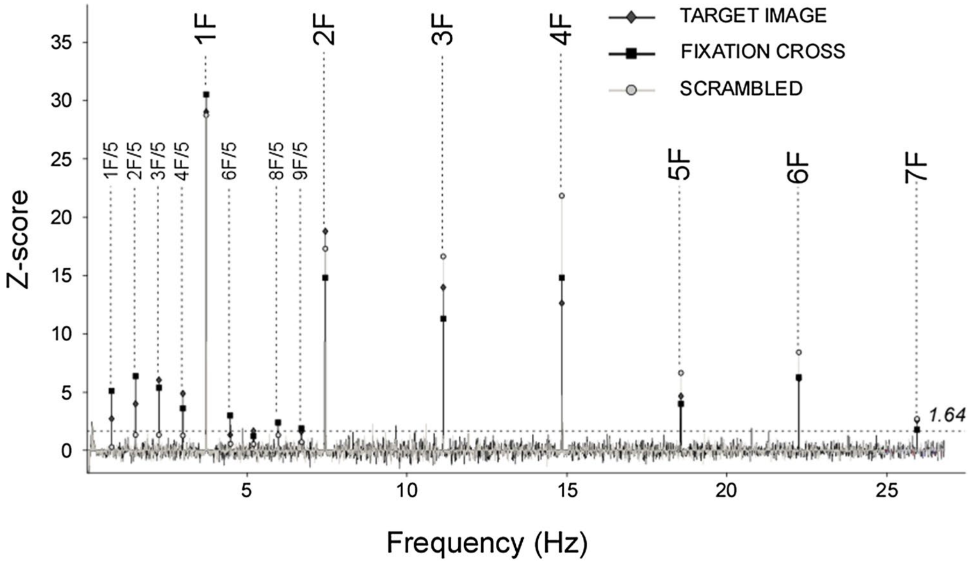

Fig. 4 Frequency spectrum of the EEG activity recorded in the TARGET IMAGE, FIXATION CROSS, and SCRAMBLED conditions, expressed as *z*-scores. The dotted line depicts the significance criterion of $z < 1.64$ (one-tailed)

central electrodes. There was no significant main effect of *condition* [$F(2,20) = 3.92$, p[GG] = 0.06, $\eta^2_p = 0.09$], and no interaction between the two factors [$F(2,20) = 1.39$, p[GG] = 0.27, $\eta^2_p = 0.01$] (Fig. 6a). Conversely, the analysis of the tool-selective response showed a main effect of *condition* [$F(2, 20) = 38.46$, $p < 0.001$, $\eta^2_p = 0.57$], a main effect of *electrode* [$F(1, 10) = 25.5$, $p < 0.001$, $\eta^2_p = 0.37$] as well as a significant interaction between the two factors [$F(2, 20) = 12.1$, $p < 0.001$, $\eta^2_p = 0.15$]. To explore the interaction, we first used paired *t* test to look at the difference between electrode pools in each condition. There appeared to be a larger activity in the OCCIPITO-TEMPORAL electrodes as compared to the CENTRAL electrodes in both FIXATION CROSS condition [$t(10) = -4.58$, $p = 0.001$] and the TARGET IMAGE condition [$t(10) = -4.79$, $p < 0.001$], but not in the SCRAMBLED condition [$t(10) = -1.7$, $p = 0.12$]. Post-hoc paired-sample *t* tests (alpha = 0.008) showed that the signal at tool-selective frequencies was significantly greater in the TARGET IMAGE condition as compared to the SCRAMBLED condition, both at OCCIPITO-TEMPORAL [$t(10) = 8.2$, $p < 0.001$] and CENTRAL electrodes [$t(10) = 4.57$, $p = 0.001$]. The response obtained in the FIXATION CROSS condition was also significantly greater than the signal obtained in SCRAMBLED condition [CENTRAL electrodes: $t(10) = 6.63$, $p < 0.001$; OCCIPITO-TEMPORAL electrodes: $t(10) = 4.98$, $p < 0.001$]. There was no significant difference in the amplitude of the tool-selective response between the TARGET IMAGE and FIXATION CROSS conditions, both at CENTRAL [$t(10) = -1.05$, $p = 0.32$] and OCCIPITO-TEMPORAL electrodes [$t(10) = -1.61$, $p = 0.14$] (Fig. 6b).

Time-domain results

Analysis in the time-domain analysis revealed a pronounced differential tool-selective response in the FIXATION CROSS and the TARGET IMAGE conditions. This differential response disappeared in the SCRAMBLED condition (Fig. 7b). The base response showed the activity to the stimulus repetition which is similar for all condition (Fig. 7a).

Discussion

In this experiment, we used fast periodic visual stimulation (FPVS) to tag EEG activity related to the differential processing of tool images compared to non-tool images. Our results showed that the periodic insertion of a tool image within a periodic stream of non-tool images separates EEG activity related to the high-order processing of visual features distinguishing tool vs. non-tool objects (Fig. 7b) from the EEG activity related to the processing of low-level visual features common to the two object categories (Fig. 7a). Specifically, we showed that an image of a tool inserted as a periodic contrasting stimulus within a stream of non-tool objects elicits a significant EEG response at the frequency of tool presentation, maximal over occipito-temporal regions, and extending towards central regions. Importantly, this tool-selective response was present regardless of whether participants attended to the content of the images (detecting the occurrence of a pre-specified target image) or performed a completely orthogonal task (detecting the occurrence of a colour change in the fixation cross). In contrast, little or no activity at the frequency of

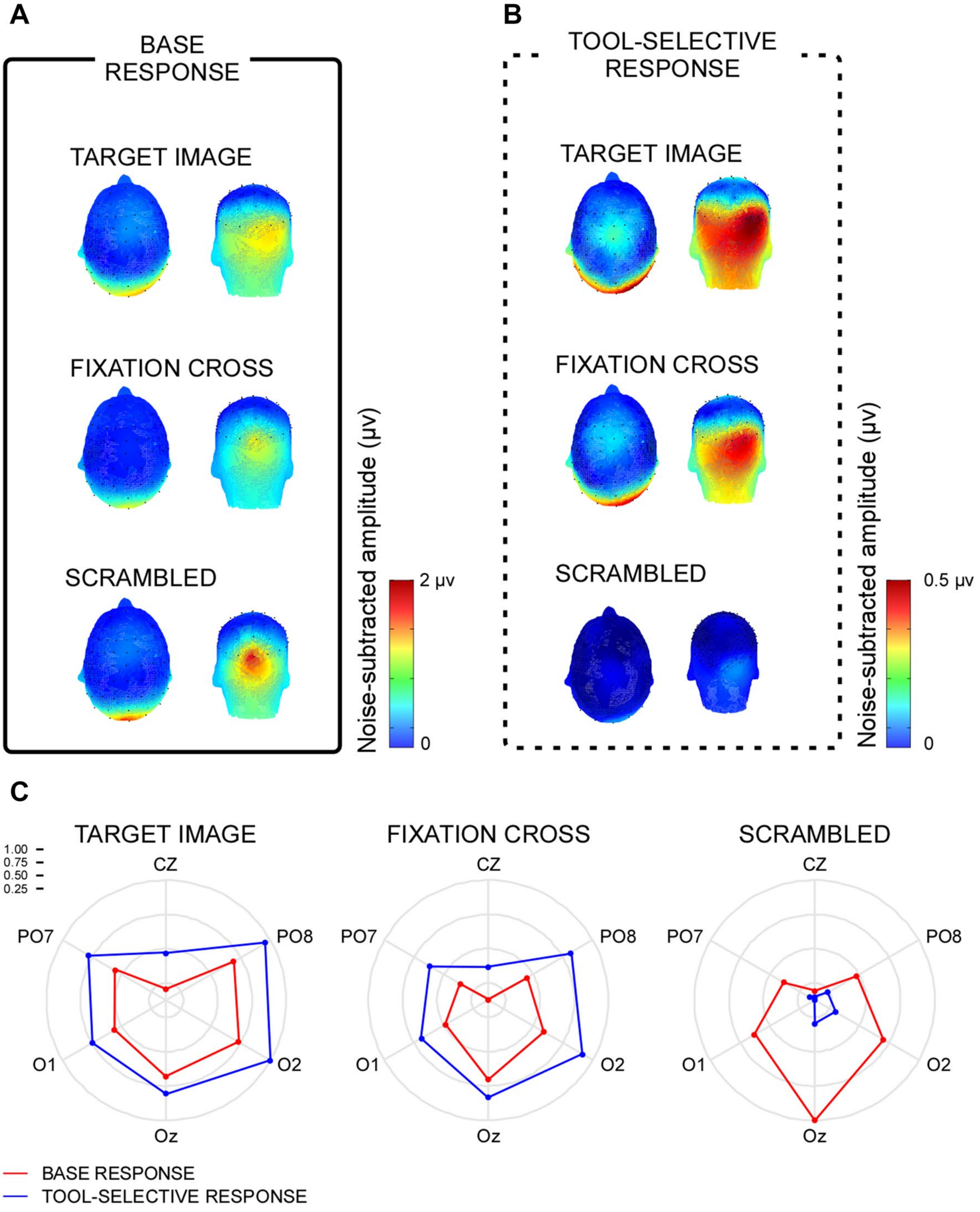

Fig. 5 Scalp topography: distribution of the noise-subtracted amplitude over the scalp electrodes of the periodic base response (**a**) and the tool-selective response (**b**) obtained in the different experimental conditions. Topographies of the base response were mainly characterized by activity over occipital electrodes. In the TARGET IMAGE and the FIXATION CROSS conditions, the tool-selective response was predominant over occipito-temporal and central electrodes. No clear activity at the tool-selective frequencies was observed in the SCRAMBLED condition. **c** Base response and tool-selective response over occipital (O1, OZ, and O2), occipito-temporal (PO7 and PO8) and central (CZ) electrodes for each condition. The data were normalized per response type (base response and tool-selective response) across the three conditions

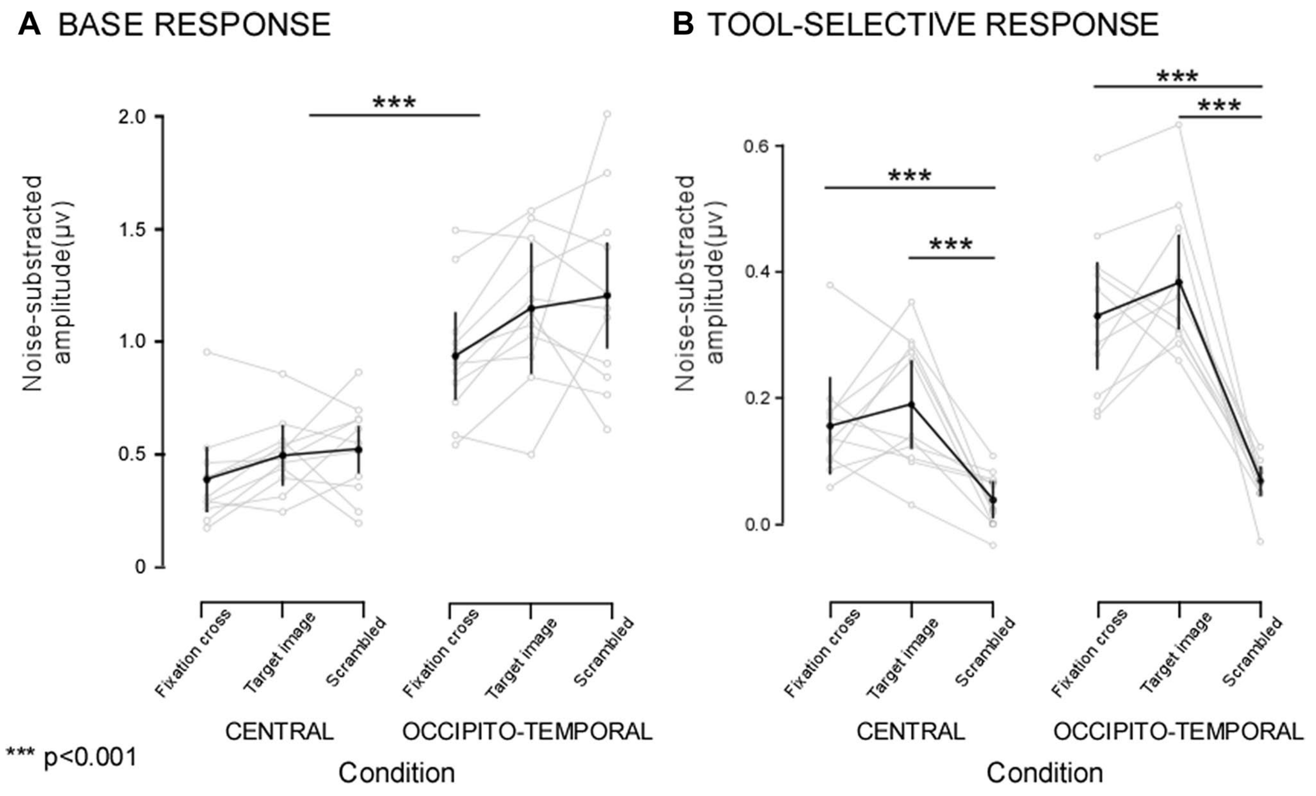

Fig. 6 Single-subject and group-level average amplitude of the base response and the tool-selective response obtained in the TARGET IMAGE, FIXATION CROSS and SCRAMBLED conditions, at occipito-temporal and central electrodes. While the base response was similar across conditions, the tool-selective response was present only in the TARGET IMAGE and the FIXATION CROSS conditions. Individual values are shown as grey connecting lines and group-level average values are shown as black connecting lines. The vertical bars represent the 95% confidence interval

the contrasting stimulus was observed when participants viewed phase-scrambled versions of the images (SCRAMBLED condition) (Fig. 6b).

The usefulness of phase scrambling comes from its ability to destroy the semantic content of an image while preserving most of the global low-level properties of the images (Ales et al. 2012) and, hence, had the tool-selective response entirely been driven by systematic differences in low-level features distinguishing tools and non-tools that are preserved in the phase-scrambled condition, a tool-selective response of the same magnitude would have been expected in the SCRAMBLED condition. However, one must take into consideration the fact that phase scrambling does not flawlessly preserve all low-level visual features of an image (Thomson 1999; Stojanoski and Cusack 2014). Hence, the absence of a tool-selective response in the SCRAMBLED condition does not allow us to definitely exclude that some unaccounted low-level features distinguishing tool from non-tool images contributed to the contrast responses observed in the TARGET IMAGE and FIXATION CROSS conditions. However, this seems highly unlikely, considering that both tool and non-tool images varied strongly across exemplars in terms of both their low-level features and their high-level features (luminance, spatial frequency and contrast, background, viewpoint, shape, lightning, etc.).

It is well known that stimulating the visual system at a fixed periodic rate with simple visual stimuli, such as flickering lights, elicits a periodic EEG signal which is maximal at occipital electrodes, and is thought to mainly reflect low-level stages of visual processing occurring in primary visual areas (Müller et al. 1997; Pastor et al. 2003; Di Russo et al. 2007; Norcia et al. 2015). Whereas the scalp topography of the base response was maximal over occipital electrodes, and thus likely reflects low-level stages of visual processing common to the processing of non-tool and tool stimuli, the scalp topography of the tool-selective response was maximal over occipito-temporal and central electrodes. Although one should be cautious to infer conclusions based on topographies (Urbach and Kutas 2002, 2006), the different topographical distribution of the tool-selective response as compared to the base response suggests that the tool-selective response originated, at least in part, from cortical regions distinct from those activated by the modulation of low-level visual features and captured in the base response. Most importantly, the scalp topography of the tool-selective response is compatible with activation of the ventral and

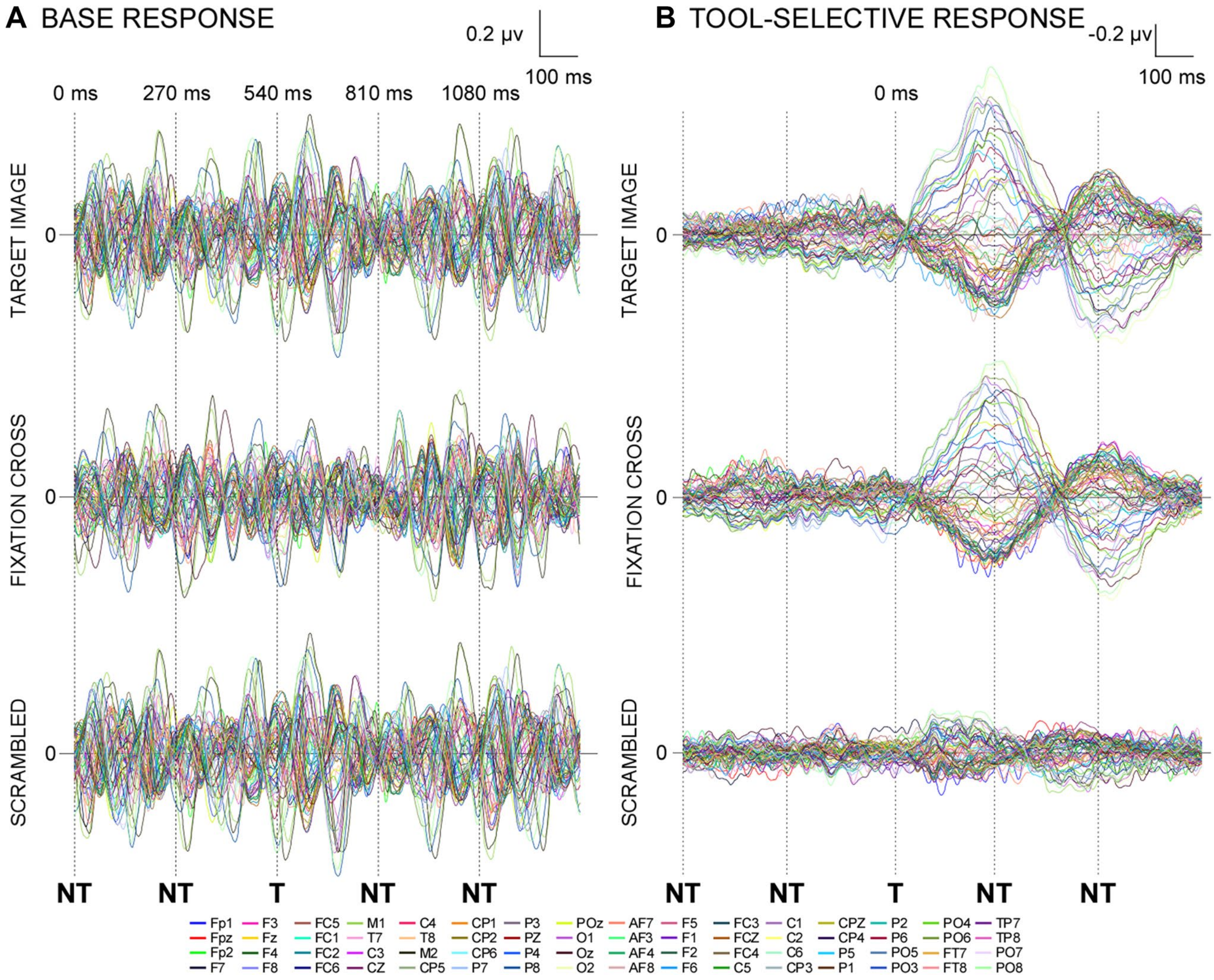

Fig. 7 Time-domain EEG waveforms averaged across repetition patterns in the TARGET IMAGE, FIXATION CROSS, and SCRAMBLED conditions. The waveforms obtained at each scalp channel are shown as different colours. **a** Base response to one full sequence (5 cycles), isolated by filtering out the tool-selective response using notch filters at 0.74 Hz and harmonics. **b** Tool-selective response to one full sequence (5 cycles), isolated by filtering out the base response using notch filters at 3.7 Hz and harmonics. NT indicates the onsets of the four non-tool images. T indicates the onsets of the contrasting tool image

dorsal visual streams. The ventral stream is located in the temporal lobe, including the fusiform gyrus which is thought to be involved in the visual processing of graspable objects (Martin et al. 1996; Chao et al. 1999; Creem-Regehr and Lee 2005). The bilateral occipito-temporal activity that we observed could thus be related to ventral stream processes involved in object semantics (Fabre-Thorpe 2011). Importantly, the finding that contrasting tool vs. non-tool objects elicits an occipito-temporal tool-selective response suggests that tool and non-tool objects differentially activate this occipito-temporal network. Supporting this hypothesis, Martin et al. (1996), Chao et al. (1999), Ishai et al. (2000) and more recently Hutchison et al. (2014) showed that different categories of objects activate the semantic network differently within the temporal lobe. The scalp topography of the tool-selective response also extended towards central electrodes. This might be related to to a recruitment of the dorsal visual stream and premotor during passive viewing of tool objects (Grafton et al. 1997). Interestingly, this extension towards central electrodes was not observed for category-selective EEG responses elicited by other kinds of visual categories using a similar FPVS paradigm. Indeed, word-selective activity has been shown to be most pronounced over left occipital electrodes (Lochy et al. 2015, 2016), while face-selective activity has been shown to be maximal over right temporo-occipital electrodes (Liu-Shuang et al. 2014; Dzhelyova et al. 2017; Xu et al. 2017; Quek and Rossion 2017). Similarly, FPVS studies have shown that numerical processing elicits selective activity maximal over medial occipital regions (Guillaume et al. 2018; Park 2018). As such, higher order category-specific activity can be measured at occipital electrodes. In other words, the topography of category-selective EEG responses obtained using the FPVS paradigm appears to depend on the eliciting object category. This suggests that this activity is not merely related to the detection of a contrasting event whatever its category.

It has also been demonstrated that stimulating the visual system at different frequencies results in different scalp topographies for the same stimulus type (Lithari et al. 2016). Therefore, testing the responses elicited by contrasting tool and non-tool objects presented at different frequencies could be of interest in future studies.

The tool-selective response could reflect selective cortical activity related to the differential processing of tool objects. One other option is that the tool-selective response does not reflect the activity related to the tool stimulus, but rather the response to a base stimulus after the presentation of the tool stimulus. However, this option appears unlikely. Indeed, we show that the deviation in signal corresponding to the tool-selective response started shortly after the occurrence of the tool stimulus and, most importantly, before the occurrence of the next base stimulus (Fig. 7b). This indicates that it was predominantly triggered by the tool image, rather than by the occurrence of a non-tool image following the presentation of a tool image.

In addition, the tool-selective response could also reflect the ability of the brain to recognize regular patterns of inputs across repetitions. Fiser and Aslin (2002) showed that fixed sequences of shapes presented repeatedly during a familiarization session can be distinguished from novel sequences of familiar shapes, indicating the ability to learn temporal sequences implicitly or explicitly. Thus, it is possible that participants in the present experiment did learn the periodic image pattern (four non-tool images followed by one tool image) over the course of the experiment. While we did not test the possible contribution of such sequence learning to the observed tool-selective response, there is good reason to think that the tool-selective response we observe here does not reflect an expectation response. Recently, Quek and Rossion (2017) showed that face stimuli embedded in a stream of non-face images elicit a similar face-selective response irrespective of whether the faces appeared at temporally predictable or unpredictable intervals (i.e., periodic vs. nonperiodic). Regardless, it should be noted that even if participants did indeed tap into the tool image periodicity, this interpretation remains compatible with the hypothesis that the tool-selective activity is due to automatic image categorization. Indeed, implicit learning of the temporal regularity requires discerning the difference in image content defining tool vs. non-tool images.

Overall, it appears that the FPVS can circumvent the need of subtracting signals from different contrasting conditions by concentrating activity related to high-level and low-level visual processing at distinct frequencies. In addition, the choice of control or base stimuli can be as diverse as needed, enabling researchers to introduce a lot of variety in the used stimuli, reducing the possibility of a bias due to low-level visual features and the attention towards the target stimuli. Moreover, this method eliminates the need to standardise images on features such as spatial frequency, luminance and contrast, as its strength lies in the variation in these features. As such, this approach allows for more ecological visual stimulation.

In conclusion, we show that it is possible to index EEG activity related to the differential processing of tool vs. non-tool objects using FPVS. Furthermore, we show that the tool-selective response related to processing tool objects cannot be explained by attention, relevance, or differences in low-level visual features. The proposed approach offers new possibilities to study, in humans, distinct processing by directly tagging and measuring the differential activity.

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Compliance with ethical standards

Conflict of interest The authors declare no competing financial interest.

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