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Objects with motor valence affect the visual processing of human body parts: Evidence from behavioural and ERP studies

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Abstract

Recent findings indicate that the mental representation of an object contains crucial information about the motor interactions relevant for its intended functional use, suggesting a possible action-specific link with body effectors. For example, in the visual system, the extrastriate body area (EBA) responds to full body and body part images according to a functional/semantic organizational principle. However, the pliancy of the relationship between objects and body parts remains under-investigated. The present study aims to i) investigate this relationship more directly by assessing whether recognition of specific body parts can be facilitated by a brief exposure to functionally-related objects (Experiment 1) and ii) whether the functional relationship between objects and body parts modulates a posterior body-sensitive ERP waveform, peaking around 200 ms, and the more centro-parietal P300, linked to item categorization processes and visual awareness (Experiment 2). Participants were asked to quickly recognize targets (pictures of hands or feet) preceded by a functionally related (e.g., drum for hand target), unrelated (e.g., drum for foot target), or neutral (e.g., unknown object for both targets) prime. Findings showed that participants' performance was significantly more accurate with related than unrelated primes and that ERP amplitudes were modulated by the relationship between the prime and the target. These findings confirm the existence of action-specific links between objects and body parts and expand on recent findings on categorical organization of neural responses to human effectors in the visual system.

Keywords: body representation · visual perception · EBA · action ·ERP

1.1 Introduction

Objects can be characterized not only on the basis of their physical characteristics (e.g., shape) but also by their intrinsic functional properties, which can be defined as the 'actions performed with/on' an object (Bonfiglioli, 2010). As originally argued by Gibson (1979), objects elicit certain action possibilities that serve to ground functionally adequate behaviour; such dynamic property implies that the mental representation of an object is not only based on perceptual characteristics (what it is) but also on how it can be used (Barsalou, 1999; 2008).

A number of studies have shown that the visual presentation of tools activates motor-related and somatosensory cortical areas such as the posterior middle temporal gyrus, the ventral premotor area and the posterior parietal cortex (Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Proverbio, 2012), highlighting that, even in the absence of actual movement, these areas are involved in the processing of objects that have a motor valence. These data suggest that our cognitive system includes a representation of the motor component associated with a given object (e.g., Bub, Masson, & Cree, 2008; Buxbaum & Saffran, 2001). Crucially, this information (the perceptual configuration of the object and related motor traces) must be integrated with the representation of our own body (de Vignemont, 2010; Gallagher, 2005; Head & Holmes, 1911; Longo & Haggard 2010) as, ultimately, we perform the actions through our body effectors. Bonfiglioli (2010) reported evidence of implicit association between objects and the body parts involved in their use, showing that the mental representation of objects includes conceptual links to body parts. A central question concerns whether, to which extent and within which time frame, viewing objects automatically evokes body parts representations.

During the last decade, a number of studies have shown that the extrastriate cortex responds selectively to specific object categories, suggesting that the visual processing of faces and bodies differs from the visual processing of non-body objects (Op de Beeck, Haushofer & Kanwisher 2008; Peelen & Downing, 2007; Kanwisher & Yovel, 2006; Thierry, Pegna, Dodds, Roberts, Basan, & Downing, 2006; Maurer, Grand, & Mondloch, 2002; Leder & Bruce, 2000; Bentin, Allison, Puce, Perez, & McCarthy, 1996). The *extrastriate body area* (EBA; Downing, Jiang, Shuman & Kanwisher, 2001), on the lateral surface of the occipitotemporal cortex, and the *fusiform body area* (FBA; Peelen & Downing, 2005), in the medial fusiform gyrus and partially overlapping with the fusiform face area, show stronger activation to visually presented bodies and body parts compared to faces, objects, and a large number of other visual categories (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006).

Evidence of the critical role of EBA in processing body information has been provided by Urgesi and colleagues (2004) who showed that disrupting this area 150–250 msec after stimulus onset using transcranial magnetic stimulation impairs individuals' perceptual discrimination on a delayed match-to-sample task for full bodies and body parts, but not for face or object parts (Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Calvo-Merino, Haggard & Aglioti, 2007; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). In addition, it has been shown that the execution of (unseen) movements with different body parts activates the EBA (Astafiev, Stanley, Shulman, & Corbetta, 2004) and, more interestingly, the movement of specific body parts partially overlap with the body parts represented within the visual body map (Orlov, Makin & Zohary, 2010). This motor-driven activation seems to suggest that visual and motor-related information converge within the occipito-temporal cortex (OTC) in a body part specific manner. In line with this hypothesis, other studies have shown that body parts are semantically coded as 'motor effectors' (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012; Bracci, Caramazza, & Peelen 2015), suggesting that the action-relatedness of a given body part is a fundamental organizational principle in the occipito-temporal pole (Bracci & Peelen 2013; Bracci et al., 2015; Lingnau & Downing, 2015).

Adding to the functional imaging and brain stimulation evidence, EEG (Thierry et al., 2006) and intracranial studies (Pourtois, Peelen, Spinelli, Seeck, & Vuilleumier, 2007) have identified a body-specific Event-Related Potential (ERP) that appears as a cortical negative deflection peaking around 200 msec after stimulus onset (this component has been named differently by different authors, for example, body-N190 and N1; because it typically peaks around 200 msec, we will use the term N200 here). This component has been observed bilaterally over the occipito-parietal electrodes (PO7, PO8, P7, P8, P9, P10) (Sadeh, Pitcher, Brandman, Eisen, Thaler, & Yovel1, 2011; Rossion & Jacques, 2008) and source localization studies have identified EBA to be the neural generator of such component (Thierry et al., 2006; Giabbiconi, Jurilj, Gruber & Vocks, 2016). Recently, Moreau and colleagues (2018) have reported theta event-related synchronization increase in response to hands and arms images compared to fingers, full bodies and non-body images in EBA. The authors argued that such frequency modulation is associated with the perception and categorical organization of body parts that are processed in action-related networks according to their functional meaning (Moreau, Pavone, Aglioti, & Candidi., 2018; Bracci et al., 2015; Lingnau & Downing, 2015).

The evidence discussed so far suggests that: i) object representations may include information on the effector involved and, ii) 'function' appears to be an intrinsic property of the body representation (Caggiano & Cocchini, 2020; Reed, McGoldrick, Shackelford & Fidopiastis, 2004). Based on these assumptions, if the organizational principle of EBA correspond to the functional meaning of body parts, then exposure to objects with motor valence could potentially affect the visual processing and categorization of body parts. With the present study, we aimed to further explore this '*functional hypothesis'* by means of a priming task. We first explored the extent of the association between objects and motor body-effector by evaluating whether recognition of body parts can be behaviourally facilitated by the presentation of functionally-related objects (Experiment 1). We adopted the same task in a second experiment (Experiment 2), in which the analysis of evoked-related potentials was used to further explore and expand on the behavioural results of Experiment 1. Because evidence in the literature indicate that the timing of the neural response to body images is characterized by a posterior body category-specific ERP that peaks around 200 msec after stimulus presentation (Thierry et al., 2006; Pourtois et al., 2007), we focused on the N200. Specifically, we predicted that the N200, recorded from P7, P8, P9, P10, PO7 and PO8 electrodes over the approximate location of EBA, would be modulated depending on whether body parts were preceded by a functional-related or functional-unrelated object. Furthermore, the P300 has been typically associated with processes involving the updating of the mental representation of stimulus context, decision making, item categorization, and visual awareness (Polich, 2007; Patel & Azzam, 2005; Picton, 1992). Therefore, to follow up on the possibility that visual processing of body parts might be influenced by prior expectations elicited by the primes, we decided to explore the potential modulation of the P300 component, over more centro-parietal sites (Linden, 2005; Proverbio, Adorni & D'Aniello, 2011; Orlandi & Proverbio, 2020). Based on these considerations, the second study aimed at determining whether the N200 and P300 components were sensitive to the potential interplay of object processing and object-effector knowledge.

1.2 Experiment 1

1.2.1 Method and procedures

In this section, we report how we determined our sample size, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

1.2.1.1 Participants

Our main hypothesis was to observe a significant difference between three conditions on the same group of participants[1]. Sample size was determined by an a priori power analysis run with G* Power 3.0.10 (Faul, Erdfelder, Buchner, & Lang, 2009) for a repeated measures F-test design with a partial η^2

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[1] An initial pilot study with a total of 10 participants was carried out to determine some aspect of the paradigm. In particular, the pilot study helped to determine the need of i) rare no-go trials to ensure a good level of attention on primes; and ii) to limit the prime nature to no-body stimuli to avoid confusion.

= .1, α = .05 and power (1-β) of .80. The 'number of groups' parameter was set a 1 and the 'number of measurements' at 3. The ‘non-sphericity correction ε’ was left at its default value of 1.

A sample of 15 participants (8 females) took part in the experiment. The Edinburgh Handedness Inventory (Oldfield, 1971) showed that the participants were right-handed (mean = .95; SD = .08; range: .79-1). Their average age was 26.13 (SD = 2.53; range= 22-31). All participants reported to have normal or corrected-to-normal vision and no history of neurological or psychiatric illness. They were naïve to the hypothesis and purpose of the study. The study was approved by the Goldsmiths Ethical Committee and all participants provided written consent.

1.2.1.2 Stimuli and materials

Stimuli consisted of a set of 20 digital greyscale photos. A subset of stimuli illustrated three types of prime objects: a drum, a foot-operated pump (pump), and an unknown object. The unknown object was a custom-built object defined as unfamiliar by an initial pilot study with participants not included in the current experiment. Each prime object was presented in four different perspectives (see Figure 1). A second set of stimuli illustrated two target body parts (hand and foot). Each stimulus (8 x 8 cm) was presented in 4 different perspectives and displayed centrally against a white background on a 19 inches CRT screen (42.06 cm x 23.66 cm). Stimuli are shown in Figure 1 (the full set of stimuli can be found

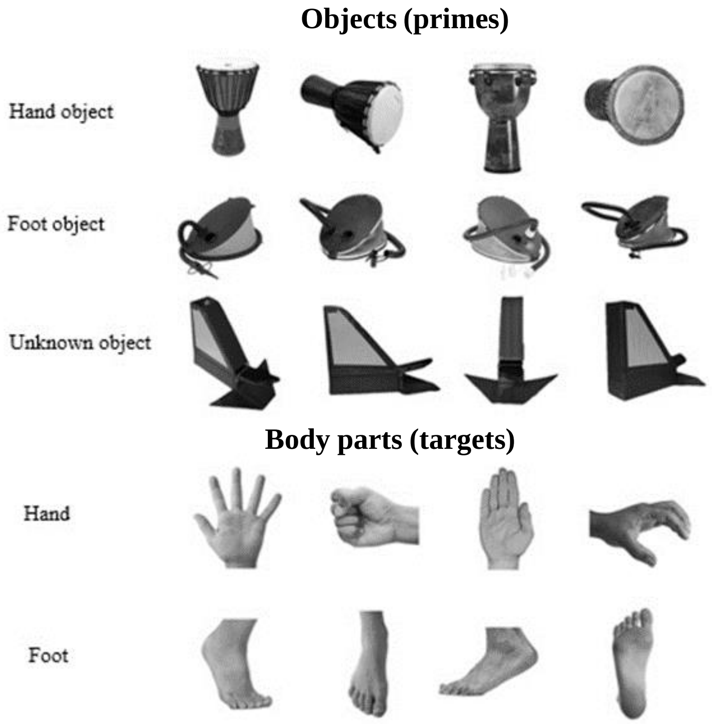

Figure 1. Illustration of stimuli (objects and body parts) presented during the task.

here: https://osf.io/5q2wv/). Stimulus presentation and data acquisition were controlled by a custom-made E-Prime 1.1 program (Schneider, Eschmann, & Zuccolotto, 2002).

1.2.1.3 Procedure

Participants sat at approximately 60 cm from the screen in an attenuated sound room and performed a priming task. The illustrations of the objects acted as prime stimuli for the target stimuli (body parts). Each trial started with the presentation of a fixation cross in the centre of the screen. After 1000 msec, one of the primes was displayed for 300 msec followed by a mask (300 msec) and then by one of the targets (see Figure 2). The relative short presentation time was meant to reduce to the minimum the possibility of participants verbally rehearsing the name of the stimuli presented while still being aware of them. Indeed, 300 msec is enough to elicit visual awareness (Pitts et al., 2014).

Participants were instructed to decide as quickly as possible, by pressing two keys on a computer keyboard with their index fingers, whether the target was a ‘hand’ or a ‘foot’. Accuracy and response latencies were recorded. Response keys were counterbalanced across participants. Depending on the type of the prime preceding the target, there were three conditions: i) Related: the prime object preceding the target was coherent with the body part that is usually used to carry out the action (i.e., drum followed by a hand or pump followed by a foot); ii) Unrelated: the prime object was not coherent with the body part that is usually used to carry out the action (i.e., drum followed by a foot or pump followed by a hand); iii) Neutral: the prime object was not related to the target (i.e., unknown object followed by either a hand or a foot). To ensure that the participants attended the event corresponding to the prime object, they were instructed to withhold their responses if a ‘star’ was superimposed to the prime object (no-go trials). The experiment was comprised of a total of 300 trials (100 for each condition), 60 of which were no-go trials equally distributed across conditions. Trials were presented in randomised order and administered in a single session, with one break, lasting approximately 15 minutes.

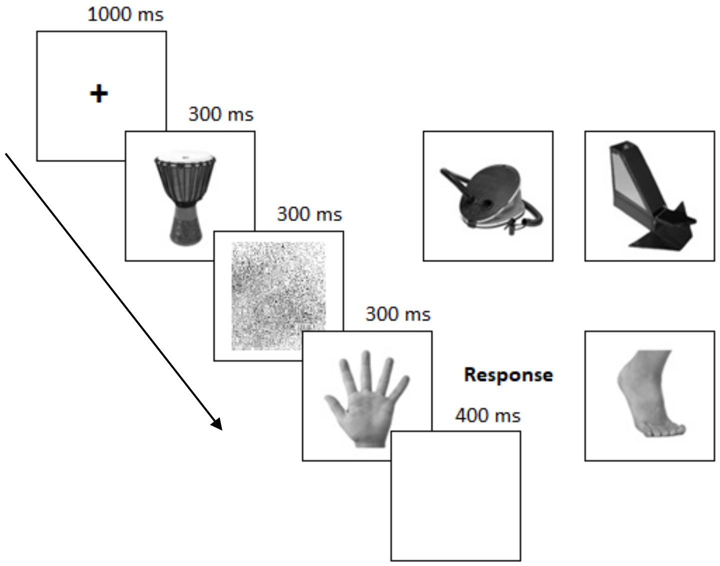

Figure 2. Schematic illustration of the task paradigm

1.2.1.4 Data Analysis

Accuracy (ACC) and response latencies (RL) for experimental trials were obtained from each participant's performance. Since the impact of primes can differently affect accuracy and speed of response across individuals, we first analysed performance for these two measures separately and then we considered a combined measure adopting the speed/accuracy trade-off formula (Soria Bauser, Suchan & Daum, 2011; Kiss, Driver & Eimer, 2009; Townsend & Ashby, 1983). Trials in which RLs were more than two standard deviations from the mean of correct trials were removed. Speed/accuracy trade-offs were calculated by dividing the mean RL for the proportion of correct responses, as in the following formula:

$$Speed/accuracy\ trade-off = \frac{RL\ (ms)}{\left(\frac{ACC}{100}\right)}$$

According to the formula, low scores indicate good performance whereas high scores indicate poor performance. This provides a measure of processing efficiency that discounts possible criterion shifts or speed/accuracy trade-offs (Kennett et al., 2001; Christie & Klein, 1995).

Shapiro-Wilk test was performed to check whether the ACC, RL and speed/accuracy trade-offs data were normally distributed. Accuracy data did not meet the normality assumption (p = .012); therefore, a non-parametric approach was used. For parametric analysis, Mauchly's test showed that the sphericity assumption was not violated ($p > .05$). Data were analyzed with the statistical package IBM SPSS 22.0 (Armonk, New York).

1.2.2 Results

Results of ACC, RLs and speed accuracy trade-offs are reported in Figure 3.

1.2.1.1 Accuracy

Participants did not show false alarms when responding to no-go trials. Overall, participants correctly responded on 88.4 % of the trials, with better performance for *Related* condition than *Unrelated* and *Neutral*. A Wilcoxon signed-rank test was used to compare accuracy between conditions. Results showed that participants were significantly more accurate on the *Related* condition compared to both *Unrelated* ($Z = 2.41$, $p = .016$) and *Neutral* ($Z = 2.16$, $p = .03$) ones. *Unrelated* and *Neutral* conditions did not show significant difference ($Z = .565$, $p = .57$).

1.2.1.2 Response latencies

Participants showed similar RLs in the three different conditions. Repeated measures ANOVA 3 (Condition) × 2 (Body Part) did not show any significant main effects for Condition [$F(2,28) = 1.04$, $p = .36$; $\eta^2_{partial} = .07$] or for Body Parts [$F(2,14) = .103$, $p = .75$; $\eta^2_{partial} = .01$]. The Condition × Body Parts interaction was also not significant [$F(2,28) = .002$, $p = .98$; $\eta^2_{partial} = .001$].

1.2.1.3 Speed-accuracy trade-off

A similar 3×2 ANOVA was also carried out for speed-accuracy trade-off data. We found a significant main effect of Condition [$F(2,28) = 4.81$, $p = .016$; $\eta^2_{partial} = .26$], whereas the main effect of Body Parts [$F(1,14) = .127$, $p = .72$; $\eta^2_{partial} = .002$] and the Condition × Body Parts interaction [$F(2,28) = .065$, $p = .93$; $\eta^2_{partial} = .001$] were not significant.

Post hoc tests on Condition adjusted for comparing a family of 3 using the Bonferroni correction (significant-$p \leq .05$), showed that participants' performance was significantly better in the *Related* compared to the *Unrelated* condition [$t\ (14) = 2.86$, $p = .037$, $d = .74$]. Differences between *Related* and

Neutral [t (14) = 2.35, p = .10, d = .61] and *Unrelated* and *Neutral* conditions were not significant [t (14) = .106, p = .9, d = .03].

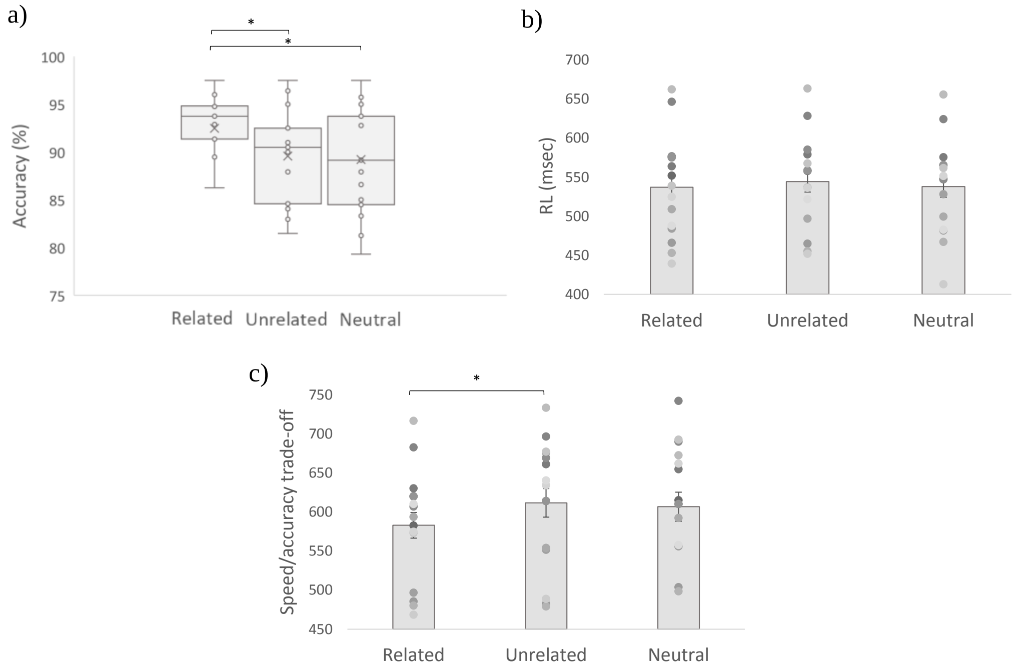

Figure 3. Participants' performance on the priming task: **a)** ACC, the middle line of the boxes represents the median, the x in the mean, the bottom line of the boxes represents the lower quartile, the top line the upper quartile, the vertical lines indicate the upper and lower extremes of each conditions; **b)** RLs, bars represents participants' averaged performance (and standard error), dots the individual participant means; **c)** speed/accuracy trade-offs, participants' averaged and individual means. * significant difference p ≤ .05

1.2.3 Discussion experiment 1

In Experiment 1 we investigated the existence of a functional relation between objects and body parts and whether such relationship is mediated by the type of action. Our findings showed that motor aspects of an object can modulate recognition of its body effectors. Specifically, when speed/accuracy trade-offs were considered, participants showed a significantly better performance on trials in the *Related* compared to the *Unrelated* conditions, suggesting a specific link between object-action-effector. This result was mainly guided by accuracy. A possible explanation for the lack of differences in RLs between conditions is that participants felt quite confident in categorizing the target stimuli because familiar (i.e., either hands or feet); however, this led to more errors (significant difference on accuracy).

Since performance on the *Neutral* condition was not significantly different either from the *Unrelated* and *Related* conditions, it is difficult to establish whether the findings should be interpreted as a benefit for object-effector congruency or a detrimental effect for object-effector incongruence. It is also possible that both interpretations are correct, that is, that performance in unrelated trials was ‘penalised’ whilst performance in related trials was advantaged. In either case, all these possible interpretations imply a pre-existing link between an object and its common body effector. In line with Bonfiglioli’s (2010) study, it seems that mental representations of objects comprise functional links with the body parts normally used to perform the related action. Similar body-action networks have been observed in language, where different areas of the motor homunculus were activated when participants passively read related action words (e.g., foot area while reading the word ‘walking’; Pulvermüller, 2005).

Further investigation of the electrophysiological signature of this process can help to better understand the aforementioned possible combination between facilitation and detrimental effects of primes across the different conditions.

1.3 Experiment 2

1.3.1 Methods and procedures

In this section, we report how we determined our sample size, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

1.3.1.1 Participants

Twenty participants were recruited for the experiment. None of these participants were included in the first experiment. Data from one participant were irredeemably corrupted due to technical problems incurred while exporting data on external disk; therefore, analyses were carried out on 19 participants (10 females). Sample size was in line with previous studies on EBA event-related potential components (Thierry et al. 2006; Moreau et al. 2018). Based on the Edinburgh Handedness Inventory (Oldfield, 1971), all participants were right-handed (mean = .98; SD = .05; range = .89-1). Their average age was 26.71 (SD = 2.76; range = 22-32). All participants reported to have normal or corrected-to-normal vision and no history of neurological or psychiatric illness. They were naïve to the hypothesis and purpose of the study. The study was approved by the Goldsmiths Ethical Committee and all participants provided written consent.

1.3.1.2 Stimuli and materials

Stimuli and material were the same as in Experiment 1.

1.3.1.3 Procedure

Procedure was the same as in Experiment 1. However, we increased the total number of trials up to 360 (120 for each condition) equally split across three conditions: *Related*, *Unrelated* and *Neutral* conditions.

It has been reported that the executing movements activate the EBA (Astafiev et al., 2004). Therefore, to minimize the effect of potential motor interference, participants were instructed to respond only if a ‘star’ was superimposed to the prime object (go-trials). This happened for a total of 60 trials (20 for each priming condition). Data recorded during the go-trials were later excluded from final analysis as their purpose was to monitor that participants maintained their attention during the entire duration of the testing session.

1.3.1.4 EEG recording and data analysis

EEG was continuously recorded using a BioSemi ActiveTwo amplifier from 64 Ag–AgCl electrodes placed according to the extended 10–20 system. All electrodes were physically referenced to the average of electrodes placed on the left and right earlobes. Four electrodes, placed at the left and right lateral canthi and above and below the left eye, were used to monitor horizontal (i.e., saccades) and vertical (i.e., blinks) eye movements, respectively. Offline pre-processing and analysis of the EEG data was conducted using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) only on trials in which participants did not provide a response. Data were filtered with a 0.1–40 Hz band-pass filter. Computerized artefact rejection was performed to discard epochs in which eye movements, excessive muscle potentials or amplifier blocking occurred. Across all participants, the rejection rate was on average of about 10%. Evoked-response potentials (ERPs) to targets were averaged over an epoch of 500 msec using a 200 msec pre-target baseline.

Statistical analysis of the ERP data focused on two time windows of interest: a N200 window and a P300 time window. In accordance with previous studies, the mean amplitude of the N200 component was measured bilaterally at posterior sites (P7, P8, P9, P10, PO7 and PO8) (Thierry et al., 2006; Rossion & Jacques, 2008; Moreau et al. 2018) between 160 and 310 msec (150 msec time window) post-target while the P300 was measured on more centro-parietal sites (CP1, CP2, P1, P2, P3 and P4) (Linden, 2005; Proverbio et al., 2011; Orlandi & Proverbio, 2020) between 265 and 395 msec (130 msec time window). These time windows were centred on the grand average post-target peak latency of N200 and P300 values (236 msec for N200 and 330 msec for P300, respectively). Mean amplitudes were normally distributed (Shapiro-Wilk test, $p > .05$) and subjected to a repeated measures analysis of variance with Condition (3 levels), Electrode (3 levels) and Hemisphere (2 levels) as factors. Mauchly's test was inspected to check for violation of the assumption of sphericity and Greenhouse–Geisser correction was used where appropriate. Post-hoc paired *t* tests were systematically adjusted using the Bonferroni correction for multiple comparisons (significant-$p \leq .05$). Data were analysed with the statistical package IBM SPSS 22.0 (Armonk, New York).

1.3.2 Results

On average, participants provided correct responses after go-trials in the 92% (SD = 4.0) of the cases, and they incorrectly provided a response after no-go trials only in 3% of the cases, demonstrating that all of them maintained a relatively high level of attention for the entire task.

1.3.2.1 Parieto-occipital N200

Figure 4 shows the grand averaged ERPs elicited on posterior sites by the target stimuli for each of the three conditions. The N200 amplitude varied according to electrode site [Electrode: $F(2,36) = 9.67$, $p < .001$; $\eta^2_{partial} = .35$] and appeared to be larger at parietal-occipital (PO7/PO8: -5.26µV) than parietal sites (P7/P8: -4.19µV; P9/P10; -4.33µV). This main effect was qualified by the interaction Electrode × Hemisphere [$F(2,36) = 5.89$, $p = .006$; $\eta^2_{partial} = .25$]. Separate follow-up analyses carried out for each hemisphere revealed that, on the left hemisphere, the N200 was larger at PO7 (-5.59µV) than at P7 (-5.52µV) [$t\ (18) = 4.40$, $p = .001$, $d = 1.01$] and P9 (-4.16µV) [$t\ (18) = 5.41$, $p < .001$, $d = 1.24$]. On the right hemisphere, the N200 was significantly more negative at PO8 (-4.93µV) than P8 (-3.87µV) only [$t\ (18) = 3.32$, $p = .011$, $d = .76$]. The main effect of Hemisphere was not significant [$F(1,18) = 0.48$, $p = .49$; $\eta^2_{partial} = .03$].

Crucially, the N200 amplitude was modulated by priming condition [Condition: F(1.53, 27.52) = 4.745 p = .030; η2 = .20]; pairwise comparisons showed that the N200 was more negative for *Related* (-4.91µV) compared to *Unrelated* (-4.19µV) stimuli [t(18) = 3.97, p = .003, *d* = .91]. The Condition effect was qualified by a significant Hemisphere × Condition interaction [F(2, 36) = 15.48, p < .001; η2 = .46]. Separate analyses run for each hemisphere showed that, at left sites, the N200 was significantly smaller in the *Unrelated* condition (-4.17µV) than both *Related* (-5.03µV) [t (18) = 4.19, p = .002, d = .96] and *Neutral* (-5.06µV) conditions [t (18) = 2.91, p = .034, d = .65], while, at right sites, a significant difference in the N200 amplitudes was observed between *Related* (-4.79µV) and *Unrelated* (-4.23µV) targets only [t (18) = 3.23, p = .014, d = .74].

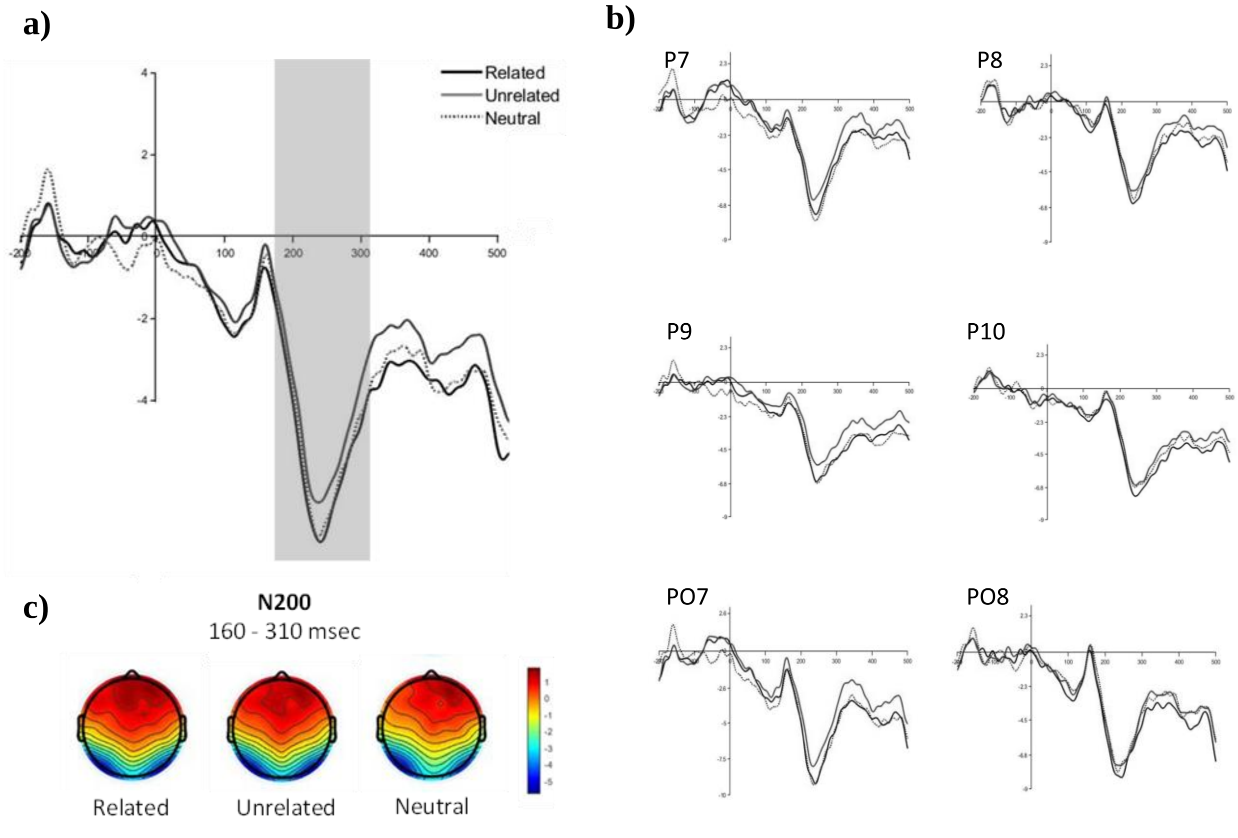

Figure 4. N200 grand average waveforms for 19 participants. Gray shadow indicates time-window of interest. **a)** Grand average waveforms collapsed across the six channels considered. **b)** Grand average waveforms for each channel **c)** Scalp topographies for each condition.

1.3.2.3 Centro-parietal P300

Figure 5 shows the grand averaged ERPs elicited on centro-parietal sites by the target stimuli for each of the three conditions. ANOVA for the P300 yielded a significant main effect of Electrode [F(1.39, 25.19) = 98.94, p < .001; $\eta^2_{partial}$ = .85] showing that this component reached its maximum amplitude at centro-parietal sites (CP1/CP2: 3.75μV) compared to the parietal ones [P1/P2, 2.21μV: t(18) = 8.86, p < .001, *d* = 2.17; P3/P4, 1.34μV: t(18) = 13.89, p < .001, *d* = 2.51]. The P300 was affected by the priming condition [Condition: F(1.36, 24.55) = 5.56 p = .018; η2 = .24]. Specifically, larger ERP responses were observed for *Unrelated* stimuli (2.94μV) compared to both R*elated* (2.25μV) [t(18) = 2.61, p = .039, *d* = .83] and *Neutral* ones (2.12μV) [t(18) = 3.09, p = .011, *d* = .78]. A significant Hemisphere × Condition interaction was also observed [F(2, 36) = 12.84, p < .001; η2 = .42]. On the left hemisphere, the P300 was significantly larger in the *Unrelated* condition (3.03μV) than both *Related* (2.18μV) [t (18) = 3.14,

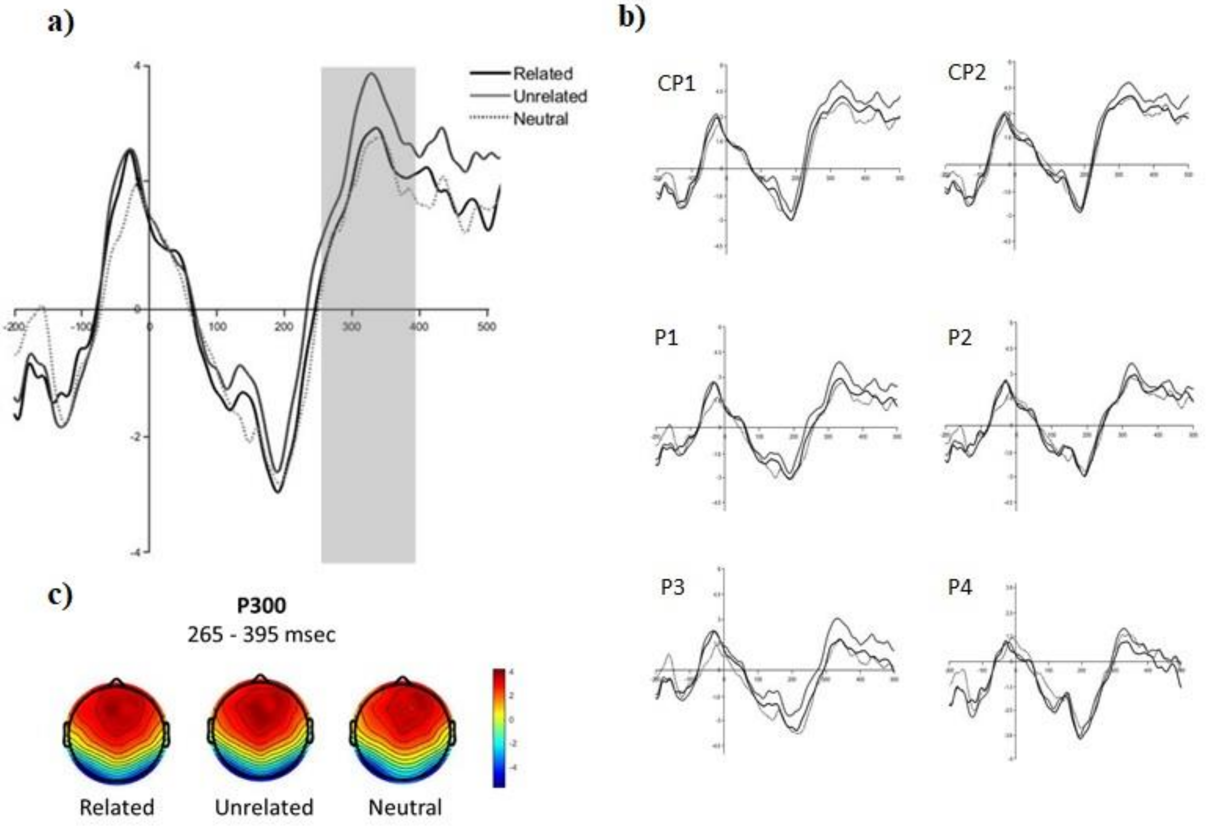

Figure 5. P300 grand average waveforms for 19 participants. Gray shadow indicates time-window of interest. **a)** Grand average waveforms collapsed across the six channels considered. **b)** Grand average waveforms for each channel **c)** Scalp topographies for each condition.

p = .002, d = .95] and *Neutral* (1.93µV) [t (18) = 4.09, p < .001, d = 1.11], while, on the right hemisphere, a significant difference in amplitudes was observed between *Unrelated* (2.85µV) and *Related* (2.32µV) targets only [t (18) = 1.97, p = .035, d = .64].

1.3.2 Discussion experiment 2

In Experiment 2, we replicated previous findings concerning the body-selective ERP amplitude peaking around 200 ms during body part and observation (Thierry et al., 2006; Pourtois et al., 2007; Taylor, Roberts, Downing, & Thierry, 2010; Sadeh et al., 2011; Rossion & Jacques, 2008). Importantly, we observed a selective modulation of N200 amplitude when identical body parts were preceded by objects functionally unrelated compared to objects functionally related. We were also able to deepen the understanding of body part visual processing by exploring the effect of such relationship on P300 component, over more centro-parietal sites which, again, was modulated according to whether primes were unrelated or related to the body parts presented. Specifically, results showed that ERPs to *Unrelated* trials were more positive, in a sustained way, than for the other two conditions starting around 200 msec on the left hemisphere, while on the right hemisphere a significant difference was observed between *Unrelated* and *Related* only. Similarly, on the left sites, *Unrelated* trials elicited a larger P300 compared to both *Related* and *Neutral* ones, while on the right hemisphere amplitude were significantly different between the *Unrelated* and *Related* conditions only. These electrophysiological data seem to be consistent with the behavioural observation from Experiment 1 and indicate that viewing objects leads to the evocation of information regarding which body part might be needed to interact with the object. Thus, body-part stimuli seem to generate specific EEG activity that may indicate a differential processing of body effectors according to their relevance for action-related objects.

1.4 General discussion

The present study aimed at investigating the potential functional link between objects (primes) and effectors (targets) by means of a priming paradigm. Based on the assumption that the representation of body parts may carry information concerning their functional role, we predicted that the visual presentation of objects with motor valence would modulate the visual recognition of the body part associated with the object. Specifically, we expected a ‘facilitation’ effect for the *Related* condition compared to both the *Unrelated* and *Neutral* ones. Behavioural data in Experiment 1 partially confirmed our original hypothesis as a significant difference in participants’ performance was observed between object-*Related* trials and object-*Unrelated* trials, but not for the object-*Neutral* ones.

It should be noted that, in a recent study adopting a similar priming paradigm, Almeida and collaborators (2018) reported different results from those observed in our first experiment. Specifically, the authors showed that unconscious processing of tools and hands images negatively influenced later recognition of hand and tool stimuli, respectively. Participants were slower in categorizing images of hands and tools when primed by a related image of a tool or a hand than by unrelated prime stimuli (e.g., animals). The authors argued that the effect might be due to inhibition resulting from close overlap between hand and tool representations in both dorsal and ventral pathways (Bracci et al., 2016; Bracci et al., 2012), which may interfere with the processing of the other category. Critically, in Almeida et al.'s (2018) study, the primes were rendered 'invisible' by presenting them for a short amount of time (i.e., 30 msec) followed by a high-contrast random noise mask. In our present study, participants were consciously aware of the prime stimuli. On one hand, although studies have shown that stimuli presented below threshold activate regions within the ventral object processing stream (Dehaene, Naccache, Cohen, Le Bihan, Mangin, Poline & Rivière, 2001), and may induce priming effects for a range of different semantic categories (Breitmeyer & Ogmen, 2000; Finkbeiner & Caramazza, 2008), 'invisible' stimuli trigger a bottom-up activation that is insufficient to elicit a large-scale reverberating state within the brain (Dehaene, Changeux, Naccache, Sackur & Sergent, 2006). On the other hand, conscious perception of sensory stimuli correlates with the activation of higher associative cortices and triggers top-down amplification increasing functional correlation between these areas and stimulus-specific areas (Dehaene et al., 2001; Haynes, Driver & Rees, 2005; Gross, Schmitz, Schnitzler, Kessler, Shapiro, Hommel & Schnitzler, 2004). In other words, in the context of the present study, the explicit identification of objects may trigger a set of expectations regarding possible interactions with the objects and lead to the formation of a 'template' of the expected stimulus, which can then be compared with the actual stimulus.

In Experiment 2, the investigation of the ERPs elicited by body parts when preceded by related, unrelated, and neutral primes helped to further elucidate the neural processing of human body parts. We observed that the functional relationship between objects and body parts affected the ERP signals associated with visual perception and categorization of body parts: *Unrelated* trials elicited a significantly smaller N200 compared to the *Related* ones and a larger P300 compared to both *Related* and *Neutral* ones. Regarding the N200 component, our findings agree with previous ERP literature describing a posterior negative deflection peaking around 200–250msec after single stimulus presentation observed when participants view recognizable and familiar images such as words, pictures, and faces (Martín- Loeches, 2007; Tanaka, Curran, Porterfield, & Collins, 2006; Schweinberger, Pfutze,

& Sommer, 1995). It has been proposed that such posterior component reflects stimulus evaluation and discrimination processes subsequent to the perceptual identification of the stimulus features (Ritter et al., 1984; Sams, Paavilainen, Alho, & Näätänen, 1985) and is sensitive to semantic expectancy (Dien, Frishkoff, Cerbone, & Tucker, 2003). Furthermore, it has been shown that ERPs after approximately 200 msec, index 'object-sensitive' activity associated with successful category decision processes in extrastriatal cortical areas (Schendan & Lucia, 2010).

It has been clearly demonstrated that EBA is ‘object-sensitive’ in the sense that it responds strongly and selectively to static images of human bodies and body parts, but not to scrambled versions of these figures and to other stimulus categories such as faces, objects, and object parts (Thierry et al., 2006). It could be argued, then, that EBA activity may index an enhanced coding of body-stimuli’s features when these are visually presented. In fact, the body (and its parts) is considered a special object for its relevance in many cognitive functions such as self-awareness, motor control and social communication. Critically, it has been argued that EBA is not a purely perceptual area, but it might also provide an interface between perceptual and motor processes (Astafiev et al., 2004; David, Cohen, Newen, Bewernick, Shah, Fink & Vogeley, 2007; Gallivan, McLean, Valyear, Pettypiece & Culham, 2011; Kühn, Keizer, Rombouts, & Hommel., 2011; Bracci et al., 2012; Tomasino, Weiss & Fink, 2012; Limanowski, Lutti & Blankenburg, 2014; Orgs, Dovern, Hagura, Haggard, Fink & Weiss, 2016; Simos et al., 2017). Remarkably, in our task, all targets were body parts yet, in the *Unrelated* condition, the N200 (and P300) amplitude significantly differed from the *Related* one. Therefore, differences between conditions can only be explained by the relationship between primes and effectors. When effectors are incongruent with the primes (*Unrelated*), they can be perceived as less salient stimuli possibly because they are negatively influenced by the prime (with motor valence) and interpreted as ‘functionally’ inappropriate. In light of the findings reported in the present study, it is reasonable to argue that, at least in this particular task, the related priming does not have a ‘facilitation’ effect (as similar amplitudes were observed also in the *Neutral* condition); rather, it is the unrelated prime that drives the ERP modulation and hampers the perceptual categorization of body parts. This effect might be the result of a pre-existing association of the objects and the body parts based on action possibilities and perceptual consequences of motor acts (Downing et al., 2001; Downing & Peelen, 2011) derived from learned knowledge and experience (Verhagen, Dijkerman, Medendorp & Toni, 2012).

In a later time-window, a second marker was observed in the form of a larger P300 in more centro-parietal areas in response to body parts for the *Unrelated* condition. This activity can be interpreted as a sign of increased attention allocation toward the body part that is ‘incongruent’ to the prime. Indeed, the

P300 component is thought to reflect neural activity related to attentional and working memory processes (Polich & Kok, 1995) and increased excitability of the posterior attention system due to orienting of visual attention (Soltani & Knight, 2000). Classically, the P300 amplitude increases as target probability gets smaller (Donchin, 1981; Luck, 2005). In this view, if it is true that a functional link exists between specific objects and body parts, then the association in the *Unrelated* condition could have been - subjectively speaking – perceived as less probable resulting in a larger P300. Crucially, probability in this particular circumstance was not based on the number of trials or targets presented (as in a classic oddball paradigm) as they were all the same number across conditions. Therefore, data may suggest that participants interpreted targets in the *Unrelated* condition as 'less probable' due to the incongruent association between the object and the body part.

The effect observed for both the N200 and P300 seems to be consistent with the cortical dynamics of visual object knowledge proposed in the two-state interactive hypothesis (Shendan & Stern, 2008; Schendan & Kutas, 2007). According to this account, an early, bottom-up, feedforward activity takes place for an initial classification of the stimulus which is sufficient for perceptual categorization (Schendan, Ganis & Kutas, 1998). However, more precise categorizations occur at a later stage (200 msec onwards), reflecting iterative neural computations critical to disambiguate the input by integrating bottom-up and top-down information (Shendan & Stern, 2008; Treisman, 2006; David, Harrison & Friston, 2005; Lamme & Roelfsema, 2000). This interpretation is also compatible with the notion that anatomical connectivity of the occipito-temporal cortex may play an important role in shaping the specificity and functional organization of this region such that, once information is extracted from the visual input, it propagates to other areas where the information is further processed, integrated with information from other modalities, and linked to previous experiences (Peelen & Caramazza, 2010; Kravitz et al., 2013). This interpretation would also explain why P300 amplitudes were not significantly different between the *Neutral* and *Related* conditions: in the *Neutral* condition, due to the novelty of the object and therefore, lack of familiarity, the incongruence might not have been perceived as strong as in the *Unrelated* due to the ambiguity of the object. However, this explanation should be taken with caution and considered a limitation of the study. In fact, the neutral stimulus consisted of a custom-made object, which was, inevitably, unfamiliar while the drum and the foot pump were not. Such unfamiliarity might have played a role in affecting the visual recognition of body parts which, due to the experimental design, we were not able to disentangle from the 'neutrality' of the object. Therefore, a further study might examine the effect of other types of prime stimuli which are familiar but neutral in terms of object-body relationship. A second limitation concerns the target stimuli that included only body parts. Although the primary aim of the study was to evaluate the association between object and body parts, based on a posteriori evaluation of the results, a non-body target stimulus could have helped in better determine EBA activity when primed by objects with motor valence. However, despite these limitations, both behavioral and the electrophysiological data clearly indicated that the visual processing of the same body part is influenced by the functional relevance of the effector in the context of its relationship with the prime objects.

1.5 Conclusions

Overall, while in literature there is substantial evidence suggesting that the observation of, for example, a hand activates motor information that can influence objects categorization (Borghi, Bonfiglioli, Lugli, Ricciardelli, Rubichi & Nicoletti, 2007; Bub, Masson, & Lin, 2013; Vainio, Symes, Ellis, Tucker, & Ottoboni, 2008), evidence evaluating the role of objects in modulating body parts' visual processing, to the best of our knowledge, is relatively scarce. Our findings provide new electrophysiological evidence that an object (with motor valence) can influence the recognition of its effector by modulating the level of activation in visual representation: the representation of specific body parts seems to be influenced by their 'functional' role. Future studies should further explore the visual processing and the link between objects and body parts, and potentially replicate the current findings by taking into account the limitations mentioned above. The notion of a functional 'architecture' of body representation is not entirely new. Previous studies have suggested that the conceptual organization of the human body is based on its ability to perform action (Bläsing, Schack & Brugger, 2010; Reed et al., 2004). In line with this hypothesis, a recent study on functional and structural connectivity profiles of EBA has shown a strong connection between EBA and parietal cortex (Zimmerman, Mars, de Lange, Toni, & Vernhagen, 2018), supporting the involvement of EBA in action planning and goal-oriented behaviour (Zimmermann, Verhagen, de Lange, & Toni, 2016; Zimmermann, Meulenbroek, & de Lange, 2012). In this view, the information related to actual (and potential) actions appears to be intrinsically carried in the representation, and knowledge, of these body parts: hands and feet are not merely parts of *a* body but they are defined, and represented, as motor effectors. Perceiving a body (part) is not solely based on visual characteristics but influenced and dynamically modulated by interacting factors such as motor experience, expectation and attention. Therefore, these factors (i.e., the prior expectation elicited by the prime) may trigger the formation of the expected body part (i.e., the one functionally related to the prime), which can then be compared with the actual visual input. The findings reported in this study provide additional support to this new reconceptualization of body representation and open a new window into the study of the weight of other potential contributors to body perception.

Data availability

The conditions stated in the informed consent form and ethics approval do not permit public archiving of data. Readers seeking access to the datasets generated and/or analyzed during the current study should contact the corresponding author. Access will be granted to named individuals. There are no further conditions.

No part of the study procedures and analyses were pre-registered prior to the research being conducted.

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