N1 responses to images of hands in occipito-temporal event-related potentials

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Abstract. Hands, much like faces, convey social information, instructions and intentions to an observer. While the neural processes of face perception have been widely studied, it was only recently that fMRI identified occipito-temporal areas sensitive to static images of hands as body parts. To complement these studies with fine-grained timing information, we measured event-related EEG potentials (ERPs) from 33 subjects who were presented with static images of hands versus faces, whole bodies, and inanimate objects as controls. Already at N1 latency, ~170 ms, hand-related ERP patterns were manifest in two results: (1) significant differences in amplitudes for images of hand versus bodies in occipito-temporal N1 responses; (2) left lateralization of responses to images of hands, and also of the difference waveforms (hands minus bodies), quantifying hand-related responses. In line with fMRI studies of hand-sensitive areas distinct from extrastriate body area (EBA), the current findings provide electrophysiological evidence for hand-sensitive brain activation, occurring at a similarly early latency as N1 responses to faces.

Introduction

From an evolutionary and social perspective effective processing of observed faces, body postures and body parts is highly important. Accordingly, neural responses to images of faces and body postures have been widely studied. Comparatively little is known about brain activation during visual processing of hands, highly conspicuous in social perception (as examples of the few studies on this topic, see Avikainen et al. 2003; Bracci et al. 2010, 2012). Here we measured event-related potentials (ERPs) in response to images of hands, compared with control conditions.

Early neuroimaging studies have shown existence of cortical regions dedicated to face processing in the fusiform gyrus (Sergent et al. 1992; Puce et al. 1996; Kanwisher et al. 1997). Likewise, regions that respond specifically to whole bodies and body parts have been found in occipito-temporal cortex (extrastriate body area, EBA: Downing et al. 2001; see de Gelder et al. 2010 for review) and in fusiform gyrus (fusiform body area, FBA: Peelen and Downing 2005). In fMRI, EBA and FBA differ in their response profiles for whole bodies and body parts (Taylor et al. 2007; Op de Beeck et al. 2010; see de Gelder et al. 2010, Downing and Peelen, 2011 for reviews). In FBA, responses are not selective for specific body parts, whereas selectivity for body parts is present in EBA (Taylor et al. 2007, Chan et al 2010). Complementary to fMRI, electrophysiological studies found event-related potential (ERP) responses to images of faces and bodies. For faces, a negative deflection (N1) was found to be sensitive to faces, with a peak latency of 170 ms after stimulus onset (N170: Bentin et al. 1996; Eimer et al. 2010; see Rossion 2014 for review). At similar latency, bodies elicited an N1 response with occipito-temporal maximum (Stekelenburg and de Gelder 2004; Thierry et al. 2006). In the study by Thierry et al. (2006), the response to bodies peaked at 190 ms and had a stable topography with maximum power at this latency (distinct from N170 topography for faces). Source analysis of this ERP to bodies was congruent with EBA

locations known from fMRI studies (Downing et al., 2001 Peelen and Downing, 2005; Op de Beeck et al. 2010; see Downing and Peelen, 2011 for review). Complementary with ERP source analysis, an EBA source of N1 responses is supported by the similar response profiles (for bodies, arms, hands, fingers) across fMRI and ERPs (Taylor et al. 2010). Dissociable responses to bodies versus faces were also found using magnetoencephalography (MEG, Meeren et al. 2013).

Not all body parts are equally important to social perception. Hands, much like faces, communicate a wide variety of social and cognitive information. Hands and body postures work together to emphasize and express language and emotions. Pointing gestures are a good way to orient attention, leading to an increased focus on hand postures during observation of arm movements (Mataric and Pomplun, 1998). Crucially, from a young age, as early as 3 months there is intense practice of different hands postures (D'Etremont et al. 1997), and larger attention to others' hands gestures rather than relying on gaze only for orientating attention (Langton et al. 2000; Yu and Smith, 2013). This suggests that hands play an important role in social and cognitive development, therefore may enjoy some form of 'special' processing like faces (McKone et al. 2006). Indeed, fMRI studies found dissociable responses between hands and bodies in the left lateral occipital cortex (LOC, Bracci et al. 2010, 2012; see also Supplementary Figure 4 in Weiner and Grill-Spector, 2011). Bracci et al. (2010, 2012) found this hand-responsive area in the left LOC whereas responses to whole bodies were represented bilaterally at the EBA. The authors proposed a double dissociation between representations of hands and whole bodies.

While the visual processing of bodies has been studied in fMRI *and* electrophysiology (as explained above), research questions regarding hand-related occipito-temporal responses have so far only been addressed in fMRI (for example, Op de Beeck et al. 2010, Bracci et al. 2010, 2012). Although ERPs to images of hands were recorded by Taylor et al. (2010), their

study did not aim to characterize hand-related response patterns as such. Their Figure 2 shows higher response amplitudes for hands than whole bodies but this amplitude difference was not formally tested. Thus, ERP evidence to complement hand-sensitive fMRI activation remains to be established. Here we search for hand-related N1 responses (versus bodies), and, in particular, we directly test laterality effects. Therefore, based on findings in fMRI studies (Bracci et al. 2010, 2012; Orlov et al. 2014), and guided by grand average waveforms in Taylor's et al. (2010), we predict the following: 1) Occipito-temporal electrodes will show different N1 amplitudes for hands compared with bodies; 2) this amplitude difference will be stronger in the left hemisphere compared to the right hemisphere; 3) underlying this hemispheric difference is an asymmetric response to hands: left N1 to hands will be more negative than right N1 to hands.

Methods

Subjects

A total of 33 subjects (24 female), of average age 24.4 years (SD = 3.4) participated in this experiment. Subjects were right-handed, with no history of neurological or psychiatric problems nor drug abuse (all by self-report). This experiment was approved by the ethics committee of the School of Psychology, University of Nottingham (Ref: 692R).

Stimuli and procedure

Subjects sat approximately 60 cm from the screen and stimuli were presented on a ViewPixx3D (VPixx Technologies, Saint-Bruno, QB, Canada) presentation monitor (1920 x 1080 pixels, 23.6", 120 Hz refresh rate, 1 ms pixel response time). Subjects viewed images of hands, bodies, faces, and objects. Hands were the stimuli of interest in this study. As a control condition, we included whole bodies which are known to elicit N1 responses that have been linked with EBA activation (Thierry et al. 2006, Taylor et al. 2010). To ensure that our N1

responses to bodies were comparable to findings in earlier work, we also included faces and objects as reported in earlier studies (Thierry et al. 2006).

Images were shown at 4 degrees of visual angle, consisting of 250 x 250 pixels. Images of hands, bodies, and faces were as in Bracci et al. (2010), with authors' permission. Face images portrayed 18 female and 18 male individuals in neutral expression with gaze diverted. Images of hands consisted of 36 hands of both sexes (not identifiable from pictures), 14 in palmar view, 19 in dorsal view and 3 viewed from the side. Of the 36 hands, 21 were in neutral positions, and 15 suggested a form of grasp or action. Images of bodies had the heads removed, bodies were all clothed and the set consisted of 18 female and 18 male models. Images of objects were acquired online from http://www.cogsci.nl/stimulus-sets and consisted of 20 man-made objects (e.g bag, button, fork, candle) and 16 natural objects (e.g. flowers, leaf, sea-shell, peanut). In total 36 different fully desaturated (black and white) images per category were presented three times. Stimulus order was pseudo-randomized in order to allow images to be repeated for purposes of a 1-back task. Each image was presented for 200 ms, immediately followed by a fixation point of jittered duration (randomized, either 1000, 1200 or 1500 ms, see Figure 1). During the presentation of these images, subjects were instructed to press a button on a Cedrus Response pad (4th generation, Cedrus Corporation, San Pedro, CA, www.cedrus.com) whenever they saw an image that was identical to the preceding image (1-back task). In total 432 stimuli were presented (4 categories x 36 images x 3 repeats), excluding 5% repeated 1-back trials and in total this task took approximately 12 minutes to complete.

----------- Figure 1 about here. -----------

Data acquisition

Subjects were asked to sit in a Faraday-cage (2.5x2.3x2.3 m) quiet room at ambient temperature. Electroencephalographic activity was recorded using a 64-channel Active-Two acquisition system (BioSemi, Amsterdam, Netherlands), sampled at 1024 Hz, and digitized at 24-bits. Triggers were sent and received using a Cedrus Stimtracker. An additional 6 Ag/AgCl electrodes were placed at M1, M2, F9, F10, T9, T10. Data were collected using ActiView 7.0.

Signal processing

Signal processing was performed in Matlab (The MathWorks Inc., Natick, MA) using Fieldtrip (Oostenveld et al. 2011) and EEGLAB (Delorme et al. 2011) routines. Due to active electrodes, BioSemi systems allow for reference-free recordings, and only at pre-processing stages the time series of the electrodes were referenced to an all-electrode average. Data were band-pass filtered between 0.4 to 35 Hz followed by a visual search (blind to condition) to identify obvious bad trials based on typical artifact waveforms (as described for example in Hari and Puce 2017, chapter 8). Such trials were removed from the dataset. A plot trial by variance was created to identify which trials had largest variance. Those that had standard deviations above 5 z-values were removed from the data. ERP data for each trial was collected, baseline corrected and averaged for each participant, with an epoch length of -200 ms to 500 ms. Subsequently, segmented trials were put through an independent component analysis (ICA) using the algorithm *runica* (see Makeig et al., 1996, 1997)*,* allowing for blind separation of the underlying component topographies. The results of the ICA were then put through an automatic artifact rejection algorithm (MARA, Winkler et al. 2011) to flag topographies containing blinks, vertical or horizontal eye movements, muscle activity, and other noise-related artefacts. This algorithm is a linear classifier that rates different features

of the topographies and provides a classification of 'reject' (for noise and outliers) or 'accept'. Even though MARA is a robust method, some artifacts can escape rejection, for example blinks that are highly correlated with stimuli presentation. Therefore, this step was complemented with visual inspection to validate the classification, searching for well-known artifact topographies (see examples in Jung et al. 2000a,b).After these steps, trials were sorted by condition and averaged, resulting in 4 averaged waveforms per subject (hands, bodies, faces, objects).

Event-related potential analyses

In order to explore the hypotheses outlined above a mass-univariate approach was taken as it requires fewer a priori assumptions, and allows to find smaller differences between conditions that extend across time as opposed to selecting a single value from a time-window (for review, see Groppe et al. 2011). Using Fieldtrip functionalities, to address hypothesis 1) we conducted a mass-univariate two-sided t-test across all time points and electrodes, for each individual subject average for the contrast *hands ≠ bodies*. For hypothesis 2), first we calculated the difference for each electrode across all time points between hands and bodies, generating one single topography of the difference for each time point. Then, we split the resulting topography into right and left hemispheres, and assigned the right hemisphere electrodes into the corresponding position of the left hemisphere- so that for example, P8 is now P7- effectively flipping the right hemisphere topography to the left. This allowed direct comparison between right and left electrodes. Following this flipping procedure, a one-tailed mass-univariate t-test was conducted to directly test for left-lateralized hand-versus-body differences. To test hypothesis 3), the same flipping procedure was done as above , but now using the waveforms for the hand condition. The electrodes in the right hemisphere were

assigned to the left, and a one-tailed mass-univariate t-test was conducted to directly test for left-lateralized brain responses to hand images.

A Monte Carlo distribution (N=2000) of t-statistic for each comparison was obtained to define the critical t-value on the tested sides of the distribution. Then, multiple comparisons were further corrected using threshold free clustering algorithm as implemented in Fieldtrip (Maris and Oostenveld, 2007; Oostenveld et al. 2011) to find significant time points where the maximum cluster t-statistic survived the threshold (cluster alpha= 0.05, minimum neighboring channels =2). Latencies were extracted based on the most negative waveform within a time interval of 150 to 200 ms within P9, PO7, P10, and PO8 electrodes, as used in Thierry et al. (2006) and tested for differences in a repeated measures ANOVA using SPSS (IBM, Armonk, NY).

Outlier identification

Outlier subjects were identified based on two criteria. First, individual subjects' condition-specific averages were visually inspected (blind to the condition) in order to find atypical waveforms. Those that did not show clear waveforms in all 4 conditions were excluded. This resulted in the removal of 2 subjects from further analysis, leaving 31 subjects. Second, behavioral performance in the 1-back task was assessed in terms of accuracy= hits/ (hits+misses) *100. Subjects with accuracy below 80% were also removed. This lead to the removal of 3 further subjects, leaving 28 subjects.

Results

Behavioral results

Accuracy analysis of hits and misses on the 1-back task (N=28, after removal of outliers) resulted in a mean accuracy of 95.5% with SEM of 1.3.

ERP waveforms and N1 peak latencies

Typical ERP waveforms were seen in all subjects (N=28): P1, N1 (N170/N190), and P2 as seen in grand averages (Figure 2). Latencies (as means over P7, P9, PO7, PO3, and P8, P10, PO8, PO4) were 167 ms (SD =8 ms, min/max = 151/186 ms) for faces, 173 ms (SD = 10 ms, min/max = 153/194 ms) for bodies, 174 ms (SD = 10 ms, min/max = 152/188 ms) for hands and 174 ms (SD =10 ms, min/max = 151/190 ms) for objects [F(1,27) = 13.73, p<0.001, repeated-measures ANOVA]. In post-hoc t tests (two-sided, Bonferroni-corrected), latency differences were significant for faces versus bodies (p<0.001), versus hands (p<0.001), and versus objects (p<0.001), also bodies versus objects (p<0.05). No other comparisons resulted in significant differences (all p>0.05).

For bodies, the overall waveforms of grand average responses, including relative amplitudes and latencies compared with faces and objects, were highly similar to responses in earlier work (Thierry et al. 2006, Figure 2). Beyond this initial comparison, faces and objects are not directly relevant to our research questions and will not be analyzed further.

----------- Figure 2 about here. -----------

Responses to hands differ from responses to bodies

A mass univariate dependent samples two-tailed t-test for hands ≠ bodies was performed in the time period of 0 to 400 ms. Significant differences were found across a wide range of electrodes. Significant amplitude negativity difference (p<0.001) between hands and bodies was found over the parietal, occipito-temporal and parieto-occipital electrodes in the time period of 75 to 275 ms after stimulus onset (see Figure 3). In these electrodes, this difference was observed in P1, N1, and P2 ERPs of the waveform. Out of these electrodes, those similar to the ones used in Thierry et al. (2006) - P7, P9, PO7, PO3, and P8, P10, PO8, PO4 - showed significant difference between 125 and 275 ms. Here we just report condition-specific

difference in the N1 latency range to which the research questions are related. Maximum

difference of the N1 occurred at 174 ms.

----------- Figure 3 about here. -----------

Hemispheric dissociation of responses to hands and bodies

In order to investigate hemispheric dissociation of the hand and body stimuli, first a

difference wave (hand-body) was calculated for each electrode and each subject (see Figure

4, note that more negative amplitude in the difference waveform indicates stronger responses

to hands than to bodies). To compare the amplitudes of difference waves from left versus

right hemisphere electrodes, a mass univariate dependent samples one-tailed t-test was

performed in the time period of 0 to 400 ms. Significant differences ($p = 0.036$) were found

in parietal, parieto-occipital, occipito-temporal and central electrodes in the time window of

140 ms to 278 ms. In occipito-temporal electrodes this difference started at the N1 but did not

extend to P2 latencies (see Figure 4). The maximum difference between body parts occurred

at PO7 where the hands-bodies amplitude difference was of -2.45 µV.

----------- Figure 4 about here. -----------

Left N1 to hands more negative than right N1 to hands

The last aim of the study was to investigate whether responses to hand stimuli are lateralized

to the left hemisphere. A mass univariate dependent samples one-tailed t-test on the

amplitude between left and right hemisphere was performed in the time window of 0 to 400

ms. The results showed that an early left versus right difference was seen in PO7/8 and P7/8

electrodes starting at 174 and 183 ms respectively, which is the time corresponding to

maximum N1 amplitude for hands. This difference then continues into P2 latency and is also

seen in C5/6, CP5/6, TP7/8, P9/10, P5/6, P3/4, PO3/4, and O1/2 electrodes from 205 ms (see

Figure 5).

----------- Figure 5 about here. -----------

Discussion

This study searched for a neural correlate of the high perceptual salience of observed hands.

We aimed to find hand-related features of the occipito-temporal N1 waveform using images

of bodies for comparison. To establish a link between our body-related N1 responses and

earlier research work, we also included images of faces and objects (as in Thierry et al.

2006). In terms of latency, responses to hands and bodies were distinct from faces, and in line

with our predictions, amplitude differences between hand stimuli and body stimuli were

found in left and right hemisphere. When comparing the amplitude difference between

hemispheres, a significant dissociation between right and left was found: the difference

between hands and bodies was larger in the left than in the right hemispheres; and responses

to hand stimuli were stronger in the left than in the right. These electrophysiological results

complement previous findings in fMRI studies indicating a hemispheric lateralization of

visual processing of hands (Bracci et al. 2010, 2012).

In terms of waveforms of responses, hands were similar to bodies which in turn were similar

to faces but different from objects (the latter 3 conditions as in as in Thierry et al. 2006).

Comparing peak amplitude latency between faces, hands and bodies, faces elicited earlier

responses than all other conditions, but this difference was of approximately 7ms . Thus, the

relative latencies of faces and bodies were as reported by Thierry et al. (2006). They

identified face- and body-related topographies starting at different time points, i.e. faces at

approximately 170 ms, and bodies at approximately 190 ms. The slightly shorter absolute

latencies in the current study (167 and 173 ms, respectively) are in line with a number of studies that used a similar setup as Thierry et al. (2006). Examples are 176 ms in Taylor et al. (2010), averaged across whole bodies and body parts, and 145 ms in Meeren et al. (2013, MEG study) and in Alho et al. (2015, MEG/EEG combined, clothed whole bodies condition). As the main result of the current study, we found a topographical difference between responses to hands and bodies, suggesting that different body parts have specific regions of the cortex dedicated for their encoding. As the current study specifically compares hands with a semantically matched control condition (bodies), it goes beyond earlier research reporting responses to observed hands in MEG (such as Avikainen et al. 2003) and EEG (such as Möhring et al. 2014). These studies found lateral-occipital responses to hands (with latencies of less than 200 ms, in line with our results), but non-hand controls were not required, due to the intended comparison between different hand postures or gestures. Furthermore, our result of stronger responses to hands than bodies is congruent with findings from fMRI research. An fMRI study compared voxel specificity to faces, non-body parts, torsos and hands, reporting hands versus torsos as the strongest between-categories difference (Op de Beeck et al. 2010). This difference lead to distinct topographical representations with hand representations overlapping more with extrastriate areas, and torsos more represented in the ventral areas of the occipito-temporal cortex, and fusiform area. Furthermore, Orlov et al. (2010) demonstrated cortical activation with well-defined borders after visual presentation of different body parts. Congruently with this evidence, the current study showed a significant difference in N1 amplitude between whole body viewing and hand viewing suggesting larger neuronal populations and/or stronger involvement of specific neuronal regions for hands. Our ERP results are also in line with grand average P7/P8 waveforms of Taylor et al. (2010, Figure 2, top panel), showing stronger N1 responses to hands than whole bodies. However,

they did not directly test this amplitude difference for significance (as not relevant to their research question of correspondence between ERP and fMRI measures of EBA activation). Our result of different hemispheric involvement in visual processing of hands - as stronger hand-related responses (versus whole bodies) in left hemisphere, and as left laterality for responses to hands as such – is in line with fMRI results: In Bracci et al. (2010) it was shown that hand viewing has dedicated processing region on the left. These results and our complementary electrophysiological data converge on left lateralization of occipito-temporal responses to hands. Again, this result matches the N1 responses to hands in Taylor et al. (2010). In the grand averages of their Figure 2, responses were stronger over the left hemisphere, but lateralization was not tested for significance. In contrast, our study contains a direct statistical test of response laterality. Not directly related to our main research questions, it is interesting to note that in contrast with fMRI results (Bracci et al. 2010, 2012), right-hemispheric occipito-temporal ERP responses are not stronger for bodies than for hands (neither in Taylor et al. 2010, Figure 2, nor in current study). To interpret this disparity, it is important to notice that fMRI, in comparison with ERPs such as N1, captures activity in a much broader time window after stimulus, in particular when stimuli of one category are grouped together in a block design (as in Bracci et al. 2012), unlike the random order of stimuli in ERP studies. The disparity could therefore hint at different temporal dynamics of responses to hands versus bodies, a topic of interest for future studies.

Returning to lateralized responses to hands as one of our main results, a key question remains to be addressed: why the left hemisphere? Brain processes involved with the representation of hands in the left occipito-temporal cortex may support a synergetic relationship between somatomotor regions and vision. Structural proximity may facilitate sensory integration allowing precise information about grasp, tool use and posture to be represented in the cortex, and therefore large hand representation in the left hemisphere may be linked to hand use as

all our subjects were right-handed (like in the fMRI study that found left-hemisphere hand-responsive clusters, Bracci et al. 2010). In a combined study of resting state and task based fMRI, occipito-temporal regions selective for observed hand movements (as compared with regions for other body part movements) showed stronger functional connectivity with motion-sensitive occipital regions (Orlov et al 2014). Motor properties of body parts influence their representation in lateral occipital cortex which does not follow a 'nearest neighbour rule' (as in somatosensory cortex), as found using fMRI (Orlov et al. 2010): Body parts that have wider range of movements largely overlapped with areas of visual motion processing (such as hMT+), and those that are restricted (e.g. trunk) had more ventral locations within the lateral occipital cortex. In addition, ROIs showing upper limb preference also produced the largest clusters of activation (Orlov et al. 2010). Lastly, Bracci et al. (2012) demonstrated that hand and tool regions of the left lateral occipital complex responded similarly and were functionally connected. However, to the authors' knowledge, so far there are no electrophysiological studies that directly addressed functional connectivity between left limb-specific lateral-occipital areas and corresponding left motor and somatosensory regions. Such studies would complement fMRI results (Orlov et al. 2010; Bracci et al. 2012; Striem-Amit et al. 2017) and create an exciting avenue for further research.

Another reason for the left lateralization could be that our static images of hands benefitted from motor-related attention. In everyday life, attention to hands is mostly attention to motor acts – those which an individual performs with her own hands, or those which an individual observes others performed with their hands. For example, in cueing tasks faster reaction times are elicited when the probe is placed closer to the responding hand (Reed et al. 2006; Morrisey and Rutherford, 2013). Infants have a stronger reaction to observed actions conducted with the hand than those with a non-hand control object (Saxe and Carey, 2006), and infants of two years will engage in imitation of hand postures, even when there are no

bodies or faces present (Slaughter et al. 2008). Motor-related attention, in turn, has been linked with left parietal cortex activation (Rushworth et al. 2001). Related left lateralization has been found for motor-planning networks (Buxbaum et al. 2005) and for activity during integration of proprioceptive information with observed congruent and incongruent limb postures (Limanowski and Blankenburg, 2016).

In conclusion, we demonstrated that occipito-temporal N1 encodes hands and not just whole bodies. Whilst complementing fMRI results of hand-specific visual brain areas (Bracci et al. 2010, 2012), this is the first electrophysiological study to empirically demonstrate a laterality effect of observing hand stimuli which suggests a specialization of the left hemisphere to hand perception. In this study, we offer support to a motor-visual integration approach which benefits from proximity to left-hemisphere motor networks. The hemisphere differences in amplitudes of the N1 to hand viewing provides strong motivation for future research to explore whether arms, legs and hands – as body parts that are frequently observed in movement - are more represented in the left extrastriate cortices versus right. In the future, the occipito-temporal N1 could be used to investigate whether this lateralization effect remains true for the observation of other body parts, especially ones involved in motion. The temporal resolution afforded by electrophysiological methods (see review: Hari and Parkkonen, 2015) allows the study of the interaction of motion-sensitive areas with areas representing body parts in the EBA. In addition, the occipito-temporal N1 may be an important tool for investigating social processes which may involve hand postures and/or observation of action and pain, providing new insights in social neuroscience at lower cost, and of easier access than fMRI.

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References

Alho, J., Salminen, N., Sams, M., Hietanen, J. K., & Nummenmaa, L. (2015). Facilitated

   early cortical processing of nude human bodies. Biol. Psychol., 109, 103-110.

Avikainen, S., Liuhanen, S., Schürmann, M., & Hari, R. (2003). Enhanced extrastriate

   activation during observation of distorted finger postures. J. Cogn. Neurosci., 15(5), 658-

   663.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological

   studies of face perception in humans. J. Cogn. Neurosci., 8(6), 551-565.

Bracci, S., Cavina-Pratesi, C., Ietswaart, M., Caramazza, A., & Peelen, M. V. (2012). Closely

   overlapping responses to tools and hands in left lateral occipitotemporal cortex. J.

   Neurophysiol., 107(5), 1443-1456.

Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable neural

   responses to hands and non-hand body parts in human left extrastriate visual cortex. J.

   Neurophysiol., 103(6), 3389-3397.

Buxbaum, L. J., Johnson-Frey, S. H., & Bartlett-Williams, M. (2005). Deficient internal

   models for planning hand–object interactions in apraxia. Neuropsychologia, 43(6), 917-

   929.

Chan, A. W., Kravitz, D. J., Truong, S., Arizpe, J., & Baker, C. I. (2010). Cortical

   representations of bodies and faces are strongest in commonly experienced configurations.

   Nat. Neurosci., 13(4), 417-418.

D'Entremont, B., Hains, S. M. J., & Muir, D. W. (1997). A demonstration of gaze following

   in 3-to 6-month-olds. Infant Behav. Dev., 20(4), 569-572.

de Gelder, B., Van den Stock, J., Meeren, H. K., Sinke, C. B., Kret, M. E., & Tamietto, M.

   (2010). Standing up for the body. Recent progress in uncovering the networks involved in

the perception of bodies and bodily expressions. Neurosci. Biobehav. Rev., 34(4), 513-527.

Delorme, A., Mullen, T., Kothe, C., Acar, Z. A., Bigdely-Shamlo, N., Vankov, A., & Makeig, S. (2011). EEGLAB, SIFT, NFT, BCILAB, and ERICA: new tools for advanced EEG processing. Comput. Intell. Neurosci., 2011:130714.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. Science, 293(5539), 2470-2473.

Downing, P. E., & Peelen, M.V. (2011). The role of occipitotemporal body-selective regions in person perception. Cogn. Neurosci., 2(3-4), 186-203.

Eimer, M., Kiss, M., & Nicholas, S. (2010). Response profile of the face-sensitive N170 component: a rapid adaptation study. Cereb. Cortex, 20(10), 2442-2452.

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. Psychophysiology, 48(12), 1711-1725.

Hari, R., & Parkkonen, L. (2015). The brain timewise: how timing shapes and supports brain function. Phil. Trans. R. Soc. B, 370(1668), pii: 20140170.

Hari, R., & Puce, A. (2017). MEG-EEG Primer. New York: Oxford University Press

Ishizu, T., Amemiya, K., Yumoto, M., & Kojima, S. (2010). Magnetoencephalographic study of the neural responses in body perception. Neurosci. Lett., 481(1), 36-40.

Jung, T.P., Makeig , S., Humphries, C., Lee, T.W., McKeown, M.J., Iragui, V., & Sejnowski, T.J. (2000a). Removing electroencephalographic artifacts by blind source separation. Psychophysiology, 37(2), 163-178.

Jung, T.P., Makeig, S., Westerfield, M., Townsend, J, Courchesne, E. & Sejnowski, T.J. (2000b). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. Clin. Neurophysiol., 111(10), 1745-1758.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci, 17(11), 4302-4311.

Langton, S. R., Watt, R. J., & Bruce, V. (2000). Do the eyes have it? Cues to the direction of social attention. Trends Cogn. Sci., 4(2), 50-59.

Limanowski, J., & Blankenburg, F. (2016). Integration of visual and proprioceptive limb position information in human posterior parietal, premotor, and extrastriate cortex. J. Neurosci, 36(9), 2582-2589.

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. J. Neurosci. Meth. 164(1), 177-190.

Makeig, S., Bell, A. J., Jung, T. P., & Sejnowski, T. J. (1996). Independent component analysis of electroencephalographic data. Adv. Neural Inf. Process. Syst. 8, 145-151.

Makeig, S., Jung, T. P., Bell, A. J., Ghahremani, D., & Sejnowski, T. J. (1997). Blind separation of auditory event-related brain responses into independent components. Proc. Natl. Acad. Sci. U.S.A., 94(20), 10979-10984.

Matarić, M. J., & Pomplun, M. (1998). Fixation behavior in observation and imitation of human movement. Cogn. Brain Res., 7(2), 191-202.

McKone, E., Kanwisher, N., & Duchaine, B. C. (2007). Can generic expertise explain special processing for faces? Trends Cogn. Sci., 11(1), 8-15.

Meeren, H. K., de Gelder, B., Ahlfors, S. P., Hämäläinen, M. S., & Hadjikhani, N. (2013). Different cortical dynamics in face and body perception: an MEG study. PLoS One, 8(9), e71408.

Möhring, N., Shen, C., & Neuhaus, A. H. (2014). Spatiotemporal dynamics of early cortical gesture processing. NeuroImage, 99, 42-49.

Morrisey, M. N., & Rutherford, M. D. (2013). Do hands attract attention? Vis. Cogn., 21(5), 647-672.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.M. (2011). FieldTrip: Open source

software for advanced analysis of MEG, EEG, and invasive electrophysiological data.

Comput. Intell. Neurosci., 2011:156869.

Op de Beeck, H. P., Brants, M., Baeck, A., & Wagemans, J. (2010). Distributed subordinate

specificity for bodies, faces, and buildings in human ventral visual cortex. NeuroImage,

49(4), 3414-3425.

Orlov, T., Makin, T. R., & Zohary, E. (2010). Topographic representation of the human body

in the occipitotemporal cortex. Neuron, 68(3), 586-600.

Orlov, T., Porat, Y., Makin, T. R., & Zohary, E. (2014). Hands in motion: an upper-limb-

selective area in the occipitotemporal cortex shows sensitivity to viewed hand kinematics.

J. Neurosci., 34(14), 4882-4895.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform

gyrus, J. Psychophysiol., 93(1), 603-608.

Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity

of human visual cortex to faces, letterstrings, and textures: a functional magnetic

resonance imaging study. J. Neurosci, 16(16), 5205-5215.

Reed, C. L., Grubb, J. D., & Steele, C. (2006). Hands up: attentional prioritization of space

near the hand. J. Exp. Psychol. [Hum. Percept.], 32(1), 166-177.

Rossion, B. (2014). Understanding face perception by means of human electrophysiology.

Trends Cogn. Sci., 18(6), 310-318.

Rushworth, M. F., Krams, M., & Passingham, R. E. (2001). The attentional role of the left

parietal cortex: the distinct lateralization and localization of motor attention in the human

brain. J. Cogn. Neurosci, 13(5), 698-710.

Saxe, R., & Carey, S. (2006). The perception of causality in infancy. Acta Psychol., 123(1),

144-165.

Sergent, J., Ohat, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. Brain, 115(1), 15-36.

Slaughter, V., Nielsen, M., & Enchelmaier, P. (2008). Interacting socially with human hands at 24 months of age. Infancy, 13(2), 185-195.

Stekelenburg, J. J., & de Gelder, B. (2004) .The neural correlates of perceiving human bodies: an ERP study on the body-inversion effect. Neuroreport, 15(5), 777-780.

Taylor, J. C., Roberts, M. V., Downing, P. E., Thierry, G. (2010). Functional characterization of the extrastriate body area based on the N1 ERP component. Brain and Cognition, 73(3), 153–159

Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. J. Neurophysiol., 98(3), 1626-1633.

Thierry, G., Pegna, A. J., Dodds, C., Roberts, M., Basan, S., & Downing, P. (2006). An event-related potential component sensitive to images of the human body. NeuroImage, 32(2), 871-879.

Yu, C., & Smith, L. B. (2013). Joint attention without gaze following: Human infants and their parents coordinate visual attention to objects through eye-hand coordination. PLoS One, 8(11), e79659.

Weiner, K. S., Grill-Spector, K. (2011). Not one extrastriate body area: Using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. NeuroImage, 56(4), 2183-2199.

Winkler, I., Haufe, S., & Tangermann, M. (2011). Automatic classification of artifactual ICA-components for artifact removal in EEG signals. Behav. Brain Func., 7(1), 1.

Legends

Figure 1. Experimental design. Images of 250 x 250 pixels presented at approximately 4 degrees of visual angle, not shown at actual size in diagram. Each trial consisted of 0.2 s presentation of a stimulus of one of the four categories, followed by a fixation mark (inter-stimulus interval either 1 s, 1.2 s, or 1.5 s). The schematic image of the hand pressing a button indicates a valid 1-back target (this occurred in 5% of trials). Images same as in Bracci et al. (2010), with authors' permission, or from http://www.cogsci.nl/stimulus-sets.

Figure 2. Top panel: Grand average event-related potential waveforms (N=28 subjects) for each viewing condition, averaged across P7, P9, PO7, PO3 (left hemisphere) and P8, P10, PO8, PO4 (right hemisphere). The N1 elicited by faces peaked approximately at 167 ms, other conditions elicited significantly later peaks – hands, 174 ms; bodies, 173 ms; objects, 174 ms (averaged across above-mentioned electrodes). Each waveform was baselined using a 200 ms pre-stimulus interval. Stimulus duration 200 ms. Bottom panel: Averaged topography for each condition over greyed-out area (160 to 190 ms) in waveform plots.

Figure 3. Grand average event-related potential waveforms (N=28 subjects) for the electrodes of interest (P7, P9, PO7, PO3, and P8, P10, PO8, PO4) similar to Thierry et al. (2006) for the observation of hands (black) and bodies (red) images. The grey panel indicates areas of significant difference (p<0.001) between conditions calculated using a mass-univariate t-test between waveforms.

Figure 4. Grand average waveforms (N=28) for the difference in amplitude between hands andbodies on the right and left hemispheres, averaged over P7, P9, PO7, PO3 and P8, P10, PO8, PO4. The difference between conditions is larger on left hemisphere (black line) versus

right hemisphere (red line). Over both hemispheres, the difference waveform is negative, indicating stringer responses for hands versus bodies (see Figure 3). To test the significance of the difference between hemispheres, the difference-wave topography was flipped (see Methods. sub-heading *Event-related Potential Analyses)* and a mass-univariate t-test was conducted on the left hemisphere electrodes. Electrodes with significant hemispheric differences (p <0.05) are highlighted with asterisks (with red asterisks corresponding to the waveform display) superimposed on the topography of the hemispheric difference-waveform [(hands - bodies left) - (hands - bodies right)]. Color bar same as in figure 2. Significance for (hands-bodies left) - (hands-bodies right) was observed in the time period of 142ms to 199 ms. This time window depicted in grey in the waveform display, and was established as the common time window of significance across the parieto-occipital electrodes.

Figure 5. Grand average event-related potential waveforms (N=28) for left (black) and right (red) hemisphere for the viewing of hand stimuli for electrodes P7/P8 and PO7/PO8 (red asterisks on the topography for P7 and PO8). To find the difference between hemispheres, the waveform topography was flipped and a mass-univariate t-test (flipped versus original) was conducted on the left hemisphere electrodes. Asterisks superimposed on the topography indicate significant differences between left and right hemisphere responses to hands (p<0.05). Color bar same as in figure 2. The results showed a significant difference between hemispheres starting at 183 ms for P7 versus P8 and at 174 ms for PO7 versus PO8 (darker grey, on the waveform plots, and red asterisks on the topography) exclusively, overlapping with the N1 component. Later significant differences were observed in other electrodes (black asterisks, starting from 205 ms ending at 400 ms), indicated by the lighter grey.

1-Back

0.2 s

←1s to 1.5s→

0.2 s

←1s to 1.5s→

0.2 s

←1s to 1.5s→

0.2 s

Figure 4