



Facilitated early cortical processing of nude human bodies



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ABSTRACT

Functional brain imaging has identified specialized neural systems supporting human body perception. Responses to nude vs. clothed bodies within this system are amplified. However, it remains unresolved whether nude and clothed bodies are processed by same cerebral networks or whether processing of nude bodies recruits additional affective and arousal processing areas. We recorded simultaneous MEG and EEG while participants viewed photographs of clothed and nude bodies. Global field power revealed a peak ~145 ms after stimulus onset to both clothed and nude bodies, and ~205 ms exclusively to nude bodies. Nude-body-sensitive responses were centered first (100–200 ms) in the extrastriate and fusiform body areas, and subsequently (200–300 ms) in affective-motivational areas including insula and anterior cingulate cortex. We conclude that visibility of sexual features facilitates early cortical processing of human bodies, the purpose of which is presumably to trigger sexual behavior and ultimately ensure reproduction.

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1. Introduction

Other human beings are arguably the most important visual stimuli in our environment. Their bodies convey information on factors that are crucial in regulating social interaction, including identity, emotion, actions, and intentions. Compatible with this, functional neuroimaging studies have revealed a distributed cortical network supporting perception of human bodies. The core regions involved in this system include the fusiform body area (FBA) in the ventral temporal cortex (VTC) and the extrastriate body area (EBA) in the lateral occipito-temporal cortex (LOTC) (de Gelder et al., 2010; Downing, Jiang, Shuman, & Kanwisher, 2001; Peelen & Downing, 2005, 2007; Pourtois, Peelen, Spinelli, Seec, & Vuilleumier, 2007). The EBA and FBA are functionally

dissociated, with EBA responding more strongly to individual body parts, while FBA is involved in configural/holistic processing of the body stimulus (for a review, see Downing & Peelen, 2011).

1.1. Processing sexual information from bodies

Electrophysiological studies have revealed that the visual N1 response, evoked by all visual objects and peaking between 140–220 ms after stimulus onset in occipito-temporal sensor sites, is especially sensitive to faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2004; Rossion & Jacques, 2008; Sams, Hietanen, Hari, Ilmoniemi, & Lounasmaa, 1997), but also stronger to bodies than to inanimate objects, such as tools or cars (de Gelder et al., 2010; Ishizu, Amemiy, Yumoto, & Kojima, 2010; Minnebusch & Daum, 2009; Thierry et al., 2006). However, in most of the previous studies on the brain basis of body perception, the bodies were presented as wearing clothes. Considering the relatively short evolutionary history of clothing, it is possible that the brain networks specialized in body perception have been tuned to respond specifically to *nude* rather than clothed bodies. Indeed, along with others' intentions and actions, bodies convey critical information also for sexual selection. Identification of mating partners in primates relies extensively on the visual system (Ghazanfar & Santos, 2004) and humans show strong preference toward

Abbreviations: ACC, anterior cingulate cortex; cBnH, clothed bodies with no head; cBmH, clothed bodies with masked head; dSPM, dynamic statistical parametric map; EBA, extrastriate body area; FBA, fusiform body area; FFA, fusiform face area; IC, insular cortex; LOTC, lateral occipito-temporal cortex; LTC, lateral temporal cortex; MNE, minimum-norm estimate; MOC, medial occipital cortex; nBnH, nude bodies with no head; nBmH, nude bodies with masked head; LOFC, lateral orbitofrontal cortex; VTC, ventral temporal cortex.

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viewing sexual signals of conspecifics (Nummenmaa, Hietanen, Santtila, & Hyona, 2012). Perception of these signals, and their evaluation as positive, leads to physiological arousal, which can subsequently trigger sexual behavior and ultimately lead to copulation (Walen & Roth, 1987).

In line with this hypothesis, fMRI studies have shown amplification of occipito-temporal responses to erotic pictures involving couples as well as to single nude bodies (for a review, see Table 1 in Bühler, Vollstädter-Klein, Klemen, & Smolka, 2008). Due to the limits of temporal resolution of fMRI, these studies have been unable to characterize the temporal dynamics of enhanced processing of sexual signals from bodies. One MEG study has found two occipito-temporal responses to be larger to nude bodies than to neutral, non-human objects: the earlier response at mean latency of 126 ms, was present only in male participants, whereas the second response at 203 ms, was observed in both male and female participants (Costa, Braun, & Birbaumer, 2003). However, as responses to nude bodies were compared with those to non-human objects rather than to clothed bodies, the study does not reveal how clothing affects the early visual responses to human bodies.

Our recent EEG study found that the N1 to bodies linearly increased from fully clothed via minimally clothed to nude bodies, with the N1 to nude bodies being even stronger than that to faces (Hietanen & Nummenmaa, 2011). This suggests that the N1 component is sensitive also to the affective arousal associated with nude bodies (Bradley, Codispoti, Cuthbert, & Lang, 2001; Codispoti & De Cesarei, 2007). Moreover, the N1 enhancement to nude bodies seems to reflect the effect of affective arousal rather than increased object-based attention to nude bodies (Hietanen, Kirjavainen, & Nummenmaa, 2014). The enhanced N1 for nude compared to clothed bodies has been confirmed also by an EEG study showing the effect to be present also under subliminal viewing conditions (Legrand, Del Zotto, Tyrand, & Pegna, 2013). Together with studies showing enhanced N1 for emotionally arousing (e.g. fearful) compared to neutral facial expressions (Batty & Taylor, 2003; Leppänen, Kauppinen, Peltola, & Hietanen, 2007), these results demonstrate that the N1 response is likely sensitive to arousal during visual object processing. However, all these studies have analyzed the data only in the sensor space, thus the spatiotemporal cascade of processing nude vs. clothed bodies remains unknown.

1.2. Effect of the presence or absence of head in body processing

In addition to the enhancement of the N1 to nude bodies, Hietanen and Nummenmaa (2011) showed that the visibility of face (i.e. intact vs. masked head) had no effect on the N1 amplitude evoked by nude or clothed bodies. In contrast, another study showed that the N1 to bodies without head had larger amplitude and longer latency than that to bodies with intact head but masked face (Minnebusch, Suchan, & Daum, 2009). This result is surprising considering that the N1 is known to reflect processing of configurationally (or holistically) represented information (Eimer, 2000), which is important for the perception of bodies (Reed, Stone, Bozova, & Tanaka, 2003). However, this result could be explained by an unusual picture of a “decapitated” human body evoking also affective responses and therefore leading to the enhanced and prolonged N1. Further, one has to take into account that the N1 to bodies with heads might not reflect only body-related visual processing, but rather summed responses to faces and bodies. Indeed, even a masked head in the context of a body has been shown to elicit enhanced activity in the face-sensitive fusiform face area (FFA) (Cox, Meyers, & Sinha, 2004). In sum, the effect of the presence or absence of head to body processing remains unclear and should therefore be controlled for.

1.3. The current study

Current evidence suggests that the early cortical responses sensitive to the visual perception of human bodies reflect not only visual processing systems specialized in body perception, but also affective-motivational processes tracking emotional arousal level, the latter occurring automatically and being beneficial in detecting threat-related social signals, identifying potential mating partners and competitors, and triggering sexual behavior. However, two critical questions remain unanswered: first, are nude and clothed bodies processed by same cerebral networks which simply respond more vigorously to nude bodies, or does processing of nude bodies recruit an extended set of circuits involved in affective and arousal processing? Second, what is the temporal cascade of cerebral processing of nude vs. clothed bodies?

To answer these questions, we recorded simultaneous MEG and EEG while male and female participants viewed photographs of nude and clothed bodies of males and females. Further, since the effect of the presence or absence of head to the processing of bodies remains unclear, the body stimuli were presented either headless or with masked head. Masked instead of intact head was selected, on the one hand, to control for the possibility that visibility of faces per se could be emotionally arousing, and on the other hand, because no difference was found between the responses to bodies with intact vs. masked head in our earlier study (Hietanen & Nummenmaa, 2011). The spatiotemporal dynamics of cortical activity evoked by the body stimuli was probed by utilizing the millisecond temporal resolution together with the increased spatial localization accuracy provided by combined MEG/EEG (Sharon, Hämäläinen, Tootell, Halgren, & Belliveau, 2007) and MNE-based source modeling (Lin, Belliveau, Dale, & Hämäläinen, 2006).

2. Materials and methods

2.1. Participants

Ten male and ten female volunteers participated in the study. Two participants were excluded from the analyses due to low signal-to-noise ratio (SNR), resulting in a final sample of 18 participants (9 females, age mean \pm SD 24.4 ± 4.0). All participants were self-reported heterosexuals and had normal or corrected-to-normal vision. The experiments were performed under written informed consent and the study protocol was approved by the Institutional review board of Aalto University.

2.2. Stimuli and task

The stimuli were color photographs of clothed and nude bodies (Fig. 1). The models in the body stimuli were attractive and normal-weight adult males and females (half and half) standing in typical modeling postures against white background. In some of the body stimuli, the upper body was slightly turned sideways, but there was no difference between the clothed body and nude body stimuli in this respect ($p > .05$ in χ^2 test). The models in clothed body stimuli wore sexually non-revealing clothing, comprising at least a sleeved shirt and long pants/jeans and, in some cases, also a jacket/coat. About 10% of the clothed stimuli had logos or emblems on their clothing, but these were equiprobable for male and female stimuli ($p > .05$ in χ^2 test). Chest and genitals were clearly exposed in the nude body stimuli. The amount of pubic hair varied, although it was typically rather modest. Penis size and turgidity also varied across nude male stimuli. None had piercings or tattoos. The subjective arousal and valence of the body stimuli has been assessed in our previous studies (Hietanen & Nummenmaa, 2011; Hietanen et al., 2014), showing higher arousal and lower valence ratings to nude than to clothed bodies.

The photographs for the stimuli were downloaded from various websites. Two variants of the body pictures were created: one with the head cropped out and one with the head masked by means of pixelation. The pixelation involved a rectangular mask around the head with the resolution decreased to an average of 4 pixels per inch. Thus, the experiment comprised a total of 8 stimulus categories, with 20 exemplars in each category. Additionally, photographs of male and female faces as well as animals were presented in the experiment; however, these data were not analyzed in the present study.

The stimuli were back-projected onto a screen in front of the participant, with an approximate viewing distance of 140 cm. The stimuli were presented for 500 ms. The inter-stimulus interval varied randomly between 1000–1200 ms. Participants' task was to pay attention to the stimuli and to indicate by a button press whenever a picture of an animal was presented. The stimuli were presented in a randomized

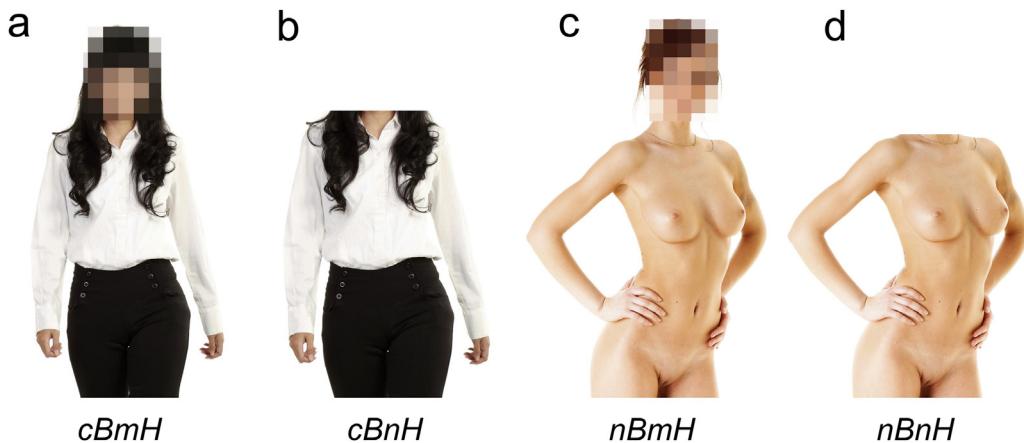


Fig. 1. Examples of the visual stimuli. (a) Clothed body with masked head (cBmH), (c) clothed body with no head (cBnH), (d) nude body with masked head (nBmH), and (e) nude body with no head (nBnH). Both male and female stimuli were used in the experiment. The images shown here do not depict the actual stimuli but are intended only as examples.

order in blocks of ~6 min between which the participants could take a break. Each block contained 20 instances of each stimulus category (a total of 220 pictures). Five stimulation blocks were presented for each participant; however, if the number of artifact-free trials was deemed insufficient on the basis of on-line averaging, an additional sixth block was run (see Section 2.3). The stimulus presentation was controlled by Presentation software.

2.3. Data acquisition

MEG was acquired with a whole-head device (VectorView, Elekta-NeuroMag, Helsinki, Finland) with 102 sensor elements each containing a magnetometer and a pair of planar gradiometers. EEG was recorded concurrently with 28 channels with the placement adhering to the 10–20 system. The data were acquired at 1 kHz sampling rate and 0.1–330 Hz pass band. The reference electrode was placed at the nose tip. Horizontal and vertical electro-oculogram (EOG) was recorded in order to monitor artifacts related to blinks and eye-movements. Prior to the recordings, the locations of three anatomical landmarks, four head-position indicator coils, and the EEG electrodes were digitized.

Responses time-locked to the onset of the visual stimulus presentation were offline-averaged across trials for each stimulus category. Trials exceeding 150 μ V or 3000 fT/cm amplitude in the EEG/EOG or MEG channels, respectively, were rejected from the average, resulting in ~200 averaged trials per stimulus category. The averaged signals were band-pass filtered between 1–30 Hz. The signal amplitudes were measured with respect to a 100-ms prestimulus baseline.

2.4. Structural magnetic resonance imaging (MRI)

Anatomical reference images were acquired with General Electric Signa 3 T MRI scanner with Excite upgrade at the Advanced Magnetic Imaging Centre of the Aalto University School of Science. Anatomical images with 1-mm isotropic voxels were acquired with a T1-weighted spoiled gradient echo (SPGR) sequence with ASSET parallel imaging (182 axial slices, no gaps, TR = 10 ms, TE = 1.9 ms, acquisition matrix = 256 \times 256, flip angle = 15°).

2.5. Data analysis

2.5.1. N1 response

As a replication of our earlier study (Hietanen & Nummenmaa, 2011), we first analyzed the amplitude and latency of the N1 responses between the stimulus categories. The N1 was identified as a negative amplitude peak at the latency range of 140–220 ms in EEG channels T5 and T6 (see Fig. 2). Amplitudes and latencies of the N1 component were analyzed using analysis of variance (ANOVA) with participant gender (male vs. female) as between-groups factor and stimulus clothing (clothed vs. nude), stimulus head (cropped vs. masked), stimulus gender (male vs. female), and laterality (left vs. right hemisphere) as within-subjects factors.

2.5.2. Mean global field power (MGFP)

We then quantified the MEG data at the sensor level with mean global field power (MGFP). The MGFP was calculated by averaging the root mean square (RMS) values separately across magnetometers and gradiometers. Both magnetometers and gradiometers were included as they differ in their depth sensitivities, i.e. magnetometers are more sensitive to deep neuronal sources (e.g. in the ventral temporal or insular cortex) but also to noise sources (e.g. heartbeat).

2.5.3. MEG/EEG source estimation

The source currents were estimated at each cortical location by computing a depth-weighted minimum-norm estimate (MNE; Hämäläinen & Ilmoniemi, 1994; Lin, Witzel, et al., 2006). The forward solutions for all source locations were computed using a three-compartment boundary element model (BEM) based on the information from individual structural MRIs and locations of the MEG sensors and EEG electrodes (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). The cortical surface of each participant, reconstructed with FreeSurfer software (<http://surfer.nmr.mgh.harvard.edu/>), was decimated to ca. 7000 source locations per hemisphere with an average 5-mm spacing between adjacent locations. A noise covariance matrix was estimated from 100-ms prestimulus baselines of the raw MEG/EEG data. Activity at each source location was estimated for each time point of the evoked response using an inverse operator computed from the forward solution and the noise covariance matrix. A loose orientation constraint was applied to favor currents perpendicular to the cortical surface (Lin, Belliveau, et al., 2006).

2.5.4. Group dSPM estimates

Dynamic statistical parametric map (dSPM) estimates were used for visualizing the mean evoked activity on the cortical surface. As a measure of signal-to-noise derived through normalizing the MNE by the noise sensitivity at each cortical location, dSPM indicates locations where the MNE amplitudes are above the noise level. The individual dSPM estimates were first morphed to the FreeSurfer average brain (Fischl, Sereno, Tootell, & Dale, 1999) and subsequently averaged across individuals at each source location.

2.5.5. Spatiotemporal cluster analysis

A nonparametric randomization test based on spatiotemporal clustering was applied for a whole-cortex statistical analysis between evoked responses to different stimulus categories (Maris & Oostenveld, 2007). The data were downsampled to 200 Hz and the individual cortical surfaces were morphed to a FreeSurfer average brain with 10,242 dipoles per hemisphere (Fischl et al., 1999). A *t*-value was calculated for each data point (i.e. dipole/time point) for the given contrast between stimulus categories using a two-sided paired-samples *t*-test. All data points with *p*-value < .05 (uncorrected for multiple comparisons) were clustered on the basis of spatial and temporal adjacency. Cluster-level statistics were then calculated by summing the *t*-values within every cluster and the maximum of the cluster-level statistics was used as the actual test statistic. A reference distribution of test statistics was produced by taking a thousand random partitions of the combined data across the conditions and by calculating a test statistic for each partition. A multiple-comparisons-corrected cluster *p*-value was obtained by comparing the test statistic of the contrast of interest against the reference distribution. The null hypothesis of no difference between the conditions was rejected if this *p*-value was smaller than .05. The tests were performed using the MNE-Python toolbox (Gramfort et al., 2013). The medial wall, as defined by automatic parcellation (Desikan et al., 2006), was excluded from the analysis due to low SNR.

3. Results

3.1. N1 responses

3.1.1. N1 amplitude

All stimulus categories elicited a prominent N1 waveform. Fig. 2 shows ERPs from two occipito-temporal channels (T5, T6). ANOVA

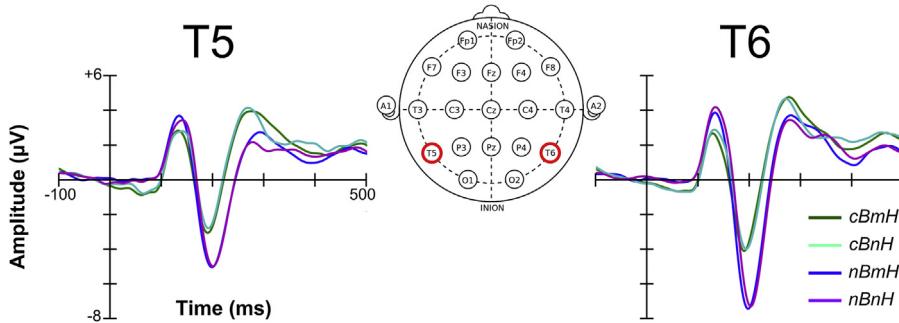


Fig. 2. ERPs from occipito-temporal channels T5 and T6 to the different stimulus categories. cBmH, clothed bodies with masked head; cBnH, clothed body with no head; nBmH, nude body with masked head; nBnH, nude body with no head.

showed main effects of stimulus clothing ($F(1,16)=25.5, p < .001, \eta_p^2 = .61$), stimulus gender ($F(1,16)=33.4, p < .001, \eta_p^2 = .68$), and laterality ($F(1,16)=5.0, p < .05, \eta_p^2 = .24$), with stronger responses to nude vs. clothed stimuli, female vs. male stimuli, and in the right vs. left hemisphere. No difference was found between headless bodies and bodies with masked head, or between participant genders. A significant interaction was found between stimulus clothing and laterality ($F(1,16)=5.1, p < .05, \eta_p^2 = .24$), caused by a larger difference in the responses to nude vs. clothed bodies in the right ($F(1,16)=29.1, p < .001, \eta_p^2 = .65$) vs. left hemisphere ($F(1,16)=15.1, p < .01, \eta_p^2 = .49$).

3.1.2. N1 latency

The N1 latency showed a main effect of stimulus clothing ($F(1,16)=35.8, p < .001, \eta_p^2 = .69$), stimulus head ($F(1,16)=14.1, p < .01, \eta_p^2 = .47$), and stimulus gender ($F(1,16)=21.7, p < .001, \eta_p^2 = .58$), with longer N1 latency to nude vs. clothed bodies, headless bodies vs. bodies with masked head, and female vs. male stimuli. A significant stimulus head X stimulus gender X laterality interaction was also found ($F(1,16)=5.6, p < .05, \eta_p^2 = .26$). Pairwise comparisons revealed that the interaction was caused by a large difference in the latencies between headless bodies vs. bodies with masked head for the male stimuli in the right hemisphere ($F(1,16)=19.3, p < .001, \eta_p^2 = .55$), whereas clearly less significant differences were observed for the other comparisons, especially in the left hemisphere (female stimuli, left hemisphere: $F(1,16)=4.9, p < .05, \eta_p^2 = .23$; male stimuli, left hemisphere: $F(1,16)=4.18, p = .06, \eta_p^2 = .21$; female stimuli, right hemisphere: $F(1,16)=8.9, p < .01, \eta_p^2 = .36$).

3.2. Mean global field power

Group-average MGFP was calculated in order to identify response maxima specific to the stimulus categories (Fig. 3). The MGFP of all stimulus categories showed a prominent peak at ~ 145 ms and another, less prominent, at ~ 265 ms after stimulus onset. The MGFP of nude bodies, but not of clothed bodies, showed a prominent peak also at ~ 205 ms.

3.3. Group dSPM estimates

Fig. 4 shows dSPM-estimated source distributions for cBnH and nBnH visualized on an inflated right-hemispheric cortical surface at the latencies of the MGFP maxima (see Section 3.2). No visible differences were observed between cBnH and cBmH or between nBnH and nBmH. The response at ~ 145 ms showed no prominent differences in the source distribution between the stimulus categories but was stronger to nBnH than to cBnH in the medial occipital cortex (MOC). At ~ 205 ms, the response to nBnH was widely distributed in the occipito-temporal areas with a right hemisphere bias, with only weak activation observed for cBnH. The response at

~ 265 showed no notable difference in the source distributions or strength between the stimulus categories.

3.4. Spatiotemporal cluster analysis

3.4.1. Visual processing of nude vs. clothed bodies

As shown in Fig. 5, nude bodies (nBmH + nBnH) elicited stronger activity than clothed bodies (cBmH + cBnH) at early latencies in bilateral areas centered in VTC and LOTC (left: 100–200 ms, $p < .001$; right: 100–200 ms, $p < .001$), and later in widespread areas including the VTC, LOTC, and lateral temporal cortex (LTC), extending to the insular (IC), lateral orbitofrontal (LOFC), and anterior cingulate (ACC) cortices (left: 200–300 ms, $p < .001$; right: 200–300 ms, $p < .001$). In contrast, stronger activity in response to clothed compared to nude body was found in the left MOC between 220 and 300 ms ($p < .05$).

3.4.2. Effect of the presence or absence of head on the visual processing of bodies

We finally asked how the presence or absence of head influences the visual processing of bodies. To that end, all bodies (i.e. clothed and nude) with masked head were contrasted against all bodies with no head (cBmH + nBmH vs. cBnH + nBnH). As shown in Fig. 6, bodies with masked head elicited significantly stronger responses than headless bodies in all four analysis time windows. Early sensitivity to the presence of head was found in the left MOC (100–185 ms, $p < .01$) and right MOC/precuneus (100–200 ms, $p < .05$), and later in bilateral VTC/MOC (left: 215–300 ms, $p < .01$; right: 225–300 ms, $p < .05$) and right LOTC (225–300 ms, $p < .05$). At longer latencies, bodies with masked head elicited stronger responses than headless bodies in the right VTC/MOC (300–400 ms, $p < .01$; 400–490 ms, $p < .05$).

4. Discussion

The current study described the spatiotemporal cascade of cerebral visual processing of nude vs. clothed human bodies. Early processing of nude bodies was enhanced compared to bodies wearing clothes. Even though both nude and clothed bodies activated a set of overlapping regions in the occipito-temporal cortices (Fig. 4), these responses were markedly stronger for nude bodies (Fig. 5). Furthermore, viewing nude but not clothed bodies recruited a set of extended regions including IC and ACC. Our findings therefore suggest that the human brain is tuned to detect sexual cues from human bodies rapidly, and that this detection process is reflected in enhanced activity in a distributed neural network, involving early (100–200 ms) facilitated responses in body processing circuits (EBA and FBA) as well as subsequent (200–300 ms) responses in affective-motivational areas (e.g. IC and ACC).

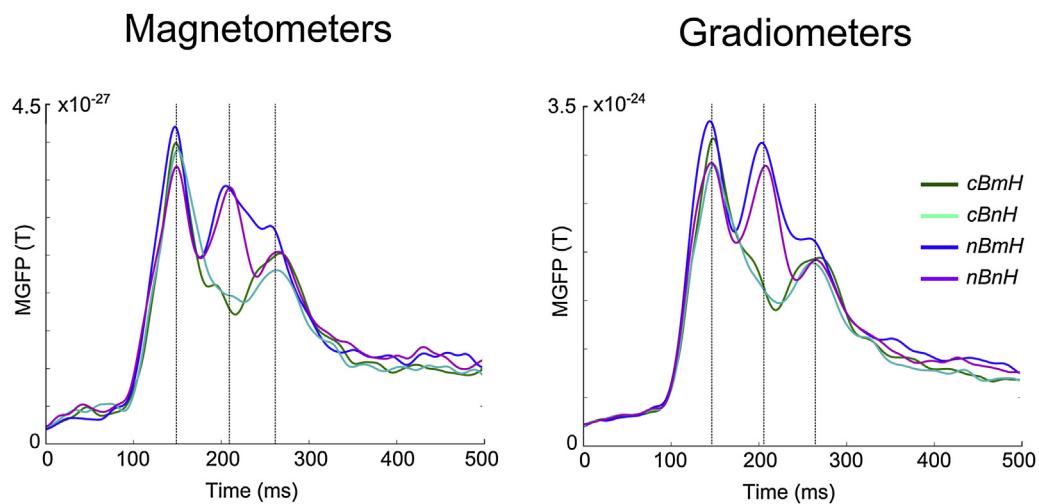


Fig. 3. Mean global field power (MGFP) of evoked MEG responses to the stimulus categories. The vertical lines indicate latencies of observed MGFP maxima. cBmH, clothed body with masked head; cBnH, clothed body with no head; nBmH, nude body with masked head; nBnH, nude body with no head.

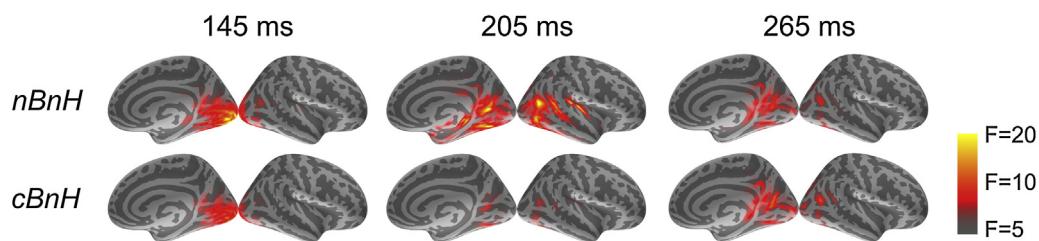


Fig. 4. Cortical source distributions estimated with dSPM and visualized on a right-hemispheric inflated cortical surface at latencies of the MGFP maxima. The color coding indicates F -values. cBnH, clothed body with no head; nBnH, nude body with no head. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

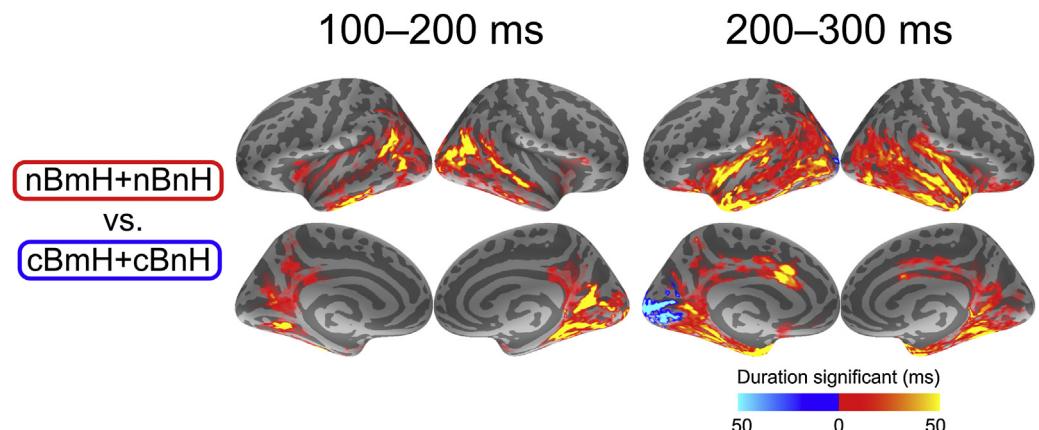


Fig. 5. Effect of clothing on the early visual processing of human bodies visualized on an inflated cortical surface. Warm and cold colors indicate nude- and clothed-body-sensitive responses, respectively. The time range indicates the analysis time window. The temporal extent of the clusters is color-coded. nBmH, nude body with masked head; nBnH, nude body with no head; cBmH, clothed body with masked head; cBnH, clothed body with no head. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

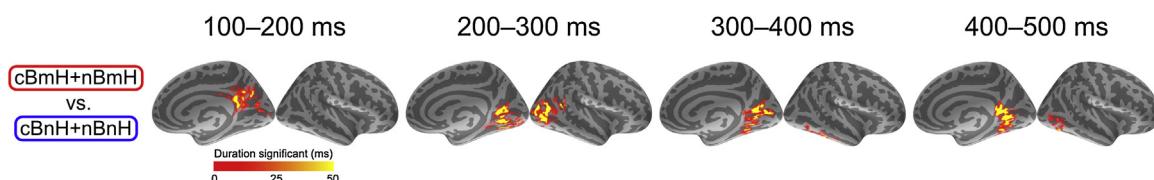


Fig. 6. The effect of the presence or absence of head in the early visual processing of bodies. Visualized on an inflated cortical surface of the right hemisphere. The color coding indicates the temporal extent of the cluster. cBmH, clothed body with masked head; nBmH, nude body with masked head; cBnH, clothed body with no head; nBnH, nude body with no head. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. Temporal dynamics of perceiving nude and clothed bodies

Supporting our earlier findings (Hietanen & Nummenmaa, 2011; Hietanen et al., 2014), the N1 amplitude was larger and latency longer for nude vs. clothed bodies (Fig. 2). MEG global field power revealed a prominent response peak at ~145 ms after stimulus onset to both clothed and nude bodies and at ~205 ms exclusively to nude bodies (Fig. 3). The nude-body-sensitive responses (i.e. nude bodies > clothed bodies) were localized to distributed areas centered at first (100–200 ms) in bilateral VTC and LOTC including the EBA and FBA, respectively, and subsequently (200–300 ms) in LOTC, VTC, and LTC, extending to the ACC, IC, and LOFC (Fig. 5). These sources accord with results from a recent study revealing locations of enhanced nude vs. clothed body processing within the N1 time range in the primary visual and body processing areas as well as in areas linked to emotion processing (Legrand et al., 2013). Stronger responses to clothed vs. nude bodies were observed only in the left MOC between 220 and 300 ms. This not only points to different cortical dynamics between the processing of nude and clothed bodies but, together with the observed N1 amplitude interaction between stimulus clothing and laterality, suggests that the processing of nude bodies is more strongly right-lateralized than the processing of clothed bodies.

4.2. Affective-motivational effects on nude body perception

The distributed activity pattern elicited by nude bodies is compatible with a recently proposed functional neuroanatomical model of body perception in which perceptual processing in the EBA/FBA interacts with expectations, associations, and internal motivational states in a fronto-insular-temporal network in order to obtain the significance of the perceived body (Amoruso, Couto, & Ibanez, 2011). The visibility of sex-related human body features changes the affective and motivational significance of the stimulus and would thus result in enhanced engagement of the fronto-insular-temporal network, particularly of the IC, which has been implicated in the integration of internal motivational drives with external stimuli (Ibanez, Gleichgerrcht, & Manes, 2010). In line with this, an fMRI study where participants viewed sexual video clips revealed a positive correlation between plethysmographic penile responses and BOLD signal in several areas, including the IC and ACC (Mouras et al., 2008). Enhanced activity in the IC has been reported also when viewing fearful vs. neutral body expressions (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004), thus suggesting that it may play a general role in extracting affective significance from bodies. At more general level, the ACC has been implicated in the evaluation of attractiveness (Platek & Singh, 2010), and both ACC and IC are associated with the elicitation of sexual interest (Georgiadis & Kringelbach, 2012).

In this context, the N1 latency difference between clothed and nude bodies (Fig. 2), along with the MGFP peaks specific to nude bodies (Fig. 3), could thus be explained by top-down influence on the processing of the presented stimulus based on prior experiences, current emotions and motivation, and future expectations (for a review, see Bar & Bubic, 2013). It has been demonstrated that interactive iterations between lower-level sensory and higher-order parietal and frontal cortices can occur already during early visual processing (<200 ms after stimulus onset), therefore implying that the early brain response components, including the N1, likely reflect the result of simultaneous bottom-up and top-down processing instead of feedforward sensory processing alone (Foxe & Simpson, 2002). Here, the MGFP response peak at ~205 ms specific to the processing of nude bodies could thus result from additional iteration triggered by emotional arousal during the first iteration, whereby a rudimentary sketch of the sensory event is obtained through feedforward and feedback projections from the early visual

areas to the prefrontal cortex and back to VTC to be integrated with the bottom-up processing (Bar et al., 2006; Bar, 2003). This would consequently be reflected as the longer N1 latency for nude vs. clothed bodies. Similarly, longer N1 latencies have been reported for emotionally arousing (e.g. fearful) vs. neutral faces (Batty & Taylor, 2003).

Importantly, even though the nude body stimuli had higher luminance ($p < .001$ in t -test) and contrast (RMS; $p < .001$ in t -test) than the clothed body stimuli, the longer N1 latency to nude vs. clothed bodies argues against the possibility that this could explain the nude-body-sensitive effect as higher level in such low-level visual features has been shown to result in decreased, rather than increased, N1 latency (Johannes, Munte, Heinze, & Mangun, 1995). Moreover, the difference in luminance and contrast between the nude and clothed body stimuli reflects a natural feature of the coloring of the body, rather than an experimental artifact. Adaptation (i.e. repetition suppression) constitutes another possibly confounding effect that needs to be considered when interpreting the results (e.g. Rugg, Soardi, & Doyle, 1995; Vuilleumier, Henson, Driver, & Dolan, 2002). However, as stronger adaptation has been demonstrated for emotionally arousing vs. neutral faces (Ishai, Pessoa, Bikle, & Ungerleider, 2004), it seems unlikely that the opposite would occur for emotionally arousing vs. neutral bodies, therefore suggesting that adaptation cannot explain the stronger responses for nude vs. clothed bodies.

Taken together, our results add to the growing pool of evidence showing enhanced ERP responses to affectively arousing visual stimuli (Olofsson, Nordin, Sequeira, & Polich, 2008) and are compatible both with body processing theories (Amoruso et al., 2011) as well as with findings on the neuroanatomical correlates of affective processing (e.g. Krolak-Salmon, Henaff, Vighetto, Bertrand, & Mauguire, 2004; Legrand et al., 2013; Sabatinelli, Lang, Keil, & Bradley, 2007). However, the present data do not allow for the dissociation between domain-general arousal mechanisms and mechanisms detecting emotionally arousing cues from human bodies. Future studies need to determine whether the present findings reflect effects specific to the visibility of sexual features from human bodies as opposed to general emotional arousal mechanisms. To resolve this issue, brain responses to clothed and nude bodies could be recorded from participants with hypoactive sexual desire disorder, who show reduced responsiveness to sexual stimuli (Basson et al., 2004). An alternative approach would involve comparing responses to sexually arousing (adults) vs. non-arousing (babies) clothed and nude bodies.

4.3. Gender differences in body perception

Female stimuli elicited greater N1 responses than male stimuli across both participant genders, which accords with our earlier findings (Hietanen & Nummenmaa, 2011). Considering that the enhancement in the processing of nude vs. clothed bodies can be accounted for by affective arousal, subsequent triggering of sexual behavior, and the ultimate purpose of reproduction (Walen & Roth, 1987), the question arises as to why were opposite-sex effects present only in male participants. These findings however accord with prior work showing that physiological and evaluative sexual responses of males are notably discriminative to opposite-sex compared to same-sex stimuli, whereas the responses of females are more evenly distributed between stimulus genders (for a review, see Rupp & Wallen, 2008; although see also Spape, Timmers, Yoon, Ponseti, & Chivers, 2014). For example, Lykins, Meana, & Strauss (2008) found that when participants were presented with erotic and non-erotic images of heterosexual couples, male participants looked at opposite-sex stimuli longer than female participants, and female participants looked at same-sex stimuli longer than male participants. Heterosexual females also tend to rate male and

female nudes as equally arousing, whereas males rate female nudes more arousing than male nudes (e.g. Costa et al., 2003). Moreover, even though reproduction requires an opposite-sex partner, sexual behavior may well be triggered by perception of a nude body regardless of the gender, for example, through associations (Amoruso et al., 2011). It has to be noted, though, that the current study with nine participants per group may simply lack statistical power for detecting potentially subtle gender differences in body perception.

4.4. Effect of head on body perception

We also investigated the effect of the presence or absence of head to the processing of bodies. While no differences were found in the N1 response amplitude between bodies with masked head vs. no head, the N1 latency to headless bodies was longer than that to bodies with masked head, which accords with Minnebusch et al. (2009). The spatiotemporal cluster analysis revealed stronger responses to bodies with masked head than to headless bodies first in bilateral MOC, and later (>200 ms) in bilateral VTC and right LOTC (Fig. 6). These effects could be explained by inadequate configural/holistic information in case of headless bodies, especially as removing internal or external features of faces has similarly been shown to attenuate and delay N1 responses (Eimer, 2000). Since enhanced activity was observed in bilateral VTC for bodies with masked head vs. no head, the interpretation is congruent also with the proposed specialization of the FBA in configural/holistic processing of the body stimulus (for a review, see Downing & Peelen, 2011). On the other hand, the stronger VTC activity for the bodies with masked head could reflect face-specific processing in a part-based rather than configural/holistic manner, as even a masked head in the context of a body has been shown to elicit enhanced activity in the face-sensitive FFA (Cox et al., 2004).

5. Conclusions

We conclude that the visibility of sexual features strongly facilitates the early cortical processing of human bodies, and that this is reflected in enhanced activity in a distributed network, including body processing areas, such as the EBA and FBA, as well as affective-motivational areas, such as the IC and ACC. The purpose of such a neural boost is presumably to trigger sexual behavior and ultimately ensure reproduction.

Conflict of interest

The authors declare no competing financial interests.

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