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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.

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, Seeck, & 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, Amemiya, 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, exstrastriate 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, Vollstädt-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 ± 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