



Additive effects of affective arousal and top-down attention on the event-related brain responses to human bodies



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ABSTRACT

The early visual event-related 'N170 response' is sensitive to human body configuration and it is enhanced to nude versus clothed bodies. We tested whether the N170 response as well as later EPN and P3/LPP responses to nude bodies reflect the effect of increased arousal elicited by these stimuli, or top-down allocation of object-based attention to the nude bodies. Participants saw pictures of clothed and nude bodies and faces. In each block, participants were asked to direct their attention towards stimuli from a specified target category while ignoring others. Object-based attention did not modulate the N170 amplitudes towards attended stimuli; instead N170 response was larger to nude bodies compared to stimuli from other categories. Top-down attention and affective arousal had additive effects on the EPN and P3/LPP responses reflecting later processing stages. We conclude that nude human bodies have a privileged status in the visual processing system due to the affective arousal they trigger.

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1. Introduction

Human bodies convey multiple sexual, social, and emotional cues and one of the most important functions of body perception is related to sexual selection (Andersson, 1994). For example, bodily features such as hip-waist-ratio (Singh, 1993), obesity (Smith, Cornelissen, & Tovée, 2007), body symmetry (Rhodes & Simmons, 2007), breast size (Manning, Scutt, Whitehouse, & Leinster, 1997) and height/weight-ratio (Fan, Dai, Liu, & Wu, 2005) all influence mate preference. Functional neuroimaging studies have revealed a specialized brain network for processing different types of biologically relevant information from others' bodies (de Gelder et al., 2010; Minnebusch & Daum, 2009; Peelen & Downing, 2007). This network includes two main components, extrastriatal body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001) in the posterior inferior temporal cortex and fusiform body area (FBA; Peelen & Downing, 2005; Peelen, Wiggett, & Downing, 2006; Schwarzlose, Baker, & Kanwisher, 2005) in the posterior fusiform gyrus. There is a functional dissociation between visual body processing in the EBA and FBA. While EBA responds more strongly to individual body parts, FBA is involved in holistic processing of the body stimulus

(see review in Downing & Peelen, 2011). Single cell recordings in primates also suggest that the visual system has circuits specialized in body perception. Neurons in the inferior temporal cortex (IT) of macaque monkeys respond selectively to the shape of both human and monkey bodies and to body parts (Kiani, Esteky, Mirpour, & Tanaka, 2007; Wachsmuth, Oram, & Perrett, 1994).

Electromagnetic studies in humans have revealed that an occipito-temporal component peaking 140–200 ms post stimulus is sensitive to presentations of bodies and their parts (Gliga & Dehaene-Lambertz, 2005; Meeren, van Heijnsbergen, & de Gelder, 2005; Righart & de Gelder, 2007; Thierry et al., 2006). This body-sensitive ERP component is often recorded from the same temporal channels as the face-sensitive N170 component (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2004; Rossion & Jacques, 2008). However, source localization and scalp voltage distribution are different for responses to faces and bodies (Gliga & Dehaene-Lambertz, 2005; Thierry et al., 2006). The N170 response to bodies reflects visual processing in both FBA and EBA, whereas the N170 response to faces originates from the fusiform face area – an area more anterior to FBA – and the lateral occipitotemporal cortex more ventral to EBA (Bötzel, Schulze, & Stodieck, 1995; Rossion, Joyce, Cottrell, & Tarr, 2003; Shibata et al., 2002) possibly also from the posterior superior temporal sulcus (Itier & Taylor, 2004). Two recent magnetoencephalography (MEG) studies comparing directly the activity to bodies versus faces reported different

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neural contributors to the electromagnetic counterpart of the N170 response. In one study, the origin of the response was localized in the posterior inferior temporal cortex for faces and in the posterior middle temporal gyrus for bodies (Ishizu, Amemiya, Yumoto, & Kojima, 2010), and in another study the response (M140) for faces was associated with activity in a large occipito-temporal network including the ventral temporal cortex, whereas the body-selective responses were restricted specifically to lateral occipito-temporal cortex (Meeren, de Gelder, Ahlfors, Hämäläinen, & Hadjikhani, 2013).

Recently, Hietanen and Nummenmaa (2011) investigated whether the N170 response to bodies is sensitive to body clothing. As efficient perception of sexual signals and categorization of conspecifics as potential mating partners or competitors is essential for both sexual selection and ensuring reproduction in humans and other primates, the visual system might be tuned to detect and process especially nude bodies rapidly. Indeed, previous imaging studies had shown increased occipitotemporal activation in response to nude bodies (e.g., Ferretti et al., 2005; Mouras et al., 2003; Walter et al., 2008). In line with this, the ERP results by Hietanen and Nummenmaa showed that the early visual body processing was enhanced to opposite and same-sex nude bodies versus clothed bodies. The authors suggested that the enhanced N170 amplitudes to nude bodies reflected the effect of increased arousal elicited by these stimuli, a suggestion supported by measurements of physiological autonomic responses (electrodermal activity) and self-reported arousal while viewing the stimulus pictures. However, another potential explanation for the enhanced N170 responses to nude bodies may be top-down allocation of attention: It is conceivable that when body stimuli appear at fixation the participants voluntarily allocate more attention to the sexually salient, nude rather than clothed bodies, and the differences in allocation of top-down, object-based attention – rather than arousal – would explain differential responses between the nude and clothed bodies.

1.1. Attentional and affective effects on brain responses

Selection of relevant environmental information is based on interplay between attentional and affective mechanisms. Both exogenous (bottom-up, stimulus-driven) and endogenous (top-down, goal-driven) gain control mechanisms control attentional selection and filtering (Posner & Dehaene, 1994; Theeuwes, 2010). These mechanisms are subserved by partially distinct brain networks spread out in the fronto-parietal cortices (Corbetta & Shulman, 2002). Affective mechanisms work in parallel with, but at least partly independent of the fronto-parietal systems in adjusting the processing of sensory information. Here the amygdala's feedforward projections to the sensory cortices are likely to play a central role in mediating top-down affective influences on sensory gain control (Vuilleumier, 2005).

In the present study we investigate the interactive effects of object-based attention and affective arousal on the visual processing of human bodies. Numerous neuroimaging studies have shown that selective attention to visual stimuli, as well as the emotional content of these stimuli, increase activation in the occipital, parietal, and infero-temporal visual areas (Kastner & Ungerleider, 2000; Pourtois, Schettino, & Vuilleumier, 2013; Vuilleumier, 2005). For example, emotion-related movements of human bodies have been shown to increase activation in the EBA and FBA areas (Peelen, Atkinson, Andersson, & Vuilleumier, 2007). Electrophysiological studies have associated the effects of attention and emotion especially with three temporally consecutive components. The first one, early posterior negativity (EPN), is a negative-going occipito-temporal potential associated with perceptual encoding and early selection of stimuli which are either voluntarily attended to or

which carry affective and motivational significance and, therefore, capture attention involuntarily. The EPN is enhanced for both attended as well as emotional pictures, the maximal enhancement occurring within 200–350 ms post-stimulus (Codispoti, Ferrari, Junghöfer, & Schupp, 2006; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Delorme, Rousselet, Mace, & Fabre-Thorpe, 2004; Junghöfer, Bradley, Elbert, & Lang, 2001; Kissler, Herbert, Winkler, & Junghöfer, 2009; Schupp et al., 2000; Schupp et al., 2004; Schupp, Junghöfer, Weike, & Hamm, 2003; Schupp et al., 2007). The second component is P3, typically observed as centro-parietal positivity between 300 and 700 ms after stimulus onset. Like EPN, P3 is enhanced to attended, task-relevant stimuli as well as to affectively arousing (i.e., both pleasant and unpleasant) versus neutral stimuli (Keil et al., 2002; Polich & Kok, 1995; Schupp et al., 2007). The third component is late positive potential (LPP), which is also observed as centro-parietal positivity beginning at about 300 ms post-stimulus. However, unlike the P3 response, the LPP is long-lasting (up till 1000 ms) and can be observed even after stimulus offset (Cuthbert et al., 2000; Hajcak & Olvet, 2008). The LPP is also enhanced to attended, task-relevant and to emotional stimuli (Cuthbert et al., 2000; Ferrari, Codispoti, Cardinale, & Bradley, 2008; Foti, Hajcak, & Dien, 2009; Schupp et al., 2000; Schupp et al., 2003).

In sum, previous research indicates that attention and affective information enhances visual processing at several stages and that the influences of attention and affect on the measured ERP components overlap in time and space, and are manifested in the same ERP components. Obviously, this is not surprising considering that the affective content of the stimuli is thought to influence attention allocation due to intrinsic stimulus significance (e.g., Nummenmaa et al., 2012; Nummenmaa, Hyönä, & Calvo, 2006). As visual processing of human bodies shares many qualities with face processing, including specialized cortical networks and high degree of automaticity, we next review the studies that have addressed attentional and emotional effects on face processing. Because the present study concerned the effects of attention directed to a specific stimulus category (object-based attention), and not the effects of attention to stimuli presented in attended versus unattended spatial locations (spatial attention), we will confine the following overview to studies investigating the effects of object-based attention on face processing.

1.2. How object-based attention and emotions influence face perception

Object-based attention does not, in general, modulate the early face-sensitive N170 response. The amplitude of the N170 response elicited by faces is independent of whether the task requires allocating attention to the centrally presented faces or to stimuli belonging to another object category (Carmel & Bentin, 2002; Cauquil, Edmonds, & Taylor, 2000; Lueschow, Sander, Boehm, Nolte, & Trahms, 2004). Only in cases, when the recognition of the facial stimuli is made difficult by degrading the stimuli (Eimer, 2000), when the discriminability of the faces was low in superimposed (e.g., face-house) images (Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009), or when task-irrelevant faces were superimposed by to-be-recognized letters (Mohamed, Neumann, & Schweinberger, 2009), top-down attention modulates the N170 amplitudes. Instead, both EEG and MEG studies have reliably shown the effects of object-based attention on face processing for later (>280 ms post stimulus) occipito-temporal and centro-parietal ERP responses (Furey et al., 2006; Lueschow et al., 2004). Also, intracranial recordings from the ventral occipito-temporal cortex have shown that the early face-sensitive N200 response is not sensitive to object-based attention, whereas attention starts to influence face-processing beginning at 240 ms post-stimulus (Engell & McCarthy, 2010).

The effects of affective information on face processing have been studied by using expressive face stimuli. In several studies, the early N170 response has been shown to be sensitive to facial emotional expressions (Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Caharel, Courtay, Bernard, Lalonde, & Rebai, 2005; Eger, Jedynak, Iwaki, & Skrandies, 2003; Leppänen, Kauppinen, Peltola, & Hietanen, 2007; Vlamings, Goffaux, & Kemner, 2009; Williams, Palmer, Liddell, Song, & Gordon, 2006; Wronka & Walentowska, 2011), although not all previous studies have found this effect (e.g., Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003; Holmes, Vuilleumier, & Eimer, 2003). Interestingly from the point of view of the present study, N170 responses to emotional versus neutral faces may actually reflect interactive effects of emotion and attention. In all the earlier studies where faces were centrally presented and the participants were instructed to direct their attention to facial expressions, modulation of N170 amplitude by facial expressions was observed (Caharel et al., 2005; Leppänen et al., 2007). In fact, one recent study specifically investigated the effects of non-spatial attention on the processing of centrally presented neutral and emotional faces. In two different conditions, the task required participants to pay attention to the gender or the emotional expression of the facial stimuli. The N170 amplitude was enhanced to emotional versus neutral faces only when attention was directed to facial expressions, but not when attention was directed to gender (Wronka & Walentowska, 2011). Like in the case of attentional modulation, facial emotional expressions have been reported to result also in enhanced occipito-temporal EPN responses (Wronka & Walentowska, 2011) as well as in broadly distributed long-lasting positivity beyond 250 ms post-stimulus (Eimer & Holmes, 2002; Eimer et al., 2003). Moreover, these later, enhanced responses (EPN and fronto-central positivity) to emotional versus neutral expression have been observed to be independent of the allocation of non-spatial attention (i.e., expression vs. gender discrimination) (Wronka & Walentowska, 2011).

1.3. The current study

To investigate the effects of affective arousal and voluntary, object-based attention on visual processing of human bodies, we recorded electroencephalographic responses while participants viewed body, face and object stimuli. To manipulate the affective arousal, we showed both clothed and nude body stimuli. Object-based attention was manipulated by showing stimulus pictures from four different categories (clothed bodies, nude bodies, faces, and cars) one at a time in random order, while the participants' task was to attend to stimuli only from one category in each block and detect specific targets belonging to this category. We quantified the effects of affective arousal and top-down attention on early visual N170 responses as well as on later occipito-temporal EPN and centro-parietal P3/LPP responses. We were especially interested in investigating whether orienting object-based attention away from the bodies would dilute the enhanced N170 responses to nude bodies (cf. Hietanen & Nummenmaa, 2011), thus revealing that the ERP modulation would be due to attentional rather than affective factors. To compare the results with earlier findings on face processing, faces were included as a control stimulus category. In order to confirm affective differences between the stimulus categories, we also assessed participants' subjective arousal and valence evaluations for each stimulus picture.

2. Methods

2.1. Participants

17 healthy volunteers (9 males, 8 females) with normal or corrected-to-normal vision participated in the experiment (age $M=21.9$, $SD=3.2$, range 18–30 years).

One male participant was left-handed and all the others were right-handed. All participants were uninformed of the purpose of the experiment. This study was approved by the Tampere Region Ethical Committee for Human Research.

2.2. Stimuli

Stimuli were 80 color pictures of clothed and nude bodies, faces, and cars, 20 from each category (see Fig. 1). Half of the human stimuli depicted males and the other half females. The pictures were downloaded from various websites. The clothed and nude models were standing in typical modeling postures. Clothed models wore conventional clothes such as t-shirts, jeans, and jackets. Face pictures were cut from similar body pictures, but not from those used for the body stimuli. In all pictures showing human models, the model was looking at the camera. In the majority of the pictures, the model had a neutral or a slightly positive expression on the face. A smiling face appeared in five clothed body pictures, in five nude body pictures, and in four face pictures ($p>.05$ in chi-square test). In most of the body pictures, the body was oriented straight towards the camera. In some pictures, the upper body was slightly turned sideways, but there was no difference between the clothed body and nude body picture categories in this respect ($p>.05$ in chi-square test). Face stimuli were rescaled 200% to make the stimulus size across stimulus types comparable. All texts (e.g., from registration plates) were removed from the car pictures. Additionally, there were two 'target pictures' (see below) per category.

The stimuli subtended (horizontal \times vertical) $4^\circ \times 8^\circ$ for the bodies ($5.4\text{ cm} \times 11.0\text{ cm}$), $5^\circ \times 4^\circ$ for the faces ($6.2\text{ cm} \times 4.8\text{ cm}$), and $8^\circ \times 5^\circ$ for the cars ($10.6\text{ cm} \times 7.4\text{ cm}$) at the viewing distance of 78 cm. All stimuli were cut from their background using Paint Shop Pro 7, and shown against white background. A black plus sign was used as a fixation point ($0.7^\circ \times 0.7^\circ$). The stimulus duration was 500 ms. The stimuli were shown on a 17" LCD-monitor set to resolution of 1024×768 . The refresh rate was 75 Hz. E-Prime software controlled stimulus delivery and response recording.

2.3. Experimental procedure

Participants were first acquainted with the laboratory and the equipment and they gave a written informed consent. The participants were told that they would be seeing pictures of nude and clothed bodies, faces, and cars in four blocks.

Participants were seated comfortably in an armchair in front of a monitor at a viewing distance of 78 cm. The laboratory room was dimly lit during stimulus presentation. The purpose of the experiment was not revealed to the participants until the end of experiment. After the EEG electrodes were attached, the participants were told that before each block, they would see two target pictures simultaneously from one of the four picture categories (nude bodies, clothed bodies, faces, cars). Participants were told to remember these pictures, focus their attention to the corresponding category while viewing the stimulus block and press the mouse button with their right index finger every time they saw either one of the targets. Participants read the instructions from the screen and the experimenter confirmed that the task was understood.

Each block was started by showing the two target stimuli side by side on the screen for 13 s. After this, a block of stimulus pictures was shown. Each picture was presented for 500 ms with an interstimulus interval (ISI) of 1500 ms. A fixation point was shown in the middle of the screen during the ISI and the participants were instructed to fixate it throughout the experiment. The stimuli were shown in random order in each block (see Fig. 1).

There were four blocks. In each block, one of the four stimulus categories was attended and the target stimuli were always from the attended category. Each block contained 400 stimuli: 80 attended and 240 (80 per category) non-attended stimuli plus 80 "filler stimuli", 20 from each stimulus category. The filler stimuli (20) from the attended stimulus category were targets requiring the manual response. Note that in order to have an equal number of stimuli in each stimulus category, we had to include also the rest of the filler stimuli (60) into each stimulus block. ERP responses in response to any of these target/filler stimuli were not analyzed. Each block lasted for 13.6 min. The blocks were interleaved with short breaks for maximizing participant comfort. Before the actual experiment, participants practiced the task for 1.6 min (40 trials) with stimuli not contained in the actual experiment. The training targets were pictures of animals in order to avoid creating an unintended attentional bias by selection history to any of the stimulus categories (see Awh, Belopolsky, & Theeuwes, 2012).

2.4. Self-reported emotional responses to pictures

After the EEG experiments, all stimulus pictures were shown again, and the participants were asked to assess how they felt when seeing them using affective arousal and valence dimensions. Participants gave answers on the computer with nine-point arousal and valence Self-Assessment Manikin scales (SAM; Bradley & Lang, 1994).

2.5. EEG recording

Continuous EEG was recorded from scalp with 64-channel actiCAP Ag/AgCl electrodes mounted to elastic cap arranged in the 10-10 international electrode

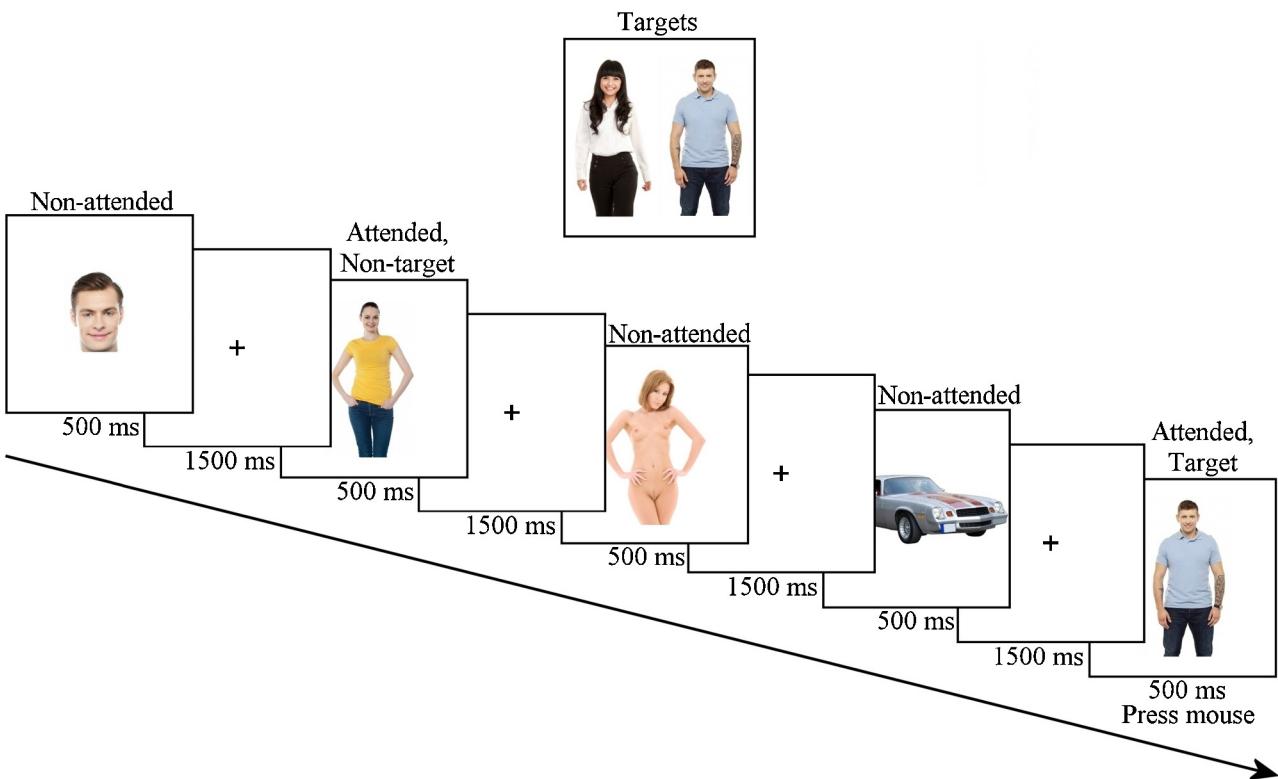


Fig. 1. A flowchart of the events during an experimental block. In the illustrated block, participants were told to attend to clothed bodies and to press a mouse button every time they see either one of the target stimuli. Examples of stimuli from different stimulus categories are also illustrated.

positioning system. The signal was amplified using quickAmp amplifier (Brain Products, Germany) and online referenced to common average. Electrode impedances were kept below 25 kOhm. Horizontal and vertical eye movements were recorded bipolarly, using the sites beside the outer canthi of both eyes and above and below the midpoint of the left eye. The EEG data were collected using Vision Recorder software. Continuous EEG-signal was digitized using 1000 Hz sampling rate and stored to a computer disk for offline analyses.

2.6. Data analysis

The raw continuous EEG-signal was first offline filtered with 0.05–30 Hz band-pass filter (50 Hz notch filter enabled) with 12 dB/oct slope on both ends. A regression-based Gratton/Coles – ocular correction algorithm (Gratton, Coles, & Donchin, 1983) was used to correct eye movement artifacts. The following automatic data inclusion criteria were used: maximal allowed voltage step was 50 μ V/ms, maximal allowed amplitude was $\pm 100 \mu$ V, and the minimum allowed voltage change during an interval of 100 ms was 0.5 μ V. If one of these criteria were exceeded, 400 ms around that point was rejected. Next, the data were visually inspected and remaining artifacts were rejected. In total, 9.1% of the trials were rejected (9.4% from clothed body trials; 8.6% from nude body trials; 9.2% from face trials; and 9.1% from car trials, no statistically significant differences across conditions). The data were then segmented to 1100-ms long epochs starting from 100 ms before the stimulus onset. A baseline adjustment was applied using the average of 100-ms pre-stimulus period. Baseline-corrected data were averaged over the trials for each stimulus type.

We analyzed data from two electrode sites. For the temporal electrodes, we selected the channels P7/8, T7/8, and TP9/10. These channels typically show the face and body sensitive N170 responses (e.g., Bentin et al., 1996; Gliga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Minnebusch, Suchan, & Daum, 2009; Righart & de Gelder, 2007; Taylor, Roberts, Downing, & Thierry, 2010). The P3/LPP response was analyzed from the centro-parietal region electrodes (CP1, CP2, CPz, P1, P2, POz, and Pz) conventionally used for the P3/LPP analysis (e.g., Cuthbert et al., 2000; Hajcak & Olvet, 2008; Schupp et al., 2004). For the temporal recording sites, N170 responses and activity in the 200–500 ms post-stimulus time window (EPN) were analyzed. N170 response was defined as the peak negative amplitude between 140 and 200 ms. For the EPN, we analyzed the mean amplitude in six consecutive 50-ms time bins. Latency of the N170 response was also measured. For P3/LPP, we analyzed activity in 100-ms time bins between 300 and 1000 ms post-stimulus. Visual inspection indicated that the P3/LPP response in the selected centro-parietal recording sites was clearly visible after the stimulus disappeared from the screen (500 ms) thus we extended the analysis to include data also between 500 and 1000 ms post-stimulus.

The data for the non-attended conditions were acquired from the attend-to-cars block. The car stimuli were included as an extra stimulus category in order to have data for the non-attended nude bodies, non-attended clothed bodies, and non-attended faces from a block where the attended stimulus did not belong to any of the categories used as attended targets. As the depth of processing of a given unattended stimulus category might vary depending on the similarity between the unattended and the attended stimulus category, comparing the effects of attention between stimulus categories would have been problematic had we taken the data for non-attended stimulus conditions from a block where the attended stimulus was one of the three investigated stimulus categories. Because we were not interested in the brain responses to the cars *per se*, these data were not analyzed further. Note that average responses from all three non-attended blocks could not be used as the baseline non-attended condition, because this resulted in different number of trials between the attended and non-attended conditions, and consequently smaller standard errors of mean (SEM) in the non-attended than attended condition thus biasing the results.

All statistical analyses were conducted using repeated-measures analysis of variance (ANOVA). A Greenhouse-Geisser correction was used when appropriate. However, for the sake of consistency, uncorrected degrees of freedom are reported. Familywise error was controlled for using the Bonferroni procedure.

3. Results

3.1. Behavioral tasks

The recognition accuracies for the targets from different stimulus categories was very high (range 90–100%; means: clothed bodies 97.5%; nude bodies 98.0%; faces 99.5%; cars 98.5%) and did not differ between the categories ($p > .05$).

Table 1 shows average affective arousal and valence scores for the four stimulus categories. An ANOVA for arousal scores showed a main effect of stimulus type ($F_{(3, 48)} = 11.4$, $p < .001$, $\eta_p^2 = .42$). Participants felt more aroused when seeing nude bodies, compared to when seeing clothed bodies ($p = .008$), faces ($p = .002$), or cars ($p = .006$). The scores for clothed bodies, faces, and cars did not differ from each other ($p > .05$). A similar ANOVA for valence scores also revealed a main effect for stimulus type ($F_{(3, 48)} = 47.5$,

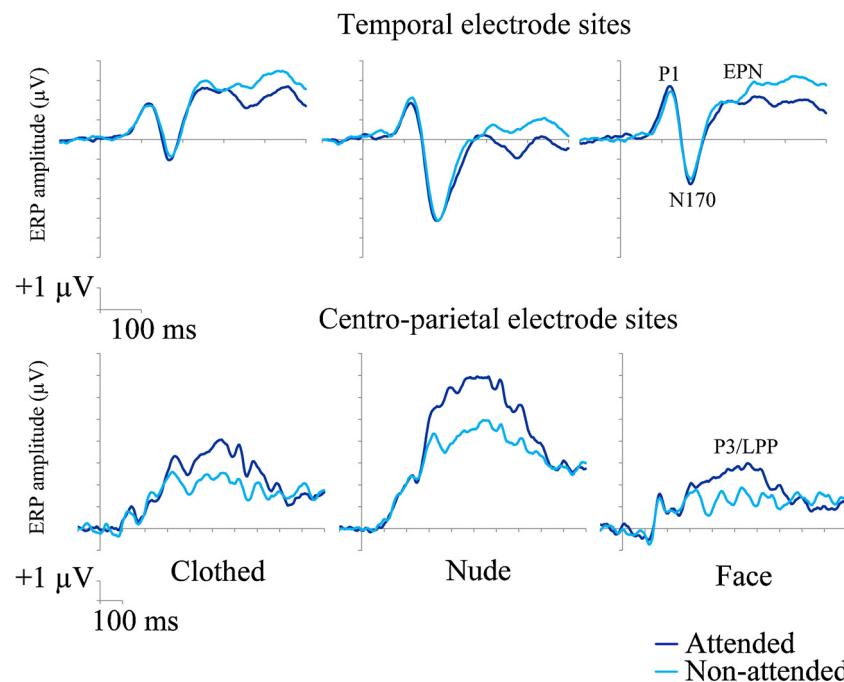


Fig. 2. ERPs from the temporal (averaged over P7, TP7, TP9, P8, TP8, and TP10) and centro-parietal electrodes (averaged over CP1, CP2, CPz, P1, P2, POz and Pz) to attended and non-attended clothed bodies, nude bodies, and faces.

$p = .002$, $\eta_p^2 = .32$). Participants experienced more pleasant feelings when seeing clothed bodies, compared to when seeing nude bodies ($p = .009$), faces ($p = .004$), or cars ($p = .021$). The scores for nude bodies, faces, and cars did not differ from each other ($ps > .05$).

3.2. N170 response

For the N170 response amplitudes, a 3 (stimulus category: clothed, nude, face) \times 2 (attention: attended, non-attended) \times 3 (electrode: P7/8, TP7/8, TP9/10) \times 2 (hemisphere: left, right) fully within-subjects ANOVA revealed a main effect of stimulus ($F_{(2, 32)} = 31.2$, $p < .001$, $\eta_p^2 = .66$). The N170 amplitude to nude bodies ($M = -5.6 \mu\text{V}$) was greater than that to faces ($M = -3.2 \mu\text{V}$, $p = .004$) or to clothed bodies ($M = -2.1 \mu\text{V}$, $p < .001$). The N170 response was also greater to faces than to clothed bodies ($p = .005$). A stimulus \times hemisphere interaction ($F_{(2, 32)} = 5.4$, $p = .009$, $\eta_p^2 = .25$) reflected the fact that, in the right hemisphere, N170 amplitude was greatest to nude bodies, followed by faces and clothed bodies ($ps < .05$). In the left hemisphere, N170 amplitude to nude bodies was greater than that to clothed bodies or to faces (both $ps < .05$), but the difference between clothed bodies and faces was not significant ($p > .05$). Attention had neither a significant main effect nor interactions with stimulus type ($ps > .05$). An attention \times electrode \times hemisphere interaction was significant ($F_{(2, 32)} = 5.0$, $p = .023$, $\eta_p^2 = .24$), likely to reflect just a spurious effect. Pairwise comparisons revealed that the N170 amplitude was greater for attended versus non-attended stimuli ($M = -2.6 \mu\text{V}$ vs. $-2.1 \mu\text{V}$, $p = .021$) at one of the left-hemispheric electrodes (TP7).

Table 1
Mean (and SD) arousal and valence rating scores for each stimulus category.

Rating	Clothed body		Nude body		Face		Car	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Arousal	3.26	1.65	4.45	1.70	3.34	1.67	2.93	1.73
Valence	6.11	1.17	4.58	0.95	5.49	1.14	4.84	1.67

For the N170 latencies, an ANOVA showed a main effect of stimulus ($F_{(2, 32)} = 19.9$, $p < .001$, $\eta_p^2 = .55$). The N170 latency for nude bodies ($M = 178 \text{ ms}$) was longer than that for clothed bodies ($M = 171 \text{ ms}$, $p < .001$) or faces ($M = 171 \text{ ms}$, $p < .001$). The main effect and interactions for attention were not significant ($ps > .05$) (see Figs. 2 and 3).¹

3.3. EPN response

The EPN response was analyzed with a $6 \times 3 \times 2 \times 3 \times 2$ ANOVA with time (six consecutive 50-ms time windows between 200 and 500 ms), stimulus category (clothed, nude, face), attention (attended, non-attended), electrode pair (P7/8, TP7/8, TP9/10), and hemisphere (left, right) as within-subject factors. This analysis revealed a main effect of attention ($F_{(1, 16)} = 13.5$, $p = .002$, $\eta_p^2 = .46$), a time \times attention interaction ($F_{(5, 80)} = 12.2$, $p < .001$, $\eta_p^2 = .43$), as well as a time \times attention \times electrode pair interaction ($F_{(10, 160)} = 7.9$, $p < .001$, $\eta_p^2 = .33$). Consequently, attended and non-attended conditions were compared separately for every electrode pair in each time window. Attention began to influence the amplitudes of the electrode pair TP9/TP10 in the 300–350 ms time window for all stimulus types and the amplitudes were more negative for the attended than non-attended stimuli ($p = .009$). The difference extended to the 450–500 ms time window ($p < .001$). For

¹ We also conducted an additional analysis to check whether there would be any effects on the earlier P1 responses measured from these same channels. P1 response was defined as the peak positive amplitude between 80 ms and 140 ms post stimulus. An ANOVA did not reveal a main effect for stimulus type or attention (both $ps > .05$). A stimulus \times electrode interaction ($F_{(4, 64)} = 4.2$, $p = .004$, $\eta^2 = .05$, $\eta_p^2 = .21$) was significant. Further analyses (data averaged across left and right recording sites) showed that the sizes of the P1 amplitudes between electrode pairs varied differently for different stimulus types but, importantly, responses to different stimulus types did not differ significantly from each other in any electrode site ($ps > .05$). There were no main effects or interactions for P1 latencies. This finding is compatible with the prevailing view suggesting that the effects of stimulus arousal on ERPs do not usually begin before the N1 response latency range (150–200 ms) (see Olofsson, Nordin, Sequeira, & Polich, 2008).

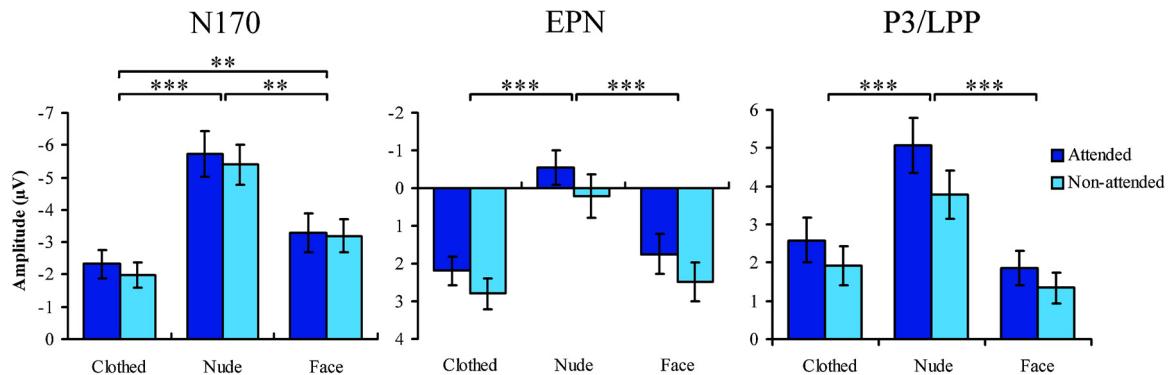


Fig. 3. The mean amplitudes (and SD) of the N170, EPN, and P3/LPP responses to clothed bodies, nude bodies, and faces in attended and non-attended conditions. The data are averaged over recording sites, hemispheres, and time-windows of analysis. For the main effect of stimulus, results of the pairwise comparisons are shown (** $p < .01$, *** $p < .001$). The main effect of attention was also significant for the EPN and P3/LPP responses. There were no interactions between stimulus and attention.

electrode pair TP7/TP8, attention effects started 200–250 ms after stimulus onset ($p = .011$), disappeared in the 250–300 ms time window ($p > .05$), and appeared again from 300 to 500 ms ($p < .01$). For the electrode pair P7/P8, attention did not modulate the amplitudes ($p > .05$). A main effect of stimulus ($F_{(2, 32)} = 53.7, p < .001, \eta_p^2 = .77$), as well as time \times stimulus ($F_{(10, 160)} = 5.8, p = .001, \eta_p^2 = .27$) and stimulus \times hemisphere ($F_{(2, 32)} = 6.3, p = .005, \eta_p^2 = .28$) interactions were also significant. Amplitudes were more negative for nude bodies than for clothed bodies or faces ($p < .001$), but the amplitudes for clothed bodies and faces did not differ from each other (see Figs. 2 and 3). Analysis of the time \times stimulus interaction revealed that the amplitudes were more negative for nude bodies than for clothed bodies or faces in all time windows ($p < .001$), but also the amplitude difference for clothed bodies versus faces was significant in the 200–250 ms time window ($M = 2.06 \mu\text{V}$ vs. $1.13 \mu\text{V}$, $p = .002$). Further analysis of the stimulus \times hemisphere interaction revealed that while nude bodies elicited greater negative amplitudes than clothed bodies or faces in both hemispheres ($p < .001$), only the amplitudes for faces differed between the left and right hemispheres ($M = 1.38 \mu\text{V}$ vs. $2.86 \mu\text{V}$, $p = .005$).

3.4. P3/LPP response

The data showed a long-lasting positive drift over centro-parietal channels (CP1, CP2, CPz, P1, P2, POz, and Pz) for all stimulus types. A 3 (stimulus type: clothed bodies, nude bodies, face) \times 2 (attention: attended, non-attended) \times 7 (time: seven 100-ms time windows between 300 and 1000 ms post-stimulus) fully within-subjects ANOVA revealed main effects of attention ($F_{(1, 16)} = 14.0, p = .002, \eta_p^2 = .47$) and stimulus type ($F_{(2, 32)} = 35.8, p < .001, \eta_p^2 = .69$). Also attention \times time ($F_{(6, 96)} = 18.3, p < .001, \eta_p^2 = .53$) and stimulus type \times time ($F_{(12, 192)} = 9.48, p < .001, \eta_p^2 = .37$) interactions were significant. Attended stimuli elicited significantly greater positive amplitudes compared to the non-attended stimuli from 300 to 700 ms ($p < .05$). The effect of arousal reflected greater positivity to nude bodies than to clothed bodies and faces ($p < .001$), and this was evident in every 100-ms time window between 300 and 1000 ms post-stimulus ($p < .05$). Also, the positive amplitudes to clothed bodies were greater than those to faces ($p < .01$), but only in 300–400 ms and 500–600 ms time windows ($p < .05$). Attention and stimulus type did not have any significant interactions ($p > .05$) (see Figs. 2 and 3). Fig. 4 summarizes the effects of attention and arousal on human body processing by showing scalp topographies of the mean voltage amplitude differences between activity in attended and non-attended conditions (averaged across nude and clothed bodies) and between activity to nude

and clothed bodies (averaged across attended and non-attended conditions).

4. Discussion

We show that both affective arousal and top-down object-based attention influence the visual processing of human bodies. Moreover, we reveal for the first time the time-course of additive attentional and arousal-driven modulations in visual processing of human bodies. In the temporal channels where early body-sensitive responses are typically recorded, no effects of attention on the amplitudes or latencies of the early N170 responses to the human body stimuli or control face stimuli were found. Our findings thus do not support the hypothesis that the enhancement of the N170 response to nude bodies reflects the effects of preferential top-down attention on the nude bodies versus other stimuli. This lack of top-down attentional modulation of the N170 potential accords with earlier findings from methodologically comparable studies investigating face processing (Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004). However, despite the lack of attentional modulation, the effects of affective arousal on the early human body processing were clear: Nude bodies, independent of the allocation of top-down object-based attention, elicited greater N170 response amplitudes than clothed bodies or faces, thus replicating the earlier results by Hietanen and Nummenmaa (2011). This result highlights that the enhancement of the N170 response to nude bodies occurs due to enhanced processing of affectively arousing stimuli. This was confirmed by self-ratings of affective arousal, which were higher for nude bodies than for other stimulus categories. Unlike the early N170 response, the later EPN and P3/LPP responses were influenced by attention as well as by affective arousal.

As reviewed in Section 1, the effects of emotion (facial expressions) on the N170 responses to faces are dependent on attention. In particular, Wronka and Walentowska (2011) showed that the N170 response is greater to emotional versus neutral faces only when participants are explicitly paying attention to the expressions, rather than the gender of the faces. Enhanced processing of nude versus clothed bodies is clearly not similarly contingent on availability of attentional resources, as N170 responses were greater to nude versus clothed bodies irrespective of the attended stimulus category. An obvious explanation relates to the degree of affective arousal elicited by nude bodies versus facial expressions of emotions. The difference between nude and clothed bodies in experienced affective arousal is likely to be greater than that for emotional versus neutral faces. In fact, previous studies have shown that the arousal ratings are lower for emotional faces than

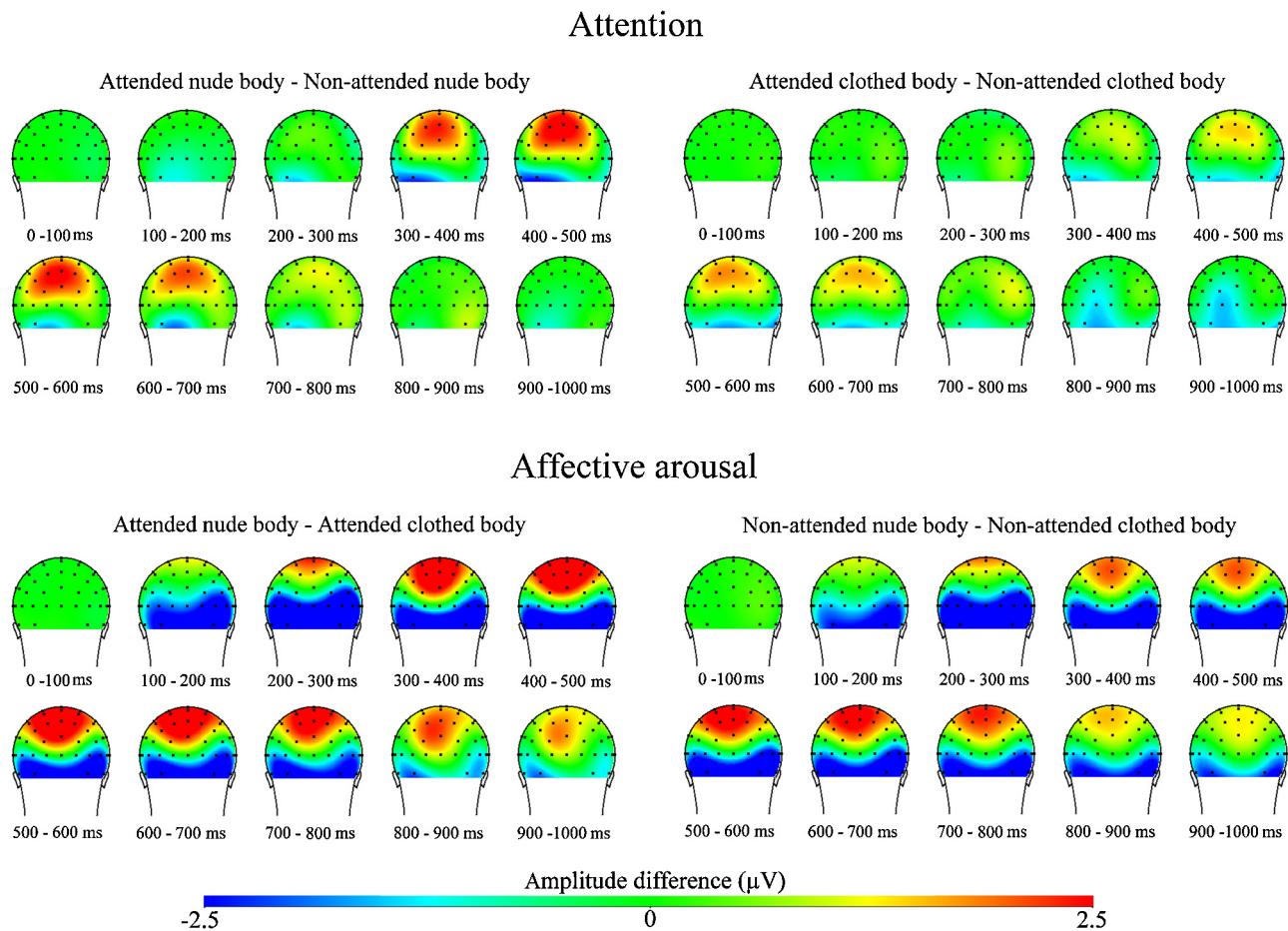


Fig. 4. Scalp topographies of the mean voltage amplitude differences between activity in attended and non-attended conditions for nude and clothed bodies (top) and between activity to nude and clothed bodies in the attended and non-attended conditions (bottom) in 100-ms time windows. The topographies are illustrated from the back view of a head to show the posterior negativity.

for emotional scenes (erotica and violence) and, moreover, that psychophysiological responses are stronger for emotional scenes than faces (Alpers, Adolph, & Pauli, 2011; Wangelin, Bradley, Kastner, & Lang, 2012). However, as we did not study the effects of affective arousal on face processing in the present experiment, more research is needed in order to investigate whether the affect-driven ERP modulations for faces and bodies depend differently on attention.

As expected, the EPN response and the centro-parietal P3/LPP response revealed significant effects of top-down attention. For EPN, irrespective of the stimulus category, attended versus unattended stimuli elicited enhanced negativity as early as 200–250 ms after the stimulus onset, and the effect sustained until the end of the analysis window (200–500 ms post-stimulus). In the same vein, for the P3/LPP response there was a positive drift over centro-parietal channels, which was enhanced for attended stimuli compared to non-attended stimuli between 300 and 700 ms post-stimulus. Affective arousal also had an additive effect on the attentional modulation of these ERPs. The EPN response was more negative for nude bodies than for clothed bodies, irrespective of the top-down attention. For P3/LPP, the positive drift was also more pronounced to nude bodies compared to clothed bodies, and this effect sustained throughout the analysis window (300–1000 ms), being thus longer lasting than that observed for the effect of attention. These results accord with the subjective ratings of affective arousal, which were higher for nude versus clothed bodies. Taken together, the present study extends earlier studies in showing the effects of attention and affective arousal on the EPN response (Codispoti et al.,

2006; Cuthbert et al., 2000; Junghöfer et al., 2001; Schupp et al., 2004; Schupp et al., 2003; Schupp et al., 2007) by revealing the additive effects of emotion and attention on the EPN response to human body stimuli. The present results also accord with prior work suggesting that both attention and affective arousal enhance the centro-parietal positivity between 300 and 700 ms after stimulus onset (P3 response) (Keil et al., 2002; Polich & Kok, 1995; Schupp et al., 2007), whereas the effects of affective arousal extended longer till 1000 ms post-stimulus (LPP response). The results are also compatible with those of a recent study showing enhanced EPN and LPP responses to arousing body parts, i.e., insulting hand gestures (Flaisch & Schupp, 2013).

Recently, Pourtois et al. (2013) suggested that the sensory processing enhancement of emotional stimuli may be realized by similar gain control mechanisms through which attentional systems (exogenous and endogenous) exert their effects on sensory processing, but importantly, this emotional gain control may be mediated by distinct neural mechanisms in amygdala and interconnected orbitofrontal areas, whereas the dorsal fronto-parietal networks mediate the attentional gain control. Based on this view, we suggest that the N170 amplitude enhancement as well as the larger EPN and P3/LPP responses to nude versus clothed bodies observed in the present study reflected the effects of the emotional gain control systems, whereas the enhancement of the EPN and P3/LPP responses to attended stimuli reflected the effects of the attentional gain control systems. The most interesting findings of the present study were that the time-course of the emotional effects was different to that of the attentional effects, and that the

effects of top-down attention and affective arousal were additive rather than interactive. The present results suggest that the early visual processing of the human body configuration, as reflected in the N170 responses, prioritizes processing of nude bodies because of their affective arousal. However, at this early stage, voluntary object-based attention does not yet modulate the processing. Instead, on the following stages as indexed by the EPN and P3/LPP responses, both affective arousal and voluntary top-down attention start to exert simultaneously their independent effects on the visual processing of human bodies. Moreover, as the data showed that the enhancement of the centro-parietal positivity lasted longer for nudity than for top-down attention, this would imply that the processing enhancement by affective arousal continued after the effect of top-down attention had ceased. It is likely that cessation of the top-down effect coincides with top-down attention disengagement after the enhanced stimulus processing required for the discrimination task was terminated. Additive effects of top-down attention and affective arousal have been reported in previous studies on EPN responses to affective pictures (erotica and mutilations) (Schupp et al., 2007) and on LPP (Ferrari et al., 2008). However, interactive effects between attention and affective arousal on centro-parietal P3 responses have also been reported (Schupp et al., 2007). Obviously, comparison of the results between studies is complicated by considerable differences in the used stimuli and experimental paradigms.

An important question relates to whether the observed larger N170 responses to nude versus clothed bodies reflect enhanced information processing in the body-specific mechanisms, or whether the N170 amplitude modulation reflects rather overlapping functioning of domain general, arousal-sensitive mechanisms which also results in the modulated EPN responses. In fact, related to face processing, there is recent evidence suggesting that the N170 component itself is not affected by the emotional expression on the face, but the emotional expressions modulate the overlapping EPN activity and this effect is superimposed on the N170 response (Rellecke, Sommer, & Schacht, 2013). However, in another recent study, investigating the N170 and EPN responses to arousing and non-arousing body parts, i.e., insulting versus pointing hand gestures, only EPN but not the N170 response was modulated by the affective arousal of the hand gestures (Flaisch & Schupp, 2013). Thus, previous research using other types of stimuli have provided evidence that the arousal-related EPN activity can overlap with the N170 component (Rellecke et al., 2013), but this is not always the case (Flaisch & Schupp, 2013). Regarding the effects of arousal on body processing, the present data do not allow resolving this issue. In one study, reporting enhanced N1 responses (with a peak latency of about 150 ms) to nude bodies, source localization algorithms were applied to compute the neural generators of the N1 response and the results showed that nude bodies elicited increased activity not only in areas playing a role in body processing, but also in other visual areas and areas involved in processing of affective information (e.g., insula and ventrolateral orbitofrontal cortex) (Legrand, Del Zotto, Tyrand, & Pegna, 2013). Future studies using, for example, magnetoencephalography which allows brain activity measurements with high temporal and spatial resolution would be valuable in resolving the issue of whether the enhanced responses to nude bodies in the N170 time-window specifically reflect enhanced activity in the allegedly body-sensitive cortical mechanisms or whether a more distributed activity enhancement in the posterior visual cortices is observed.

5. Conclusions

We conclude that the early visual processing (<200 ms) of human bodies and faces is unaffected by top-down object-based attention. Instead, affective arousal enhances processing already

at this early stage as evidenced by greater N170 responses to nude versus clothed human bodies independently of endogenous top-down attention. The enhanced N170 responses to nude bodies reflect the effects of emotional gain control systems on processing of affective stimuli. Top-down attention begins to influence stimulus processing around 200–250 ms post-stimulus, and more consistently only after 300 ms. At these processing stages, the effects of object-based attention and affective arousal are additive. We thus propose that the early enhancement of visual processing of nude bodies ensures that biologically and socially important information from the human bodies is processed fast and effectively despite the current task goals.

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References

- Alpers, G. W., Adolph, D., & Pauli, P. (2011). Emotional scenes and facial expressions elicit different psychophysiological responses. *International Journal of Psychophysiology*, 80, 173–181.
- Andersson, M. B. (1994). *Sexual selection*. New Jersey: Princeton University Press.
- Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, 16, 437–443.
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, 17, 613–620.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551–565.
- Blau, V. C., Maurer, U., Tottenham, N., & McCandliss, B. D. (2007). The face-specific N170 component is modulated by emotional facial expression. *Behavioral and Brain Functions*, 3, 7.
- Bötzel, K., Schulze, S., & Stodieck, S. R. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, 104, 135–143.
- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The Self-Assessment Manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, 25, 49–59.
- Caharel, S., Courtay, N., Bernard, C., Lalonde, R., & Rebai, M. (2005). Familiarity and emotional expression influence an early stage of face processing: An electrophysiological study. *Brain and Cognition*, 59, 96–100.
- Carmel, D., & Bentin, S. (2002). Domain specificity versus expertise: Factors influencing distinct processing of faces. *Cognition*, 83, 1–29.
- Caquail, A. S., Edmonds, G. E., & Taylor, M. J. (2000). Is the face sensitive N170 the only ERP not affected by selective attention? *Neuroreport*, 11, 2167–2172.
- Codispoti, M., Ferrari, V., Junghöfer, M., & Schupp, H. T. (2006). The categorization of natural scenes: Brain attention networks revealed by dense sensor ERPs. *Neuroimage*, 32, 583–591.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 201–215.
- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology*, 52, 95–111.
- de Gelder, B., Van den Stock, J., Meeren, H. K. M., Sinke, C. B. A., 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. *Neuroscience and Biobehavioral Reviews*, 34, 513–527.
- Delorme, A., Rousselet, G. A., Mace, M. J., & Fabre-Thorpe, M. (2004). Interaction of top-down and bottom-up processing in the fast visual analysis of natural scenes. *Cognitive Brain Research*, 19, 103–113.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293, 2470–2473.
- Downing, P. E., & Peelen, M. V. (2011). The occipitotemporal body-selective regions in person perception. *Cognitive Neuroscience*, 2, 186–203.
- Eger, E., Jedynak, A., Iwaki, T., & Skrandies, W. (2003). Rapid extraction of emotional expression: Evidence from evoked potential fields during brief presentation of face stimuli. *Neuropsychologia*, 41, 808–817.
- Eimer, M. (2000). Attentional modulations of event-related brain potentials sensitive to faces. *Cognitive Neuropsychology*, 17, 103–116.
- Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport*, 13, 427–431.
- Eimer, M., Holmes, A., & McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: An ERP study of rapid brain responses to six basic emotions. *Cognitive, Affective, & Behavioral Neuroscience*, 3, 97–110.

- Engell, A. D., & McCarthy, G. (2010). Selective attention modulates face-specific induced gamma oscillations recorded from ventral occipitotemporal cortex. *The Journal of Neuroscience*, 30, 8780–8786.
- Fan, J., Dai, W., Liu, F., & Wu, J. (2005). Visual perception of male body attractiveness. *Proceedings of the Royal Society B*, 272, 219–226.
- Ferrari, V., Codispoti, M., Cardinale, R., & Bradley, M. M. (2008). Directed and motivated attention during processing of natural scenes. *Journal of Cognitive Neuroscience*, 20, 1753–1761.
- Ferretti, A., Caufo, M., Del Gratta, C., Di Matteo, R., Merla, A., et al. (2005). Dynamics of male sexual arousal: Distinct components of brain activation revealed by fMRI. *Neuroimage*, 26, 1086–1096.
- Flaisch, T., & Schupp, H. T. (2013). Tracing the time course of emotion perception: The impact of stimulus physics and semantics on gesture processing. *Social Cognitive and Affective Neuroscience*, 8, 820–827.
- Foti, D., Hajcak, G., & Dien, J. (2009). Differentiating neural responses to emotional pictures: Evidence from temporal-spatial PCA. *Psychophysiology*, 46, 521–530.
- Furey, M. L., Tanskanen, T., Beauchamp, M. S., Avikainen, S., Uutela, K., Hari, R., et al. (2006). Dissociation of face selective cortical responses by attention. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 1065–1070.
- Gliga, T., & Dehaene-Lambertz, G. (2005). Structural encoding of body and face in human infants and adults. *Journal of Cognitive Neuroscience*, 17, 1328–1340.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for the off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55, 468–484.
- Hajcak, G., & Olvet, D. M. (2008). The persistence of attention to emotion: Brain potentials during and after picture presentation. *Emotion*, 8, 250–255.
- Hietanen, J. K., & Nummenmaa, L. (2011). The naked truth: The face and body sensitive N170 response is enhanced for nude bodies. *PLoS ONE*, 6, e24408.
- Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research*, 16, 174–184.
- Ishizu, T., Amemiya, K., Yumoto, M., & Kojima, S. (2010). Magnetoencephalographic study of the neural responses in body perception. *Neuroscience Letters*, 481, 36–40.
- Itier, R. J., & Taylor, M. J. (2004). Source analysis of the N170 to faces and objects. *Neuroreport*, 15, 1261–1265.
- Junghöfer, M., Bradley, M. M., Elbert, T. R., & Lang, P. J. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology*, 38, 175–178.
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341.
- Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large-scale neural correlates of affective picture processing. *Psychophysiology*, 39, 641–649.
- Kiani, R., Esteky, H., Mirpour, K., & Tanaka, K. (2007). Object category structure in response patterns of neuronal population in monkey inferior temporal cortex. *Journal of Neurophysiology*, 97, 4296–4309.
- Kissler, J., Herbert, C., Winkler, I., & Junghöfer, M. (2009). Emotion and attention in visual word processing: An ERP study. *Biological Psychology*, 80, 75–83.
- Legrand, L. B., Del Zotto, M., Tyrand, R., & Pegna, A. J. (2013). Basic instinct undressed: Early spatiotemporal processing for primary sexual characteristics. *PLoS ONE*, 8, e69726.
- Leppänen, J. M., Kauppinen, P., Peltola, M. J., & Hietanen, J. K. (2007). Differential electrocortical responses to increasing intensities of fearful and happy emotional expressions. *Brain Research*, 1166, 103–109.
- Lueschow, A., Sander, T., Boehm, S. G., Nolte, G., & Trahms, L. (2004). Looking for faces: Attention modulates early occipitotemporal object processing. *Psychophysiology*, 41, 350–360.
- Manning, J. T., Scutt, D., Whitehouse, G. H., & Leinster, S. J. (1997). Breast asymmetry and phenotypic quality in women. *Evolution and Human Behavior*, 18, 223–236.
- 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, e71408.
- Meeren, H. K., van Heijnsbergen, C. C., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 16518–16523.
- Minnebusch, D. A., & Daum, I. (2009). Neuropsychological mechanisms of visual face and body perception. *Neuroscience and Biobehavioral Reviews*, 33, 1133–1144.
- Minnebusch, D. A., Suchan, B., & Daum, I. (2009). Losing your head: Behavioral and electrophysiological effects of body inversion. *Journal of Cognitive Neuroscience*, 21, 865–874.
- Mohamed, T. N., Neumann, M. F., & Schweinberger, S. R. (2009). Perceptual load manipulation reveals sensitivity of the face-selective N170 to attention. *NeuroReport*, 20, 782–787.
- Mouras, H., Stoléru, S., Bittoun, J., Glutron, D., Péligrini-Issac, M., Paradis, A., et al. (2003). Brain processing of visual sexual stimuli in healthy men: A functional magnetic resonance imaging study. *Neuroimage*, 20, 855–869.
- Nummenmaa, L., Glerean, E., Viinikainen, M., Jääskeläinen, I. P., Hari, R., & Sams, M. (2012). Emotions promote social interaction by synchronizing brain activity across individuals. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 9599–9604.
- Nummenmaa, L., Hyönen, J., & Calvo, M. G. (2006). Eye movement assessment of selective attentional capture by emotional pictures. *Emotion*, 6, 257–268.
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology*, 77, 247–265.
- Peelen, M. V., Atkinson, A. P., Andersson, F., & Vuilleumier, P. (2007). Emotional modulation of body-selective visual areas. *Social Cognitive and Affective Neuroscience*, 2, 274–283.
- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93, 603–608.
- Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8, 636–648.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, 49, 815–822.
- Polich, J., & Kok, A. (1995). Cognitive and biological determinants of P300: An integrative review. *Biological Psychology*, 41, 103–146.
- Posner, M. I., & Dehaene, S. (1994). Attentional networks. *Trends in Neuroscience*, 17, 75–79.
- Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*, 92, 492–512.
- Rellecke, J., Sommer, W., & Schacht, A. (2013). Emotion effects on the N170: A question of reference? *Brain Topography*, 26, 62–71.
- Rhodes, G., & Simmons, L. W. (2007). Symmetry, attractiveness and sexual selection. In R. I. M. Dunbar, & L. Barrett (Eds.), *The Oxford handbook of evolutionary psychology* (pp. 333–364). New York: Oxford University Press.
- Righart, R., & de Gelder, B. (2007). Impaired face and body perception in developmental prosopagnosia. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 17234–17238.
- Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, 39, 1959–1979.
- Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage*, 20, 1609–1624.
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Tiffany, I., & Lang, P. J. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology*, 37, 257–261.
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Hillman, C. H., Hamm, A. O., & Lang, P. J. (2004). Brain processes in emotional perception: Motivated attention. *Cognition and Emotion*, 18, 593–611.
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Emotional facilitation of sensory processing in the visual cortex. *Psychological Science*, 14, 7–13.
- Schupp, H. T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2007). Selective visual attention to emotion. *The Journal of Neuroscience*, 27, 1082–1089.
- Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *The Journal of Neuroscience*, 25, 11055–11059.
- Shibata, T., Nishijo, H., Tamura, R., Miyamoto, K., Eifuku, S., Endo, S., et al. (2002). Generators of visual evoked potentials for faces and eyes in the human brain as determined by dipole localization. *Brain Topography*, 15, 51–63.
- Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, 59, 1191–1201.
- Smith, K. L., Cornelissen, P. L., & Tovée, M. J. (2007). Color 3D bodies and judgements of human female attractiveness. *Evolution and Human Behavior*, 28, 48–54.
- Sreenivasan, K. K., Goldstein, J. M., Lustig, A. G., Rivas, R. R., & Jha, A. P. (2009). Attention to faces modulates early face processing during low but not high face discriminability. *Attention, Perception, & Psychophysics*, 71, 837–846.
- Taylor, J. C., Roberts, M. V., Downing, P. E., & Thierry, G. (2010). Functional characterisation of the extrastriate body area based on the N1 ERP component. *Brain and Cognition*, 73, 153–159.
- Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*, 135, 77–99.
- 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, 871–879.
- Vlamings, P. H. J. M., Goffaux, V., & Kemner, C. (2009). Is the early modulation of brain activity by fearful facial expressions primarily mediated by coarse low spatial frequency information? *Journal of Vision*, 9, 1–13.
- Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, 9, 585–594.
- Wachsmuth, E., Oram, M. W., & Perrett, D. I. (1994). Recognition of objects and their component parts: Responses of single units in the temporal cortex of the macaque. *Cerebral Cortex*, 4, 509–522.
- Walter, M., Bermpohl, F., Mouras, H., Schiltz, K., Tempelmann, C., Rotte, M., et al. (2008). Distinguishing specific sexual and general emotional effects in fMRI-subcortical and cortical arousal during erotic picture viewing. *Neuroimage*, 40, 1482–1494.
- Wangelin, B. C., Bradley, M. M., Kastner, A., & Lang, P. J. (2012). Affective engagement for facial expressions and emotional scenes: The influence of social anxiety. *Biological Psychology*, 91, 103–110.
- Williams, L. M., Palmer, D., Liddell, B. J., Song, L., & Gordon, E. (2006). The 'when' and 'where' of perceiving signals of threat versus non-threat. *Neuroimage*, 31, 458–467.
- Wronka, R., & Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology*, 48, 1047–1056.