

**EARLY VISUAL BODY PROCESSING IS NOT MODULATED BY TOP-DOWN OBJECT-
BASED ATTENTION IN THE HUMAN BRAIN**

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Human bodies are a rich source of socially relevant information. Electrophysiological and imaging studies have revealed that specialized mechanisms in the brain are used to extract social information, for example, from faces, eyes, and bodies. An event-related component called N170 has been demonstrated to reflect face and body processing, while EEG components like early posterior negativity (EPN) and late positive potential (LPP) have been shown to reflect processes of attention and memory.

In this experiment, it was tested whether top-down object-based attention modulates early visual body processing and corresponding ERPs, P1 and N170. EEG was measured from 64 channels while participants saw pictures of both clothed and nude bodies, faces, and cars and directed their top-down attention towards different stimulus categories. It was found that N170 response amplitude was not enhanced when seeing attended compared to non-attended body stimuli in the parieto-occipital channels (P3/4, PO3/4 and P5/6). Also for face processing, such modulation did not occur in the temporal channels (P7/8, TP7/8 and TP9/10). However, early attentional modulation of the P1 response amplitude occurred in the occipital channels (PO9/10, O1/2). Clear attentional modulation of the ERP components was found after 300 ms for all stimulus categories. LPP response measured from centro-parietal channels was also enhanced for attended stimuli in the time window of 300 – 700 ms.

It is concluded that the initial body and face processing are unaffected by the modulation of top-down object-based attention. Top-down attention begins to affect visual body and face processing after 300 ms post-stimulus and probably is reflected in activation of a larger cortical network related to body and face processing. Early attentional modulation in the occipital channels could reflect spatial attentional processes related to differing stimulus sizes between stimulus categories. Human visual perception is tuned to detect human bodies, and top-down attention cannot rapidly modulate this processing. This ensures that evolutionarily important information from other peoples' bodies is processed fast and accurately in the human brain despite of where attention is directed at any moment.

Keywords: visual body processing, top-down, object-based, attention, ERP

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1. Introduction

Undoubtedly, human bodies are important sources of biologically, sexually, socially and emotionally relevant information. The visual information about another person's posture, biological motion, gestures, and body composition is used to enrich social interaction. For example, aspects of personality, internal states, sexuality, attitudes, intelligence, power, relationships between two persons, and future behavior can be inferred to some extent from the bodies of other people (See Adams, Ambady, Nakayama, & Shimojo, 2011). One of the important functions of body perception is obviously related to sexual selection (Andersson, 1994). For example, the role of body composition in mate-preference has been studied intensively (Currie & Little, 2009). Hip-waist-ratio (Singh, 1993), obesity (Smith, Cornelissen, & Tovee, 2007), face and body symmetry (Rhodes & Simmons, 2007), breast size (Manning, Scutt, Whitehouse, & Leinster, 1997), and height/weight-ratio (Fan, Dai, Liu, & Wu, 2005) have been shown to guide mate preference.

In line with this, it is no wonder that information from the bodies of other people is processed accurately, efficiently, and to some extent automatically in the brain and that there are specialized cortical areas devoted to processing visual body-related information (de Gelder, Van den Stock, Meeren, Sinke, Kret et al., 2009; Minnebusch & Daum, 2009; Peelen & Downing, 2007). In the present study, it was examined whether the visual body areas process information in an automatic, bottom-up fashion, resistant to top-down attention or whether top-down attentional processes modulate visual processing of body information. To this end, event-related potentials (ERP) were measured to pictures of human bodies while the participants' attention was directed either to bodies or to other pictures.

While attentional effects to face processing have been studied extensively (Carlson & Reinke, 2010; Carmel & Bentin, 2002; Crist, Wu, Karp, & Woldorff, 2008; Furey, Tanskanen, Beauchamp, Avikainen, Uutela, et al., 2006; Holmes, Villeumier, & Eimer, 2003; Lueschow, Sander, Boehm, Nolte, Trahms, et al., 2004; Mohamed, Neumann, & Schweinberger, 2009; Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009), no studies have examined attentional effects on visual body processing. In the face perception literature, the results are also mixed, some studies reporting that top-down object-based attention modulates early face processing reflected in a face-sensitive N170 response (Mohamed et al., 2009; Sreenivasan et al., 2009), while others have found negative results (Carmel et al., 2002; Furey et al., 2006; Lueschow et al., 2004). Exactly the same questions can be asked regarding visual body processing.

Recently, Hietanen and Nummenmaa (2011) found that visual body processing is enhanced when a body is seen naked compared to a clothed one. They suggested a possibility that a part of the enhancement could be attributed to increased top-down object-based attention towards nude body stimuli. In order to explore that possibility, specifically the effects of top-down object-based attention on visual body processing were studied. In the experiment, the effects of attentional modulation to processing of clothed bodies, nude bodies, faces, and cars were investigated.

1.1 Neural mechanisms of body perception

Accordingly with the need for fast and accurate body perception, distinct neural mechanisms have been found devoted to processing of other peoples' bodies (Peelen & Downing, 2007). Functional imaging has provided evidence that perception of human bodies and deriving of useful social information from them is achieved by a specialized brain network (de Gelder et al., 2010; Minnebusch & Daum, 2009; Peelen & Downing, 2007). The network includes two main areas, extrastriatal body area (EBA) and fusiform body area (FBA). EBA is located in a focal region of lateral occipitotemporal cortex and responds strongly to both photographic and non-photographic depictions of bodies and body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). FBA, located in posterior fusiform gyrus, also responds to bodies in a similar fashion as EBA (Peelen & Downing, 2005; Peelen, Wiggett, & Downing, 2006; Schwarzlose, Baker, & Kanwisher, 2005). Taylor, Wiggett, and Downing (2007), however, found evidence of functional specialization between EBA and FBA, as EBA seems to respond more strongly to individual body parts while FBA is associated with more holistic processing of complete body stimuli. Also, some evidence of a larger cortical network devoted to body detection and identification has been found (Hodzic et al., 2009a, 2009b). The network includes not only EBA and FBA, but also various other cortical areas devoted to processing of body information, such as an area in the inferior parietal lobe and areas in inferior frontal gyrus, cingulate gyrus, and the post-central sulcus.

Evidence of specialized regions that process body information has also come from single cell recordings. For example, studies with macaque monkeys have shown that neurons in inferior temporal cortex (IT) respond selectively to the shape of both human and monkey bodies while some cells respond most vigorously to body parts (Desimone, Albright, Gross, & Bruce, 1984; Gross, Bender, & Rocha-Miranda, 1969; Kiani, Esteky, Mirpour, & Tanaka, 2006; Wachsmuth, Oram, & Perrett, 1994). Similar cells have been found from corresponding regions in the human temporal

cortex by using intracranial recordings (Pourtois, Peelen, Spinelli, Seeck, & Vuilleumier, 2007), and especially EBA seems to contain high density of such cells. It is important to note that cell populations responding to bodies and faces seem to be somewhat dissociated spatially (Peelen, Wiggett, & Downing, 2006; Schwarzlose et al., 2005).

Neural mechanisms of body perception have also been studied by using electroencephalography (EEG) and magnetoencephalography (MEG). Such studies have found EEG components with short (<200 ms) latencies that are modulated by body stimuli. The main body-related component with a short latency is an event-related potential (ERP) measured over the occipito-temporal cortex peaking somewhere between 140 and 200 ms after a picture of a body is seen (Stekelenburg & de Gelder, 2004; Thierry et al., 2006). This negative ERP component named “N170” (after its negativity and typical afterstimulus peaking time) has been extensively studied, and much debate has been over which type of information processing the component reflects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bukach, Gauthier, & Tarr, 2006; Carmel & Bentin, 2002; Eimer, 2000; Hietanen & Nummenmaa, 2011; Thierry, Martin, Downing, & Pegna, 2007). N170 has been argued to reflect face perception (Bentin et al., 1996; Carmel & Bentin, 2002; Rossion & Jacques, 2008), general expertise in object perception (Bukach et al., 2006), configural processing (Eimer, 2000), interstimulus perceptual variance (Thierry et al., 2007) and also body perception (Hietanen & Nummenmaa, 2011). However, the source localization and voltage distribution over the scalp are apparently different between the body and face perception and perception of other objects (Gliga & Dehaene-Lambertz, 2005; Hietanen & Nummenmaa, 2011; Thierry et al., 2006). Thus, N170 responses to bodies probably reflect the processing in specialized cortical structures tuned to detect bodies and body parts, FBA and EBA, respectively. Also, in one study (Thierry et al., 2006) the N1 component to a clothed body stimulus was found to have a latency of 190 ms, which further points to a separate neural source from the face-related N170.

1.2 Attentional modulation of high-level visual processing

Considering above, the processing of body information in the brain seems to be fairly modular and automatic. There is behavioral evidence that schematic body stimuli capture attention more efficiently than other stimulus categories (for example schematic hands, cars, trees, but excluding faces), even when the stimuli were shown for only 200 ms (Downing, Bray, Rogers, & Childs, 2004). Such results suggest that bodies are prioritized for attentional selection and point to a

conclusion that visual system assigns attentional priority to stimuli that are represented in strongly selective cortical regions (Downing et al., 2004). The experiment indicated also that attention influences body processing in a bottom-up way. However, it is interesting to ask whether the neural top-down attentional mechanisms can influence visual body processing and consequently, the related EEG components. It might be that automatic neural processes devoted to body processing are in fact immune to attentional modulation.

In face perception literature, such questions have already been asked (Carlson & Reinke, 2010; Carmel & Bentin, 2002; Crist et al., 2008; Furey et al., 2006; Holmes et al., 2003; Lueschow et al., 2004; Mohamed et al., 2009; Sreenivasan et al., 2009). Because neural face processing shares many qualities with body processing, including modularity and high degree of automaticity, it is reasonable to ask similar questions regarding body processing. This rationale is enhanced by the fact that body and face stimuli themselves share also many characteristics, such as that they convey information relevant for social communication and that they contribute to recognition and identification of individuals, age, gender, intentions, and emotions (Minnebusch & Daum, 2009). Additionally, within-differences in both stimulus categories are quantitative rather than qualitative, both stimuli are symmetric, and made of specific elements. Visual discrimination in both categories requires fine-grained analysis of size, shape, and relative location of parts.

The visual system cannot process all the information that is projected to the retinas and has to select only some of it for further processing. Thus, it would be adaptive to be able to select the most relevant information for the current task at hand, while ignoring irrelevant information. This can be achieved with either bottom-up or top-down processing, that are central information processing principles in the human brain (Theeuwes, 2010). A combination of both is also possible. Distinct areas or neural networks that detect and process highly specific information automatically, like faces or bodies, are examples of possible bottom-up mechanisms. Top-down processing involves voluntary allocation of attentional resources to processing of such stimuli. However, a clear picture of how body information is processed in the human brain has only recently begun to emerge (de Gelder et al., 2010; Minnebusch & Daum, 2009; Peelen & Downing, 2007). As noted, there is evidence of bottom-up processing of bodies, but the role of top-down processing and the interaction between the two remain to be studied.

Neural mechanisms of visual attention have been studied for long and various neurocognitive models have been suggested (Heslenfeld, Kenemans, Kok, & Molenaar, 1997). In many models, some kind of a neural mechanism is suggested to be responsible for selecting stimuli to be attended while leaving others unattended. Usually, the mechanism is inhibition of the neural

networks processing the unattended stimuli, excitation of the networks related to processing the attended stimuli or a combination of both (Aron, Robbins, & Poldrack, 2004; Dagenbach & Carr, 1994; Heslenfeld et al., 1997). There are more recent results supporting both inhibition and excitation hypothesis (see Nieuwenhuis & Yeung, 2005). However, some studies seem to have given more support to the excitation hypothesis (Egner & Hirsch, 2005). Therefore, if top-down attention influences body processing, it could be manifested in both exciting and inhibiting activity in the body processing areas, depending on whether body stimuli are attended or ignored. Research also suggests that top-down selection of stimuli can occur only after an initial sweep of information through the brain and after the selection based on bottom-up salience detection (Theeuwes, 2010). This implies that selection of stimuli relies on both bottom-up and top-down processing. Now, a question arises about when top-down attention can begin to influence stimulus selection and enhance the processing of selected stimuli or various aspects of it, such as location, color, or orientation. Also, does the minimum time of top-down influence differ between various kinds of information, for example between different objects?

Visual top-down attention is usually divided into two distinct types: spatial (Cheal, Lyon, & Gottlob, 1994) and object-based (Kahneman & Henik, 1981) attention. Spatial attention refers to enhanced processing of stimuli presented in a certain attended location in space, while object-based attention refers to enhanced processing of a certain attended stimulus quality (e.g. orientation, color, or size) or stimulus type (e.g. car, house, or face). Spatial attention has been found to modulate the very early stages (80 - 130 ms) of cortical visual processing (Heinze, 1994; Moran & Desimone, 1985; Motter, 1993; Poghosyan, Shibata, & Ioannides, 2005) and modulatory effects have been found already in primary visual area V1 (Posner & Gilbert, 1999; Smith, Cotillon-Williams, & Williams, 2006). When attention is directed towards elementary features such as motion or color, attention starts to modulate visual ERPs only after 150 ms (Anllo-Vento, Luck, & Hillyard, 1998; Harter & Guido, 1980; Torriente, Valdes-Sosa, Ramirez, & Bobes, 1999). In case of complex objects, such as faces, attentional top-down object-based modulation begins later, somewhere between 170 and 350 ms (Carmel & Bentin, 2002; Furey et al., 2006; Lueschow et al., 2004; Mohamed et al., 2009; Sreenivasan et al., 2009).

The role of top-down attention in modulating the early body-related N170 response has not been studied. However, the effects of top-down attention on face processing have attracted more interest. In the face perception literature, the possibility of the modulatory role of attention has been explored in a number of studies, with inconclusive results. Such studies often focus on either spatial or object based attention. In some studies, it has been found that spatial (Carlson & Reinke., 2010;

Crist et al., 2008; Holmes et al., 2003) or object-based (Mohamed et al., 2009; Sreenivasan et al., 2009) selective attention can modulate N170 responses related to faces. On the other hand, many studies have failed to find such modulatory effects (Carmel & Bentin, 2002; Furey et al., 2006; Lueschow et al., 2004).

Carmel and Bentin (2002) found that attention to cars increased the N170 response compared to when cars were left unattended, but for faces N170 was equally high regardless of whether the stimulus was attended or not. Also, Lueschow et al. (2004) did not find face-related N170 modulation by attention. They showed both pictures of faces and houses, while participants had to attend either to faces or houses and press a mouse button if a target picture from the attended category appeared. Furey et al. (2006) also failed to demonstrate top-down attention effects on face-related N170. They showed superimposed face-house pictures while participants had to attend to either one of the stimuli and to determine whether the present picture of a face or house was the same as shown in the immediately preceding picture.

On the other hand, Mohamed et al. (2009) found that perceptual load manipulation revealed a sensitivity of face-selective N170 to attention. The participants perceived task-irrelevant houses and faces during a low or high perceptual load task. The authors found that if perceptual load was high, face-related N170 attenuated greatly compared to low perceptual load condition. In another study, conducted by Sreenivasan et al. (2009), participants were told to attend to either faces or houses while showing superimposed face-scene images. Discriminability of the faces and houses was modulated parametrically. The results showed that if the discriminability of the faces was low, top-down attention had an effect on N170, but if the faces could easily be spotted from the superimposed stimulus, attention effects vanished. Taken together, it might be that the greatest N170 modulation by top-down object-based attention might occur if perceptual load is high or discriminability of the faces is low, and if it is not the case, attentional modulation would be smaller or non-existent. Thus, if attentional resources are heavily focused elsewhere or if the face stimulus is not salient enough, it is not processed as effectively in the brain as if the face was attended and no additional tasks were present.

If the experiments that failed to show attentional effects on face-related N170 (Carmel & Bentin, 2002; Furey et al., 2006; Lueschow et al., 2004) are considered in the context of face discriminability and attentional load of the task, the results make more sense. In the study by Carmel and Bentin (2002), visual discriminability of the faces was high and perceptual load was relatively small because the task was to just press a mouse button when a face or a car was seen or to decide if a stimulus depicted a living thing or not. Also in the study by Lueschow et al. (2004),

the face stimuli were of high discriminability and the perceptual load was low. However, the results by Furey et al. (2006) are more difficult to explain by this reasoning. While the perceptual load might have been relatively low because the participants had just to tell if the attended picture in the superimposed face-house stimulus was the same or different than in the previous one, the discriminability of the faces was not high.

Whether the case is similar when studying top-down object-based attentional effects to body-evoked N170 remains to be studied. In studies where no attentional effects are found, the results have been explained by suggesting that faces have a privileged status in the visual processing system and are processed automatically without a possibility of top-down modulation (Cauquil, Edmonds, & Taylor, 2000; Farah et al. 1995; Lavie, Ro, & Russell, 2003). The opposite results have been suggested to reduce or even question the automaticity and special status of face perception in human information processing.

Even in studies where top-down object-based attention has not modulated the face-related N170 component, effects of attention on later EEG components have been found (Furey et al., 2006; Lueschow et al., 2004). Lueschow et al. (2004) found that attention influenced face processing at 300 ms after stimulus presentation. Also Furey et al. (2006) found later differences in EEG between attended and non-attended conditions starting from 250 ms after stimulus presentation. These findings fit well to previous results showing that changes in attention are reflected in two distinct EEG components, early posterior negativity (EPN) and late positive potential (LPP) that are usually associated with affective significance of stimuli and increased allocation of attentional resources (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000, Foti, Hajcak, & Dien, 2009, Hajcak, Dunning, & Foti, 2007, Hajcak & Olvet, 2008; Schupp et al., 2000; Schupp Junghofer, Weike, & Hamm, 2003; Schupp et al., 2004). EPN is enhanced by early selective attention to the stimuli and the increased LPP amplitudes reflect the sustained processing and encoding of the stimuli (Foti et al., 2009). It has been found that attentional modulation of the ERP components can be different depending on the timescale and component. Schupp et al. (2007) showed high- and low-arousing stimuli while modulating top-down attention. They found that attention and arousal operated additively in the latency range of 200 – 300 ms post-stimulus but the interaction was multiplicative at 400 – 600 ms post-stimulus (Schupp et al. 2007). They argued that the early processing (200 – 300 ms post-stimulus) reflects perceptual encoding, while the later processing (400 – 600 ms post-stimulus) reflects stimulus evaluation.

All in all, the question of whether early neural body processing is influenced by top-down object-based attention remains open. If early body processing is outside attentional influences, it would be reasonable to ask when such modulation begins to occur.

1.3 Attention and enhanced processing of nude bodies

Recent research has found that N170 to nude bodies is larger than to clothed bodies (Hietanen & Nummenmaa, 2011). The authors argued that this kind of a preference of the visual system to nude bodies can indicate that human visual system is tuned to detect especially nude bodies. This tuning could have happened for evolutive reasons. Specifically, there is evidence that humans have begun to use clothing only $72,000 \pm 42,000$ years ago (Kittler, Kayser, & Stoneking, 2003) and it could be that the brain circuits originally tuned to detect nude bodies, show attenuated responses towards bodies that wear clothes. On the other hand, the larger amplitudes could be reflecting the activation of brain mechanisms responsible for affective arousal that lead to improved information processing of nude stimuli. However, Hietanen and Nummenmaa (2011) also stated the possible influence of top-down attention in enhancing the response. It is possible that more top-down attention was allocated to nude than to clothed bodies and that the N170 response was enhanced at least partially because of such processing.

The N170 response to clothed bodies has been found to be usually either smaller (Righart & de Gelder, 2007; Thierry et al., 2006) or equal (Gliga, Dehaene-Lambertz, 2005; Meeren, van Heijnsbergen, de Gelder, 2007) to the amplitude of the N170 response to faces. However, Hietanen and Nummenmaa (2011) found that N170 to nude bodies was even bigger than N170 to faces or cars. Therefore, it was also investigated, how top-down attention affects this response. Further, it was examined whether the N170 response to nude bodies remains the greatest when attention is directed to other stimuli.

1.4 Aims of the study

In this study, an object based attention paradigm, similar to that in Lueschow et al. (2004), was used to determine whether the early and later visual processing of body information is influenced by top-down object-based attention. Stimulus pictures from different categories (clothed body, nude body,

face, and car) were shown in random order in succession, one at a time, and the participants' task was to attend to stimuli of one stimulus category in each block (four blocks in total). Within a block, participants were shown two specific target stimuli from the attended category, to which the participants were told to respond when seeing them. Because at the moment, only literature concerning the effects of attention on face perception exists, faces were included as a stimulus category to enable comparison. Car pictures were used as non-human control stimuli.

Specifically, it was tested whether top-down object-based attention modulates body processing and the related EEG-components. It was hypothesized that:

1. If attention modulates the early stages of body processing, N170 or even P1 responses in the body-sensitive channels should be greater when body stimuli are attended compared to when left non-attended.
2. If the attentional modulation of the ERP components differs between the stimulus categories, it indicates that the sensitivity of top-down attentional influence to visual processing is different between stimulus types.
3. Later object processing should be modulated by top-down attention and it should be reflected in the ERP-components occurring after N170. For attended stimuli, the ERP-component amplitudes should be greater than for non-attended stimuli.
4. If there is no top-down attentional modulation of the N170 response when nude bodies are seen, the N170 response to nude bodies must be explained by other means, e.g., by enhanced body processing and activation of the networks related to affective processing.

In addition to the EEG recording, the participants' subjective evaluation of their feelings when seeing each stimulus picture was asked. Participants had to assess how positive or negative and how aroused they felt during seeing each stimulus picture.

2. Methods

2.1 Participants

20 healthy volunteers (10 male, 10 female) with normal or corrected-to-normal vision participated in the experiment (age $M=21.8$, $SD=2.98$, range 18 – 30 years). One of the male participants was left-handed and all the others were right-handed. All participants were uninformed of the purpose of the experiment. One male and two female participants were excluded from further analysis due to noisy signal on relevant electrodes.

2.2 Stimuli

Color pictures of clothed and nude bodies, faces, and cars were used as stimuli. The pictures were downloaded from various websites. The models in both clothed and nude categories were standing in typical modeling postures. Clothing on clothed models was conventional such as t-shirts, jeans and jackets. For face pictures, the faces were first cut from the body pictures. The face stimuli were not taken from the same individuals that were used for the body stimuli. The size of the face stimuli was doubled so that the stimulus size across stimulus types remained as similar as possible. Cars in car stimuli were depicted from varying angles. All texts (e.g. from registration plates) were removed from the car pictures. There were 80 stimulus pictures: 20 cars, 20 faces, 20 clothed bodies, 20 nude bodies. Additionally, there were two target pictures (see below) in each category. In human stimulus categories, half of the pictures showed a male and the other half a female model. Also, one of the two target pictures in the human target categories was a male and the other one was a female.

The stimulus sizes (horizontal \times vertical) at the distance of 78 cm were $4^\circ \times 8^\circ$ for the bodies (5.4 cm \times 11.0 cm), $5^\circ \times 4^\circ$ for the faces (6.2 cm \times 4.8 cm), and $8^\circ \times 5^\circ$ for the cars (10.6 cm \times 7.4 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 that was set to resolution 1024 \times 768. The refresh rate was 75Hz. E-Prime was used as the stimulus presentation software.



Figure 1. Illustration of the stimuli used in the experiment. Image (male head) courtesy of stockimages / FreeDigitalPhotos.net.

2.3 Experimental procedure

The laboratory and the equipment were first introduced to the participants. The participants were instructed that, in the experiment, they would be seeing pictures of nude and clothed bodies, faces, and cars in four blocks. Before starting, participants gave a written informed consent. 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 recording 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. Participants were encouraged to remember those pictures, focus their attention to that stimulus category during the block and press left mouse button (mouse used with right hand) 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 two target stimuli side by side for 13 seconds. 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 encouraged to fixate it during the experiment. The stimuli were shown in random order in each block.

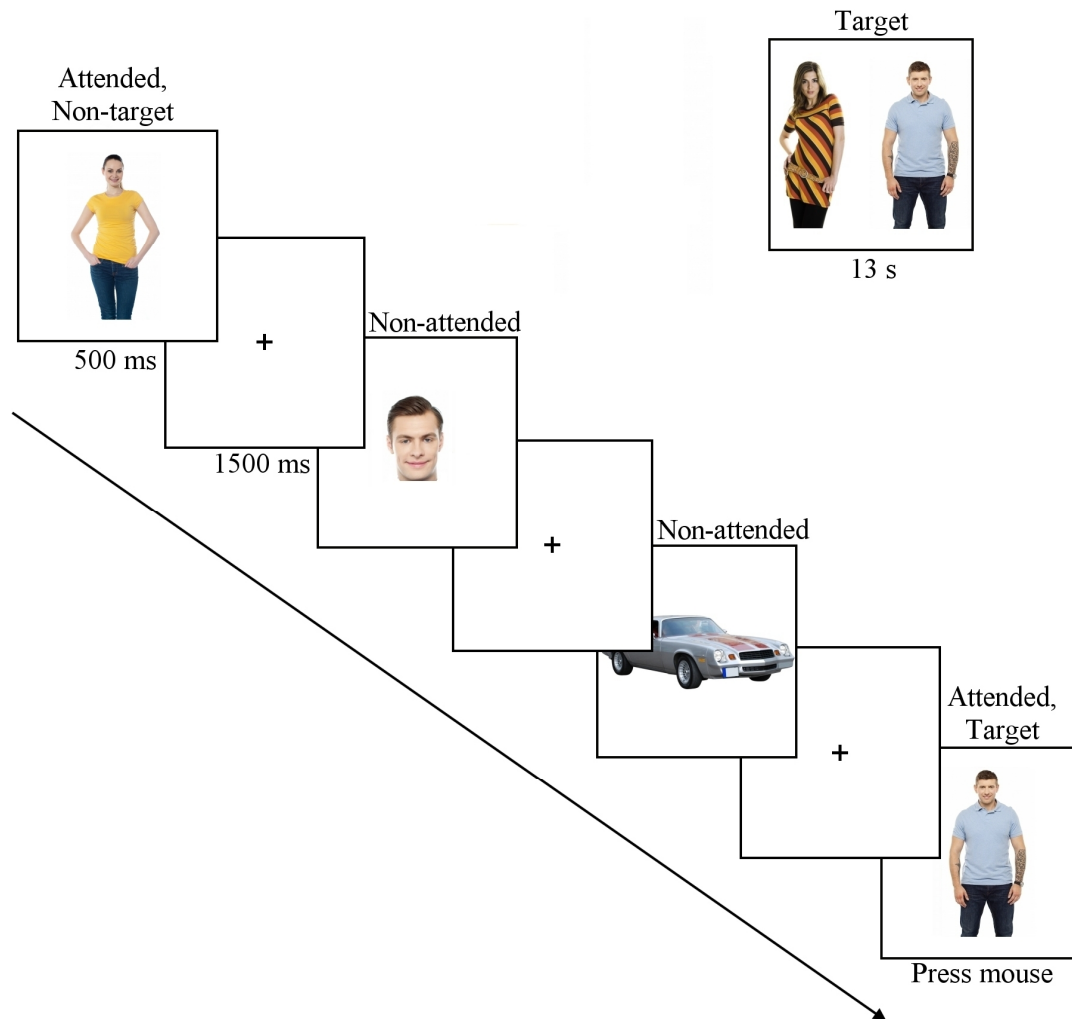


Figure 2. A flowchart of events during an experimental block. In the illustrated block, participants were told to attend to human clothed bodies and to press a mouse button every time they see either one of the target stimuli. Images (male body, female body wearing yellow t-shirt, male head) courtesy of stockimages / FreeDigitalPhotos.net.

In the experiment, there were four blocks. In each block, one of the four stimulus categories was attended and the target stimuli were always from the same category. Each block contained 400 stimuli. Data were collected for 320 stimuli: 80 attended and 240 non-attended stimuli. The

remaining 80 stimuli were pictures labeled as “targets”, 20 targets for each stimulus category. Each block lasted approximately 13.6 minutes. Between the blocks, there was a short pause during which the participants were encouraged to move a bit, to get comfortable, and to read instructions for the next block. Before the actual experiment, there was a short training block in order to familiarize the participants with the attentional and behavioral task. The stimuli for that block were not contained in the actual experiment. Also, the training targets were pictures of animals in order to avoid creating an attentional bias to any of the stimulus categories.

2.4 Questionnaires

Immediately after the four blocks, the participants saw every picture in the stimulus set again, and they were instructed to assess how they felt when seeing them. They assessed their feelings on the dimensions of affective arousal and valence. On the computerized questionnaire, there were two nine-point SAM scales (Self-Assessment Manikin; Bradley & Lang, 1994) per stimulus; one for arousal and the other for valence.

2.5 EEG-recording

The EEG data were collected using Vision Recorder software. Continuous EEG was recorded from scalp with 64-channel actiCAP Ag/AgCl electrodes mounted to elastic cap. A 10-10 international electrode positioning system was used. The signal was amplified using quickAmp amplifier (Brain products, Germany) and online referenced to common average. The impedances were kept below 25kOhm. Horizontal and vertical eye movements were recorded using bipolar channel recording, using the sites beside the outer canthi of both eyes and above and below the midpoint of the left eye. Continuous EEG-signal was digitized using 1000 Hz sampling rate and stored to a computer disk for offline analyses.

2.6 Data analysis

Offline, the raw continuous EEG-signal was first filtered with 0.05 – 30 Hz band-pass filter (50 Hz notch filter enabled) with 12 dB/oct slope on both ends. After that a regression-based Gratton/Coles

ocular correction algorithm (Gratton, Coles, & Donchin, 1983) was used to correct artifacts resulting from the eye movements. The following automatic data inclusion criteria were also used: maximal allowed voltage step was 50 $\mu\text{V}/\text{ms}$, maximal allowed amplitude was $\pm 100 \mu\text{V}$, and the minimum allowed voltage change during an interval of 100 ms was 0.5 μV . If one of these criteria were exceeded, 400 ms around that point was rejected. After applying the algorithms, the data were visually inspected and remaining artifacts were rejected. In total, 9.1 % of the data was rejected (9.4 % from clothed body trials; 8.6 % from nude body trials; 9.2 % from face trials; and 9.1 % from car trials). The data were then segmented to 1100 ms long epochs starting from 100 ms before the stimulus onset. In the analyses, only 500 ms in the beginning of each epoch were used because the stimulus duration was 500 ms. However, 1100-ms long epochs were selected because LPP-responses usually span from 400 ms to 1000 ms and this way it was possible to identify possible LPP-responses more reliably. A baseline correction was applied using the average of 100-ms pre-stimulus period. Baseline-corrected data were averaged over the trials for each stimulus type.

2.6.1 EEG components and the electrode sites for the analyses

EEG components that were analyzed were P1, N170, EEG components in the 200 – 400 ms time window, and LPP.

P1 component was defined as the peak positive amplitude between 80 ms and 140 ms. N170 component was defined as the peak negative amplitude between 140 ms and 200 ms. Latency was also analyzed for P1 and N170 components. For the time window from 200 ms to 400 ms post-stimulus, amplitude averages of 50-ms time windows were used. The latest component of interest was LPP. Visual inspection indicated that LPP response began approximately 300 ms post-stimulus and was clearly visible also after the stimulus disappeared from the screen. Thus, the data after 500 ms post-stimulus could be included in the analysis. LPP was analyzed in 100-ms time windows between 200 ms and 1000 ms post-stimulus in centro-parietal channels (CP1, CP2, CPz, P1, P2, POz, and Pz).

To find the electrode locations whose amplitudes would reflect body processing, it was inspected visually where N170 differentiated the most between the clothed bodies and the control stimuli (cars). By using this criterion, the most body sensitive electrode sites were found from the parieto-occipital channels (electrodes P3/4, PO3/4, P5/6). Note that in these channels, the absolute amplitudes for clothed body stimuli were not the greatest. It is noteworthy, that these electrodes

somewhat overlap the EBA area (Downing et al., 2001). In previous studies investigating ERP responses to bodies, P7/8 (or corresponding T5/6) electrodes were selected for the analysis because N170 responses are most pronounced at these sites (Taylor, Roberts, Downing, Thierry, 2010) or without any explicit explanation (Gliga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Minnebusch, Suchan, & Daum, 2009; Righart & de Gelder, 2007). For temporal channels, P7/8, TP7/8, and TP9/10 (Bentin et al., 1996) were selected. Finally, independent of the stimulus categories, channels where the early attentional effects on stimulus processing would be greatest were searched. Based on visual inspection, channels PO9/10 and O1/2 were chosen for that analysis. P1 and N170 responses and activity in the 200 – 400 ms time window were analyzed from parieto-occipital, temporal, and occipital channels. In the 200 – 400 ms time window, EPN-component was found and analyzed in temporal and occipital channels, while the component on the parieto-occipital channels reminded P3, which has also been found to reflect attentional processes (Schupp et al. 2007). LPP was analyzed only from centro-parietal channels.

For the attended vs. non-attended condition comparisons, data for the attended conditions were analyzed from the blocks where the particular stimulus category was attended. The data for the non-attended condition was analyzed from the attend-to-cars block (except for the cars vs. clothed bodies analysis, for which the data from the attend-to-clothed bodies block was used for non-attended car condition). Originally, the averages of the responses from all three non-attended blocks were intended to be used to quantify the responses for the non-attended condition. However, such a conduct resulted in different amounts of trials between the attended and non-attended conditions, resulting in smaller standard errors of mean (SEM) in the non-attended than attended condition and thus false attentional effects.

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 brevity, original degrees of freedom are reported. Bonferroni corrected *p*-values were used for all multiple comparisons.

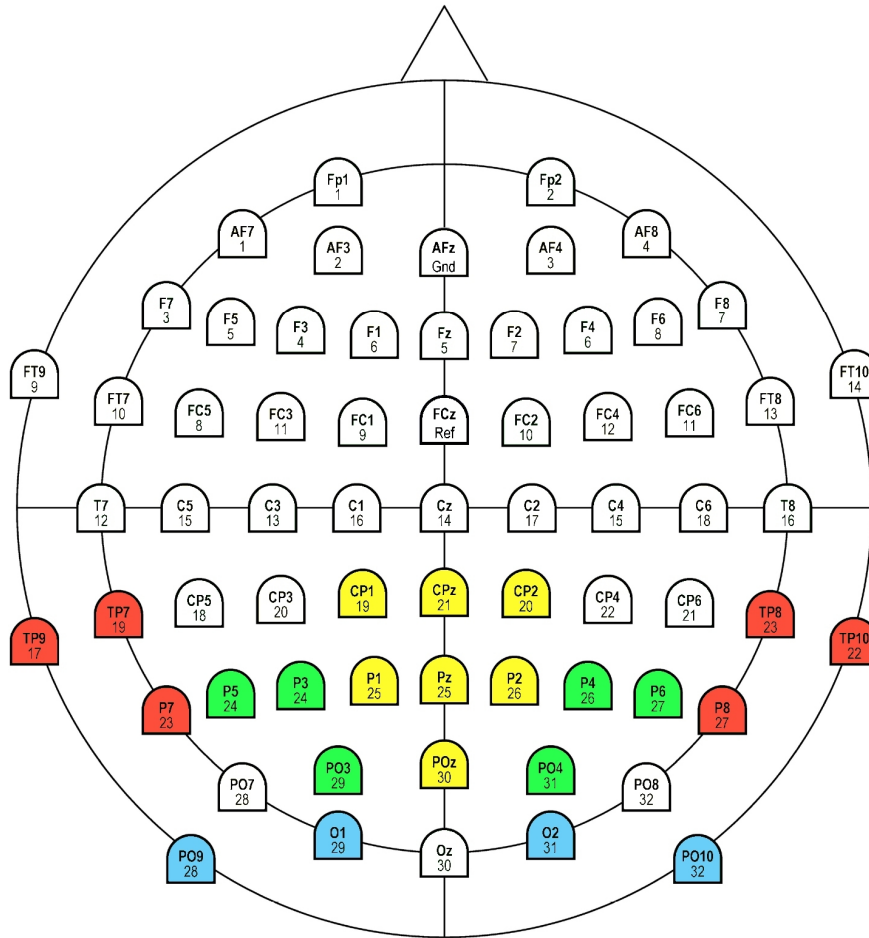


Figure 3. The 64 channel ActiCAP electrode net with 10-10 layout is displayed above. Channels that are used to separately analyze P1, N170, and later EEG components are highlighted: green – parieto-occipital channels; red – temporal channels; blue – occipital channels; yellow – centro-parietal channels.

2.6.2 Questionnaires

Both scales of SAM were analyzed for all stimulus types and average arousal/valence scores were calculated. Differences in stimulus valence/arousal were assessed using ANOVA.

3. Results

Before separate analyses in different channels, scalp topographies of the mean voltage amplitude differences between attended and non-attended conditions are presented (see Figure 4). Visual inspection indicated that scalp topographies between the attended and non-attended conditions begin to differ 300 – 350 ms post-stimulus continuing approximately to 700 – 750 ms post-stimulus.

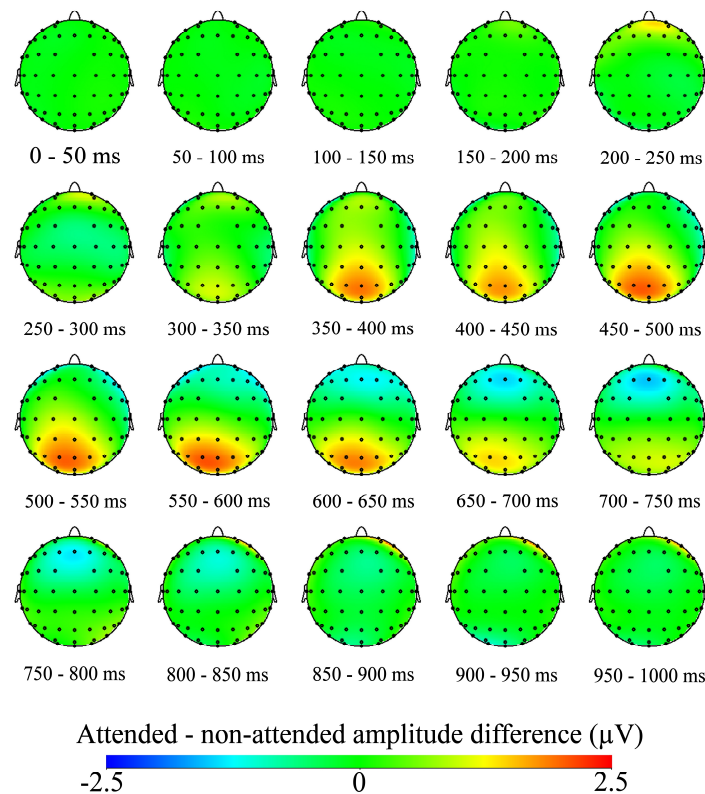


Figure 4. Scalp topographies of the mean voltage amplitude differences between attended and non-attended conditions in 20 consecutive 50-ms time windows.

3.1 Parieto-occipital channels and body sensitivity

First, P1 and N170 -responses to non-attended clothed bodies (data from attend-to-cars block) and non-attended cars (data from attend-to-clothed bodies block) were analyzed from the parieto-occipital channels (see figure 5). For P1 response, a $2 \times 3 \times 2$ ANOVA with stimulus category (clothed body, car), electrode (P3/4, PO3/4, P5/6) and hemisphere (left, right) as within-subject

factors revealed a main effect of stimulus ($F_{(1, 16)} = 14.5, p = .002, \eta^2 = .06, \eta_p^2 = .48$). P1 response to clothed bodies was greater than that to cars ($M = 4.5 \mu\text{V}$ vs. $3.5 \mu\text{V}$). Also a stimulus \times electrode interaction ($F_{(2, 32)} = 14.7, p < .001, \eta^2 = .03, \eta_p^2 = .48$) was significant. Pairwise comparisons revealed that the P1 amplitude to bodies differed from that to cars in electrodes PO3/4 and P3/4 (both p s = .001), but the difference was not significant in P5/6 electrodes ($p > .05$). Also, the difference in P1 amplitude between body and car stimuli was greater at the electrode pair PO3/4 than P3/P4 ($M = 1.9 \mu\text{V}$ vs. $1.0 \mu\text{V}, p = .015$). For the P1 response latency, analysis was restricted to electrodes P5/6 because the P1 responses were clear for both stimulus categories only in these channels. An ANOVA did not reveal significant main effects or interactions. (all p s $> .05$).

For N170 response, a similar ANOVA as above showed a main effect of stimulus ($F_{(1, 16)} = 29.6, p < .001, \eta^2 = .09, \eta_p^2 = .65$). The N170 response to clothed bodies was greater than that to cars ($M = -0.4 \mu\text{V}$ vs. $0.9 \mu\text{V}$). Also a stimulus \times electrode interaction ($F_{(2, 32)} = 6.4, p = .011, \eta^2 = .02, \eta_p^2 = .29$) was significant. Pairwise comparisons revealed that the N170 response to bodies was greater than that to cars in all electrode pairs (for PO3/4 $p < .001$ and for P5/6 $p = .01$). The difference in the N170 amplitudes in response to bodies and cars was greater in the electrode pair PO3/4 than in P5/6 ($p = .04$). For the N170 response latency, analysis was restricted to electrodes P5/6 because the N170 responses were clear for both stimulus categories only in these channels. An ANOVA did not reveal significant main effects or interactions. (all p s $> .05$).

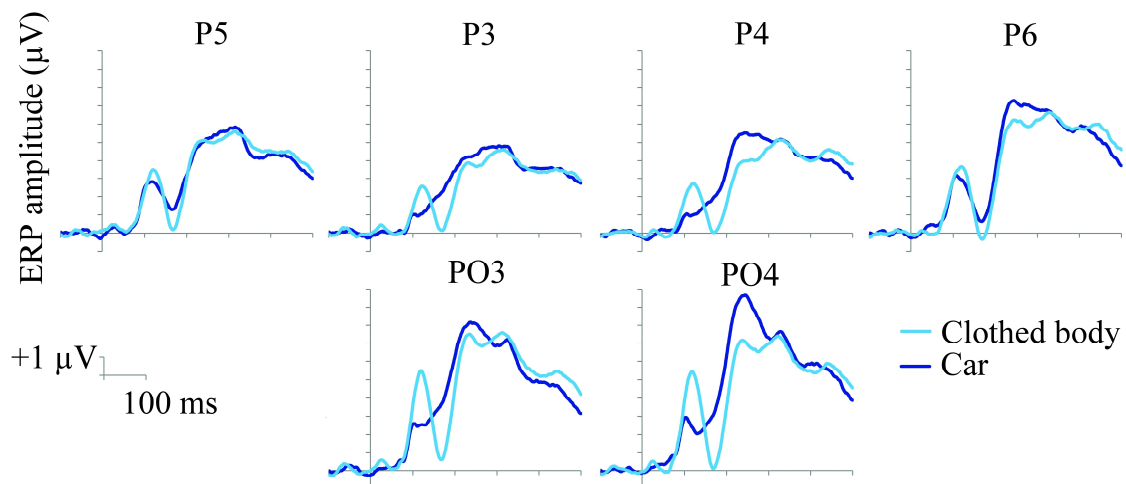


Figure 5. ERPs from parieto-occipital channels (left: P5, P3, PO3; right: P6, P4, PO4) to non-attended clothed bodies and cars.

3.2 Attentional effects in the parieto-occipital channels

Next it was tested whether attention affects body-related ERPs in the parieto-occipital channels. To this analysis, the data from the attend-to-clothed bodies block and attend-to-cars block were included. Responses to attended and non-attended clothed bodies and cars were analyzed with a $2 \times 2 \times 3 \times 2$ ANOVA with stimulus category (clothed body, car), attention (attended, non-attended), electrode (P3/4, PO3/4, P5/6) and hemisphere (left, right) as within-subject factors. Such an ANOVA for P1 response amplitudes did not show a main effect or any interactions involving attention. Also, a similar ANOVA for P1 latency did not reveal any main effects or interactions. An ANOVA conducted for the N170 amplitudes did not show a main effect for attention ($F_{(1, 16)} = 0.2$, $p = .659$). However, an attention \times stimulus \times electrode ($F_{(2, 32)} = 4.5$, $p = .019$, $\eta^2 = .002$, $\eta_p^2 = .22$) interaction was significant. Therefore, the attention effects in different electrode pairs (P3/4, PO3/4, P5/6) and stimulus categories were analyzed separately. Pairwise comparisons did not reveal significant differences in response to attended vs. non-attended categories for either stimulus type in any of three electrode pairs (all $ps > .05$). The significant interaction resulted from the fact that different stimuli and attention conditions had differential influences on the amplitudes between the electrode pairs. Attention \times electrode \times hemisphere ($F_{(2, 32)} = 3.4$, $p = .046$, $\eta^2 = .000$, $\eta_p^2 = .05$) interaction was also significant. Pairwise comparisons did not reveal significant differences in response to attended vs. non-attended categories for any electrode (all $ps > .05$). The significant interaction resulted from the fact that in the left and right hemispheres, different attention conditions had differential influences on the amplitudes between the electrodes. For the N170 response latency, a similar ANOVA did not show a main effect or any interactions for attention.

Next, the effects of attention on the responses in the time-window at 200 – 400 ms were analyzed from the parieto-occipital electrodes. A $4 \times 2 \times 2 \times 2$ ANOVA with time (200 – 250, 250 – 300, 300 – 350, 350 – 400 ms), stimulus category (clothed bodies, cars), attention (attended, non-attended) and hemisphere (left, right) as within-subject factors did not show a main effect of attention ($p > .05$), but a time \times attention interaction ($F_{(3, 48)} = 10.4$, $p < .001$, $\eta^2 = .02$, $\eta_p^2 = .39$) and a time \times attention \times stimulus type interaction ($F_{(3, 48)} = 7.1$, $p = .003$, $\eta^2 = .01$, $\eta_p^2 = .31$) were significant. Pairwise comparisons showed that for body stimuli, attention affected amplitudes only in the 300 – 350 ms time window. Response amplitudes for bodies were more positive in the attended than in the non-attended condition ($p = .026$). For cars, attention began to affect responses already in the 200 – 250 ms time window ($p = .007$), but the amplitudes were more positive in the

non-attended than in the attended conditions. For cars, amplitudes were more positive in the attended than in the non-attended condition in the 350 – 400 ms time window ($p = .020$).

3.3 Effects of body clothing

Here, it was analyzed whether the ERP components would differ in response to nude vs. clothed bodies in the parieto-occipital channels and also whether the attentional effects are different when seeing nude compared to clothed bodies. (see figure 6) For non-attended clothed and nude bodies, the data were acquired from the attend-to-cars block. When analyzing the P1 response, a $2 \times 2 \times 3 \times 2$ ANOVA with stimulus category (clothed, nude), attention (attended, non-attended), electrode (P3/4, PO3/4, P5/6) and hemisphere (left, right) as within-subject factors did not show a significant main effect of stimulus type or attention ($ps < .05$). However, a stimulus \times hemisphere interaction ($F_{(1, 16)} = 4.5, p = .049, \eta^2 = .01, \eta_p^2 = .22$) was significant. Pairwise comparisons showed that clothed bodies elicited a greater P1 response than nude bodies in the left hemisphere ($M = 4.6 \mu V$ vs. $4.0 \mu V, p = .023$). In the right hemisphere there was no significant difference ($p < .05$). A similar ANOVA for P1 latency did not reveal any significant main effects or interactions.

For the N170 response, a similar ANOVA revealed a main effect of stimulus type ($F_{(1, 16)} = 6.5, p = .022, \eta^2 = .04, \eta_p^2 = .29$). The N170 amplitude was greater to nude than to clothed bodies ($M = -1.2 \mu V$ vs. $-0.3 \mu V, p = .022$). A stimulus \times hemisphere interaction was also significant ($F_{(1, 16)} = 10.5, p = .005, \eta^2 = .02, \eta_p^2 = .40$). Pairwise comparisons revealed that nude bodies elicited significantly greater amplitudes only in the right hemisphere ($p = .001$). Attention did not show a significant main effect ($p < .05$). However, attention \times stimulus \times electrode \times hemisphere interaction ($F_{(2, 32)} = 4.4, p = .022, \eta^2 = .001, \eta_p^2 = .40$) was significant. Therefore, attentional effects were analyzed separately for clothed and nude bodies and for each electrode. N170 was greater when seeing non-attended than when seeing attended clothed bodies in electrodes P6 ($M = -1.0 \mu V$ vs. $-0.5 \mu V, p = .031$) and PO4 ($M = -0.4 \mu V$ vs. $0.1 \mu V, p = .040$).

For N170 response latency, an ANOVA revealed a main effect of attention ($F_{(1, 16)} = 4.7, p = .045, \eta^2 = .02, \eta_p^2 = .23$). For attended stimuli, the latency of the N170 response was reduced compared to non-attended stimuli ($M = 169$ ms vs. 172 ms, $p = .045$). There was no significant main effect for stimulus type ($p > .05$). However, a stimulus \times hemisphere interaction ($F_{(1, 16)} = 10.5, p = .005, \eta^2 = .01, \eta_p^2 = .40$) was significant. Pairwise comparisons indicated that in the right hemisphere N170 peaked later when a nude body was seen compared to when a clothed body was

seen ($M = 173$ ms vs. 168 ms, $p = .029$). No significant difference was found in the left hemisphere ($p > .05$).

Next, the effects of attention on the responses in the time-window of 200 – 400 ms (P3/4, PO3/4, P5/6) were analyzed. A $4 \times 2 \times 2 \times 2$ ANOVA with time (200 – 250, 250 – 300, 300 – 350, 350 – 400 ms), stimulus category (clothed, nude), attention (attended, non-attended) and hemisphere (left, right) as within-subject factors showed a main effect of attention ($F_{(1, 16)} = 7.3$, $p = .016$, $\eta^2 = .03$, $\eta_p^2 = .31$), time \times attention interaction ($F_{(3, 48)} = 7.4$, $p < .001$, $\eta^2 = .02$, $\eta_p^2 = .31$) and a time \times attention \times stimulus type interaction ($F_{(3, 48)} = 9.5$, $p < .001$, $\eta^2 = .01$, $\eta_p^2 = .37$). Further analyses showed that for both clothed and nude body stimuli, attention began to affect amplitudes in the 300 – 350 ms time window. Amplitudes were more positive in the attended than non-attended condition (for clothed bodies, $p = .026$; for nude bodies, $p = .018$). The difference continued to 350 – 400 ms only for nude bodies ($p = .002$) and seemed to continue even after that.

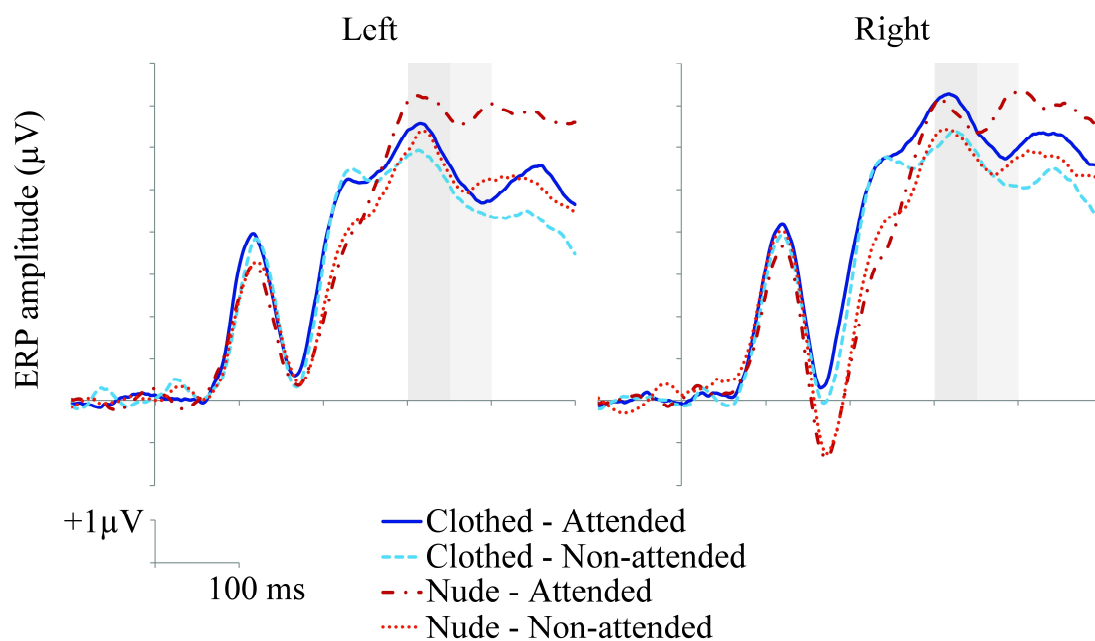


Figure 6. ERPs from parieto-occipital channels (left averaged over P5, P3, and PO3; right averaged over P6, P4, and PO4) to attended and non-attended clothed and nude bodies. Dark gray area represents the time window of significant attentional effects for clothed bodies. For nude bodies, significant attentional effects are indicated by both gray areas.

3.4 Responses in the temporal channels

The ERP responses to bodies and faces were also examined by analyzing the data from the temporal electrodes where body- and face-related N170 responses have been analyzed in previous studies (see figure 7). For non-attended clothed and nude bodies and faces, the data were acquired from the attend-to-cars block. For the P1 response amplitude, a $3 \times 2 \times 3 \times 2$ ANOVA with stimulus category (clothed, nude, face), attention (attended, non-attended), electrode (P7/8, TP7/8, TP9/10) and hemisphere (left, right) as within-subject factors did not reveal a main effect for attention or stimulus type (both $ps > .05$). However, a stimulus \times electrode interaction ($F_{(4, 64)} = 4.2, p = .004, \eta^2 = .05, \eta_p^2 = .21$) was significant. Thus, a one-way ANOVA was conducted separately for each electrode pair. Responses to different stimulus categories did not differ significantly from each other in any electrode site ($ps > .05$). When analyzing P1 responses to each stimulus type separately, for nude and clothed bodies responses in P7/8 electrode pair were greater than in TP7/8 ($ps < .001$) or in TP9/10 ($ps < .001$). For faces, responses in P7/8 were greater only from responses in TP7/8 ($p < .001$). Similar ANOVA for P1 latency did not show any main effects or interactions.

For the N170 amplitude, an ANOVA revealed a main effect of stimulus ($F_{(2, 32)} = 31.2, p < .001, \eta^2 = .31, \eta_p^2 = .66$). N170 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 ($M = -2.1 \mu\text{V}, p < .001$). Also N170 to faces was greater than N170 to clothed bodies ($p = .005$). A stimulus \times hemisphere interaction ($F_{(2, 32)} = 31.2, p < .001, \eta^2 = .04, \eta_p^2 = .25$) was significant. In the left hemisphere, N170 to nude bodies ($M = -4.3 \mu\text{V}$) was greater than that to clothed bodies ($M = -1.8 \mu\text{V}, p < .001$) or to faces ($M = -2.8 \mu\text{V}, p = .043$). The difference between clothed bodies and faces was not significant ($p > .05$). In the right hemisphere, the pattern of differences replicated the pattern for the main effect of stimulus. Attention did not show a significant main effect ($p > .05$), but an attention \times electrode \times hemisphere interaction was significant ($F_{(2, 32)} = 5.0, p = .023, \eta^2 = .002, \eta_p^2 = .24$). Pairwise comparisons revealed that TP7 was the only electrode where attention had a significant effect. N170 in that location was greater for attended stimuli compared to non-attended stimuli ($M = -2.6 \mu\text{V}$ vs. $-2.1 \mu\text{V}, p = .021$).

A $3 \times 2 \times 3 \times 2$ ANOVA for N170 latencies indicated a main effect of stimulus ($F_{(2, 32)} = 19.9, p < .001, \eta^2 = .06, \eta_p^2 = .55$). The N170 latency for nude bodies ($M = 178$ ms) was greater than that for clothed bodies ($M = 171$ ms, $p < .001$) or faces ($M = 171$ ms, $p < .001$). The main effect and interactions for attention were not significant ($ps > .05$).

Lastly, the effects of attention on the responses were examined in the time-window of 200 – 400 ms post-stimulus. A $4 \times 3 \times 2 \times 2$ ANOVA with time (200 – 250, 250 – 300, 300 – 350, 350 –

400 ms), stimulus category (clothed, nude, face), attention (attended, non-attended) and hemisphere (left, right) as within-subject factors elicited a main effect of attention ($F_{(1, 16)} = 9.6, p = .007, \eta^2 = .02, \eta_p^2 = .37$) and a time \times attention interaction ($F_{(3, 48)} = 13.7, p < .001, \eta^2 = .01, \eta_p^2 = .46$). Therefore, attended and non-attended conditions were compared separately in each time window. Attention began to affect the amplitudes at 300 – 350 ms time window for all stimulus types and the amplitudes were more negative for the attended than non-attended condition ($p = .007$). The difference continued to the 350 – 400 ms time window ($p = .001$), and seemed to continue even after that.

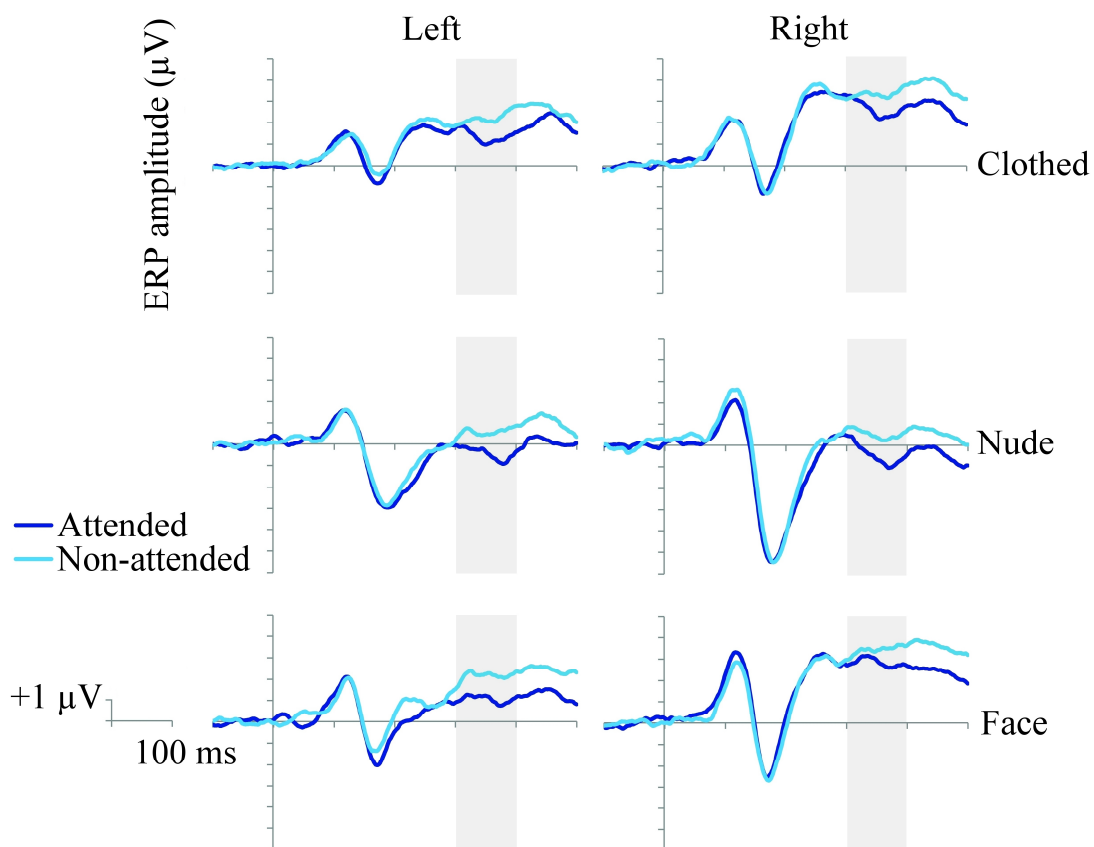


Figure 7. ERPs from temporal channels (left averaged over P7, TP7, and TP9; right averaged over P8, TP8, and TP10) to attended and non-attended clothed bodies, nude bodies, and faces. The gray area represents the time window of significant attentional effects.

3.5 Occipital and centro-parietal channels

It was also investigated if there are any channels where attention affects early stimulus processing more clearly than in the parieto-occipital and temporal electrodes. (see figure 8). Also the LPP responses in the centro-parietal channels were analyzed. Visual inspection indicated that the largest early attentional effects occurred in the occipital electrodes PO9/10 and O1/2. For non-attended clothed and nude bodies and faces, the data were acquired from the attend-to-cars block. For P1 amplitude, a $3 \times 2 \times 2 \times 2$ ANOVA with stimulus category (clothed, nude, face), attention (attended, non-attended), electrode (PO9/10, O1/2) and hemisphere (left, right) as within-subject factors revealed a main effect of attention ($F_{(1, 16)} = 14.8, p = .001, \eta^2 = .01, \eta_p^2 = .48$). The P1 responses to attended stimuli were greater than those to non-attended stimuli ($M = 7.8 \mu\text{V}$ vs. $7.3 \mu\text{V}, p = .001$). No interactions were found for attention (all $ps > .05$). A similar ANOVA for P1 latency did not show any main effects or interactions. An ANOVA for N170 amplitudes did not show a significant main effect of attention ($p > .05$). However, an attention \times hemisphere interaction ($F_{(1, 16)} = 5.7, p = .030, \eta^2 = .004, \eta_p^2 = .26$) was significant. Pairwise comparisons indicated that there was no significant difference between attended and non-attended conditions in either hemisphere (both $ps > .05$). Also, when analyzing attended and non-attended conditions separately, N170 did not differ between the hemispheres ($ps > .05$).

In the 200 – 400 ms time window, a $4 \times 3 \times 2 \times 2$ ANOVA did not reveal a main effect of attention ($p > .05$), but a time \times attention interaction ($F_{(3, 48)} = 3.6, p < .020, \eta^2 = .01, \eta_p^2 = .18$) and time \times attention \times stimulus type interaction ($F_{(6, 96)} = 2.4, p = .034, \eta^2 = .03, \eta_p^2 = .13$) were significant. No significant differences were found between attended and non-attended conditions for any stimulus type in any time window (all $ps > .05$). The significant interaction resulted from the fact that different stimuli and attention conditions had differential influences on the amplitudes between different time windows.

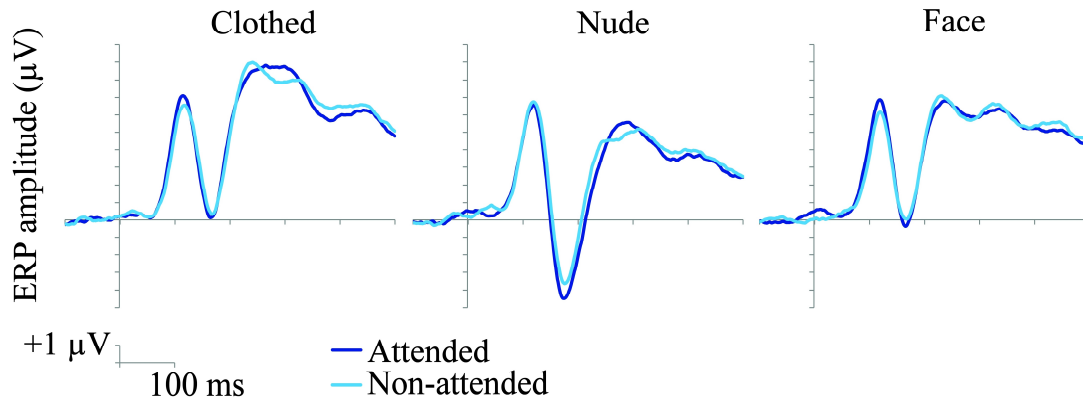


Figure 8. ERPs from occipital channels (averaged over PO9/10 and O1/2) to attended and non-attended clothed bodies, nude bodies, and faces.

Finally, the LPP responses were analyzed (see figure 9). The data showed a long-lasting positive LPP drift over centro-parietal channels (CP1, CP2, CPz, P1, P2, POz and Pz) for all stimulus types both when attended and non-attended. A $2 \times 3 \times 8$ ANOVA with attention, stimulus type, and time as factors revealed main effects of attention ($F_{(1, 16)} = 11.8, p = .003, \eta^2 = .06, \eta_p^2 = .43$) and stimulus type ($F_{(2, 32)} = 37.7, p < .001, \eta^2 = .36, \eta_p^2 = .70$). Also attention \times time ($F_{(7, 112)} = 18.5, p < .001, \eta^2 = .06, \eta_p^2 = .37$) and stimulus type \times time ($F_{(14, 224)} = 9.2, p < .001, \eta^2 = .05, \eta_p^2 = .37$) interactions were significant. Seeing attended stimuli elicited significantly greater LPP amplitudes compared to the non-attended stimuli from 300 to 700 ms ($ps < .05$). LPP to nude bodies was greater in every 100-ms time window ($ps < .05$). Attention and stimulus type did not have any significant interactions ($ps > .05$).

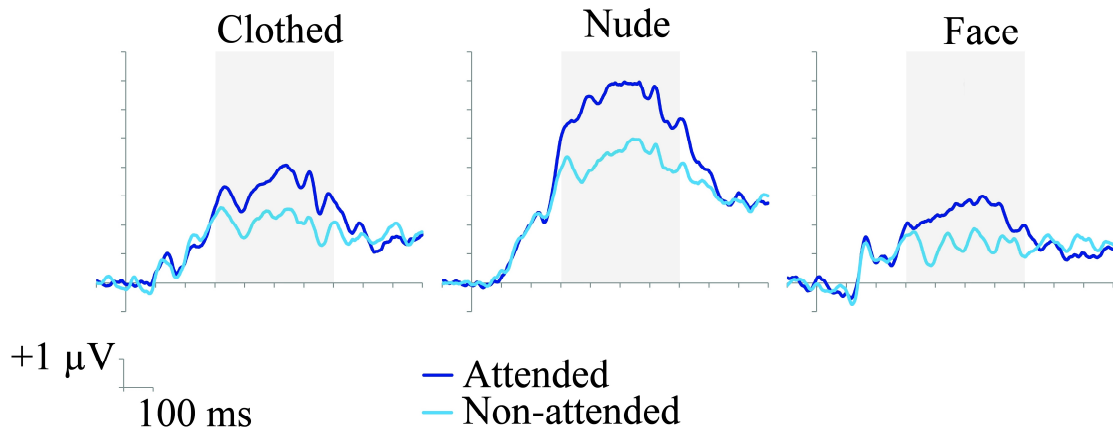


Figure 9. ERP responses from centro-parietal electrodes (averaged over CP1, CP2, CPz, P1, P2, POz and Pz) to attended and non-attended clothed bodies, nude bodies, and faces. The gray area indicates where LPP responses differed significantly between attended and non-attended conditions.

3.6 Questionnaires

Table 1 shows average affective arousal and valence scores attributed to all four stimulus categories. An ANOVA for arousal scores showed a main effect of stimulus type ($F_{(3, 48)} = 11,4, p < .001, \eta^2 = .11, \eta_p^2 = .42$). 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 ($ps > .05$). A similar ANOVA for valence scores also revealed a main effect for stimulus type ($F_{(3, 48)} = 47,5, p = .002, \eta^2 = .19, \eta_p^2 = .32$). Participants felt more positive 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 ($ps > .05$).

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

Table 1. Mean and SD of arousal and valence scores for each stimulus category.

4. Discussion

In this experiment, the main aim was to find out whether object-based top-down attention influences early human visual body processing. It was also examined whether attentional modulation differs between processing of human bodies and human faces or between nude and clothed body stimuli. Attention was manipulated by instructing the participants to attend to a given stimulus category while pictures of clothed bodies, nude bodies, faces, and cars were shown. Attention allocation was controlled by showing target stimuli from the attended category, to which participants had to respond by clicking a mouse. The ERP-components of interest were P1, N170, EPN, P3, and LPP. These components were analyzed separately from parieto-occipital channels (P3/4, PO3/4, and P5/6), temporal channels P7/8, TP7/8, and TP9/10), and occipital channels (O1/2, PO9/10), except for LPP, which was analyzed from centro-parietal channels (CP1, CP2, CPz, P1, P2, POz and Pz).

Statistical analyses confirmed that the parieto-occipital channels (P3/4, PO3/4, and P5/6) are specifically body sensitive, i.e., both P1 and N170 responses to clothed bodies were greater than those to cars. Because this scalp location is somewhat overlapping the EBA area (Downing et al., 2001), it is possible that activity in that area was reflected in the ERPs measured from the overlying electrodes. From the selected electrodes for the analysis (based on visual inspection) PO3/4 was the most body sensitive.

Importantly, top-down object-based attention did not modulate early body processing. Attention allocation did not have an effect on P1 or N170 in the parieto-occipital channels, based on the analysis when cars and clothed bodies were compared. However, in the analysis where the responses to clothed and nude bodies were compared, top-down attention decreased the N170 latency, while the amplitudes were not modulated. The difference was significant, and could in principle indicate that top-down attention speeds up the processing of visual body information. Regarding the automaticity of early face processing, Cauquil et al. (2000) suggested that if the processing is not completely automatic, top-down attentional modulation could show as enhanced ERP amplitudes or reduced latencies. Similar reasoning could be applied to the present findings. However, the mean difference in latency between responses to attended and non-attended stimuli was only 3 ms and the effect size was small. Thus, one should be cautious in interpreting this result. The difference probably does not reflect any meaningful enhancement to visual body processing. Also the fact that the N170 latency was not decreased by attention, points to a conclusion that early visual body processing in the parieto-occipital channels is not modulated by top-down object-based

attention. A finding that was not straightforward to interpret was that, at two electrodes in the right hemisphere (PO4 and PO6), N170 response was smaller in the attended than non-attended condition for clothed stimuli. However, because this effect was found only on two electrodes and for one stimulus category, no far-reaching conclusions should be made based on this result.

In the parieto-occipital channels, the visual processing of bodies was enhanced to nude vs. clothed bodies; N170 response amplitudes were greater to nude than to clothed bodies. This effect was found only in the right hemisphere. Also, surprisingly in the left hemisphere, the P1 response was actually smaller to nude than to clothed bodies. Overall however, the amplitude differences between the responses to clothed and nude bodies were small. The small amplitude differences could be explained by findings that EBA is activated when individual body parts (Taylor, Wiggett, & Downing, 2007) or stick figure body stimuli (Peelen & Downing, 2005) are seen. These findings suggest that at this stage of visual body processing, only general body features and forms are recognized, and whether the body is clothed or nude is not yet analyzed. This fits well with the theories by Taylor et al. (2007) and Hodzic et al. (2009a,b) stating that the processing in EBA precedes processing in FBA in which body configuration or whole bodies are identified.

In the temporal channels, there were no attention effects on P1 or N170 amplitudes or latencies for any stimulus type. Thus, it seems that top-down attention does not modulate object processing in the temporal channels. Only at the electrode TP7 some attentional modulation occurred. However, because the findings were restricted to just one electrode, no far-reaching conclusions can be made.

The previous results by Hietanen and Nummenmaa (2011) were replicated in the temporal channels. Nude bodies elicited greater N170 responses than did faces, while N170 to clothed bodies was the smallest of the three. It is probable that the N170 response in these channels reflects both visual body and face processing. Hietanen and Nummenmaa (2011) also further argued that the enhancement of the N170 response resulted from brain activity tuned to detect sexual signals from other peoples' bodies. The current results support that argument. They also suggested that possibly, top-down attention could account for some of the enhancement of N170 to nude bodies. The results of the current experiment did not support that suggestion. The greater N170 amplitudes towards nude bodies than towards other stimuli are not due to additional allocation of top-down attention.

Analysis of the later components in the parieto-occipital (P3/4, PO3/4, P5/6) and temporal channels (P7/8, TP7/8, TP9/10) revealed that attention modulated the processing of all stimulus types 300 ms after stimulus onset. At the electrodes located in the temporal region, the ERP-component in the 200 – 400 ms time window, from which the attentional modulation was found,

reminded early posterior negativity (EPN). In the parieto-occipital channels, later activity was instead somewhat similar to that in the nearby centro-parietal channels where LPP was found. The component from which attentional differences were found in the parieto-occipital channels reminded P3 response. P3 is the one of the most studied ERP components, and has been found to be enhanced by motivational significance of the stimuli, as well as detection of a target stimulus among other stimuli (see Luck & Kappenman, 2012). The time window of this modulation replicates the findings by Lueschow et al. (2004), where attentional modulation was found to begin 250 – 340 ms after stimulus presentation, depending on the electrode, and peaked between 300 and 350 ms. Also, Schupp et al. (2007) found top-down attentional modulation in 200 – 300 ms post-stimulus time window. Apparently, top-down attention begins to enhance visual processing of attended human stimuli (clothed bodies, nude bodies, and faces) at somewhere near 300 ms post-stimulus latency.

The earliest top-down attentional modulation occurred surprisingly in the occipital channels (PO9/10 and O1/2) and was reflected in the P1 response, which was greater for attended than non-attended stimuli. Previous studies have reported that attention can modulate P1 response, but usually only in case of spatial attention. (Heinze et al., 1994; Motter, 1993; Poghosyan et al., 2005). The effects of object-based attention have been observed 140 ms after stimulus onset, but only when elementary features such as motion or color are concerned (Anllo-Vento & Hillyard, 1996; Anllo-Vento et al., 1998; Harter & Guido, 1980; Torriente et al., 1999). Also, for face processing, object-based attentional modulation has not been found to occur until 170 ms post-stimulus (Mohamed et al., 2009; Sreenivasan et al., 2009). The earlier results suggest that also in the present experiment, spatial attention played some role, when attending to different stimulus types. However, all the stimuli were shown in the center of the screen, and in that regard spatial attentional modulation seems unlikely.

The most plausible explanation for the early attentional modulation observed in the present study is related to the “zoom lense”-model of spatial attention (Eriksen & James, 1986; Posner & Peterson, 1990). Usually when spatial attention is studied, same sized stimuli are shown to different locations in the visual field activating corresponding visuotopic locations in the striate cortex. When attention is directed to one of the locations, anticipatory activity increases in the corresponding location in the striate cortex. Results from an fMRI study (Müller, Bartelt, Donner, Villringer, & Brandt, 2003) indicate also, that even if stimuli are shown in the same location, different-sized neural networks will be activated depending on the stimulus size, and attention can focus on perceiving only one-sized stimuli. Thus, attention to small stimuli could increase anticipatory

activity in a small neural network in the striate cortex, while attention to large stimuli increases anticipatory activity over larger region in the striate cortex. If the pattern of the stimulus-elicited neural activity matches with the pattern of the anticipatory activity, an effective categorization of the object could in principle be made by using that information. For example, faces could have been recognized fast by attending to small-sized round objects. In such a way, spatial attention could have influenced the results of the present experiment also.

The LPP response showed a similar attentional modulation as the earlier attentional effects in the 300 – 700 ms latency, that is, attention increased the amplitude of LPP in all stimulus categories. This might reflect increased processing in the extended neural network that processes information of other peoples' bodies (Hodzic et al., 2009a, 2009b). Also, LPP was increased when nude bodies were seen compared to other stimulus categories. These results fit well with earlier studies examining the relationship between attention and affective arousal (Cuthbert et al., 2000, Foti et al., 2009, Hajcak et al., 2007, Hajcak & Olvet, 2008, Schupp et al., 2000, Schupp et al., 2003; Schupp et al., 2004) indicating enhanced attention for emotional stimuli. Also, as in Schupp et al. (2007) study, late attentional effects were increased when highly arousing stimuli were seen.

Analysis of the SAM questionnaires revealed that the participants felt the most positive when clothed bodies were seen, but most aroused, when a nude body was seen. This replicates earlier findings (Hietanen & Nummenmaa, 2011), and suggests that affective arousal is a key component in enhancing visual body processing when a nude body is seen. Such an effect has been well-documented in the literature (See Olofsson, Nordin, Sequeira, & Polich, 2008).

Taken together, the present results indicate that early body and face processing are not modulated by top-down object-based attention. Attention modulates body processing clearly at 300 ms latency in the parieto-occipital, temporal, and centro-parietal channels. In the parieto-occipital channels, the modulation is more pronounced for nude than clothed bodies, which could indicate that emotional significance of a stimulus enhances the attentional modulation. Attentional modulation of object processing as early as 100 ms post-stimulus at the occipital channels is a novel result as such a modulation of visual object processing has not been found before. It is possible that spatial attention could have been used to some extent to distinguish between different stimulus types. However, because no early attentional modulation of body or face processing was found, it is more probable that early visual body and face processing are not susceptible to top-down attentional modulation, as have been found before (Carmel & Bentin, 2002; Furey et al., 2006; Lueschow et al., 2004).

Because the question of attentional modulation has been asked before regarding face perception, and as the responses to face stimuli were also recorded, the current results can be compared to the results of previous experiments. When comparing the present results to those by Mohamed et al. (2009), they seem to disagree regarding faces. However, it should be noted that the attention manipulation was different between these two studies. Mohamed et al. (2009) found a rather large attentional effect in the temporal region. They used a perceptual load task to manipulate object-based attention and found that when perceptual load was high, face processing was attenuated greatly, compared to a low load condition. In the current experiment the perceptual load was low, and that can explain why attentional effects were not found. The current results indicate that also body processing cannot be manipulated if perceptual load is low. The results by Sreenivasan et al. (2009) seem consistent with the present results, because they found attentional modulation only when faces were not easy to discriminate and argued that the capability of attention to affect early face perception depends on the stimulus signal quality and as the quality lowers, possible attentional modulation increases. In the current experiment, the stimuli were not faded or made difficult to discriminate in any way. Thus, processing of visual body information is not modulated when the body stimuli are easy to discriminate.

Further, the findings of the current experiment agree with those by Carmel and Bentin (2002), Lueschow et al. (2004), and Furey et al. (2006), who did not find top-down attentional modulation of face perception within 170 ms post-stimulus latency. Also, in their experiment, Lueschow et al. (2004) found attentional modulation to face perception (by using MEG) to begin 190 ms after stimulus presentation. However, they also did not find as early modulation when analyzing the ERP responses.

Taken together, it is argued that because in the present experiment the visual discriminability of all the stimuli was high and the perceptual load was low, the effects of attention to early body and face processing were not detectable even though the attention manipulation itself was probably stronger than in the study by Lueschow et al. (2004). Thus, top-down object-based attention is not yet able to influence body processing within the first 290 ms. after stimulus onset. This supports the findings that top-down selection of stimuli can occur only after an initial sweep of information through the brain and after the selection based on bottom-up salience detection (Theeuwes, 2010). It is possible that before attention can begin to modulate processing of an object, stimulus feature, or location, that object, feature, or location has to be recognized first. That would explain why the timescales of attentional modulation differs between spatial, feature-based, and complex-object-based visual processing. In this context, spatial attention can affect visual

processing earliest, because the location of an object is determined early in the visual analysis. Then, when form and color of the object are determined, attention can begin to influence the processing of those. Lastly, somewhere after 170 ms post-stimulus, after an object has been recognized, top-down attention can begin to influence its processing. By analyzing ERP responses, such a modulation is apparent only after 300 ms post-stimulus.

Based on the current results, it seems that the early N170 response is reflecting different processes depending on whether it is recorded over body- or face-sensitive channels. In the parieto-occipital channels, N170 seems to reflect the processes of body part and form -perception but not the processing of affective significance. In the temporal channels, however, the N170 response reflects body and face processing but also affective processing. The affective significance of a stimulus seems to be determined already in the timescale of 170 ms. It has been argued that the early coding of emotional features of stimuli are performed in amygdala (Bacter & Murray, 2002; Childress, Ehrman, Wang, & Sciortino, 2008; Zald, 2003). That activation could be reflected to ERPs recorded from cortical areas. It is also a possibility that emotional processing could occur in the cortical areas without subcortical influence (Pessoa & Adolphs, 2010). This activation could also contribute to perceived enhancement of ERPs when seeing affectively arousing stimuli.

It is possible that top-down object based attentional effects on the body-related N170 response could not be found in the present experiment because of the experimental procedure. At the beginning of a block, a participant was instructed to attend to one of the four stimulus categories. Also, they saw two target pictures from the same category. Thus, when seeing a stream of pictures, they had to remember which stimulus category was to be attended and also the two specific target stimuli. What happens then, when a participant sees a stimulus? First, they have to recognize the stimulus type as a nude body, clothed body, face or car. Then they have to decide if the stimulus type was to be attended or not. Further, if the stimulus was to be attended, they have to compare if the attended stimulus matches with the target or not. At that point, attention has to be focused on the finer details of the stimulus. So in the current experiment, every stimulus category received at least some attention. Only after stimulus recognition and determination of whether the stimulus was to be attended, participants could ignore the non-attended stimulus. Because of initial attention to every stimulus category, it could be that the attentional effects to early ERP responses would not show.

In the future, a combined EEG and functional imaging study could confirm if EBA-related processing is genuinely reflected in the ERP responses measured over the parieto-occipital channels. Additionally, in future studies the possible effects of spatial attention should be controlled

more carefully by controlling the stimulus size between categories. On the other hand, if stimulus size for all the stimuli is the same, the natural size relations between different object categories would be lost.

4.1 Conclusions

It is concluded that both initial body and face processing are unaffected by the modulation of top-down object-based attention. Top-down attention begins to affect visual body and face processing 300 ms after stimulus presentation, and probably is reflected in activation of a larger cortical network related to body and face processing. Early attentional modulation in the occipital channels could reflect spatial attentional processes that occurred because of differing stimulus sizes between stimulus categories. Human visual perception is tuned to detect human bodies, and top-down attention cannot rapidly modulate this processing. This ensures that evolutionarily important information from human bodies is processed fast and accurately in the human brain despite of where attention is directed at any moment.

References

- Andersson, M., B. (1994). *Sexual selection*. New Jersey: Princeton University Press.
- Anllo-Vento, L., & Hillyard, S.A. (1996). Selective attention to the color and direction of moving stimuli: electrophysiological correlates of hierarchical feature selection. *Perception & Psychophysics*, *58*, 191–206.
- Anllo-Vento, L., Luck, S. J., & Hillyard, S. A. (1998). Spatio-temporal dynamics of attention to color: evidence from human electrophysiology. *Human Brain Mapping*, *6*, 216–238.
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*, 170–177.
- Baxter, M. G., & Murray, E. A. (2002). The amygdala and reward. *Nature Reviews Neuroscience*, *3*, 563–573.
- 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.
- 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.
- Bukach, C. M., Gauthier, I., & Tarr, M. J. (2006). Beyond faces and modularity: the power of an expertise framework. *Trends in Cognitive Sciences*, *10*, 159–166.
- Carlson, J. M., & Reinke, K. S. (2010). Spatial attention-related modulation of the N170 by backward masked fearful faces. *Brain and Cognition*, *73*, 20–27.
- Carmel, D., & Bentin, S. (2002). Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition*, *83*, 1–29.

- Cauquil, 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.
- Cheal, M. L., Lyon, D. R., & Gottlob, L. R. (1994). A framework for understanding the allocation of attention in location-precued discrimination. *Quarterly Journal of Experimental Psychology*, *47*, 699–739.
- Childress, A. R., Ehrman, R. N., Wang, Z., Li, Y., Sciortino, N., Hakun, J., et al. (2008). Prelude to passion: limbic activation by “unseen” drug and sexual cues. *PLoS ONE*, *3*, e1506.
- Crist, R. E., Wu, C-T., Karp, C., & Woldorff, M. G. (2008). Face processing is gated by visual spatial attention. *Frontiers in Human Neuroscience*, *1*, 10.
- Currie, T. E., & Little, A. C. (2009). The relative importance of the face and body in judgements of human physical attractiveness. *Evolution and Human Behavior*, *30*, 409–416.
- 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.
- Dagenbach, D., & Carr, T. H. (1994). *Inhibitory Processes in Attention, Memory, and Language*. San Diego: Academic Press.
- 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.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, *4*, 2051–2062.
- Downing, P. E., Bray, D., Rogers, J., & Childs, C. (2004). Bodies capture attention when nothing is expected. *Cognition*, *93*, 27–38.

- 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.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, *8*, 1784–1790.
- Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, *11*, 2319–2324.
- Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention: a zoom lens model. *Perception & Psychophysics*, *40*, 225–240.
- Fan, J., Dai, W., Liu, F., & Wu, J. (2005). Visual perception of male body attractiveness. *Proceedings of The Royal Society B*, *272*, 219–226.
- Farah, M. J., Wilson, K. D., Drain, H. M., & Tanaka, J. R. (1995). The inverted face inversion effect in prosopagnosia: evidence for mandatory, face-specific perceptual mechanisms. *Vision Research*, *35*, 2089-2093.
- 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., et al. (2006). Dissociation of face selective cortical responses by attention. *Proceedings of the National Academy of Sciences USA*, *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.

- Gross, C. G., Bender, D. B., & Rocha-Miranda, C. E. (1969). Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, *166*, 1303–1306.
- Hajcak, G., Dunning, J. P., & Foti, D. (2007). Neural response to emotional pictures is unaffected by concurrent task difficulty: an event-related potential study. *Behavioral Neuroscience*, *121*, 1156–1162.
- Hajcak, G., & Olvet, D. M. (2008). The persistence of attention to emotion: brain potentials during and after picture presentation. *Emotion*, *8*, 250–255.
- Harter, M. R., & Guido, W. (1980). Attention to pattern orientation: negative cortical potentials, reaction time, and the selection process. *Electroencephalography and Clinical Neurophysiology*, *49*, 461–475.
- Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Munte, T. F., et al. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature*, *372*, 543–546.
- Heslenfeld, D. J., Kenemans, J. L., Kok, A., & Molenaar, P. C. (1997). Feature processing and attention in the human visual system: an overview. *Biological Psychology*, *45*, 183–215.
- 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.
- Hodzic, A., Kaas, A., Muckli, L., Stirn, A., & Singer, W. (2009a). Distinct cortical networks for the detection and identification of human body. *Neuroimage*, *45*, 1264–1271.
- Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009b). Cortical responses to self and others. *Human Brain Mapping*, *30*, 951–962.
- 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.

- Kahneman, D., & Henik, A. (1981). Perceptual organization and attention. In M. Kuvoby, J. Pomerantz (Eds.), *Perceptual organization* (pp. 181–211). Hillsdale, NJ: Erlbaum.
- 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.
- Kittler, R., Kayser, M., & Stoneking, M. (2003). Molecular evolution of *Pedicularis humanus* and the origin of clothing. *Current Biology*, *13*, 1414–1417.
- Lavie, N., Ro, T., & Russell, C. (2003). The role of perceptual load in processing distractor faces. *Psychological Science*, *14*, 510–515.
- Luck, S. J., & Kappenman, E. S. (2012). *The Oxford handbook of event-related potential components*. New York: Oxford University Press, Inc.
- 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.
- McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. II: response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex*, *9*, 431–444.
- 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 USA*, *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.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*, 782–784.
- Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, *70*, 909–919.
- Müller, N. G., Bartelt, O. A., Donner, T. H., Villringer, A., & Brandt, S. A. (2003). A physiological correlate of the "zoom lens" of visual attention. *The Journal of Neuroscience*, *23*, 3561 – 3565.
- Nieuwenhuis, S., & Yeung, N. (2005). Neural mechanisms of attention and control: losing our inhibitions? *Nature Neuroscience*, *8*, 1631-1633.
- 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., & 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.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, *11*, 773–782.

- Poghosyan, V., Shibata, T., & Ioannides, A. A. (2005). Effects of attention and arousal on early responses in striate cortex. *European Journal of Neuroscience*, *22*, 225–234.
- Posner, M. I., & Gilbert, C. D. (1999). Attention and primary visual cortex. *Proceedings of the National Academy of Sciences USA*, *96*, 2585–2587.
- Posner M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Pourtois, G., Peelen, M. V., Spinelli, L., Seeck, M., & Vuilleumier, P. (2007). Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia*, *45*, 2621–2625.
- Rhodes, G., & Simmons, L. W. (2007). Symmetry, attractiveness and sexual selection. In Dunbar, R. I. M., & Barrett, L. (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 USA*, *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.
- 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., Junghofer, M., Weike, A. I., & Hamm, A. O. (2003). Attention and emotion: an ERP analysis of facilitated emotional stimulus processing. *Neuroreport*, *14*, 1107–1110.
- 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.
- 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, A. T., Cotillon-Williams, N. M., & Williams, A. L. (2006). Attentional modulation in the human visual cortex: the time-course of the BOLD response and its implications. *Neuroimage*, *29*, 328–334.
- 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.
- Stekelenburg, J. J., & de Gelder, B. (2004). The neural correlates of perceiving human bodies: an ERP study on the body-inversion effect. *Neuroreport*, *15*, 777–780.
- 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.
- Taylor, J., Wiggett, A., & Downing, P. (2007). fMRI analysis of body and body part representations in the extrastriate and fusiform body areas. *Journal of Neurophysiology*, *98*, 1626–1633.

- Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*, *135*, 77–99.
- Thierry, G., Martin, C. D., Downing, P., & Pegna A. J. (2007). Controlling for interstimulus perceptual variance abolishes N170 face selectivity. *Nature Neuroscience*, *10*, 505–511.
- 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.
- Torriente, I., Valdes-Sosa, M., Ramirez, D., & Bobes, M. A. (1999). Visual evoked potentials related to motion-onset are modulated by attention. *Vision Research*, *39*, 4122–4139.
- 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.
- Weisbuch, M., & Ambady, N. (2011). Thin-slice vision. In Adams, R. B., Ambady, N., Nakayama, K., & Shimojo, S. (2011). *The Science of Social Vision*. (pp. 228–247). New York: Oxford University Press, Inc.
- Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, *41*, 88–123.