



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



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ARTICLE INFO

Article history:

Received 27 January 2014

Accepted 7 September 2014

Available online 16 September 2014

Keywords:

Arousal

Attention

Visual body processing

Object-based attention

EEG

N170

EPN

P3

LPP

ABSTRACT

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

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1. Introduction

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

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

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

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

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

1.1. Attentional and affective effects on brain responses

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

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

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

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

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

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

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