



Neural Correlates and Perceived Attractiveness of Male and Female Shoulder-to-Hip Ratio in Men and Women: An EEG Study

Farid Pazhoohi¹ · Joana Arantes² · Alan Kingstone¹ · Diego Pinal³

Received: 6 September 2022 / Revised: 18 April 2023 / Accepted: 20 April 2023

© The Author(s), under exclusive licence to Springer Science+Business Media, LLC, part of Springer Nature 2023

Abstract

While there are studies regarding the neural correlates of human facial attractiveness, there are few investigations considering neural responses for body form attractiveness. The most prominent physical feature defining men's attractiveness is their physical fitness and upper body strength. Shoulder-to-hip ratio (SHR), a sexually dimorphic trait in humans, is an indicator of men's attractiveness for both men and women. The current study is the first to report on the neurophysiological responses to male and female body forms varying in SHR in healthy heterosexual men and women observers. Electroencephalographic (EEG) signals were acquired while participants completed an oddball task as well as a subsequent attractiveness judgement task. Behavioral results showed larger SHRs were considered more attractive than smaller SHRs, regardless of stimuli and participants' sex. The electrophysiological results for both the oddball task and the explicit judgement of attractiveness showed that brain activity related to male SHR body stimuli differed depending on the specific ratios, both at early and late processing stages. For female avatars, SHR did not modulate neural activity. Collectively the data implicate posterior brain regions in the perception of body forms that differ in attractiveness vis-a-vis variation of SHR, and frontal brain regions when such perceptions are rated explicitly.

Keywords Body size · Shoulder-to-hip ratio (SHR) · Attractiveness · EEG · ERP

Introduction

Visual perception of the human body activates a distinct region in human visual cortex, a region that selectively responds to the appearance of human bodies but not faces (Downing et al., 2001; Peelen & Downing, 2007). This region is called the extrastriate body area (EBA; Downing et al., 2001) and is located in the lateral occipito-temporal cortex. In addition to the EBA, the fusiform body area (FBA) is a region in extrastriate visual cortex that responds selectively to visual depictions of the human body (Peelen & Downing, 2005; Schwarzlose et al., 2005). It is suggested that EBA neurons respond to parts of the body while FBA neurons are

more responsive to the appearance of the whole body (Taylor et al., 2007). For example, pictures of the human body elicit a negative event-related potential (ERP) component peaking at 190 ms (N190) that differs from the N170 component which tends to be elicited selectively by faces (Gliga & Dehaene-Lambertz, 2005; Thierry et al., 2006).

While there are studies regarding the neural correlates of facial attractiveness that have used, for example, functional magnetic resonance imaging (fMRI) or ERP (e.g., Calvo et al., 2018; Cloutier et al., 2008; Hahn et al., 2016; Trujillo et al., 2014), there are relatively few investigations that have considered the neural responses for the attractiveness of the body form using fMRI (Holliday et al., 2011; Platek & Singh, 2010) or ERP measures (Del Zotto & Pegna, 2017; Pazhoohi et al., 2020b). For example, Del Zotto and Pegna investigated attractiveness of the female body form by testing the association of patterns of brain activation with different waist-to-hip ratios (WHRs; lower values yield a “curvier” figure). They showed that men generated a P1 that had a higher amplitude for the WHR 0.7 compared to 0.6, 0.8 and 0.9, and the N190 showed a higher amplitude for WHR 0.6 for both the male and female observers. Furthermore,

✉ Farid Pazhoohi
pazhoohi@gmail.com

¹ Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, BC V6T 1Z4, Canada

² Department of Basic Psychology, School of Psychology, University of Minho, Braga, Portugal

³ Psychological Neuroscience Lab, CIPsi, School of Psychology, University of Minho, Braga, Portugal

Pazhoohi et al. (2020b), reported that the perception of women's lower WHR and larger breasts show different temporal and spatial patterns of activation compared to the perception of larger WHR and smaller breasts. Specifically, in an implicit evaluation (i.e., an oddball task), as well as during an explicit evaluation of women's bodies (i.e., an attractiveness judgement task), attractive WHRs and breast sizes differently influenced brain activity related to visual processing than less attractive WHRs and breast sizes, both at early and late temporal stages in men and women.

While WHR is a factor in perceptions of female body form attractiveness (Barber, 1995; Bovet & Raymond, 2015; Singh, 1993), the most prominent physical feature linked to perceptions of male body form attractiveness is physical fitness and upper body strength (Dixson et al., 2003; Hönekopp et al., 2007). Shoulder to hip ratio (SHR), the circumference of the shoulders relative to the hips, is a sexually dimorphic trait in humans and a higher SHR is positively associated with attractiveness in men (Fan et al., 2005; Horvath, 1981; Tovée et al., 1999). In general, women visually attend more to muscular male body forms and consider muscular men with broader shoulder more attractive than overweight and lean men (Dixson et al., 2014; Garza et al., 2017). Moreover, women desire men portraying a more masculine SHR and upper body as their potential partners (Braun & Bryan, 2006; Sell et al., 2017). It appears that women are drawn to these characteristics because they are linked to good genes, masculinity, and immune system strength, which may offer both indirect advantages, such as healthier offspring, and direct benefits, such as acquiring resources (Frederick & Haselton, 2007; Garza & Byrd-Craven, 2021; Gray & Frederick, 2012; Pazhoohi et al., 2023b; Puts et al., 2012).

Additionally, men are generally more attentive of a rival's upper-body, and exposure to a rival with a high SHR may evoke jealousy (Buunk & Dijkstra, 2005; Massar & Buunk, 2009). Men also desire more masculine body forms as they consider (correctly it would seem) that such body forms increase their attractiveness to women and may increase their success in intrasexual competitions (Frederick et al., 2007; Kordsmeyer et al., 2018). Moreover, men with higher SHR self-report higher body esteem (Pazhoohi et al., 2012), a higher number of sexual partners, more extra-pair copulations, and an earlier age of initiation to sexual activities and masturbation (Hughes & Gallup, 2003). Men are more attentive to other men's characteristics such as increased muscularity because it could be a cue to formidability, fighting ability and resource holding power (Durkee et al., 2018, 2019; Puts, 2010; Sell et al., 2009, 2012).

A recent eye-tracking study ventured to investigate, for the first time, men and women's preference for male and female bodies that varied in terms of SHR (Pazhoohi et al., 2019). In line with previous research, men looked longer at the chest of

males with higher SHRs; but a similar pattern was not observed for women. Nonetheless, men rated males with higher SHRs and women with lower SHRs as more attractive, while women rated an intermediate SHR as most attractive for both male and female images (Pazhoohi et al., 2019). The difference in how men and women visually prefer and rate attractiveness based on SHR raises the question of whether there are sex differences at the neural level for processing male and female bodies with varying upper body sizes (SHR).

While previous studies investigated neural and behavioral correlates of women's WHRs (Del Zotto & Pegna, 2017; Holliday et al., 2011; Pazhoohi et al., 2020a, 2020b; Platek & Singh, 2010), to the best of our knowledge no previous investigation has considered the neural correlates of male and female upper body size perception. In the current study we aimed to determine the behavioral and neurophysiological correlates of male and female observers when viewing male and female body forms varying in SHR. This will provide insights into the cognitive mechanisms responsive to these bodily features, and how these are affected by the observer-stimulus sex relationship. Based on Pazhoohi et al. (2019), we expected: (1) males would rate women with lower SHRs as more attractive, while women would prefer an intermediate SHR, and (2) males would rate males with a large SHR as more attractive and females would again prefer an intermediate SHR. As for the brain activity, though this research is largely explorative in nature, in line with the findings of Pazhoohi et al. (2019) we tentatively predict prominent brain activity differences for male than female participants both in response to female and male avatars.

In order to address the above, we examined electroencephalographic (EEG) signals to male and female body forms varying in SHR in healthy heterosexual men and women observers, while they completed an oddball task (Squires et al., 1975) and a subsequent attractiveness judgement task. In both tasks, participants were exposed to images of female and male body figures varying in SHR. The oddball task, where participants were engaged in a task irrelevant to body size judgement, was used as an implicit measurement of attractiveness while the rating task was an explicit measurement of attractiveness. Previous research has shown differences in implicit and explicit processing of nonverbal social signals such as facial expressions (Critchley et al., 2000). Accordingly, in the current study we aimed to explore whether there are dissociations between these two forms of measurement of body size perception.

Method

Participants

In this study, 48 heterosexual individuals (28 females) between 18 and 37 years old ($M = 23$; $SD = 4.36$) were included as the final number of participants. They were recruited from University of Minho students through an institutional credit system. None of the participants had any history of major psychiatric or neurological disorders, nor were they on medication; they also reported the absence of any psychoactive drugs during the last month prior to participation. Participants either received course credit or 10 Euros gift cards in exchange for their participation.

Prior to the beginning of the study, a consent form was signed by the participants and sociodemographic information was collected. The participants were also asked to complete a brief battery of questionnaires; namely, the NEO-FFI-20 Personality Inventory (Bertoquini & Pais-Ribeiro, 2006), which is a validated Portuguese short version of the NEO-PI-R (Costa & McCrae, 1995); the Brief Symptoms Inventory (Derogatis, 1993) validated in Portuguese (Canavarro, 1999); the Edinburgh Handedness Inventory (Oldfield, 1971); and the Graffar Social Classification Scale (Graffar, 1956). All participants, but one, were right-handed. All participants had normal or corrected to normal vision. Further, there were no differences between participating men and women in any of the aforementioned tests (Table 1).

Procedure and Measures

Stimuli

The stimuli were generated using DAZ 3D studio version 4.6 (Daz Productions, Inc., Salt Lake City, UT, USA). Six stimuli (see Fig. 1) were generated using one female model and one male model, each with three SHRs of small (1.1), medium (1.2) and large (1.3) ratios. Previous studies determined that men's SHR ranged from 1.03 to 1.40, with an average of 1.18 ± 0.07 , as reported by Hughes and Gallup (2003). As a result, we categorized an SHR of 1.2 as intermediate and developed two alternative ratios, namely a lower (1.1) and a higher (1.3) ratio. Head and feet of the stimuli were cropped. For the oddball task, another set of stimuli were created for each sex with flowers on the chest area of the stimuli's upper clothing (see Fig. 1). All the stimuli were presented in grayscale and equated for exposure value and luminance.

Task Design and Paradigm

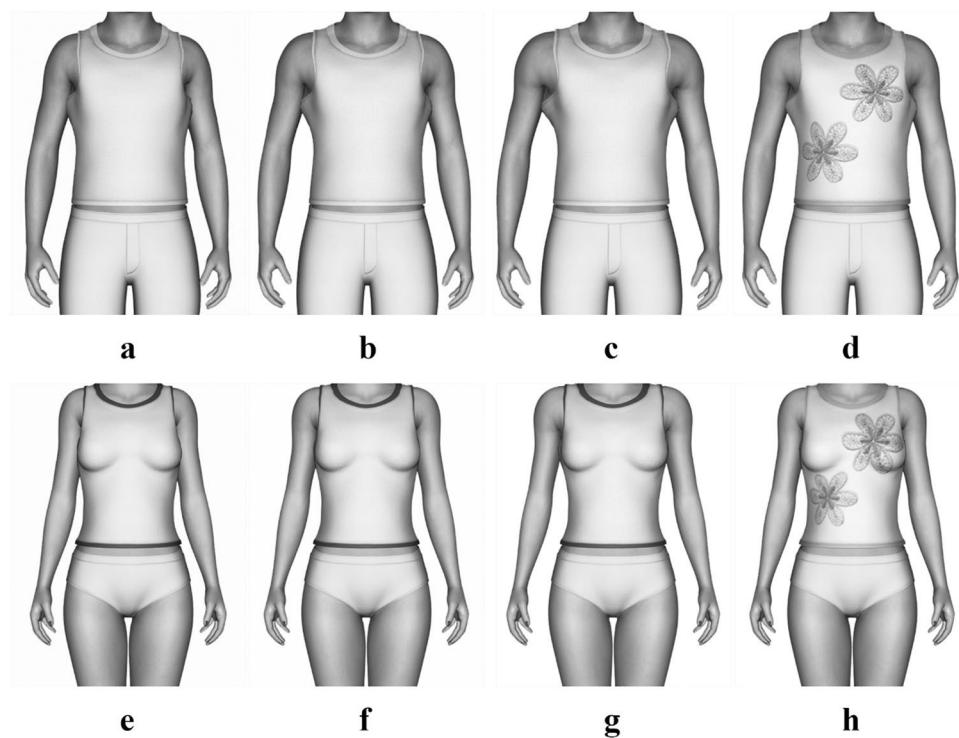
Participants were seated in a comfortable armchair in front of a 19" LCD monitor on which the stimuli were presented. The experiment consisted of two blocks: an oddball task and an attractiveness judgement task, the latter which was always completed last to avoid priming performance on the oddball task. In the oddball task participants viewed stimuli varying in sex (i.e., male and female avatars) and SHR centered on the screen while they were asked to press the "M" key on the computer's keyboard whenever they saw flowers (the oddball event) on a T-shirt. Stimuli were presented and responses were recorded using Presentation® software (Neurobehavioral Systems, Inc., Albany, CA, USA). Each trial consisted of a pre-stimulus black screen with a white fixation cross in the center that lasted between 300 and 500 ms, followed by the stimulus display in the middle of the screen for 750 ms. There was a jittered intertrial interval of 1200–1700 ms.

Table 1 Independent group *t*-test results comparing male and female participants for sociodemographic, personality and neuropsychological variables

	Male (<i>n</i> =20)		Female (<i>n</i> =28)		<i>t</i>	<i>p</i>
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>		
Age (in years)	24.15	5.16	22.18	3.56	1.57	.124
GSC Score	12.95	2.14	13.25	2.08	-.49	.629
Neo-FFI-20						
Neuroticism	7.05	2.19	6.86	2.53	.27	.785
Extraversion	10.70	2.30	9.86	2.03	1.34	.186
Openness	10.70	4.17	11.04	2.43	-.35	.727
Kindness	10.80	2.46	9.93	2.79	1.12	.269
Self-consciousness	12.80	1.91	12.25	1.62	1.08	.288
BSI						
Global symptom index	.43	.25	.52	.38	-.94	.351

GSC score: Graffar Social Classification score, BSI: Brief Symptoms Inventory

Fig. 1 Examples of the stimuli used in this study: male avatars with **a** small SHR, **b** medium SHR, and **c** large SHR; **d** oddball stimulus for male avatar and medium SHR; female avatars with **e** small SHR, **f** medium SHR, and **g** large SHR; **h** oddball stimulus for female avatar and medium SHR



(300–500 ms pre-stimulus + 900–1200 ms post-stimulus), with a white fixation cross in the center of the black screen; Fig. 2A). Both the standard stimuli and the oddballs were presented in random order (180 trials for standard stimuli and 48 trials for oddball stimuli).

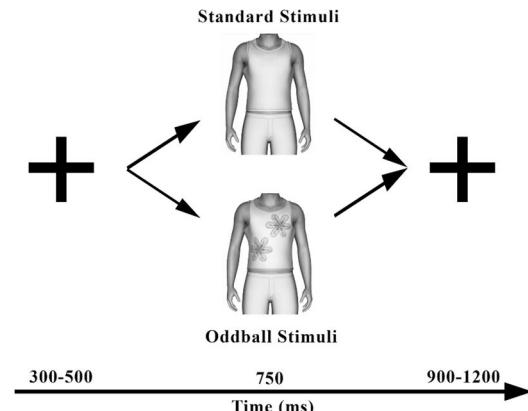
In the second block, participants completed an active attractiveness judgement task while EEG was recorded. Stimuli varying in sex and SHR were presented in random order. There were 150 trials and each trial consisted of a variable interstimulus interval of 700 to 1000 ms (600–900 ms pre-stimulus + 100 ms post-stimulus), followed by stimulus presentation for 750 ms before a 7-point Likert scale replaced the stimulus (Fig. 2B). The Likert scale was present on screen until the participant's response indicating the perceived attractiveness of the stimulus (1 = not attractive at all; 7 = highly attractive).

Behavioral Analysis

Behavioral analyses were performed using SPSS. An independent-samples *t*-test was conducted to test for sex differences in oddball response accuracy and reaction time. Oddball reaction time was measured as the time between the onset of an oddball stimulus and the execution of a response key.

A mixed ANOVA tested the effects of participant sex (male and female observers) and SHR (small, medium, and large) on perceived attractiveness ratings, and another mixed ANOVA on reaction times for providing the ratings. Ratings were considered the numeric value entered upon presentation

A) Oddball paradigm procedure



B) Attractiveness judgement procedure

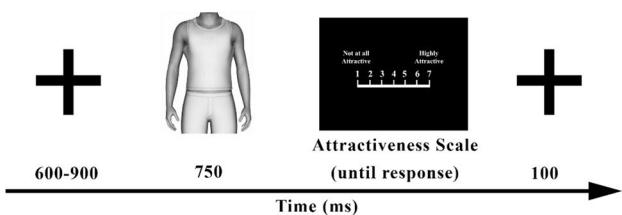


Fig. 2 Experimental procedures for **A** oddball paradigm and **B** attractiveness judgement task

of the Likert scale and the reaction time the time elapsed from scale presentation to button press.

EEG Recording and Processing

Experimental sessions took place in an electrically and acoustically shielded room. EEG was recorded with a 64-channels BioSemi ActiveTwo system (BioSemi B.V., The Netherlands), with the active electrodes placed at standard positions of the international 10–10 system of an elastic cap and using a Common Mode Sense recording montage, which produces reference free recordings. Additionally, electrooculogram signals were monitored via two electrodes in the outer canthi of the eyes and another one below left eye in order to correct EEG signals for ocular movements artifacts. All electrodes were adjusted to maintain their offset lower than 30 mV. EEG signals were amplified and digitized at a rate of 512 Hz, and the signal was bandpass filtered online between 0.01 and 100 Hz.

EEG Analyses

EEG data were processed and visualized using BrainVision Analyzer 2.1 (Brain Products GmbH, München, Germany). The signals were filtered digitally off-line between 0.1 and 30 Hz via a phase shift free fourth-order Butterworth filter and re-referenced to average reference. Then the signals were corrected for ocular artifacts using the procedure developed by Gratton et al. (1983). Semi-automatic artifact rejection was also applied. EEG was segmented offline into epochs from 200 ms prior to stimulus onset to 750 ms after the onset of the stimulus. Mean activity during the pre-stimulus interval was used as baseline. Artifact free epochs were averaged across participants for the combination of the three SHRs (small, medium and large) for each of the avatar sex conditions (male and female).

For ERP analysis, temporal Principal Component Analysis (tPCA) was applied to each of the participant's data for each condition and avatar sex. This method allows us to avoid the potential errors that may arise from visual inspection of the ERP waveforms during the decomposition of the ERPs into its constituent components (Dien et al., 2005). tPCA results produce a matrix for factor scores and another one for factor loadings. Factor scores are the transformation of the amplitude values representing magnitudes of the latent variables (i.e., transformations of the original microvolt values for each participant, condition, and electrode) and factor loadings are the data points based on the number of channels, epoch length, and frequency showing the distribution of each factor over time (Dien, 1998).

Application of tPCA to the oddball task related EEG signals showed eight temporal factors (TFs), altogether accounting for 92.05% of the variance (Fig. 3A). In temporal order

from stimulus onset, the largest factor loadings for TF4 were observed between 85 and 95 ms post-stimulus, while its largest positive factor scores were found at parietal and parieto-occipital electrodes (Pz, P1, P2, P3, P4 POz, PO3, and PO4). The largest factor loadings for TF8 were identified between 95 and 115 ms post-stimulus and the largest positive factor scores were at parieto-occipital electrodes (Oz, O1, O2, PO7, PO8, P7, P8, P9, and P10). TF6 largest factor loadings were obtained between 125 and 150 ms post-stimulus and its largest factor scores were observed at parieto-occipital electrodes (Oz, O1, O2, POz, PO3, PO4, PO7, and PO8). From 150 to 185 ms post-stimulus, TF5 had its maximum factor loadings with its largest negative factor scores located at parietal and parieto-temporal electrodes (TP7, TP8, P7, P8, P9, and P10), corresponding to the negative going part of N190. The maximum factor loadings for TF2 were obtained between 200 and 300 ms after the onset of the stimulus and largest positive factor scores were maximal at parieto-occipital electrodes (POz, PO3, PO4, PO7, PO8, Oz, O1, and O2). From 350 to 500 ms post-stimulus, TF3 had the largest factor loadings with its highest negative factor scores observed at frontal electrodes (FPz, FP1, FP2, AFz, AF3, AF4, AF7, and AF8). TF7 highest factor loadings were observed from 480 to 580 ms post-stimulus and its highest factor scores were located at frontal and frontocentral electrodes (Fz, F1, F2, F3, F4, FCz, FC1, and FC2). Finally, TF1 was corresponding with a negative slow wave (NSW) with its factor loadings being maximal from 600 ms post-stimulus to the end of the recording epoch (750 ms) and its factor scores being maximal at frontal electrodes (FPz, FP1, FP2, AFz, AF3, AF4, AF7, and AF8).

After applying the tPCA to ERP data for the attractiveness judgement task, six temporal factors explaining 92.14% of the variance were identified (Fig. 3B). In temporal order from stimulus onset, TF3 factor loadings were maximal from 125 to 160 ms post-stimulus and its factor scores were highest at occipital and parieto-occipital electrodes (Oz, O1, O2, POz, PO3, PO4, PO7, and PO8), probably corresponding with the classical P1 component. TF5 was probably related to an early N190 component, since it showed the highest factor loadings from 165 to 175 ms after the onset of stimulus with the largest negative factor scores observed at parietal and parieto-occipital electrodes (PO7, PO8, P7, P8, P9, and P10). TF2 largest factor loadings were observed between 175 and 315 ms post-stimulus with its highest factor scores found at parieto-occipital and occipital regions (Oz, O1, O2, POz, PO3, PO4, PO7, and PO8). TF6 factor loadings were highest between 300 and 330 ms post-stimulus and its largest negative factor scores were observed at occipital, parietal and parieto-occipital regions (Oz, O1, O2, PO7, PO8, P7, P8, P9, and P10). Maximal TF4 factor loadings were between 320 and 500 ms post-stimulus with its highest negative factor scores observed at frontal electrodes (FPz, FP1, FP2, AFz, AF7, AF8, F7, and F8). Finally, TF1 was associated with a

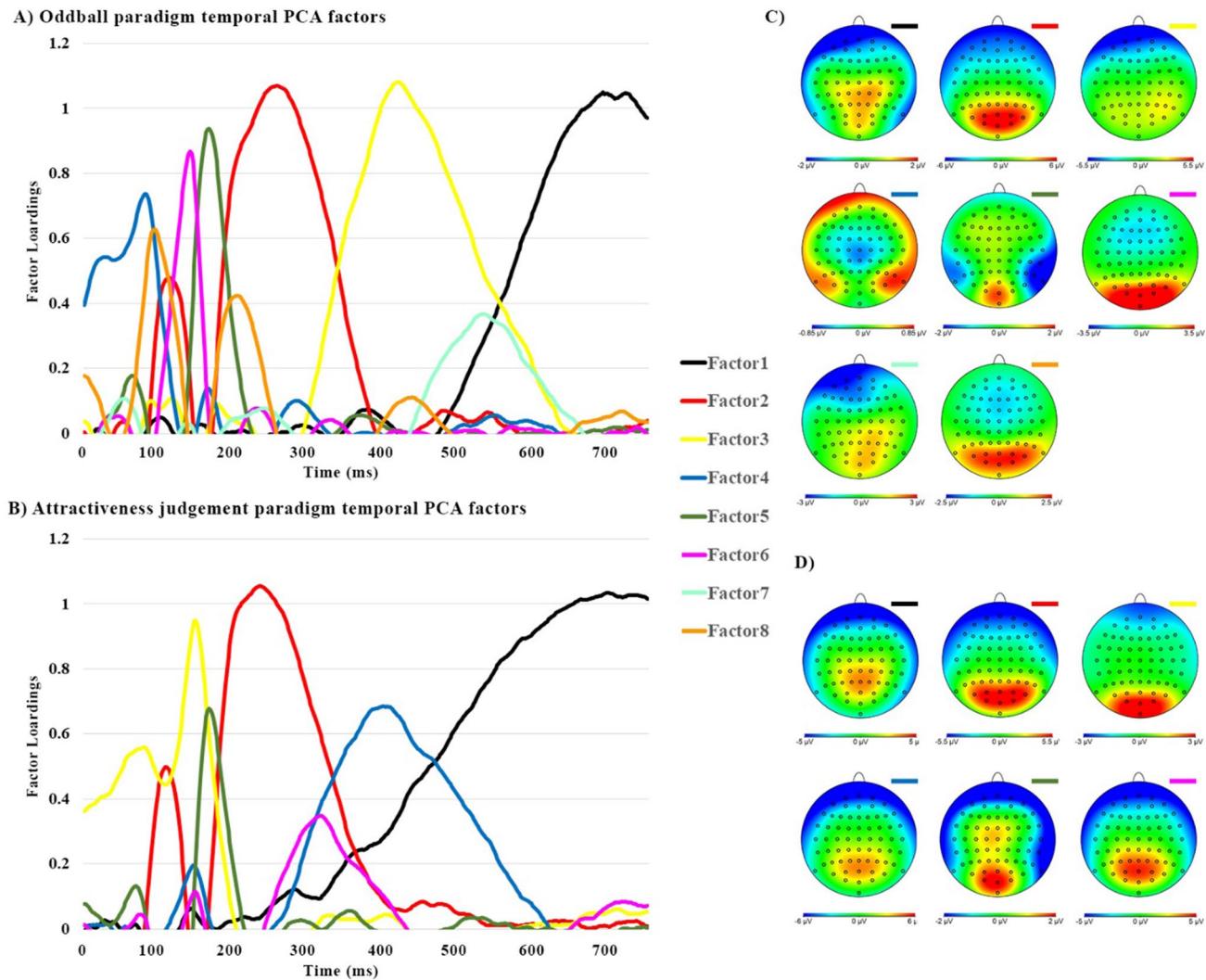


Fig. 3 **A** Extracted temporal principal components analysis factors for the oddball task. **B** extracted temporal principal components analysis factors for attractiveness judgement task. **C** voltage maps of

PCA factors for oddball paradigm. **D** voltage maps of PCA factors for attractiveness judgement paradigm

NSW as the maximal factor loadings were observed between 500 ms and the end of the analyzed epoch, while the maximal negative factor scores were recorded at frontal electrodes (FPz, FP1, FP2, AFz, AF7, AF8, F7, and F8).

To analyze the ERP data for both oddball and attractiveness judgement tasks, factor scores were averaged before entering statistical analysis across three laterality levels (midline, left and right hemispheres) for those electrodes showing maximal factor scores for each temporal factor independently. No midline region was available for TF5 of both oddball and attractiveness judgement tasks, therefore the laterality effect had only two levels (left and right hemispheres) for this temporal factor. A mixed ANOVA tested the effects of participant sex (male and female), SHR (small, medium, and large), and Laterality (midline, left and right hemispheres) on factor scores for each TF and independently for male and

female avatars. For all the ANOVAs carried out, Greenhouse-Geisser correction was applied whenever there was violation of the sphericity assumption, and the Bonferroni test was applied in post hoc comparisons whenever necessary, with significance cut-off at $p \leq 0.05$.

Additionally, standard low resolution brain electromagnetic tomography (sLORETA) was used to explore differences between conditions in the estimated cortical sources of electric activity signals recorded at the scalp (Pascual-Marqui et al., 1994). This algorithm is a discrete, 3D distributed, linear, weighted minimum norm inverse solution. Thus, this procedure yields images of current density with exact localization, albeit with low spatial resolution (i.e. neighboring neuronal sources will be highly correlated) (Pascual-Marqui, 1999; Pascual-Marqui et al., 1994). sLORETA computations were made in a realistic head model (Fuchs et al., 2002) based

on the MNI152 template (Mazziotta et al., 2001), for which the three-dimensional solution space was restricted to cortical gray matter partitioned in 6239 voxels at 5 mm spatial resolution. Thus, sLORETA generates functional images that represent the brain regions that showed activation at a given

time window for a specific experimental condition. Current source distribution maps for each TF were generated via the implementation of LORETA algorithms in Brain Vision Analyzer 2.0 (Fig. 4) and the coordinates of the voxel with higher estimated activity for each TF are gathered at Table 2.

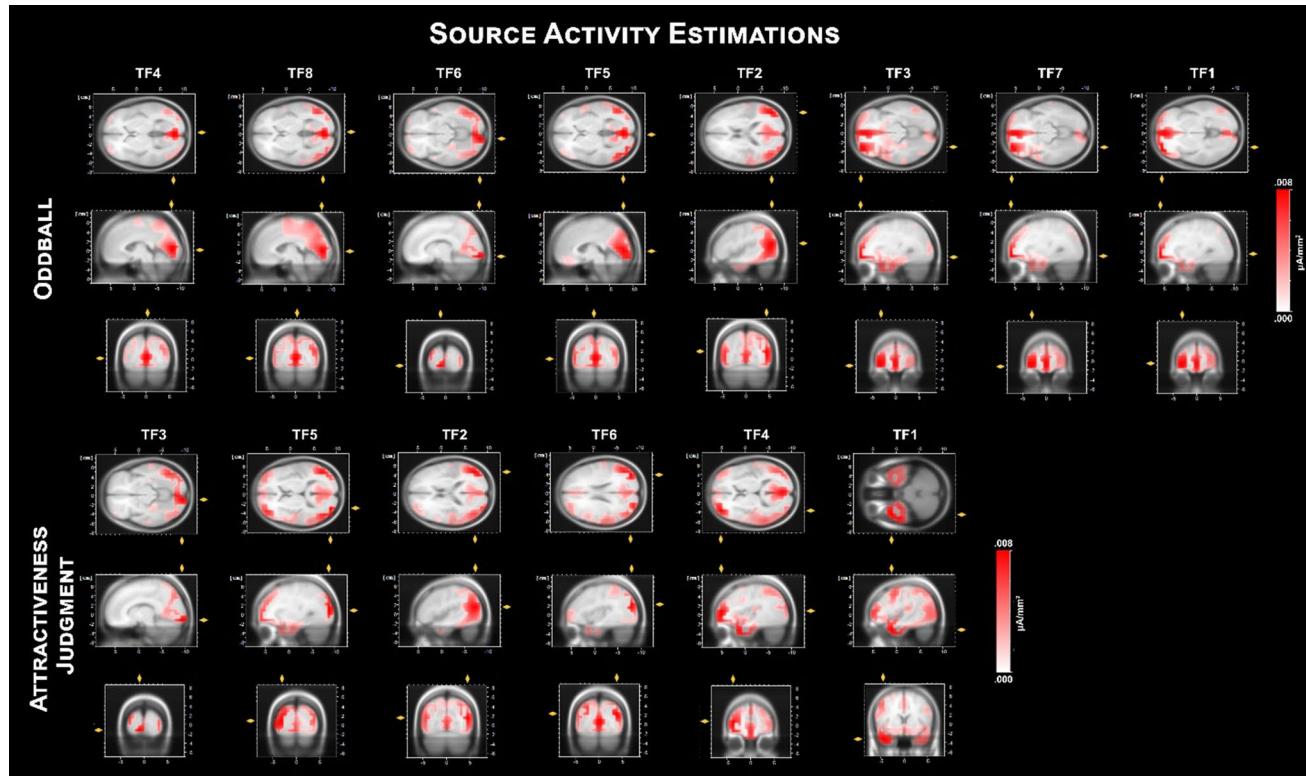


Fig. 4 Source activity estimation maps for each task and temporal factor showing the brain regions with maximal activation for each temporal factor

Table 2 Areas of activation in the Oddball and Attractiveness Judgement tasks

Task	Temporal factor (time range in ms)	Anatomical region	Brodmann area	MNI Coordinates		
				x	y	z
Oddball	4 (85–95)	Right lingual gyrus	18	4	-81	1
	8 (95–115)	Right lingual gyrus	18	4	-81	1
	6 (125–150)	Left inferior occipital gyrus	17	-10	-95	-13
	5 (150–185)	Left lingual gyrus	18	-3	-81	1
	2 (200–300)	Right middle temporal gyrus	39	46	-74	15
	3 (300–500)	Left superior frontal gyrus	11	-31	59	-13
	7 (480–580)	Left superior frontal gyrus	11	-31	59	-13
	1 (600–750)	Left middle frontal gyrus	10	-31	59	-6
	3 (125–160)	Left inferior occipital gyrus	17	-10	-95	-13
	5 (165–175)	Left middle occipital gyrus	19	-31	-88	8
Attractiveness judgement	2 (175–315)	Right middle temporal gyrus	39	46	-74	15
	6 (300–330)	Right middle temporal gyrus	19	39	-81	22
	4 (320–500)	Left middle frontal gyrus	10	-38	52	8
	1 (500–750)	Left middle temporal gyrus	21	-45	10	-34

Further, the estimated current source density distributions were compared between each pair of experimental conditions for each TF and avatar sex separately by running a nonparametric statistical mapping procedure (Nichols & Holmes, 2002) in LORETA software. In this procedure a paired samples *t*-test for each single voxel for each temporal factor was run to compare the current source density distribution for each pair of conditions. Then, 5000 randomizations with the statistical procedure applied in each run were conducted to determine a statistical threshold ($p < 0.05$) corrected for multiple comparisons.

Results

Behavioral Results

Oddball Accuracy and Reaction Time

An independent-samples *t*-test was conducted to compare oddball accuracy between men and women. There was no significant difference between men ($M = 99.90\%$, $SD = 0.46\%$) and women ($M = 99.93\%$, $SD = 0.39\%$) in oddball accuracy, $t(46) = -0.23$, $p = 0.812$. Also, there was no difference in the reaction time between men ($M = 466.83$, $SD = 38.51$ ms) and women ($M = 453.83$, $SD = 48.67$, $t(46) = 0.99$, $p = 0.328$).

Attractiveness Judgements and Reaction Time

Male Avatars A 2 (Participant Sex: Male and Female) \times 3 (SHR: Small, Medium, and Large) mixed analysis of variance (ANOVA) was performed for male avatars, with Participant Sex as a between-subjects factor and SHR as a within-subjects factor. The main effect for Participant Sex was significant, $F(1, 46) = 45.62$, $p < 0.001$, $\eta^2 = 0.49$; women rated the stimuli ($M = 4.68$, $SEM = 0.23$) more attractive than men ($M = 2.24$, $SEM = 0.27$).

Results also showed a significant main effect for SHR, $F(1.36, 62.56) = 22.24$, $p < 0.001$, $\eta^2 = 0.32$; large SHR ($M = 3.79$, $SEM = 0.22$) was rated more attractive than both medium ($M = 3.53$, $SEM = 0.18$, $p = 0.044$) and small SHRs ($M = 3.05$, $SEM = 0.16$, $p < 0.001$). Also, medium SHR was rated significantly more attractive than small SHR ($p < 0.001$). The Participant Sex \times SHR interaction was not significant ($p = 0.230$).

To investigate the reaction time, a 2 (Participant Sex) \times 3 (SHR: small, medium, and large) mixed ANOVA was performed, with Participant Sex as a between-subjects factor and SHR as a within-subjects factor. No significant differences were observed for the main effects and their interaction (all $ps > 0.178$).

Female Avatars A 2 (Participant Sex: Male and Female) \times 3 (SHR: Small, Medium, and Large) mixed ANOVA was performed for female avatars, with Participant Sex as a between-subjects factor and SHR as within-subjects factor. Results showed a significant main effect for SHR, $F(1.66, 76.65) = 22.24$, $p < 0.001$, $\eta^2 = 0.55$; large SHR ($M = 4.88$, $SEM = 0.15$) was rated more attractive than both medium ($M = 4.65$, $SEM = 0.14$, $p = 0.001$) and small SHRs ($M = 4.14$, $SEM = 0.14$, $p < 0.001$). Also, medium SHR was rated significantly more attractive than small SHR ($p < 0.001$). Participant Sex main effect ($p = 0.259$) and Participant Sex \times SHR interaction were not significant ($p = 0.247$).

No significant main effects or interactions between the aforementioned factors were observed for reaction times (all $ps > 0.153$).

EEG results

Male Avatars

Oddball Task *Factor Scores Analysis of Variance.* A 2 (Participant Sex: Male and Female) \times 3 (SHR: Small, Medium, and Large) \times 3 (Laterality: Midline, Left, and Right Hemispheres) mixed ANOVA was performed, with Participant Sex as a between-subjects factor and SHR and Laterality as within-subjects factors.

Results showed a main effect of SHR for TF5 (negative going part of N190), $F(2, 92) = 3.98$, $p = 0.022$, $\eta^2 = 0.08$. Pairwise comparisons showed that large SHR ($M = -0.50$, $SEM = 0.13$) had more negative factor scores than medium SHR ($M = -0.33$, $SEM = 0.13$, $p = 0.014$; see Fig. 5 for TF5 ERPs and voltage maps).

LORETA Analysis. Using LORETA software, *t*-tests were conducted to compare neural activation between different SHR conditions. LORETA results showed that TF4 current source activity was significantly higher for large SHR than medium SHR at right Postcentral gyrus ($t = 3.687$, $p = 0.047$). Additionally, *t*-tests for TF3 showed significantly higher activation for small SHR than medium SHR at right Cuneus ($t = -3.760$, $p = 0.033$; see Fig. 6).

Attractiveness Judgment Task *Factor Scores Analysis of Variance.* A 2 (Participant Sex: Male and Female) \times 3 (SHR: Small, Medium, and Large) \times 3 (Laterality: Midline, Left, and Right Hemispheres) mixed ANOVA was performed, with Participant Sex as a between-subjects factor and SHR and Laterality as within-subjects factors.

For TF5 (early N190), results showed a significant main effect for SHR, $F(2, 92) = 4.79$, $p = 0.010$, $\eta^2 = 0.09$; small SHR ($M = -1.11$, $SEM = 0.14$) had higher negative factor scores than medium SHR ($M = -0.82$, $SEM = 0.15$, $p = 0.006$; see Fig. 7 for TF5 ERPs and voltage maps).

Fig. 5 Event-related potentials and voltage maps for temporal factor 5 of Oddball task showing left, midline, and right pools for male avatar SHR (small, medium, and large)

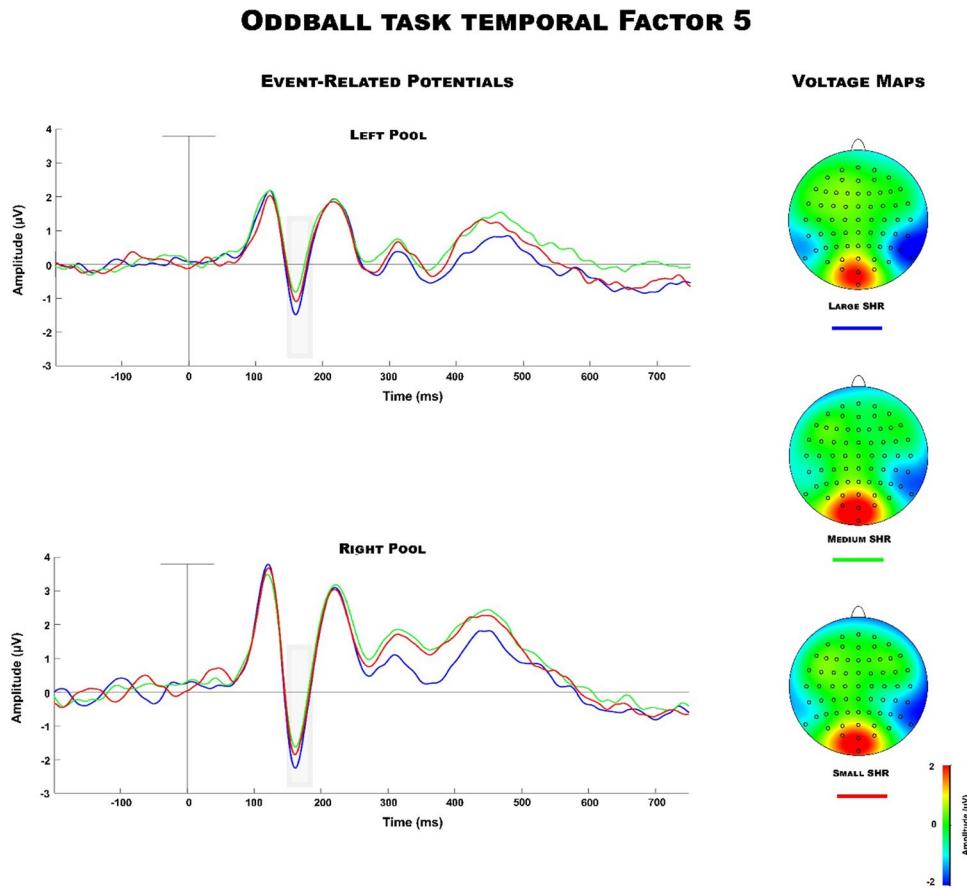


Fig. 6 Sectional views and 3D cortex images showing the estimated cortical sources of electric activity for temporal factors 4 and 3 in the Oddball task for male avatars

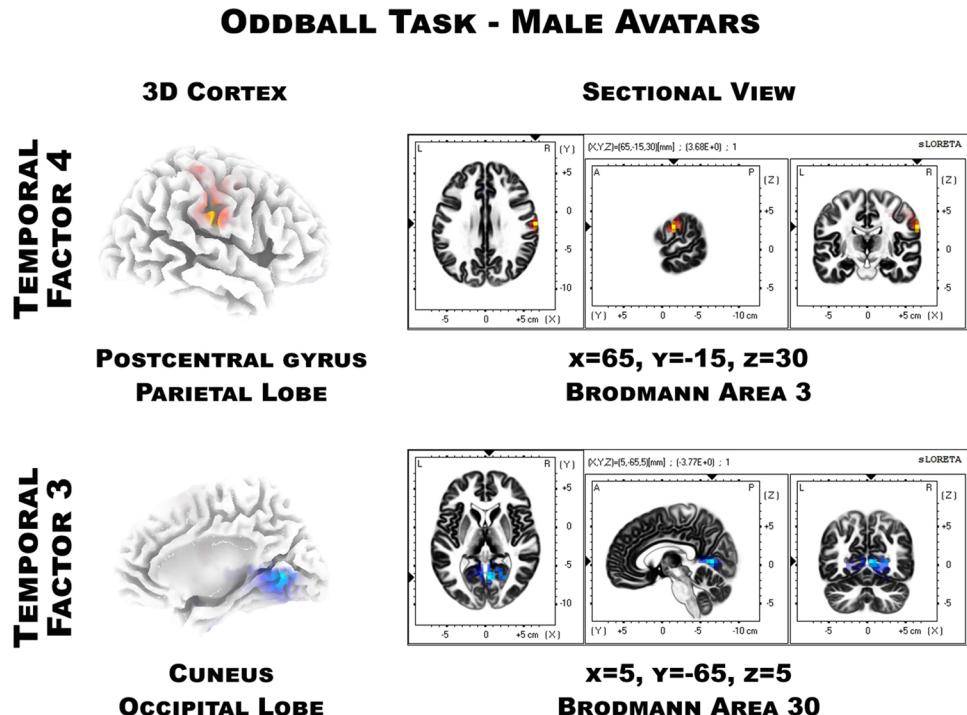
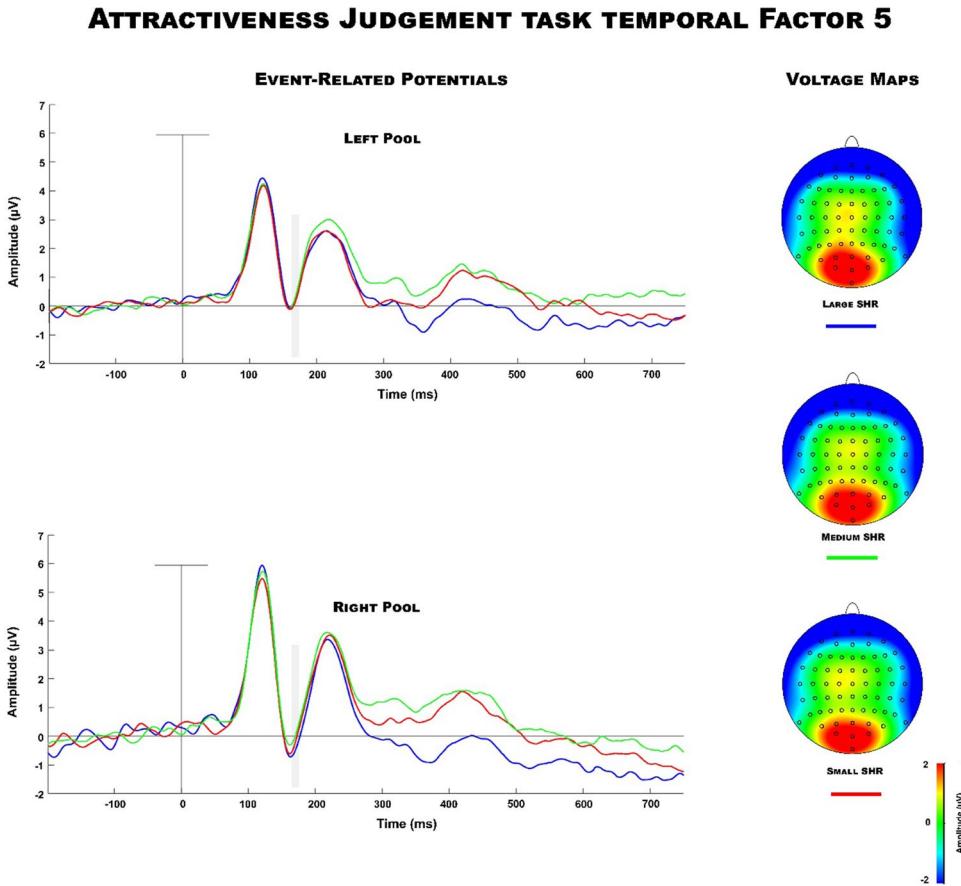


Fig. 7 Event-related potentials and voltage maps for temporal factor 5 of attractiveness judgement task showing left, midline, and right pools for male avatar SHR (small, medium, and large)



For TF2, results showed a main effect of SHR, $F(2, 92) = 3.85, p = 0.025, \eta^2 = 0.07$. Pairwise comparisons showed that medium SHR ($M = 1.37, SEM = 0.13, p = 0.024$) had higher factor scores than large SHR ($M = 1.22, SEM = 0.12$; see Fig. 8 for TF2 ERPs and voltage maps).

Results showed a significant main effect of SHR for TF6, $F(2, 92) = 5.34, p = 0.006, \eta^2 = 0.10$. Moreover, the SHR x Laterality interaction was significant, $F(3.05, 140.71) = 3.11, p = 0.017, \eta^2 = 0.06$; on the midline electrodes, small SHR ($M = -1.29, SEM = 0.17$) had higher negative factor scores than medium ($M = -0.93, SEM = 0.17, p = 0.003$) and large SHRs ($M = -0.92, SEM = 0.15, p = 0.019$). Also, on the left hemisphere, small SHR ($M = -1.11, SEM = 0.12$) had lower factor scores than medium SHR ($M = -0.77, SEM = 0.15, p = 0.004$; see Fig. 9 for TF6 ERPs and voltage maps).

Finally, results showed a significant main effect of SHR for TF4, $F(2, 92) = 6.65, p = 0.002, \eta^2 = 0.12$; large SHR ($M = -0.89, SEM = 0.12$) had lower negative factor scores than medium SHR ($M = -1.31, SEM = 0.12, p = 0.003$; see Fig. 10 for TF4 ERPs and voltage maps).

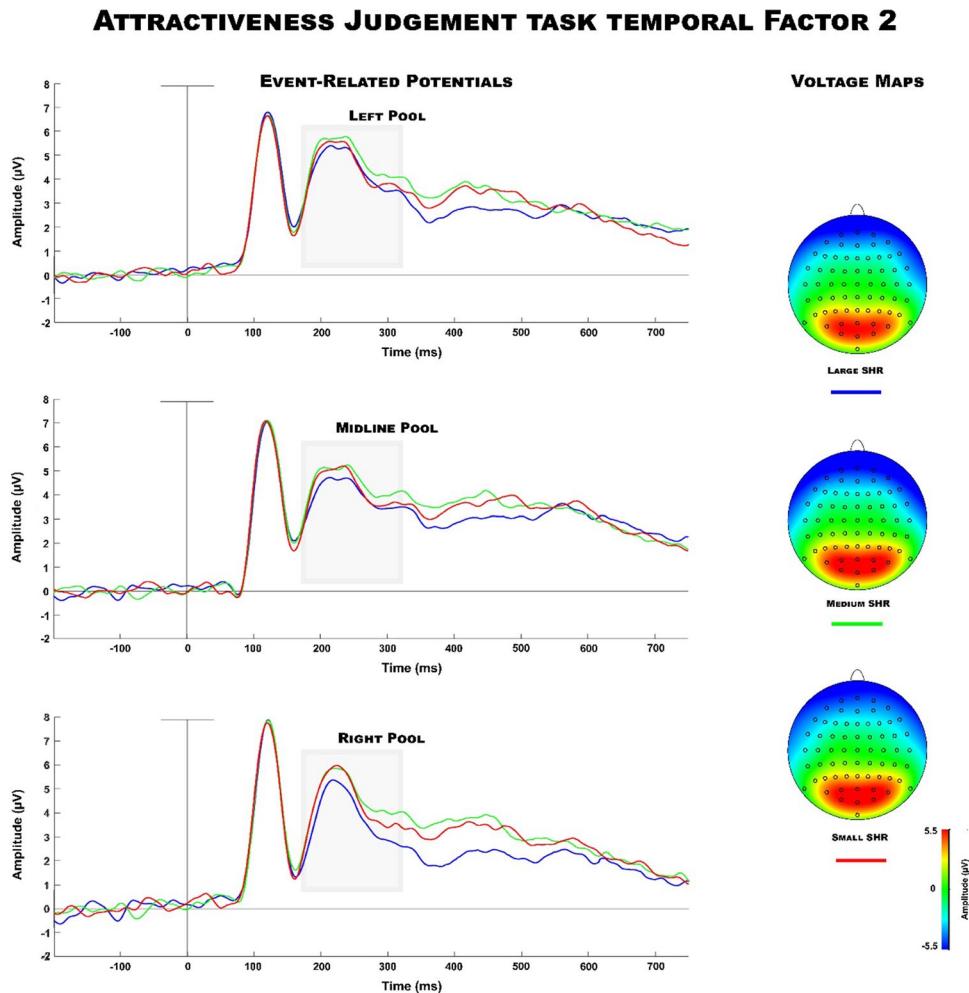
LORETA Analysis. LORETA t -tests results for TF2 showed that source estimated activity was significantly

higher for medium SHR than large SHR at right postcentral gyrus ($t = -4.48, p \leq 0.004$). In contrast, for TF6 activation was significantly higher for large than medium SHR at right parahippocampal gyrus ($t = 3.84, p = 0.029$) and significantly higher for larger than small SHR at right posterior cingulate and Cuneus ($t = 3.74, p = 0.036$). Similarly, TF1 showed significant results when comparing large SHR with medium SHR ($t = 3.94, p \leq 0.029$). Current source density estimates indicate higher activation at right posterior cingulate for large SHR than medium SHR (see Fig. 11).

Female Avatars

Factor Scores Analysis of Variance A 2 (Participant Sex: Male and Female) \times 3 (SHR: Small, Medium, and Large) \times 3 (Laterality: Midline, Left, and Right Hemispheres) mixed ANOVA was performed for female avatars, with Participant Sex as a between-subjects factor and SHR and Laterality as within-subjects factors. No significant difference was observed, for temporal factors either in oddball or attractiveness judgement tasks.

Fig. 8 Event-related potentials and voltage maps for temporal factor 2 of Attractiveness Judgement task showing left, midline, and right pools for male avatar SHR (small, medium, and large)



LORETA Analysis Oddball Task. LORETA *t*-test results for the oddball task for female avatars showed that medium SHR was related to significantly higher activation at middle temporal gyrus than small SHR for TF6 ($t = 3.80$, $p = 0.043$). Also, for TF7 activation at middle occipital gyrus was significantly higher for medium than large SHR ($t = -4.06$, $p = 0.008$; see Fig. 12).

Attractiveness Judgement Task. Loreta *t*-test results for the attractiveness judgment of female avatars showed significant differences only for TF2. Large SHR showed significantly lower activation than medium SHR at precentral gyrus ($t = 3.92$, $p = 0.024$), but significantly higher Cuneus activation than Small SHR ($t = 3.75$, $p = 0.041$; see Fig. 13).

Discussion

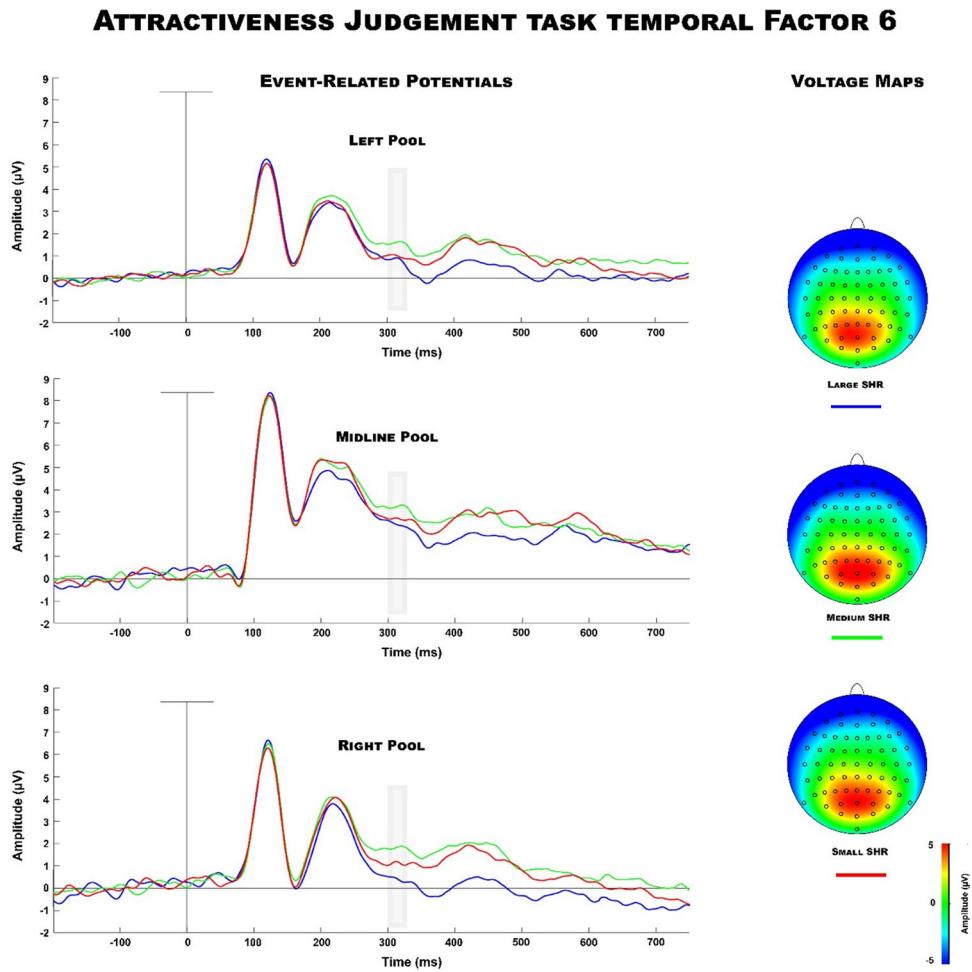
In the current study we investigated neural and behavioral correlates of perceived attractiveness of male and female avatars' as a function of the SHR. Behavioral results showed that compared to men, women rated male avatars as more

attractive. Moreover, all the participants rated large SHR more attractive than medium and small SHRs, and preferred medium SHR over small SHR independently of avatar sex.

Behavioral results regarding the preference for larger SHR in male models are in accordance to previous behavioral studies showing preference for more masculine and bigger upper body for men (Braun & Bryan, 2006; Dixson et al., 2014; Fan et al., 2005; Frederick et al., 2007; Kordsmeyer et al., 2018; Pazhoohi et al., 2012, 2023b; Sell et al., 2017; Tovée et al., 1999). Interestingly, there was no difference in the preference pattern observed between female and male avatars, meaning participants also considered higher SHRs more attractive for female avatars. This is in contrast with Pazhoohi et al. (2019) behavioral findings which led to our predictions that men would prefer male avatars with higher SHRs and female avatars with a lower SHR, whereas women would prefer intermediate SHRs for both sexes.

One reason for the present result could be that in the current study male and female avatars were shown in a random order within the same single block. This might have influenced the results in a way that participants opted for general preference to

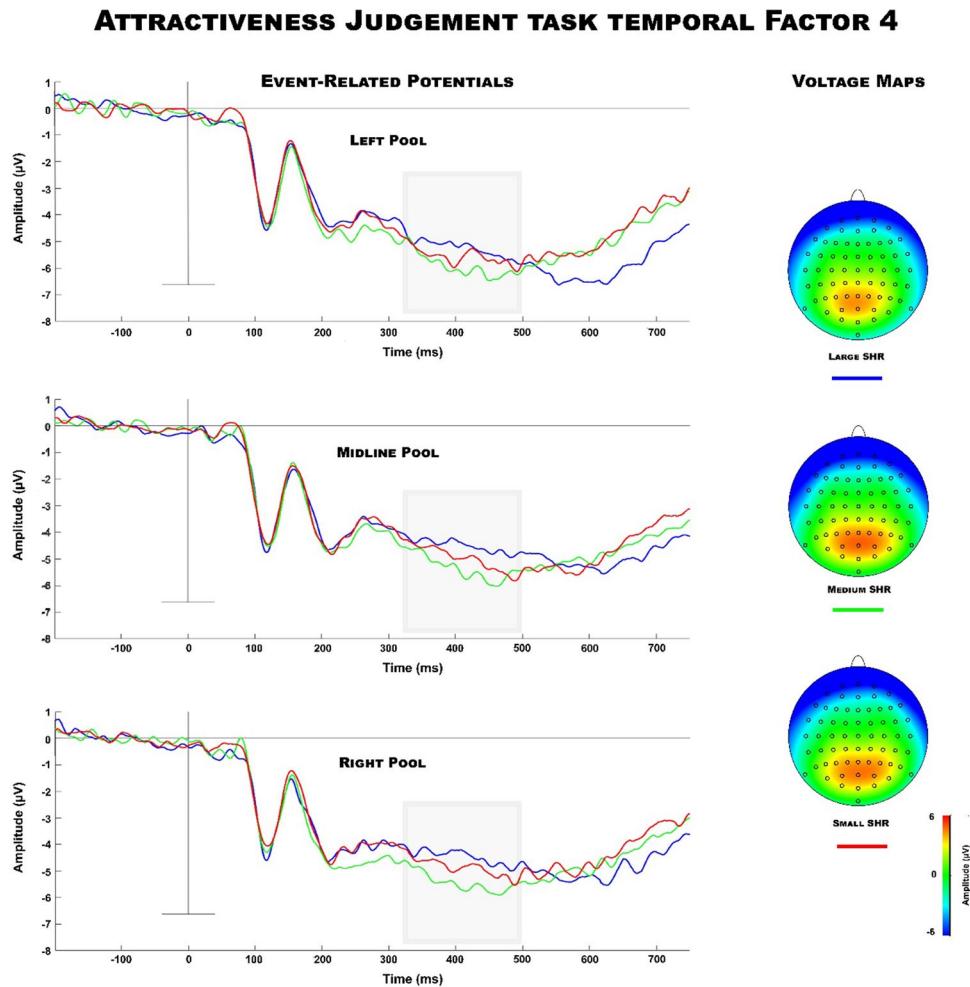
Fig. 9 Event-related potentials and voltage maps for temporal factor 6 of Attractiveness Judgement task showing left, midline, and right pools for male avatar SHR (small, medium, and large)



higher SHRs, irrespective of the sex of the avatars. Another possibility is that the preference for more masculine body forms of the female avatars could reflect an increase pressure for women to be physically toned (e.g., the yoga culture in social media) and equating that with beauty. While we did not measure our participants' social media use and exposure, future research might choose to test how such a variable might affect preferences for women's SHR. Another potential reason for the unexpected finding that participants preferred women with higher SHR could be due to the positioning of the arms, as increase in shoulder size has resulted in increase of distance between arms and the body in stimulus with high SHR compared to low SHR, thereby might have led into the illusion that women with higher SHR has a thinner body, hence more attractive. To address this confound, we cropped the upper body below the breasts and post-hoc asked a separate sample of participants

to rate the attractiveness of the three stimuli differing in arm positioning. No difference was found between the stimuli. It should be noted that research on attractiveness perception of women's upper body size is limited to the current study and Pazhoohi et al. (2019); therefore, future research is needed to further investigate the role of women's SHR on interpersonal perception and attraction. Moreover, the study has a drawback in that it only used three levels of SHR. To enhance the study's ecological validity, future research should obtain a broader range of SHR (e.g., Pazhoohi et al., 2023a).

Fig. 10 Event-related potentials and voltage maps for temporal factor 4 of Attractiveness Judgement task showing left, midline, and right pools for male avatar SHR (small, medium, and large)



Male Avatars

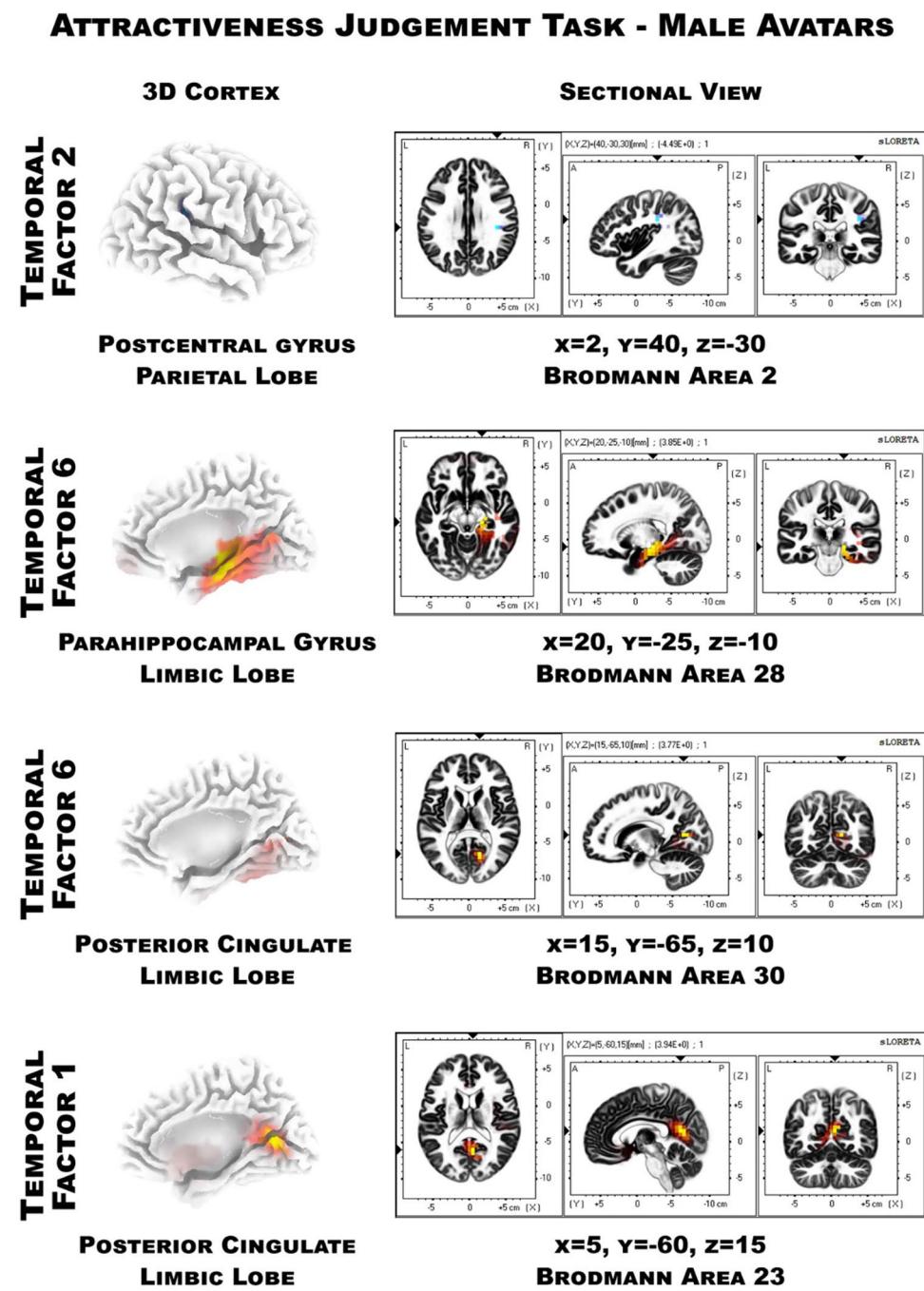
Oddball Task

The electrophysiological results for the oddball task (implicit attractiveness) showed an effect for the TF5 (negative-going part of N190) component, peaking between 150 and 185 ms post-stimulus with the largest factor scores at parietal and parieto-temporal electrodes. Using a LORETA brain electromagnetic tomography the source of maximal activity for TF8 was estimated at the left lingual gyrus in Brodmann area 18 (secondary visual cortex). Results showed that for male avatars, large SHR had higher negative factor scores than medium SHR of male avatars. The lingual gyrus (Brodmann area 18) or the secondary visual cortex (V2) is selectively activated during complex shape recognition and texture perception (Freeman et al., 2013; Hegdé & Van Essen, 2000), and emerging less than 100 ms after stimulus presentation (Hegdé & Van Essen, 2004). Brodmann area 18 alongside Brodmann area 19 form the extrastriate visual cortex, where EBA and FBA are also situated, and, therefore, the results of the current study highlight the role of these body sensitive

brain regions in the processing of male SHR variations early in the analysis of visual stimuli. Furthermore, this result is in accordance with the previous studies showing an N190 body processing specificity (Gliga & Dehaene-Lambertz, 2005; Pourtois et al., 2007; Thierry et al., 2006) and its modulation by factors determining the attractiveness of body forms (e.g. WHR in females, Del Zotto & Pegna, 2017).

LORETA Analysis The LORETA results comparing neural activity of SHR conditions for each TF showed that TF4 had higher neural activity for large SHR at the right postcentral gyrus compared with medium SHR. Right postcentral gyrus was previously shown to play a role in facial attractiveness rating (Shen et al., 2016). Similarly, right postcentral gyrus showed different activation in response to implicit attractiveness perception, as well as judgements of attractiveness of different male SHRs (see below). Additionally, for TF3 small SHR had higher activation at right Cuneus than medium SHR. Cuneus is one of the brain areas that shows higher activation to body stimuli than face stimuli (Kret et al., 2011), and the current results from both the oddball task as well as

Fig. 11 Sectional views and 3D cortex images showing the estimated cortical sources of electric activity for temporal factors 2, 6, and 1 in the Attractiveness Judgement task for male avatars



the attractiveness judgement task (see below) highlight its role in perception of male body attractiveness.

Attractiveness Judgment Task

The electrophysiological results for active judgements of attractiveness showed an effect for the TF5 (early N190) component peaking from 165 to 175 ms. The source of maximal activity during the time-window of TF5 was estimated at Brodmann area 19 (left middle occipital gyrus). Small SHR

of male avatars had higher negative amplitude than medium male SHR. Middle occipital gyrus has been shown to be activated in response to facial attractiveness perception and rating (Vartanian et al., 2013). Moreover, Brodmann area 19 is associated with several visual functions and along with area 18 constitute extrastriate visual cortex, in which EBA and FBA areas are located (Downing et al., 2001; Peelen & Downing, 2005, 2007; Schwarzlose et al., 2005), and suggests an early N190 normal activity regarding perception and attractiveness rating of stimuli differing in SHR, supporting

Fig. 12 Sectional views and 3D cortex images showing the estimated cortical sources of electric activity for temporal factors 6 and 7 in the Oddball task for female avatars

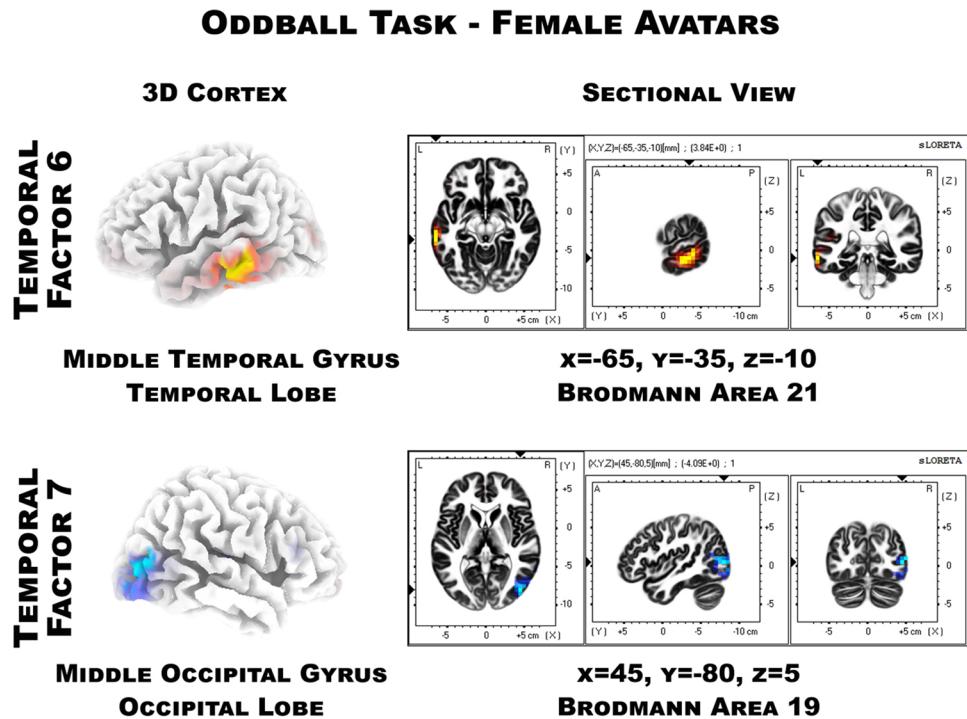
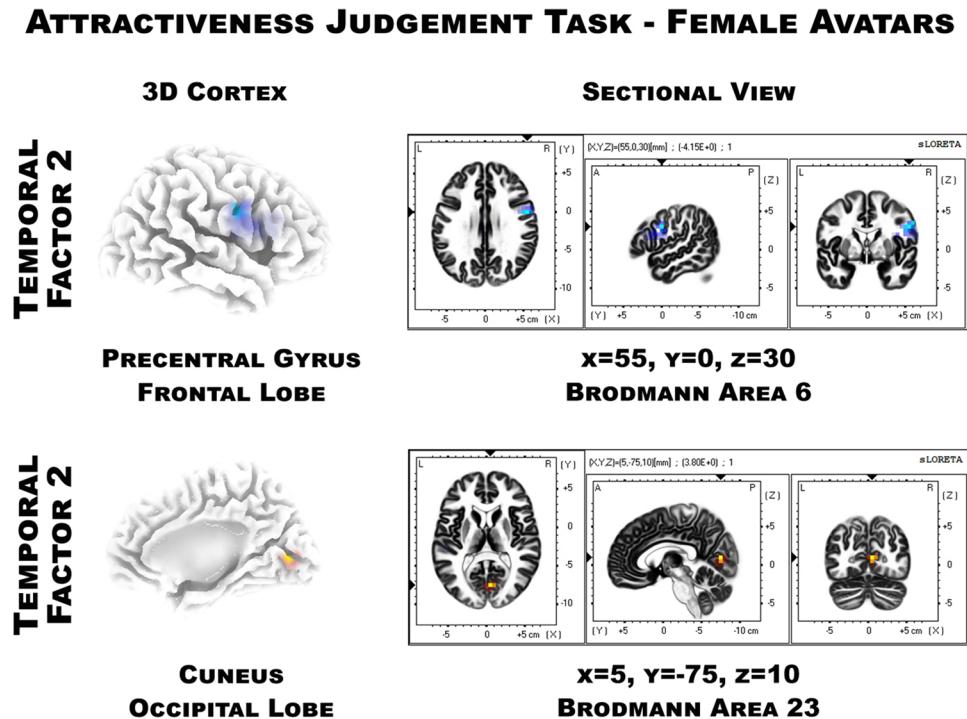


Fig. 13 Sectional views and 3D cortex images showing the estimated cortical sources of electric activity for temporal factor 2 in the Attractiveness Judgement task for female avatars



results from the previous studies in this regard (Thierry et al., 2006).

The results for TF2 showed higher amplitude for medium SHR than large SHR. This component peaked between 175 and 315 ms after the onset of the stimulus presentation maximizing at parieto-occipital electrodes and showing maximal current source activity at Brodmann area 39 (right middle

temporal gyrus). Middle temporal gyrus is suggested to be involved with convergence of information across different modalities related to vision, action, haptics, and language (Weiner & Grill-Spector, 2013). For example, it was shown to be involved in perception of facial attractiveness though this region is not necessarily within face processing areas (Vartanian et al., 2013). Brodmann area 39 is identified as

angular area (Triarhou, 2007) and the activation of middle temporal gyrus and angular area in the processing of human body images in the current study extends their role to the perception and judgements of attractiveness of body figures.

Component TF6 factor loadings peaked between 300 and 330 ms and the source of its maximal activity was identified at Brodmann area 19 (right middle temporal gyrus) using LORETA. For male avatars, small SHR had higher negative amplitude than medium and large SHRs. Previous research has shown a negative component with a latency close to 300 ms (i.e. N300) is linked to image classification (Hamm et al., 2002). Further, a higher N300 amplitude to attractive facial stimuli than unattractive faces has been previously reported (Zhang & Deng, 2012; Zhang et al., 2011). Interestingly, results of the present study show the opposite relation of N300 with attractiveness, since it was more negative to small than large SHR. Given the scarce research on the involvement of this component in facial and body form attractiveness processing, the present results warrant further investigation on the role of N300 during perception and attribution of attractiveness to different body morphs and its evaluation during active attractiveness judgement.

For the TF4 component the highest peak was observed between 320 and 500 ms post-stimulus with the highest factor scores at frontal electrodes. LORETA identified the source of maximal brain activity associated with TF4 at Brodmann area 10 (left middle frontal gyrus). For male avatars, medium SHR had higher negative amplitude than large SHR. Previous fMRI studies have shown activation in the left middle frontal gyrus to attractive stimuli such as attractive body depictions (Martín-Lloeches et al., 2014; see Di Dio et al., 2007, for activation in right middle frontal gyrus associated to attractive bodies perception). Collectively, it seems late components in the current study, such as TF4, are associated with the judgement of attractiveness, selection of the rating, and also the consecutive response execution related to the judgement.

LORETA Analysis LORETA results showed that TF2 had higher neural activity for medium SHR than large SHR at right postcentral gyrus. In contrast, activation for TF6 was higher for large than medium SHR at the right parahippocampal gyrus and higher for large than small SHR at the right posterior cingulate and Cuneus. Right parahippocampal gyrus has been shown to be activated during facial trustworthiness ratings (Platek et al., 2009), while right posterior cingulate was shown to be more activated to masculinized than feminized faces (Rupp et al., 2009). Results of the current study extend the role of right posterior cingulate in preference to more masculine faces to masculine male body forms. Similarly, TF1 showed large SHR had higher brain activation than medium SHR at the right posterior cingulate. Our results extend the role of postcentral gyrus, parahippocampal gyrus, and right posterior cingulate to attractiveness judgements of male upper bodies.

Female Avatars

LORETA Analysis

LORETA results for female avatars showed activations in regions similar to those for male avatars, however the time intervals for such activations were different for the female avatars. Specifically, LORETA results of the oddball task for female avatars showed higher activation for medium SHR than small SHR at the middle temporal gyrus for TF6. Also, for TF7 activation at the middle occipital gyrus was higher for medium SHR than large SHR. Middle occipital gyrus has been shown to be activated in response to facial attractiveness perception and ratings (Vartanian et al., 2013).

In the attractiveness judgement task, LORETA results showed lower activation of large SHR compared to medium SHR at the precentral gyrus for TF2, while large SHR had higher Cuneus activation than small SHR in the same temporal factor. Similarly, for male avatars, LORETA results showed higher activity for large than small SHR at the right Cuneus, suggesting Cuneus activity related to SHR, irrespective of sex of the avatars. Precentral gyrus has been shown to be involved in body part processing and body expression perception (Grezes et al., 2007; Suzuki et al., 1997) and our results extends its role to body size perception.

Conclusions

Accurate identification of bodily features plays a significant role in human social interactions (Pazhoohi & Liddle, 2012). Researchers have noted the evolutionary benefits of ability to determine an individual's body size, shape, and posture in human's interactions, including in the contexts of men's intrasexual competition (Puts, 2010; Sell et al., 2009, 2012) as well as intersexual selection (Dixson et al., 2014; Frederick & Haselton, 2007; Garza & Byrd-Craven, 2021; Garza et al., 2017; Pazhoohi et al., 2023b; Puts et al., 2012). This research identified behavioral and neural correlates of male and female SHR for men and women observers. Behavioral results showed that both men and women rated larger SHR as more attractive than smaller ones for both male and female avatars. The EEG results of both the oddball task and the explicit judgement of attractiveness showed that brain activity related to male SHR body stimuli differs depending on the specific ratios, both at early and late processing stages. However, the differences in neural activity regarding female SHR were less conspicuous. In other words, while for male avatars brain activity differences depending on SHR were evident both at scalp and source level, for female avatars SHR related differences were only observable at current source activity level and in a more restricted time window than those observed for male avatars. As the first study investigating the brain activity in response to upper body size perception,

findings of the current research signify evolutionary adaptive importance of men's upper body size compared to that of women's at the neural level.

In sum, the results of the current study reveal that variation in SHR modulates attractiveness ratings for male and female avatars alike. However, different patterns of brain activity dynamics accompany such ratings. Specifically, for male avatars, SHR variations modulate early and late activity during visual processing. These modulations are present at posterior brain regions related to body form perception, and attractiveness processing, as well as some frontal regions associated with judgement and decision making. This paper extends the results of previous studies on facial attractiveness to body attractiveness, namely SHR, and establish the basis for future studies assessing the specific role of different ERP components and brain regions in the determination of SHR in perceptions of attractiveness of female and male body figures.

Acknowledgments This study was conducted at Psychology Research Centre (UID/PSI/01662/2013), University of Minho, and supported by the Portuguese Foundation for Science and Technology and the Portuguese Ministry of Science, Technology and Higher Education through national funds and co-financed by FEDER through COMPETE2020 under the PT2020 Partnership Agreement (POCI-01-0145-FEDER-007653). JA receives funding from FCT Portugal through grants PTDC/MHC-PCN/4589/2012 and IF/01298/2014 and DP is supported by grant SFRH/BPD/120111/2016.

Funding The authors have not disclosed any funding.

Data Availability Authors will share upon request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical Approval This research was approved by the Behavioural Research Ethics Committee of the University of Minho and was conducted in accordance with the Declaration of Helsinki as it pertains to research with human participants.

Informed Consent All participants consented to taking part in the study.

References

Barber, N. (1995). The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Evolution and Human Behavior*, 16(5), 395–424. [https://doi.org/10.1016/0162-3095\(95\)00068-2](https://doi.org/10.1016/0162-3095(95)00068-2)

Bertoquini, V., & Pais-Ribeiro, J. (2006). Estudo de formas reduzidas do NEO-PI-R: Exame do NeoFFI, do Neo-FFI-R, e do Neo FFI-P para o contexto português. *Psicologia: Teoria, Investigação e Prática*, 11, 85–102.

Bovet, J., & Raymond, M. (2015). Preferred women's waist-to-hip ratio variation over the last 2500 years. *PLoS ONE*, 10(4), e0123284. <https://doi.org/10.1371/journal.pone.0123284>

Braun, M. F., & Bryan, A. (2006). Female waist-to-hip and male waist-to-shoulder ratios as determinants of romantic partner desirability. *Journal of Social and Personal Relationships*, 23(5), 805–819. <https://doi.org/10.1177/0265407506068264>

Buunk, B. P., & Dijkstra, P. (2005). A narrow waist versus broad shoulders: Sex and age differences in the jealousy-evoking characteristics of a rival's body build. *Personality and Individual Differences*, 39(2), 379–389. <https://doi.org/10.1016/j.paid.2005.01.020>

Calvo, M. G., Gutiérrez-García, A., & Beltrán, D. (2018). Neural time course and brain sources of facial attractiveness vs. trustworthiness judgment. *Cognitive, Affective, & Behavioral Neuroscience*, 18, 1233–1247. <https://doi.org/10.3758/s13415-018-0634-0>

Canavarro, M. C. (1999). Inventário de sintomas psicopatológicos: BSI. In M. R. Simões, M. Gonçalves, & L. S. Almeida (Eds.), *Testes e provas psicológicas em Portugal* (Vol. 2, pp. 87–109). SHO/APORT.

Cloutier, J., Heatherton, T. F., Whalen, P. J., & Kelley, W. M. (2008). Are attractive people rewarding? Sex differences in the neural substrates of facial attractiveness. *Journal of Cognitive Neuroscience*, 20(6), 941–951. <https://doi.org/10.1162/jocn.2008.20062>

Costa, P. T., Jr., & McCrae, R. R. (1995). Domains and facets: Hierarchical personality assessment using the Revised NEO Personality Inventory. *Journal of Personality Assessment*, 64(1), 21–50. https://doi.org/10.1207/s15327752ja6401_2

Crutchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van Amelsvoort, T., Robertson, D., David, A., & Murphy, D. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Human Brain Mapping*, 9(2), 93–105.

Del Zotto, M., & Pegna, A. J. (2017). Electrophysiological evidence of perceived sexual attractiveness for human female bodies varying in waist-to-hip ratio. *Cognitive, Affective, & Behavioral Neuroscience*, 17(3), 577–591. <https://doi.org/10.3758/s13415-017-0498-8>

Derogatis, L. R. (1993). *BSI: Brief Symptom Inventory* (3rd ed.). National Computers Systems.

Di Dio, C., Macaluso, E., & Rizzolatti, G. (2007). The golden beauty: Brain response to classical and renaissance sculptures. *PLoS ONE*, 2(11), e1201. <https://doi.org/10.1371/journal.pone.0001201>

Dien, J. (1998). Addressing misallocation of variance in principal components analysis of event-related potentials. *Brain Topography*, 11(1), 43–55. <https://doi.org/10.1023/A:1022218503558>

Dien, J., Beal, D. J., & Berg, P. (2005). Optimizing principal components analysis of event-related potentials: Matrix type, factor loading weighting, extraction, and rotations. *Clinical Neurophysiology*, 116(8), 1808–1825. <https://doi.org/10.1016/j.clinph.2004.11.025>

Dixon, A. F., Halliwell, G., East, R., Wignarajah, P., & Anderson, M. J. (2003). Masculine somatotype and hirsuteness as determinants of sexual attractiveness to women. *Archives of Sexual Behavior*, 32(1), 29–39. <https://doi.org/10.1023/A:1021889228469>

Dixon, B. J., Grimshaw, G. M., Ormsby, D. K., & Dixon, A. F. (2014). Eye-tracking women's preferences for men's somatotypes. *Evolution and Human Behavior*, 35(2), 73–79. <https://doi.org/10.1016/j.evolhumbehav.2013.10.003>

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293(5539), 2470–2473. <https://doi.org/10.1126/science.1063414>

Durkee, P. K., Goetz, A. T., & Lukaszewski, A. W. (2018). Formidability assessment mechanisms: Examining their speed and automaticity. *Evolution and Human Behavior*, 39(2), 170–178. <https://doi.org/10.1016/j.evolhumbehav.2017.12.006>

Durkee, P. K., Polo, P., Muñoz-Reyes, J. A., Rodríguez-Ruiz, C., Losada-Pérez, M., Fernández-Martínez, A. B., Turiégano, E., Buss, D. M., & Pita, M. (2019). Men's bodily attractiveness: Muscles as fitness indicators. *Evolutionary Psychology*, 17. <https://doi.org/10.1177/1474704919852918>

Fan, J., Dai, W., Liu, F., & Wu, J. (2005). Visual perception of male body attractiveness. *Proceedings of the Royal Society of London*

B: Biological Sciences, 272(1560), 219–226. <https://doi.org/10.1098/rspb.2004.2922>

Frederick, D. A., Buchanan, G. M., Sadehgari-Azar, L., Peplau, L. A., Haselton, M. G., Berezovskaya, A., & Lipinski, R. E. (2007). Desiring the muscular ideal: Men's body satisfaction in the United States, Ukraine, and Ghana. *Psychology of Men & Masculinity*, 8(2), 103–117. <https://doi.org/10.1037/1524-9220.8.2.103>

Frederick, D. A., & Haselton, M. G. (2007). Why is muscularity sexy? Tests of the fitness indicator hypothesis. *Personality and Social Psychology Bulletin*, 33(8), 1167–1183. <https://doi.org/10.1177/0146167207303022>

Freeman, J., Ziomba, C. M., Heeger, D. J., Simoncelli, E. P., & Movshon, J. A. (2013). A functional and perceptual signature of the second visual area in primates. *Nature Neuroscience*, 16(7), 974–981. <https://doi.org/10.1038/nn.3402>

Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology*, 113(5), 702–712. [https://doi.org/10.1016/S1388-2457\(02\)00030-5](https://doi.org/10.1016/S1388-2457(02)00030-5)

Garza, R., & Byrd-Craven, J. (2021). Effects of women's short-term mating orientation and self-perceived attractiveness in rating and viewing men's waist to chest ratios. *Archives of Sexual Behavior*, 50, 543–551. <https://doi.org/10.1007/s10508-020-01846-0>

Garza, R., Heredia, R. R., & Cieślicka, A. B. (2017). An eye tracking examination of men's attractiveness by conception risk women. *Evolutionary Psychology*, 15(1), 1474704917690741. <https://doi.org/10.1177/1474704917690741>

Gliga, T., & Dehaene-Lambertz, G. (2005). Structural encoding of body and face in human infants and adults. *Journal of Cognitive Neuroscience*, 17(8), 1328–1340. <https://doi.org/10.1162/0898929055002481>

Graffar, M. (1956). Une méthode de classification sociale d'échantillons de population. *Courrier*, 6(8), 455–459.

Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55(4), 468–484. [https://doi.org/10.1016/0013-4694\(83\)90135-9](https://doi.org/10.1016/0013-4694(83)90135-9)

Gray, P. B., & Frederick, D. A. (2012). Body image and body type preferences in St. Kitts, Caribbean: A cross-cultural comparison with US samples regarding attitudes towards muscularity, body fat, and breast size. *Evolutionary Psychology*, 10. <https://doi.org/10.1177/147470491201000319>

Grezes, J., Pichon, S., & De Gelder, B. (2007). Perceiving fear in dynamic body expressions. *NeuroImage*, 35(2), 959–967. <https://doi.org/10.1016/j.neuroimage.2006.11.030>

Hahn, A. C., Symons, L. A., Kredel, T., Hanson, K., Hodgson, L., Schiavone, L., & Jantzen, K. J. (2016). Early and late event-related potentials are modulated by infant and adult faces of high and low attractiveness. *Social Neuroscience*, 11(2), 207–220. <https://doi.org/10.1080/17470919.2015.1059361>

Hamm, J. P., Johnson, B. W., & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology*, 113(8), 1339–1350. [https://doi.org/10.1016/S1388-2457\(02\)00161-X](https://doi.org/10.1016/S1388-2457(02)00161-X)

Hegdé, J., & Van Essen, D. C. (2000). Selectivity for complex shapes in primate visual area V2. *Journal of Neuroscience*, 20(5), RC61. <https://doi.org/10.1523/jneurosci.20-05-j0001.2000>

Hegdé, J., & Van Essen, D. C. (2004). Temporal dynamics of shape analysis in macaque visual area V2. *Journal of Neurophysiology*, 92(5), 3030–3042. <https://doi.org/10.1152/jn.00822.2003>

Holliday, I. E., Longe, O. A., Thai, N. J., Hancock, P. J., & Tovée, M. J. (2011). BMI not WHR modulates BOLD fMRI responses in a subcortical reward network when participants judge the attractiveness of human female bodies. *PLoS ONE*, 6(11), e27255. <https://doi.org/10.1371/journal.pone.0027255>

Hönekopp, J., Rudolph, U., Beier, L., Liebert, A., & Müller, C. (2007). Physical attractiveness of face and body as indicators of physical fitness in men. *Evolution and Human Behavior*, 28(2), 106–111. <https://doi.org/10.1016/j.evolhumbehav.2006.09.001>

Horvath, T. (1981). Physical attractiveness: The influence of selected torso parameters. *Archives of Sexual Behavior*, 10(1), 21–24. <https://doi.org/10.1007/BF01542671>

Hughes, S. M., & Gallup, G. G. (2003). Sex differences in morphological predictors of sexual behavior: Shoulder to hip and waist to hip ratios. *Evolution and Human Behavior*, 24(3), 173–178. [https://doi.org/10.1016/S1090-5138\(02\)00149-6](https://doi.org/10.1016/S1090-5138(02)00149-6)

Kordsmeyer, T. L., Hunt, J., Puts, D. A., Ostner, J., & Penke, L. (2018). The relative importance of intra-and intersexual selection on human male sexually dimorphic traits. *Evolution and Human Behavior*, 39, 424–436. <https://doi.org/10.1016/j.evolhumbehav.2018.03.008>

Kret, M. E., Pichon, S., Grèzes, J., & de Gelder, B. (2011). Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI Study. *NeuroImage*, 54(2), 1755–1762. <https://doi.org/10.1016/j.neuroimage.2010.08.012>

Martín-Loches, M., Hernández-Tamames, J. A., Martín, A., & Urrutia, M. (2014). Beauty and ugliness in the bodies and faces of others: An fMRI study of person esthetic judgement. *Neuroscience*, 277, 486–497. <https://doi.org/10.1016/j.neuroscience.2014.07.040>

Massar, K., & Buunk, A. P. (2009). Rivals in the mind's eye: Jealous responses after subliminal exposure to body shapes. *Personality and Individual Differences*, 46(2), 129–134. <https://doi.org/10.1016/j.paid.2008.09.016>

Mazzotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., Woods, R., Paus, T., Simpson, G., Pike, B., & Holmes, C. (2001). A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 356, 1293–1322. <https://doi.org/10.1098/rstb.2001.0915>

Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, 15(1), 1–25. <https://doi.org/10.1002/hbm.1058>

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)

Pascual-Marqui, R. D. (1999). Review of methods for solving the EEG inverse problem. *International Journal of Bioelectromagnetism*, 1(1), 75–86.

Pascual-Marqui, R. D., Michel, C. M., & Lehmann, D. (1994). Low resolution electromagnetic tomography: A new method for localizing electrical activity in the brain. *International Journal of Psychophysiology*, 18(1), 49–65. [https://doi.org/10.1016/0167-8760\(84\)90014-X](https://doi.org/10.1016/0167-8760(84)90014-X)

Pazhoohi, F., & Liddle, J. R. (2012). Identifying feminine and masculine ranges for waist-to-hip ratio. *Journal of Social, Evolutionary, and Cultural Psychology*, 6(2), 227–232. <https://doi.org/10.1037/h0099212>

Pazhoohi, F., Hosseinichari, M., & Doyle, J. F. (2012). Iranian men's waist-to-hip ratios, shoulder-to-hip ratios, body esteem and self-efficacy. *Journal of Evolutionary Psychology*, 10(2), 61–67. <https://doi.org/10.1556/jep.10.2012.2.2>

Pazhoohi, F., Garza, R., Doyle, J. F., Macedo, A. F., & Arantes, J. (2019). Sex differences for preferences of shoulder to hip ratio in men and women: An eye tracking study. *Evolutionary Psychological Science*, 5, 405–415. <https://doi.org/10.1007/s40806-019-00198-w>

Pazhoohi, F., Arantes, J., Kingstone, A., & Pinal, D. (2020a). Becoming sexy: Contrapposto pose increases attractiveness ratings and modulates observers' brain activity. *Biological Psychology*, 151, 107842. <https://doi.org/10.1016/j.biopsycho.2020.107842>

Pazhoohi, F., Arantes, J., Kingstone, A., & Pinal, D. (2020b). Waist to hip ratio and breast size modulate the processing of female body

silhouettes: An EEG study. *Evolution and Human Behavior*, 41(2), 150–169. <https://doi.org/10.1016/j.evolhumbehav.2020.01.001>

Pazhoohi, F., Hassan, S. B., & Kingstone, A. (2023a). The interacting effects of men's height and shoulder-to-hip ratio on comfort distance: A virtual reality study. *Adaptive Human Behavior and Physiology*. <https://doi.org/10.1007/s40750-023-00216-z>

Pazhoohi, F., Garza, R., & Kingstone, A. (2023b). The interacting effects of height and shoulder-to-hip ratio on perceptions of attractiveness, masculinity, and fighting ability: Experimental design and ecological validity considerations. *Archives of Sexual Behavior*, 52(1), 301–314.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93(1), 603–608. <https://doi.org/10.1152/jn.00513.2004s>

Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8(8), 636. <https://doi.org/10.1038/nrn2195>

Platek, S. M., Krill, A. L., & Wilson, B. (2009). Implicit trustworthiness ratings of self-resembling faces activate brain centers involved in reward. *Neuropsychologia*, 47(1), 289–293. <https://doi.org/10.1016/j.neuropsychologia.2008.07.018>

Platek, S. M., & Singh, D. (2010). Optimal waist-to-hip ratios in women activate neural reward centers in men. *PLoS ONE*, 5(2), e9042. <https://doi.org/10.1371/journal.pone.0009042>

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(11), 2621–2625. <https://doi.org/10.1016/j.neuropsychologia.2007.04.005>

Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, 31(3), 157–175. <https://doi.org/10.1016/j.evolhumbehav.2010.02.005>

Puts, D. A., Welling, L. L., Burriss, R. P., & Dawood, K. (2012). Men's masculinity and attractiveness predict their female partners' reported orgasm frequency and timing. *Evolution and Human Behavior*, 33(1), 1–9. <https://doi.org/10.1016/j.evolhumbehav.2011.03.003>

Rupp, H. A., James, T. W., Ketterson, E. D., Sengelaub, D. R., Janssen, E., & Heiman, J. R. (2009). Neural activation in women in response to masculinized male faces: Mediation by hormones and psychosexual factors. *Evolution and Human Behavior*, 30(1), 1–10. <https://doi.org/10.1016/j.evolhumbehav.2008.08.006>

Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *Journal of Neuroscience*, 25(47), 11055–11059. <https://doi.org/10.1523/JNEUROSCI.2621-05.2005>

Sell, A., Cosmides, L., Tooby, J., Sznycer, D., Von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society B: Biological Sciences*, 276(1656), 575–584.

Sell, A., Hone, L. S., & Pound, N. (2012). The importance of physical strength to human males. *Human Nature*, 23, 30–44.

Sell, A., Lukazsweski, A. W., & Townsley, M. (2017). Cues of upper body strength account for most of the variance in men's bodily attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, 284(1869), 20171819. <https://doi.org/10.1098/rspb.2017.1819>

Shen, H., Chau, D. K., Su, J., Zeng, L. L., Jiang, W., He, J., Fan, J., & Hu, D. (2016). Brain responses to facial attractiveness induced by facial proportions: Evidence from an fMRI study. *Scientific Reports*, 6(1), 35905. <https://doi.org/10.1038/srep35905>

Singh, D. (1993). Adaptive significance of female physical attractiveness: role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, 65(2), 293–307. <https://doi.org/10.1037/0022-3514.65.2.293>

Squires, N. K., Squires, K. C., & Hillyard, S. A. (1975). Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*, 38(4), 387–401. [https://doi.org/10.1016/0013-4694\(75\)90263-1](https://doi.org/10.1016/0013-4694(75)90263-1)

Suzuki, K., Yamadori, A., & Fuji, T. (1997). Category-specific comprehension deficit restricted to body parts. *Neurocase*, 3(3), 193–200. <https://doi.org/10.1080/13554799708404054>

Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). fMRI analysis of body and body part representations in the extrastriate and fusiform body areas. *Journal of Neurophysiology*, 98(3), 1626–1633. <https://doi.org/10.1152/jn.00012.2007>

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(2), 871–879. <https://doi.org/10.1016/j.neuroimage.2006.03.060>

Tovée, M. J., Maisey, D. S., Vale, E. L., & Cornelissen, P. L. (1999). Characteristics of male attractiveness for women. *The Lancet*, 353(9163), 1500. [https://doi.org/10.1016/S0140-6736\(99\)00438-9](https://doi.org/10.1016/S0140-6736(99)00438-9)

Triarhou, L. C. (2007). A proposed number system for the 107 cortical areas of Economo and Koskinas, and Brodmann area correlations. *Stereotactic and Functional Neurosurgery*, 85(5), 204–215. <https://doi.org/10.1159/000103259>

Trujillo, L. T., Jankowitsch, J. M., & Langlois, J. H. (2014). Beauty is in the ease of the beholding: A neurophysiological test of the averageness theory of facial attractiveness. *Cognitive, Affective, & Behavioral Neuroscience*, 14(3), 1061–1076. <https://doi.org/10.3758/s13415-013-0230-2>

Vartanian, O., Goel, V., Lam, E., Fisher, M., & Granic, J. (2013). Middle temporal gyrus encodes individual differences in perceived facial attractiveness. *Psychology of Aesthetics, Creativity, and the Arts*, 7(1), 38. <https://doi.org/10.1037/a0031591>

Weiner, K. S., & Grill-Spector, K. (2013). Neural representations of faces and limbs neighbor in human high-level visual cortex: Evidence for a new organization principle. *Psychological Research Psychologische Forschung*, 77(1), 74–97. <https://doi.org/10.1007/s00426-011-0392-x>

Zhang, Y., Kong, F., Chen, H., Jackson, T., Han, L., Meng, J., Yang, Z., Gao, J., & Najam ul Hasan, A. (2011). Identifying cognitive preferences for attractive female faces: An event-related potential experiment using a study-test paradigm. *Journal of Neuroscience Research*, 89(11), 1887–1893. <https://doi.org/10.1002/jnr.22724>

Zhang, Z., & Deng, Z. (2012). Gender, facial attractiveness, and early and late event-related potential components. *Journal of Integrative Neuroscience*, 11(04), 477–487. <https://doi.org/10.1142/S0219635212500306>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.