Beauty in everyday motion: Electrophysiological correlates of aesthetic preference for human walking

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Beauty in everyday motion: electrophysiological correlates of aesthetic preference for human walking

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Abstract

Aesthetic preference occurs in everyday experience. Studies have suggested that aesthetic preference (such as observing other's motion) affects social interaction via enhanced neural processing. This study investigated the effect of aesthetic preference on neural activities, in response to walking motion. Twenty participants observed biological motion (BM) representing three walking types (model-posture, good-posture, and bad-posture) and their scrambled motion (SM) during the event-related potentials measurement. The N200 and N300 amplitudes, reflecting the early sensory and the later integrational processes, were analyzed. The results revealed that the N200 amplitude of BM was greater than that of SM in the good- and bad-posture conditions. The N300 amplitude was larger in BM than SM regardless of the walking type. Exploratory regression analyses indicated that the N300 for BM, but not for SM or N200, was more negatively deflected with the increase of aesthetic preference scores. Our findings suggest that aesthetic preference enhances the later integrational process of BM represented in the N300 amplitude, whereas the early perceptual process (reflected by the N200 amplitude) is potentially modulated by familiarity rather than aesthetic preference in other's motion.

Keywords

Beauty, walk, event-related potentials, point-light display, biological motion

Introduction

Aesthetic preference—beauty, fondness, and attractiveness—permeates our lives. It occurs in both everyday experiences and qualitatively different and special experiences such as art appreciation (Langlois, et al., 2000). In accordance with the evidence of aesthetic preference for artistic activities (e.g., ballet dance) (Chang, et al., 2016; Cross, Kirsch, Ticini, & Schutz-Bosbach, 2011), Johnson and Tassinary (2007) demonstrated that human beings form aesthetic preferences by observing others' daily body motions (i.e., walking). This study presented various walking animations, which differ in terms of sex, gait, and movement, and requested the participants to evaluate aesthetic preference for each walking motion. Participants' aesthetic preferences varied accordingly among the animations. These suggest that aesthetic preference of others' daily body motion has significance for social interactions. Thus, identifying the processing of aesthetic preferences for everyday experience would contribute toward understanding the underlying mechanisms of human social interaction. This study investigated how aesthetic preferences affect event-related potential in response to the observation of human walking. The high temporal resolution of the measure used can contribute toward understanding neurocognitive mechanisms (Luck, 2014) for the processing of aesthetic preferences for daily body motion.

Neuroaesthetic studies have revealed that high aesthetic preference is associated with the enhancement of both sensory and general processes. Previous studies have indicated that strong aesthetic preference induces enhanced neural activity in the sensory region corresponding to the modality of a presented stimulus (Boccia, et al., 2016; Cattaneo, 2020; Chatterjee, Thomas, Smith, & Aguirre, 2009; Di Dio, Macaluso, & Rizzolatti, 2007). For example, Chatterjee, et al. (2009) demonstrated that beautiful faces automatically generate neural activities in the brain regions specialized for visual and facial perception. On the other hand, several studies have suggested that, being independent from the sensory modality of the presented objects (Ishizu & Zeki, 2011), high aesthetic preference enhances the neural activities in brain regions—the areas partially involved in the attention, social, and emotion networks (Ishizu & Zeki, 2011; Jacobsen, Schubotz, Hofel, & Cramon, 2006; Kawabata & Zeki, 2004; Nadal, Munar, Capo, Rossello, & Cela-Conde, 2008). For example, Kawabata and Zeki (2004) demonstrated that beautiful paintings caused increased activation in the medial orbitofrontal cortex, anterior cingulate gyrus, and left parietal cortex than neutral paintings, regardless of the modalities of the painted objects. Although these studies suggest that aesthetic preference facilitates the visual sensory and the general processes, the majority of these findings were obtained by utilizing the static stimuli, rather than videos of human motion.

Previous studies focusing on dance provide clues that are more direct regarding understanding the relationship between aesthetic preference for bodily motion and the neural activities associated with visual sensory and general processing. For example, Cross, et al. (2011) reported associations between the high aesthetic preference for dance performances and the enhanced neural activities of visual areas involved in motion and form processing (V5/MT+; inferior temporal gyrus, middle temporal gyrus, and middle occipital gyrus; and inferior parietal lobule). Calvo-Merino et al. (2010) also showed that enhancement of the activities of the extrastriate body area are associated with aesthetic preference for a dance posture. On the other hand, Kirsch et al. (2015) reported that the increased activities of the posterior temporal region (i.e., superior temporal sulcus: STS)—involved in processing multisensory integration with modulation from attention, social, and emotion networks (Allison, Puce, & McCarthy, 2000)—are associated with high aesthetic preferences for a dance motion after training in dance performance. These studies revealed the enhanced activities involved in visual sensory and general processing in response to bodily motion with the high aesthetic preference. However, the majority of research thus far has only analyzed artistic body motion (i.e., dance movement). Therefore, it remains unknown as to how aesthetic preference for bodily motion in everyday experience (i.e., walking) is processed.

Biological motion (BM) stimuli—expressed in point-light displays—are appropriate for investigating the influence of aesthetic preference. BM transmits information, such as emotion (Bachmann, Munzert, & Kruger, 2018; Wenderoth, et al., 2012), gender (Johnson & Tassinary, 2005; Kozlowski & Cutting, 1977), and person identification (Cutting & Kozlowski, 2013). BM has been used to investigate the neural mechanisms involved in the perception of bodily motion. Giese and Poggio (2003) proposed a neurocognitive model of BM perception: two sensory streams and later processes involved in the integration of their sensory information. The first sensory stream is a ventral pathway that is specialized for the analysis of body forms. The second is a dorsal pathway that is specialized for the processing of optic-flow/motion information. This sensory information are integrated within the STS (Giese & Poggio, 2003). In line with Giese and Poggio (2003), functional imaging studies in humans have identified that point-light display of body motion selectively activates areas in the STS (Beauchamp, Lee, Haxby, & Martin, 2003; Bonda, Petrides, Ostry, & Evans, 1996; Grossman, et al., 2000; Howard, et al., 1996; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Other areas in the ventral pathway, namely, fusiform face areas (Beauchamp, et al., 2003; Grossman & Blake, 2002; Vaina, et al., 2001) and lingual gyrus (Cignetti, et al., 2017; Servos, 2002) are identified as being activated. Moreover, event-related potentials (ERPs) have shown that BMs elicit two ERPs (i.e., N200 and N300) corresponding to the early sensory and later integration processes. Given the high temporal resolution of ERPs, these electrophysiological measures could permit the separate investigation of the two processes and contribute toward understanding the cognitive processing of aesthetic preference.

The N200, a negative ERP component approximately 200 ms after stimulus onset at occipitotemporal (OT) areas, represents the visual sensory processes involving the perception of both form and motion (Baccus, Mozgova, & Thompson, 2009; Buzzell, Chubb, Safford, Thompson, & McDonald, 2013). These studies reported that BM for walking produced larger amplitudes of the N200 compared with the scrambled motion (SM) and static point-light image of a walking human. This suggested that the N200 is sensitive to both form and motion information (Baccus, et al., 2009; Buzzell, et al., 2013). Another ERPs study proposed that the N200 amplitude was more attenuated by the adaptation to BM and SM than the static point-light image (Hirai & Kakigi, 2008). This suggested that the N200 was sensitive to the motion of BM and SM. These findings suggest that the N200 represents the sensory process involved in the encoding of body form and motion of BM and local motion analysis. Jokisch et al. (2005) showed that the N200 is mainly located in posterior areas near the midline. We hypothesized that high aesthetic preference for a human walking is associated with the large amplitude of the N200, representing activities of the sensory process. This is based on the studies demonstrating the association of high aesthetic preference—with the enhanced neural activities in the sensory regions—including main sources of the N200 (Boccia, et al., 2016; Cattaneo, 2020; Chatterjee, et al., 2009; Di Dio, et al., 2007; Kirk, 2008; Li & Zhang, 2020; Luo, Yu, Li, & Mo, 2019; Mizokami, et al., 2014). This expectation is consistent with ERP studies showing that enhanced a negative peak around 200 ms at the occipitotemporal areas is associated with aesthetic preference for a face (Meng, Li, Peng, Li, & Shen, 2020; Y. Zhang, et al., 2020).

The N300, the negative component at approximately 300 ms in OT areas, represents the activities of the later process of BM perception. ERP studies on BM have shown that the main sources of the N300 are the STS and fusiform gyrus (Jokisch, et al., 2005). Jokisch et al. (2005) indicated that the N300 has larger amplitude for upright and inverted BM compared to SM. Moreover, Hirai and Kakigi (2008) found that the amplitude of N300 in response to BM was attenuated following an adaptation to BM but not for SM and static point-light image. These studies suggest that the process reflected in the N300 is associated with the processing of biologically relevant motion patterns based on the integration of the form and motion information in STS co-acting attention, social, and emotion networks (Giese & Poggio, 2003). We considered the association of high aesthetic preference with enhanced activities in the STS (Alluri, et al., 2013; Sachs, Ellis, Schlaug, & Loui, 2016) and previous ERP studies showing a negative deflection around 300 ms in the occipitotemporal areas to aesthetic objects (Shi, Huo, & Hou, 2021; Wiese, Altmann, & Schweinberger, 2014; Zhang & Deng, 2012). Hence, we hypothesized that high aesthetic preference is associated with the large amplitude of the N300.

This study investigated whether aesthetic preference for human walking motion is associated with the early sensory (N200) and later integrational processes (N300). The ERPs were measured in response to three types of BMs (model-posture, good-posture, and bad-posture) and their SM as a control condition. Additionally, a rating task was conducted to confirm whether BM of the model- and good-posture conditions was judged as more aesthetically preferable than the bad-posture condition. Statistical analysis was conducted to examine whether the N200 and N300 amplitudes—elicited by BM with high aesthetic preference (i.e., model and good posture)—were larger than with low aesthetic preference (i.e., bad posture). Previous studies have reported that the right hemisphere is dominant in BM perception (Bonda, et al., 1996; Grossman, et al., 2000), and another study reported that the association of the aesthetics preference for dance with activities of the posterior temporal region is only observed in the left hemisphere (Kirsch, et al., 2015). These observations suggest that the neural activity of aesthetic preference of BM is modulated by laterality (i.e., right and left occipitotemporal sites). Thus, this study included the factor of laterality in the statistical analysis. Further, exploratory regression analyses were conducted to examine whether aesthetic preference to each stimulus was associated with the amplitude of the ERPs separately in BM and SM conditions.

Materials and Methods

Participants

A total of 23 male students from Kyushu University aged between 20 and 25 years (M = 22.3, SD = 1.4) participated in this study. The data of three participants were excluded from the analysis due to the disconnection of a reference electrode or the electrodes placed on the right and left OT regions. Finally, data from the remaining 20 participants were analyzed. All participants provided written informed consent for the experimental procedure approved by the Ethical Committee of Kyushu University (Approval No. 191).

Stimuli

The stimuli were 180 point-light displays of BM (representing a human walking, 60 per walking type [model-, good-, and bad-posture]) and 180 point-light displays of SM (60 per walking type). The stimuli were produced in three steps: capturing motion data of three forms of walking, converting the data to BM, and creating SM by manipulating BM.

Capturing walking motion

Male and female walking instructors were required to wear 15 reflective markers on the top of their heads and on the joints of their limbs. The instructors were subsequently required to walk like a model on a runway, with a good posture (as seen in daily life), and in a bad-looking posture (as seen in daily life). Their walking movements were recorded by a three-dimensional motion analysis system consisting of nine infrared cameras (Raptor Hawk, Motion Analysis, USA) at 100 Hz. Eighteen motions, three motions for each condition (i.e., walking type [model, good, and bad-posture]) in each sex, were recorded.

Converting to the biological motion

Using editing software and a motion capture acquisition (Cortex, Motion Analysis, USA), the vertical, horizontal, and time axis of each motion data were modified to unify the height of walkers and their walking pace. The preprocessed data were converted to point-light displays consisting of 15 moving white dots on a black background with 800 ms duration (Figure 1). To cover different phases of the walking cycle, ten stimuli were created from each motion data by sliding the time window for 100 ms each. A total of 180 BM stimuli were used in the experiment. Supplementary File 1 shows examples of BM stimuli.

Making the scrambled motion

A total of 180 SM stimuli were created by randomizing the starting position of the dot of each BM. Consequently, the global configuration of human walking was collapsed in SM; however, the local motions (i.e., velocity and speed of the dots) in SM were the same as those in BM.

Experimental procedure

The experiment was conducted in an electromagnetic shield room. In the initial session, participants sat 60 cm away from the display monitor (E2351VR-BN, LG Electronics, Korea) with a multichannel electroencephalogram (EEG) cap (64ch Geodesic Sensor

Net, Electrical Geodesics, Inc., USA). The task in the first session was conducted according to a previous study (Jokisch, et al., 2005) (Figure 1a). A white cross was presented on the center of the monitor for 2,000 ms to alert the participants the beginning of trial. A BM or SM stimuli with 800 ms duration were subsequently displayed on the same location. The next trial was immediately initiated following completion of the previous trial. Participants were asked to answer whether they perceived a human (or not) by pressing one of the assigned buttons (num 1: person, num 3: not person). The correct rate and response times remained similar across conditions (see Supplementary File 2). The first session consisted the three blocks. The stimuli (360 stimuli) were presented once per block in a random order. The total number of trials for each participant was 1080. The participants were instructed to maintain their gaze on the center of the monitor throughout each trial. Additionally, they were required to reduce blinking and body movements, except for stimuli responses. The stimulus presentation and data acquisition were controlled using Presentation v18.1 (Neurobehavioral Systems, Inc., USA) on a Windows computer (Dell, Inc., USA; windows 10.0 64bit, Microsoft Corp., USA).

In the second session, the participants rated the stimuli displayed on the monitor by placing a mark using a mouse on the following eight visual analog scales: beautiful/not beautiful, beautiful move/not beautiful move, human/not human, beautiful human/not beautiful human, masculine/feminine, like/not like, elegant/not elegant, and attractive/unattractive (see Supplementary File 3). These scales were used to cover various expressions of aesthetic preference, based on a previous study suggesting that aesthetic preference can be judged as being largely beautiful, elegant, attractive, and likable (Marković, 2012). Considering that human beauty is different from the beauty of non-human objects especially in terms of function (Yarosh, 2019), the evaluation included both scales reflecting human beauty (a beautiful human) and beauty of non-human aspects (a beautiful motion). The scores of the analog scales were integrated using principal component analysis (PCA). Finally, the value of the principal component was used as a comprehensive score for aesthetic preference (see Supplementary File 4). The total number of presented stimuli was 36 (6 stimuli for every 6 conditions [model-BM, good-posture-BM, bad-posture-BM, model-SC, good-posture-SC, bad-posture-SC]). The duration of the stimuli was 6,000 ms, including three walking cycles. Participants could repeat a playback of each stimulus until they marked the scales with confidence. Participants observed only one among ten stimuli with different phases of an original walking cycle. The selection of the presented stimuli and the order of their presentation were randomized among participants.

EEG recordings and analysis

The EEG was recorded from 64 sites on the scalp using a multichannel EEG measurement system (Net Amps 200 64-channel EEG Amplifier and Net Station ver. 4.1.2; Electrical Geodesics Inc., USA). The EEG signals were sampled at 500 Hz with an online filter (passband: 0.01–200 Hz). Their impedances were maintained at less than 70 kΩ. A reference followed the default setting of the multichannel EEG cap (64-channel Geodesic Sensor Net, Electrical Geodesics, Inc., USA).

The EEGLAB toolbox (Brunner, Delorme, & Makeig, 2013; Delorme & Makeig, 2004) implemented on MATLAB (The MathWorks, Inc., USA) was used for the EEG preprocessing and ERP calculation. For the preprocessing, an offline band-pass filter (finite impulse response filter: 0.5–40 Hz; transition bandwidth: 1 Hz) was applied. Normalized spectrum power (frequency range: 0–200 Hz) and kurtosis for each EEG channel were calculated for automatic channel rejection. The threshold of rejection was over 5 SD for both measures using all EEG channels in each participant. The continuous EEG signals were epoched into 1,000 ms segments for each trial. Prestimulus baseline data were collected for 200 ms, and experimental data were collected for 800 ms following stimulus onset. The epochs containing abnormal activities were automatically rejected based on their spectrum power [frequency range: 0–40 Hz; threshold: −60–40 dB; kurtosis (thresholds: 5); and linear trends (a number of consecutive points for the detection of linear patterns: 750, a threshold of absolute slope: 50, a threshold of coefficient: 0.3)]. The EEG signals were then re-referenced to the common average reference. The independent components (ICs) analysis using the Infomax algorithm was performed for separating the EEG signals and artifacts. ICs representing eye artifacts, heartbeats, or muscle activities were manually rejected based on the topographical map and the frequency spectrum. The remaining components were projected back to the EEG sensor space. The number of trials without artifact contamination remained similar across conditions (M = 152.9, SD = 9.85; $F_{\text{motion type (1,19)}} = 1.53$, $F_{\text{walking type (2,38)}} = 0.34$, $F_{\text{motion type} \times \text{walking type (2,38)}} = 0.10$, $ps > 0.05$).

For the analysis of ERPs (i.e., N200 and N300), the averaged EEG signals in each left and right occipitotemporal area (left OT: E29, E30, E32, right OT: E43, E44, E47; Figure 2b) were used (Hirai, Fukushima, & Hiraki, 2003; Hirai, Senju, Fukushima, & Hiraki, 2005). We found a negative peak approximately 260 ms for N200 and approximately 350 ms for N300. These results are similar to a study conducted by Inuggi et al. (2018) on BM perception. The time windows were set to 40 (Inuggi, et al., 2018) and 100 (Masahiro Hirai & Hiraki, 2006) ms wide, including the peaks of N200 and N300, respectively (Figure 2a). The mean amplitudes of the N200 (240–280 ms) and N300 (300–400 ms) with a baseline correction (−200–0 ms) were used for the statistical analysis.

Statistical analysis

An analysis of variance (ANOVA) with motion type (BM/SM), walking type (model/good/bad-posture), and laterality (right OT/left OT) as within-participant factors with Greenhouse–Geisser correction was conducted for the ERPs (i.e., N200 and N300 amplitudes at the left and right OT). Further analysis included tests of simple effects and multiple comparisons using Shaffer's procedure.

To investigate the effects of aesthetic preference on the ERPs, exploratory regression analyses with the evaluated score of the stimuli as an independent variable were performed (see Supplementary File 4). The factor of the laterality (right OT/left OT) was not included in the regression analyses because the ANOVA did not show interaction effects between laterality and walking type. Prior to the regression analyses, PCA was applied to the scores of eight visual analog scales for dimensional compression of the scores reflecting aesthetic preference. The first principal component (PC1) was selected as the score of aesthetic preference for each stimulus. This score was used for the regression analyses. The results of the PCA are highlighted in Supplementary File 4, indicating that the PC1 can well extract variance of items associated with beauty and attractiveness. In addition, parallel analysis (Franklin, Gibson, Robertson, Pohlmann, & Fralish, 1995) confirmed that the PC1 can sufficiently explain the variance of the data.

R, R packages (Franklin, et al., 1995; Kuznetsova, Brockhoff, & Christensen, 2017; Revelle, 2021), and R function—including anovakun ver. 4.8.5 (Iseki, 2020)—were used for the statistical analysis. Significance α level was set to 0.05.

Results

The evaluated score of the stimuli

The ANOVA for the score of the PC1 revealed a significant main effect of motion type ($F_{(1,19)} = 106.1$, $p < 0.0001$, partial$\eta^2 = 0.85$). This indicates that BM were evaluated as more beautiful than SM. Additionally, there was a significant main effect of walking type ($F_{(2,38)} = 17.6$, $p < 0.0001$, partial$\eta^2 = 0.48$) and motion type × walking type interaction ($F_{(2,38)} = 15.6$, $p < 0.0001$, partial$\eta^2 = 0.45$). The follow-up analysis indicates a simple effect of walking type only for BM condition (BM: $F_{(2,38)} = 26.4$, $p < 0.0001$, partial$\eta^2 = 0.58$, SM: $F_{(2,38)} = 0.41$, $p = 0.667$, partial$\eta^2 = 0.02$). BM of the good- and model-posture conditions were evaluated as more beautiful than those of the bad-posture condition (model posture vs. bad posture: $t_{(19)} = 5.10$, $adj.p = 0.0001$; good posture vs. bad posture: $t_{(19)} = 7.29$, $adj.p < 0.0001$).

ERP results

N200

The ANOVA for N200 indicated a significant main effect of motion type ($F_{(1,19)} = 7.67$, $p = 0.012$, partial$\eta^2 = 0.29$). This was qualified by a significant motion type × walking type interaction ($F_{(2,38)} = 4.23$, $p = 0.022$, partial$\eta^2 = 0.18$). Follow-up analyses indicated significant simple main effects of motion type for good-posture ($F_{(1,19)} = 8.56$, $p = 0.0087$, partial$\eta^2 = 0.31$) and bad-posture conditions ($F_{(1,19)} = 8.51$, $p = 0.0088$, partial$\eta^2 = 0.31$), however, not for the model-posture condition ($F_{(1,19)} = 2.09$, $p = 0.164$, partial$\eta^2 = 0.10$). The N200 amplitude of BM was larger than that of SM, except for the model-posture condition (see Figure 3). The simple effect of walking type was not significant for both motion type conditions (BM: $F_{(1.5,28.2)} = 2.30$, $p = 0.130$, partial$\eta^2 = 0.11$, SM: $F_{(2,38)} = 2.86$, $p = 0.070$, partial$\eta^2 = 0.13$). In addition, there was a significant main effect of laterality ($F_{(1,19)} = 6.76$, $p = 0.018$, partial$\eta^2 = 0.26$), indicating that the N200 amplitude of the right OT was larger than that of the left OT. There were no significant interactions of laterality with motion type ($F_{(1,19)} = 0.016$, $p = 0.900$, partial$\eta^2 = 0.001$) nor walking type ($F_{(1,19)} = 0.819$, $p = 0.448$, partial$\eta^2 = 0.04$).

N300

There were significant main effects of motion type ($F_{(1,19)} = 107.5$, $p < 0.0001$, partial$\eta^2 = 0.85$) and walking type ($F_{(2,38)} = 3.69$, $p = 0.034$, partial$\eta^2 = 0.16$), which were qualified by a significant motion type × walking type interaction ($F_{(2,38)} = 4.84$, $p = 0.014$, partial$\eta^2 = 0.20$). N300 amplitude for BM was larger than that for SM among all walking types (model posture: $F_{(1,19)} = 53.13$, $p < 0.0001$, partial$\eta^2 = 0.74$, good posture: $F_{(1,19)} = 119.7$, $p < 0.0001$, partial$\eta^2 = 0.86$, bad posture: $F_{(1,19)} = 125.1$, $p < 0.0001$, partial$\eta^2 = 0.87$, see Figure 3). However, the simple effect of walking type was observed for SM (BM: $F_{(2,38)} = 1.05$, $p = 0.361$, partial$\eta^2 = 0.05$, SM: $F_{(2,38)} = 8.81$, $p = 0.0028$, partial$\eta^2 = 0.32$). The effects associated with laterality were not significant (main effect: $F_{(1,19)} = 0.16$, $p = 0.697$, partial$\eta^2 = 0.01$, motion type × laterality interaction: $F_{(1,19)} = 2.71$, $p = 0.116$, partial$\eta^2 = 0.13$, walking type × laterality interaction: $F_{(1,19)} = 0.060$, $p = 0.942$, partial$\eta^2 = 0.003$).

Exploratory regression analyses

The regression analyses, with the score of aesthetic preference as an independent variable, indicated that the N300 amplitude for BM was more negatively deflected with increasing the score ($\beta = -0.263$, $t_{(118)} = -3.80$, $p = 0.0002$; $R^2 = 0.102$, $F_{(1,118)} = 14.46$, $p = 0.0002$). There was no significant effect in SM condition (see Figure 4). For the N200 amplitude, the analyses did not reveal the significant effect of aesthetic preference for BM and SM conditions.

Discussion

This study investigated the influence of aesthetic preference for a human walking on ERPs involved in the early and later processes of BM. Participants observed BM of three types of walks (i.e., model-, good-, and bad-posture) and their SM during ERP measurement. Participants also rated aesthetic preference for each stimulus. The results of the rating task confirmed that the participants had higher aesthetic preferences for BM in the model and good postures than those in the bad posture. There are two main findings from the ERP analyses. First, the N300 amplitude of BM was larger than that of SM, and the N200 amplitude of BM was greater than that of SM only in the conditions of good and bad posture. This finding suggests that the two ERP components are associated with different psychological functions. Second, the exploratory regression analysis indicated that aesthetic preference was positively correlated with the N300 amplitude for BM, whereas the factorial analysis did not reveal the systematic relationship between aesthetic preference and electrophysiological measures. This finding suggests that aesthetic preference moderates the later process of BM.

The results indicate that the amplitude of the N300 is enhanced in response to BM, regardless of the walking types. Previous studies have reported the larger amplitude of the N300 for BM representing human walking than SM (M. Hirai, et al., 2005; Jokisch, et al., 2005; Puce & Perrett, 2003). An ERP study also revealed that the N300 showed larger amplitudes for upright and inverted BM than for SM (Jokisch, et al., 2005). This suggests that the N300 component reflects the fine visual analysis of motion patterns specific to BM. Additionally, the fMRI study showed that viewing upright and inverted BM activated the posterior STS. This is the main source of the N300 (Jokisch, et al., 2005; Krakowski, et al., 2011; Safford, Hussey, Parasuraman, & Thompson, 2010), compared to SM (E. D. Grossman & Blake, 2001). These findings suggest that the N300 represents neural activities in the STS that reflect the processing of fine global structure from motion at the later stage of BM perception. In addition, the results revealed that the N300 amplitude was sensitive to BM in all walking styles. This further supports the proposal of the previous study that the stage of processing in N300 reflects the integrative analysis of socially relevant motion patterns (Jokisch, et al., 2005).

The regression analyses highlighted the possibility of the association between the higher aesthetic preference for BM and the larger amplitude of the N300 (Figure 3). Previous ERP studies also reported the association of aesthetic preference for objects (i.e., a product (Shi, et al., 2021)and face [(Wiese, et al., 2014; Z. Zhang & Deng, 2012) with ERP components, showing a negative deflection at approximately 300 ms after stimulus presentation in the occipitotemporal areas. These findings suggest that aesthetic preference is processed in the later stage of visual perception. Furthermore, neuroaesthetic studies highlight the psychological function of this processing stage. The studies suggest that the brain regions associated with aesthetic preference overlap considerably with attention, emotion, and social networks (Cela-Conde, Agnati, Huston, Mora, & Nadal, 2011; Chatterjee, et al., 2009; Chatterjee & Vartanian, 2014). Holmes and Zanker (2012) also indicated that aesthetic preference induced visual attention toward the objects regardless of the task demands. A previous ERP study revealed that the attention to the motion in BM enhanced the N300 amplitude when compared with the participants attending to an irrelevant aspect of the objects (M. Hirai, et al., 2005). Our results indicate that aesthetic preference of BM is processed after 300–400 ms stimulus onset—at the latest. This suggests the possibility of high aesthetic preference, enhancing the extraction of socially relevant motion patterns effectively via the enhanced attention to BM.

Our results highlighted that the N200 amplitude of BM is larger than that of SM in the good- and bad-posture conditions. However, the N200 amplitude was not differentiated for BM in the model-posture condition and their SM. As some ERP studies have shown such an attenuation of the negative potential around 200 ms for attractive faces when compared with a corresponding potential for less attractive faces

(Hahn, et al., 2016; Hsiao, Tagai, Shimakura, Isobe, & Nittono, 2017), it is possible that the attenuation of the N200 to the model posture is the reflection of aesthetic processing. However, this interpretation is inconsistent with another studies demonstrating the enhancement of the negative potential around 200 ms for aesthetically preferred objects (Meng, et al., 2020; Y. Zhang, et al., 2020). The behavioral results also contradicted with the modulated pattern of the N200 amplitudes. There were no differences in the score of aesthetic preference between the model and the good-posture condition. The score of the bad-posture condition was lower than that of each of the other conditions. The regression analyses did not identify the relationship between the N200 amplitude and the score for aesthetic preference. These results suggest that the N200 was modulated by other factors rather than aesthetic preferences of BM. We speculated that differences in N200 amplitude might be affected by familiarity although there is no direct evidence supporting this interpretation in the present study. The familiarity of the walking stimuli was controlled during the experiment because participants observed each stimulus the same number of times. However, the experience of each type of walking differs before the experiment. The participants hardly, if ever, had seen a model walk the runway as a fashion model. This suggests that less familiarity of the walking stimuli under the model-posture condition attenuates the effectiveness of visual processing. Previous studies have shown that familiarity with the motion (i.e., expertise or doing experience) influences the perception of the motion. For example, ballet dancers can discriminate the exemplars of dance better than non-experts (Calvo-Merino, Ehrenberg, Leung, & Haggard, 2010). Studies using fMRI (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006) and EEG (Di Nota, Chartrand, Levkov, Montefusco-Siegmund, & DeSouza, 2017; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008) have shown that familiarity enhances brain activity involved in the perception of body motion. In addition, the ERP study reported that the repeated exposure to stimuli enhances the negative peak amplitude 230–280 ms after stimuli onset in the occipitotemporal areas (Han, et al., 2020). Similarly, another BM study suggested that the N200 amplitude was related to the ease of BM perception, demonstrating the attenuation of the N200 amplitude for inverted BM compared with upright BM (Jokisch, et al., 2005). Given these findings, we speculate that the N200 is sensitive to familiarity with human motion, and amplitude is attenuated when the stimuli represent unusual motion (i.e., model walking). This may be due to the difficulty of simulating the specific motion in the brain (Inuggi, et al., 2018). Future studies directly manipulating the familiarity and aesthetic preference of stimuli are needed to elucidate the processing reflected in the N200.

The present study provides several implications for the neurocognitive model of BM perception and for future studies. A recent review paper proposed that the ERPs associated with BM (i.e., N200 and N300) represent the cortical processing of fine configural information including action types, styles, and visual features (i.e., bodily action evaluator (Hirai & Senju, 2020)) following the detection stage in the subcortical regions (i.e., Step Detector). Our results suggest that the "bodily action evaluator" processes contain at least two functionally and temporally distinct processes. The early process was affected by the walking type, suggesting the effect of familiarity, while the later process was associated with aesthetic preference for BM. However, various neuroaesthetic studies have reported evidence contrary to our findings. The rTMS study suggested that enhancement of neural activities in the later processes caused negative sifting of aesthetic preferences (Calvo-Merino, Urgesi, et al., 2010). In addition, other rTMS studies indicated a critical role of the early processes in mediating the aesthetic evaluation of bodies (Cazzato, Mele, & Urgesi, 2014, 2016). Cattaneo (2020) suggests the possibility that the degree to which aesthetic preference relies on early or later processes depends on stimuli features, such as static vs. dynamic bodies and dance vs. ordinary dynamic postures. These rTMS studies used static images with implied motion, while the present study used BM without featural information. It is possible that the differences in stimuli features caused inconsistent results between our study and the rTMS studies. Such features of objects should be further considered for the understanding of the underlying neural mechanisms for aesthetic preference in BM perception.

There are a number of limitations that require acknowledgment. First, the present study included only male participants. This has an advantage for avoiding the contamination of hormonal effects with the menstrual cycle on judgments of the attractiveness to others (Sundstrom Poromaa & Gingnell, 2014). Previous studies have demonstrated sex difference in the efficacy of BM perception (Cela-Conde, et al., 2009). Second, the stimuli were point-light displays without the appearance of the walkers, and they looked like they were walking toward observers. It is possible that participants had difficulty rating aesthetic preference for various stimuli, and the onset of the ERP components was relatively delayed. However, the participants rated BM of the model- and good-posture conditions as more beautiful than those of the bad-posture condition. We found the positive correlation between aesthetic preference and ERP was elicited by BM. The difference of motion patterns in BM allowed the emergence of aesthetic preference and exploration of its underlying neural processes. Third, the regression analyses—with the score of aesthetic preference as an independent variable—were conducted as an exploratory analysis. The results are preliminary, and further studies are required to replicate whether an aesthetic preference enhances neural processes (especially at the later stage of BM perception).

In summary, the findings of this study suggest that aesthetic preference for others' everyday motions enhances the perceptual processes. Aesthetic preference is associated with the neural activities in the later stage of BM perception. The neural activities represent an integration of the sensory information via modulation from other neural networks including attention and social networks. Aesthetic preference may drive the neural processes involving the integration of sensory information in everyday experience.

Authors’ Contributions

SHa, YN, and YI designed and performed the experiment and analyzed data with advice from SHi. HN contributed to making stimuli and experiment design. SHa, YN, YI, SU, YE, MU, TO, and SHi contributed to the data interpretation. SHa and SU wrote the manuscript, and all authors revised it. All authors read and approved the final manuscript.

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Figure Captions

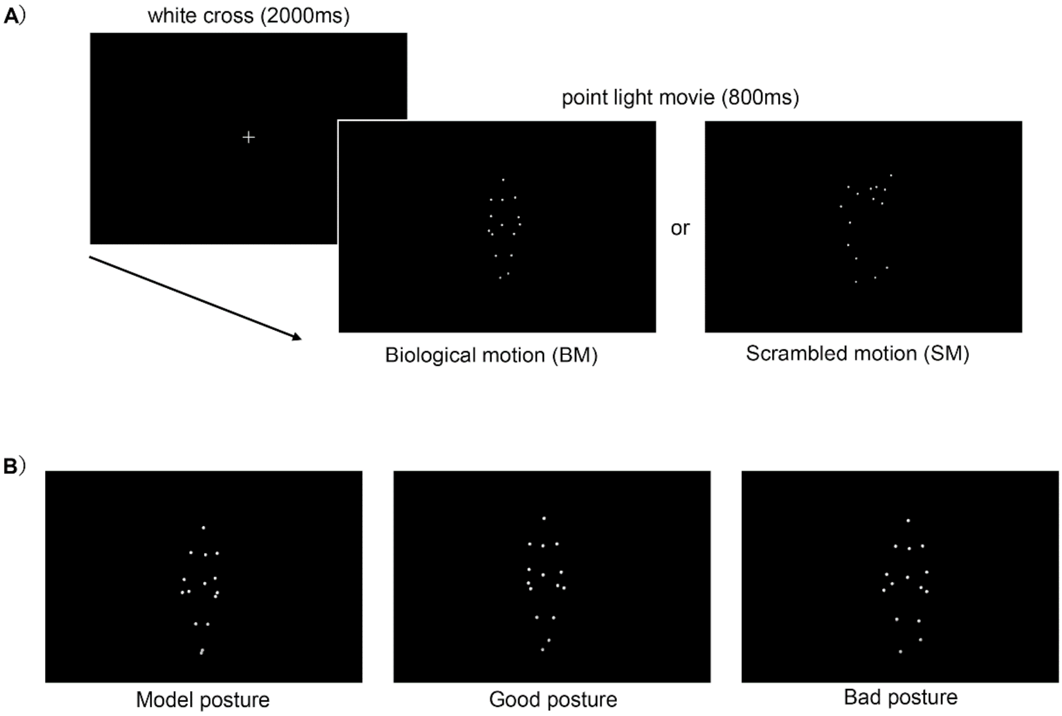

Figure 1. Illustration of the task in the first session

A: an example of a trial of the experiment task. B: examples of BM for each walk type.

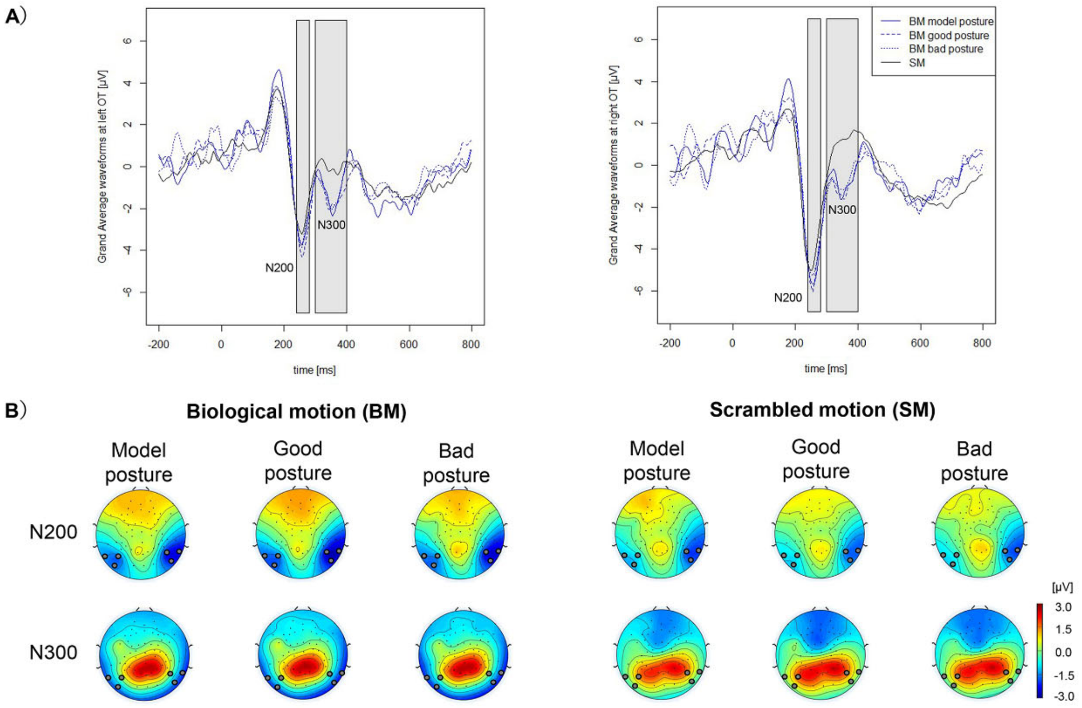

Figure 2. Grand average waveforms and scalp topography maps for each condition A: Grand average waveforms at the left and right OT. The blue and black lines indicate grand average waveforms elicited by BM and SM. The line type indicates the walking type. A solid line indicates model posture, a dashed line indicates good posture, and a dotted line indicates bad posture. The rectangles indicate time windows of N200 and N300. The left figure illustrates the waveforms at the left OT, and the right shows them at the right OT. B: Scalp topographies maps of N200 and N300 time windows. Gray circles indicate electrodes included in ERP calculations.

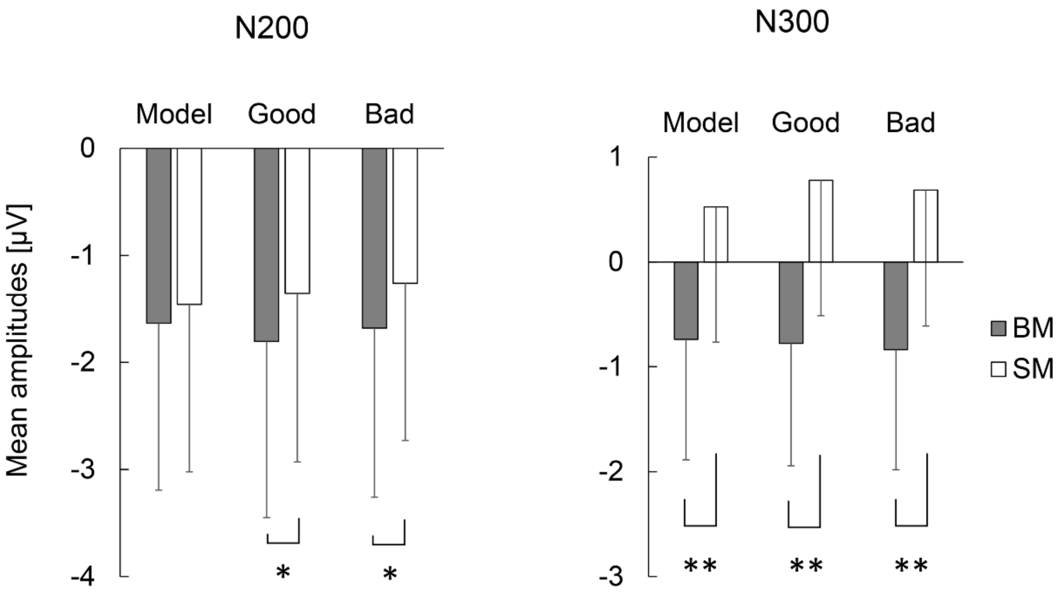

Figure 3. Mean amplitudes of N200 and N300 elicited by BM and SM in the three walking types (bad, model, and good postures). The effort bar indicates the standard deviation. *: $p < 0.01$; **$p < 0.001$

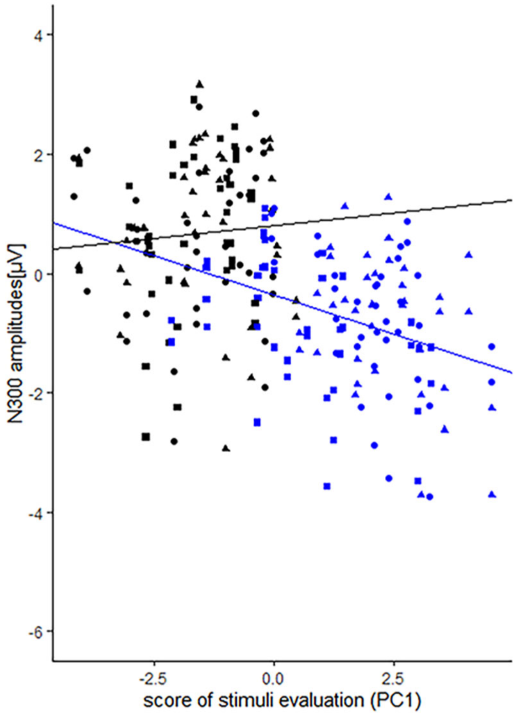

Figure 4 Scatter plots of the score of PC1 and ERPs (elicited by both BM and SM)

Scatter plots of the score of PC1 and N300 amplitudes. The color of the dots and lines indicates the motion types. The blue and black indicate BM and SM condition, respectively. The lines show regression expressions for each motion type. The sharps of the dots represent walking type; ● shows the model posture, ▲ is the good posture, and ■ is the bad posture. The amplitudes of the N300 for BM were negatively deflected with increasing participants' impression of beauty representing as the score of PC1 ($\beta = -0.263$, $t_{(118)} = -3.80$, $p = 0.0002$; $R^2 = 0.102$, $F_{(1,118)} = 14.46$, $p = 0.0002$).