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Temporal dynamics of neural activity in an integration of

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task

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ABSTRACT

While viewing works of art in galleries, we evaluate them by integrating at least two types of information: their visual properties (e.g., colors, symmetry, and proportion) and contextual information accompanying them (e.g., titles and names of artists). How rapidly the brain integrates visual and contextual information of artworks remains to be investigated. Using electroencephalography (EEG), we investigated neural activity when subjects with no professional experience in art viewed images of sculptures (masterpieces from the Classical and Renaissance periods, characterized by a canonical proportion of the golden ratio) and performed a five-scale rating of how appealing they were. At the beginning of each trial, we manipulated the expectations of the subjects for an upcoming sculpture by presenting information about its authenticity (either "genuine" or "fake"), although all images were actually taken from genuine artworks. The image of the sculpture was then presented, either in its original proportion or after being deformed by a photo-editing software. This 2×2 factorial design enabled us to identify whether each component of the EEG response was sensitive to contextual information (genuine or fake), visual information (original or deformed), or both. Results revealed that amplitudes of a positive EEG component emerging at 200-300 ms after the presentation of the artworks (mainly distributed over the parietal cortex) were significantly modulated by both visual and contextual factors, indicating a rapid integration of these two types of information in the brain.

1. Introduction

While viewing objects in daily life, our perception is usually oriented toward recognizing or identifying those objects. In contrast, viewing artworks in galleries and museums sometimes provides us with more than an opportunity to engage in object identification *per se*, evoking subjective experiences and reactions to their styles and structures. These esthetic experiences are regarded as a special psychological process, typically characterized by focused attention on objects (artworks) and suppression of everyday concerns (Cupchik, Vartanian, Crawley, & Mikulis, 2009). Other researchers defined an esthetic experience as being able to "perceive—feel—sense" an artwork (from the Greek *aisthese-aisthanomai*), implying an involvement of cognitive, emotional, and reward-related processes in the evaluation of artworks (Di Dio & Gallese, 2009; Di Dio, Macaluso, & Rizzolatti, 2007).

Increasing number of studies have recently attempted to explore the neural basis of the esthetic experience using neuroimaging techniques (Cela-Conde, Agnati, Huston, Mora, & Nadal, 2011; Chatterjee, 2011; Di Dio & Gallese, 2009; Nadal & Pearce, 2011; Zeki, 1999) such as functional magnetic resonance imaging (fMRI) (Cupchik et al., 2009; Di Dio et al., 2007; Jacobsen, Schubotz, Hofel, & Cramon, 2006; Kirk, Skov, Hulme, Christensen, & Zeki, 2009; Kornysheva, von Cramon, Jacobsen, & Schubotz, 2010), electroencephalography (EEG) (Brazdil et al., 2009; de Tommaso et al., 2008; Hofel & Jacobsen, 2007; Jacobsen & Hofel, 2003), and magnetoencephalography (MEG) (Cela-Conde et al., 2009; Munar et al., 2011). In a typical paradigm of these studies (called "neuroesthetics"), subjects were presented with various images of artworks such as paintings and sculptures, and they judged each work as beautiful or not. By comparing neural responses to stimuli judged as beautiful with those judged as not beautiful, these studies identified brain regions showing selective activity for "beautiful" artworks, such as the amygdala (Di Dio et al., 2007), superior and

inferior parietal lobules (Cela-Conde et al., 2009; Jacobsen et al., 2006), and medial frontal regions (Jacobsen et al., 2006; Kawabata & Zeki, 2004).

Although these studies identified a network of brain regions related to the perception and evaluation of art, which aspects of artworks evoke and modulate our esthetic experiences remains relatively unknown. Some studies argue that stimulus parameters in artworks (e.g., colors, symmetry, and proportions) play an important role in inducing esthetic experiences of viewers (Di Dio et al., 2007; Jacobsen & Hofel, 2002). For example, Di Dio et al. (2007) used subjects with no experience in art theory and compared their neural activity induced by two sets of images of sculptures, one composed of original sculptures with a proportion of the golden ratio and the other composed of deformed versions of those images. They found increased responses in the insula, precuneus, and prefrontal regions to the original stimuli compared with those to the deformed stimuli. These results indicated that neural responses in the brain are substantially modulated by some stimulus parameters (in this case, proportion) in artworks (visual factor).

On the other hand, other studies reported a critical role of contextual information of artworks in esthetic experiences. They indicated that titles, text, and other forms of cognitive information accompanying artworks could influence the results of esthetic evaluations performed by observers (Leder, Carbon, & Ripsas, 2006; Russell, 2003). This view was supported by an fMRI study by Kirk et al. (2009). In their study, subjects were presented with the same set of images under two different contexts: as being sourced from a prestigious gallery ("gallery" label) and as being generated through a computer program ("computer" label). They observed that neural activity in the orbitofrontal cortex, one of the regions related to the processing of artworks, was significantly elevated when the images were given the "gallery" label, demonstrating an influence of contextual factor in esthetic evaluations. A similar modulation by contextual factor was also observed in a more recent

study (Lacey et al., 2011).

These previous studies suggest that the complexity of esthetic experiences is shaped through an integration of visual and contextual information in the brain. However, neural mechanisms underlying this integration are mostly unclear, particularly in the temporal domain. Do these two types of information (visual and contextual) affect the neural processing of artworks in different time windows? If so, when (and where) does the integration of visual and contextual factors take place? To address these issues, we investigated EEG signals related to the evaluation of artworks (sculptures) by independently modulating both visual and contextual factors. As in the previous study (Kirk et al., 2009), we manipulated contextual information of artworks by presenting the information about the authenticity of sculptures (genuine or fake). Furthermore, half of the sculpture images were deformed to modulate visual factors of esthetic experiences (Di Dio et al., 2007). This 2 (genuine/fake) × 2 (original/deformed) factorial design would allow us to explore which components of EEG responses were sensitive to each factor, thereby identifying time windows in which the two types of information are separately processed and integrated in the brain.

2. Methods

2.1. Subjects

Fifteen subjects (age: 19–24 years) with no professional experience in art participated in this study. The EEG data of one subject were excluded from analyses because of excessive noise in EEG waveforms (presumably resulting from head movements). They had normal or corrected-to-normal visual acuity. Informed consent was obtained from each subject after the nature of the study was explained. An approval for the study was obtained from the Ethics Committee of Kobe University, Japan.

2.2. Stimuli and task

All visual stimuli were generated and presented through the Matlab Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The subjects' task was to provide esthetic rating for artworks (various images of sculptures representing human bodies) displayed on a cathode ray tube (CRT) monitor (resolution: 1024×768 pixels, refresh rate: 60 Hz). As shown in Figure 1A, every trial began with information about the authenticity of an upcoming image of a sculpture (either "genuine" or "fake," 1 s), although all images were actually taken from genuine artworks. The subjects were informed that the "genuine" sculptures were chosen from masterpieces in the Classical and Renaissance periods, whereas the "fake" sculptures were imitations of these masterpieces prepared by students from art colleges. After a fixation period of 0.8 s, an image of a sculpture (target stimulus) appeared on the screen for 7 s (target period). Unknown to the subjects, body proportions in half of these sculptures were deformed by a photo-editing software (deformed condition, see below for details), whereas the remaining were presented in original proportions (original condition). The experimental procedures produced four types of trials (genuine-original, genuine-deformed, fake-original, and fake-deformed) defined by a combination of contextual and visual factors. To avoid noise in EEG data caused by blinks and eye movements of the subjects, we placed a white rectangular frame around the sculpture for an initial 1 s of the target period. The subjects were instructed to not move their eyes while the frame remained on the screen, although they were allowed to move their eyes freely when the frame disappeared. After the removal of the target image, they provided esthetic rating for the sculpture using a scale from 1 (very unappealing) to 5 (very appealing) (Kirk et al., 2009). No time limit was imposed for these esthetic ratings.

Images of the sculptures for the target stimulus were chosen from 24 artworks from the

Classical and Renaissance periods (e.g., Doryphoros by Polykleitos, Fig. 1A). satisfied the criteria of the golden ratio and were characterized by a canonical foot-to-navel:navel-to-head proportion of 1:0.60–0.63 (Di Dio et al., 2007; Livio, 2002). As observed in a previous study (Di Dio et al., 2007), we applied two types of deformation to the sculpture images, one into a short-leg (long-trunk) proportion and the other into a long-leg (short-trunk) proportion. The foot-to-navel:navel-to-head proportions were 1:0.64–0.82 and 1:0.45–0.59 in the former and latter types of deformation, respectively. Although the face and forelimb areas of the sculptures were kept identical between original and deformed conditions in the previous study (Di Dio et al., 2007), the deformations in the present study included the head and forelimb areas. Before the experiment, the 24 sculptures were divided into four groups (groups A-D, six sculptures for each), with an equivalent mean luminance [A: $2.7 \pm 0.87 \text{ cd/m}^2$, B: $2.6 \pm 0.75 \text{ cd/m}^2$, C: $2.4 \pm 0.68 \text{ cd/m}^2$, D: $2.2 \pm 0.54 \text{ cd/m}^2$, mean \pm standard error (SE)]. The sculptures in these four groups were assigned to the aforementioned four experimental conditions (genuine-original, genuine-deformed, fake-original, and fake-deformed). The images from the groups (A-D) and the experimental conditions were randomly varied across subjects so that a given image of sculpture (e.g., Doryphoros) was assigned to different conditions across subjects. These procedures ensured that any differences in grand-averaged EEG responses among conditions could not be attributed to differences in the stimuli used in each condition. The images in original proportions were used for sculptures classified into the genuine-original and fake-original conditions, whereas the deformed images were used for stimuli assigned to the genuine-deformed and fake-deformed conditions. Half of the deformed stimuli had the short-leg (long-trunk) proportion, and the other half had the long-leg (short-trunk) proportion. An experimental session consisted of 24 trials in which stimuli in the four conditions were randomly intermixed (six trials for each). Each session was repeated six times in each

experiment, with the order of the 24 stimuli being randomly changed across the sessions.

2.3. EEG measurement and data analyses

Signals from 19 points (Fp1, Fp2, F3, Fz, F4, F7, F8, C3, Cz, C4, T3, T4, T5, T6, P3, Pz, P4, O1, and O2) over the scalp of the subjects were recorded (EEG1200, NihonKoden, Tokyo, Japan). These signals were sampled at 500 Hz and referenced with an average potential measured from the right and left earlobes. Neural activities in response to the target (sculpture) images were investigated by recording visual-evoked potentials (VEPs) time-locked to the onset of the images. For each of the four aforementioned conditions, EEG waveforms from 36 trials were averaged. The epoch for the averaging ranged from −100 to 800 ms relative to the onset of the target images, with signals in the prestimulus period (from −100 to 0 ms) used as a baseline. Trials with signal variations larger than 100 μV were discarded from analyses (Suzuki & Noguchi, 2013). Finally, a band-pass filter of 0.5–30 Hz was applied to these VEPs.

The presentation of visual stimuli evokes a series of EEG responses with positive and negative polarities, such as the P1 and N1 (Hillyard & Anllo-Vento, 1998). We searched for the peak amplitude of each component within a given time window and compared these peaks across the four conditions. As observed in a previous study (Keyes, Brady, Reilly, & Foxe, 2010), the time windows for searching for the peaks were 90–144 ms for the P1, 146–200 ms for the N1, and 202–286 ms for the P2 responses. Furthermore, a recent study in neuroesthetics reported an EEG component at 300–400 ms that differentiated between stimuli judged as "beautiful" and those "not beautiful" (Hofel & Jacobsen, 2007; Jacobsen & Hofel, 2003). Thus, we investigated the mean amplitude of EEG signals at that interval (300–400 ms, a delayed activity). A total of four EEG responses (P1, N1, P2, and the delayed activity)

were compared across the four conditions (genuine-original, genuine-deformed, fake-original, and fake-deformed).

2.4. Source estimations of EEG signals

Using VEPs and their differential waveforms across conditions, we estimated three-dimensional (3D) source locations for EEG signals (Fig. 4) by the multiple sparse priors (MSP) approach (Friston et al., 2008) implemented in Statistical Parametric Mapping 5 (SPM5). First, a tessellated cortical mesh was created for each subject using a template brain from the Montreal Neurological Institute (MNI). This mesh contained 7200 vertices and served as a model brain to estimate current source distributions. Positions of current dipoles were restricted to the cortical surface, and they were evenly placed at each node of the mesh. Second, this dipole mesh was spatially co-registered with a sensor space of EEG consisting of 3D locations for the 19 electrodes. We then constructed a single-shell, spherical head model for forward solutions. Finally, these forward models were inverted with the MSP approach, mapping the contribution (source strength) of each dipole on the mesh to EEG waveforms. We estimated the current source densities for each time point, condition, and subject.

For second-level (group-level) analyses across all subjects, the MSP solutions for each condition and each subject were averaged over all time points belonging to a time window of interest. In the present analyses, the time window was set at 202–286 ms after the onset of the sculpture images because the activity at that interval (the P2 component) was significantly modulated by visual and contextual factors (see below). The resultant MSP averages were then submitted to random-effect analyses of SPM (Cela-Conde et al., 2009; Henson et al., 2007). The difference between conditions (e.g., genuine vs. fake) was evaluated by voxel-wise *t*-tests implemented on SPM5. The threshold for a significant difference was set

at p < 0.0001, uncorrected for multiple comparisons. Activation clusters >10 voxels were considered as significant (Noguchi, Kaneoke, Kakigi, Tanabe, & Sadato, 2005).

2.5. A questionnaire after the EEG measurement

To confirm that subjects in the present study had no professional training or education in art, they were asked to complete a questionnaire about their experience in art after the experiment. Structures and items in this questionnaire were based on those in a previous study (Furnham & Walker, 2001). They were first asked how much art they had studied (Art The subjects chose from the following three options (scores in studied, Fig. 1C). parentheses): junior-high level (1), high-school level (2), and undergraduate level or higher (3). They then answered the second question about how much they had studied the history of art by choosing one of the three aforementioned options. The next two questions asked were how often they had visited art galleries in the previous year (Galleries past) and how often they intended to go in the next year (Galleries future). Possible responses were not at all (0), once or twice (1), once a month (2), once every two weeks (3), and once a week (4). In the fifth question, they were asked to assume that they had a free day and were presented with 10 options of leisure activities (an appraisal of artworks and nine other activities such as camping and drinking). They were asked to rank these activities in an order of preference. The score was 9 if they had ranked the appraisal of artworks at the top of a list, whereas the score was 0 if they ranked it at the bottom. We then assessed their knowledge of art using an objective test. The subjects were presented with images of nine well-known sculptures (e.g., The Thinker by Rodin and Ecstasy of Saint Teresa by Bernini) and asked to provide the names of artists, titles, and the years (centuries) in which they were made. Because each correct answer scored 1 point, the possible minimum and maximum scores of the test were 0 and 27, respectively. As a control, all the aforementioned questions were also presented to 18 students (graduates and undergraduates) who majored in the history of art at Kobe University,

Japan. Scores of these expert students are compared with those of EEG subjects

(non-experts) in Figure 1C.

In the final section of the questionnaire, the EEG subjects were asked whether they felt something odd about the stimuli presented during the experiment. This was to check the possibility that they had noticed anything odd about our experimental manipulations (the 2 × 2 factorial design of genuine/fake and original/deformed). None of the subjects raised any points related to our experimental design, which suggested that they had not been aware of the purpose or manipulations in the present experiment.

3. Results

3.1. Behavioral data

Results of the esthetic ratings during the EEG measurements are displayed in Figure 1B. Two-way analysis of variance (ANOVA) of contextual (genuine or fake) and visual (original or deformed) factors yielded a significant main effect of contextual factor [F(1,42) = 5.99, p = 0.019, effect size $\eta_p^2 = 0.125$]. This result indicated that we successfully manipulated the expectations of subjects regarding artworks by presenting them with authenticity information. We also found a marginally significant main effect of the visual factor [F(1,42) = 4.00, p = 0.052, $\eta_p^2 = 0.087$]. No interaction between the two factors was observed [F(1,42) = 0.34, p = 0.57, $\eta_p^2 = 0.008$]. As supplementary analysis, we tested the effect of the two types of deformations (short-leg or long-leg). Two-way ANOVA (genuine/fake × short-leg/long-leg) of the ratings in deformed conditions again yielded a significant main effect of contextual factor [genuine > fake, F(1,42) = 4.32, p = 0.04, $\eta_p^2 = 0.093$]; however, no main effect of deformation [F(1,42) = 0.87, p = 0.36, $\eta_p^2 = 0.020$] or interaction [F(1,42) = 0.19, p = 0.67, $\eta_p^2 = 0.005$] was observed.

Scores from the postexperimental questionnaire are shown in Figure 1C. For all items, significant differences in scores were observed between the experts and EEG subjects [t(30) > 3.7, p < 0.001 for all]. These behavioral data indicated that participants in the present EEG experiment had no professional experience in art. However, they could somehow feel a difference between the original and deformed sculptures, as suggested by the main effect of visual factor in the ratings (Fig. 1B).

3.2. EEG data

VEPs at all 19 electrodes of EEG (averaged across all subjects) are displayed in Figure 2A. In all the conditions, the presentation of the target image (sculpture) elicited the P1 (90–144 ms) and N1 (146–200 ms) components at posterior sites over the visual cortex (O1, O2, T5, T6, P3, and P4). These initial responses were followed by the P2 component that appeared at 200-300 ms after the stimulus onset. Consistent with a previous study (Freunberger, Klimesch, Doppelmayr, & Holler, 2007), distinct P2 responses were observed over the parieto-occipital cortex (O1, O2, P3, P4, and Pz). As shown in enlarged VEPs at two electrodes over the parietal region (P3 and P4, Fig. 2B), the largest P2 amplitude was observed in the genuine-original condition (red lines) in which subjects expecting genuine artworks were presented with sculptures in original proportions. In contrast, the smallest P2 amplitude was observed when subjects with low expectations viewed deformed images (fake-deformed condition, black lines). The P2 amplitudes in the other conditions (genuine-deformed and fake-original, green and blue lines, respectively) were intermediate between these two. The relationships among the four conditions remained unchanged in the delayed activity at 300-400 ms.

Using the data of peak amplitudes at the P3 (left parietal) and P4 (right parietal) electrodes, we statistically evaluated the modulation of EEG waveforms by contextual and

visual factors. Considering the possibility of a functional difference between the right and left parietal cortices in the processing of artworks (Cela-Conde et al., 2009), three-way ANOVA comprising contextual (genuine/fake), visual (original/fake), and electrode (P3/P4) factors was applied for each EEG component (Fig. 3, left). In P1 (Fig. 3A) and N1 (Fig. 3B), these ANOVAs revealed no main effect or interaction [F(1,92) < 2.74, p > 0.10, $\eta_p^2 < 0.029$ for all]. Means \pm SEs of these peak amplitudes were as follows: the P1 component, genuine–original: $3.8 \pm 0.6 \,\mu\text{V}$, genuine–deformed: $3.4 \pm 0.5 \,\mu\text{V}$, fake–original: $3.4 \pm 0.6 \,\mu\text{V}$, fake–deformed: $3.0 \pm 0.4 \,\mu\text{V}$; N1 component, genuine–original: $0.3 \pm 0.4 \,\mu\text{V}$, genuine–deformed: $-0.1 \pm 0.5 \,\mu\text{V}$, fake–original: $-0.3 \pm 0.4 \,\mu\text{V}$, fake–deformed: $-0.5 \pm 0.4 \,\mu\text{V}$. These results can be explained by the similarity of visual inputs across the four conditions. Although we created some deformations in the sculptures assigned to the genuine–deformed and fake–deformed conditions, the target stimuli in all the conditions were images of human bodies with their luminance controlled (see Methods). Therefore, resultant EEG waveforms showed similar responses, particularly in initial VEP components such as P1 and N1.

In contrast to these initial responses, amplitudes of later EEG components (P2 and delayed activity) were strongly modulated by experimental manipulations. Means \pm SEs of the peak amplitudes were as follows: the P2 component, genuine–original: $8.9 \pm 0.5 \mu V$, genuine–deformed: $8.6 \pm 0.5 \mu V$, fake–original: $8.6 \pm 0.5 \mu V$, fake–deformed: $7.6 \pm 0.5 \mu V$, delayed activity, genuine–original: $3.4 \pm 0.4 \mu V$, genuine–deformed: $2.9 \pm 0.5 \mu V$, fake–original: $2.9 \pm 0.4 \mu V$, fake–deformed: $2.3 \pm 0.4 \mu V$. In the P2 component (Fig. 3C), we found a significant main effect of contextual factor [F(1,92) = 4.82, p = 0.03, $\eta_p^2 = 0.050$] and a main effect of the visual factor [F(1,92) = 4.29, p = 0.04, $\eta_p^2 = 0.045$). A significant main effect of electrodes (P4 > P3) was also observed [F(1,92) = 7.47, p = 0.008, $\eta_p^2 = 0.075$], which may be related to the right-hemispheric dominance of the parietal cortex in an esthetic

preference task (Cela-Conde et al., 2009). Similar statistical results were obtained for the delayed activity at 300–400 ms (Fig. 3D). Three-way ANOVA indicated main effects of contextual $[F(1,92)=7.58, p=0.007, \eta_p^2=0.076]$ and visual $[F(1,92)=7.11, p=0.009, \eta_p^2=0.072]$ factors, although no main effect of electrodes was observed $[F(1,92)=0, p=0.99, \eta_p^2<0.001]$. No interaction among two or three factors was observed in either components $[F(1,92)<1.19, p>0.28, \eta_p^2<0.013$ for all]. These results indicated that EEG responses after 200 ms reflected both contextual and visual factors in an esthetic preference task, indicating a rapid integration of these two types of information in the brain.

These views were further strengthened by the results of correlation analyses between behavioral (ratings) and EEG data (Fig. 3, right). We found that the amplitudes of the P1 and N1 components were not correlated with the ratings provided during the EEG experiment (P1: r = 0.16, p = 0.25; N1: r = 0.06, p = 0.67). In contrast, a significant correlation with these ratings was observed for the P2 amplitudes (r = 0.27, p = 0.04), although the correlation became somewhat weaker for the delayed activity (r = 0.22, p = 0.10). Neural correlates for contextual modulation of the esthetic rating (Fig. 1B) could therefore be observed in the EEG responses as early as 200–300 ms after the stimulus onset.

3.3. Source estimations of the P2 component

As shown in Figure 3, the mean amplitudes of the P2 component and the delayed activity were significantly influenced by contextual and visual factors. We thus estimated the source locations of the EEG signal underlying these modulations (Fig. 4) using differential VEPs across conditions. Second-level (group-level) comparison of MSP solutions (see Methods) between "genuine" and "fake" conditions revealed significant responses in the parietal regions (Fig. 4A). A medial region in the frontal cortex was also activated, which is consistent with the findings of a previous study by Kirk et al. (2009).

In Figure 4B, the effect of visual factors (original vs. deformed proportions) is displayed. In addition to the occipital cortex (right panel), significant differences between the original and deformed conditions were observed in the parietal cortex (left panel), the same regions as those shown in Figure 4A (contextual effect). Neural responses in the parietal regions were thus modulated by both visual and contextual factors, which resembled the results of esthetic ratings (Fig. 1B). These results imply that visual information of sculpture images evoked neural responses in the parietal cortex by interacting with contextual information, suggesting an integration (or convergence) of the two types of esthetic information in the brain within an initial 200–300 ms of visual processing.

4. Discussion

In the present study, we investigated how visual and contextual factors in an appraisal of artworks modulated brain responses. Our results indicated that neural activity in the P2 time range (200–286 ms) was closely related to the processing of both contextual (genuine/fake) and visual (original/deformed) information. Source estimations of the P2 component (Fig. 4) further indicated that these modulations of neural activity mainly originated from the parietal regions, which is consistent with previous studies of neuroesthetics showing an involvement of the parietal cortex in the processing of artworks (Cela-Conde et al., 2009; Cupchik et al., 2009; Di Dio et al., 2007; Jacobsen et al., 2006).

4.1. A possibility of the P300 component in ERP waveforms

Notably, the P2 component in the present study was different from the early P300 response that reflects arousal or general attention driven by the stimuli. If ERP waveforms in the present study contained the P300 component, that component would be strongly induced in the deformed rather than original conditions because sculpture images with

unusual proportions were presented in the deformed conditions. However, no component (P1, N1, or P2) actually showed a larger amplitude to the deformed images than that to the original images, which is inconsistent with the view that the present data were affected by the P300 response. Moreover, the presentation ratio of the original and deformed images was set at 50:50 throughout the experiment. Because P300 is typically induced by an oddball stimulus with a low presentation rate (Duncan et al., 2009), it is probable that the high presentation rate (50%) of the deformed images in our experiment precluded an emergence of P300, even when subjects were surprised by viewing the deformed images.

4.2. The effect of contextual information in the P2 component

In contrast to the P1 (90–144 ms) and N1 (146–200 ms) components that showed similar responses across the four conditions (genuine–original, genuine–deformed, fake–original, and fake–deformed), we found a larger amplitude of the P2 component (202–286 ms) in the genuine condition than that in the fake condition. Moreover, these P2 responses were significantly correlated with the esthetic rating (Fig. 3C). These results are congruent with previous reports that presentations of subjectively "pleasant" stimuli such as attractive faces (Marzi & Viggiano, 2010) and beautiful pictures (de Tommaso et al., 2008) evoked stronger positive-going EEG waveforms than those of "unpleasant" stimuli.

What types of psychological processes were implicated in this enlargement of P2? One possibility could be attention to the target stimuli. In the present study, the subjects had a higher level of expectation when the sculpture was preceded by "genuine" information compared with that when it was preceded "fake" information (Fig. 1B). Therefore, one may argue that the enhanced attention caused by the "genuine" instruction induced the larger amplitude of P2 in response to the target stimuli (attentional modulation). However, this explanation seems unlikely because the attentional modulation was *not* observed in the P1 and

N1 components (Fig. 3A and B). If the increase in P2 was caused by the enhanced attention to "genuine" stimuli, the magnified EEG responses should also have been observed in other components (P1 and N1) of VEPs (Hillyard & Anllo-Vento, 1998), which was not the case.

We thus hypothesized that contextual modulation of P2 is related to a memory process in the esthetic preference task. Several studies have indicated a close relationship of P2 with the memory system (Evans & Federmeier, 2009; Freunberger et al., 2007). For example, Evans and Federmeier (2009) found a stronger P2 response to repeatedly presented words than that to novel ones, suggesting that the brain refers to memories of the past in the time range of P2 (202–286 ms). In the present case, the subjects evaluated the target stimulus (sculpture) by remembering the authenticity information at the beginning of each trial (Fig. 1B). If the information of "genuine" instruction was recollected, this would alter the target stimulus into the "pleasant" stimuli (contextual effect). These "pleasant" stimuli induced a lager amplitude of the P2 response in genuine conditions than that that in fake conditions, as attractive faces (Marzi & Viggiano, 2010) and beautiful pictures (de Tommaso et al., 2008) did in previous studies.

4.3. A neural mechanism reacting to visual properties in artworks

In addition to contextual effect described above, amplitudes of the P2 component were also significantly modulated by visual factor (proportion) of sculptures. Our data were consistent with a previous fMRI study (Di Dio et al., 2007) reporting an increased response in the insula and medial parietal (precuneus) regions to sculptures in canonical proportions compared with that to sculptures in deformed proportions. Although a direct comparison of locations of the activated regions is difficult because of limited spatial resolution in the present EEG measurements, the high temporal resolution of EEG revealed that these responses to visual factor appeared rapidly, within several hundreds of milliseconds after the

presentation of the artwork.

This rapid integration of contextual and visual factors within an initial 200–300 ms is consistent with a previous view (Di Dio & Gallese, 2009) in which esthetic experiences are defined as being able to "perceive–feel–sense" an artwork and not as a product of deep contemplation about the artwork over a long period of time. In fact, the previous fMRI study reported that the esthetic experience for canonical artworks was most evident during an observation task rather than during an explicit esthetic preference task (Di Dio et al., 2007), which highlighted the rapid and implicit aspects of esthetic evaluations. The rapid integration of contextual and visual factors observed in the present study provides further temporal evidence for these previous data.

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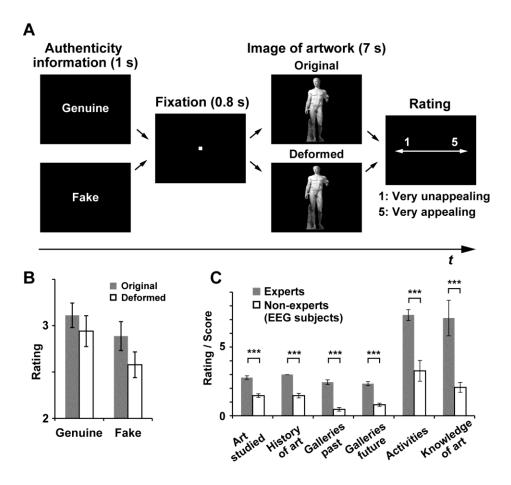


Figure 1. Stimuli, task, and behavioral results. (A) Structure of one trial. Each trial began with the authenticity information ("genuine" or "fake") about the artwork (a masterpiece sculpture representing a human body) subsequently presented. However, all images of sculptures were actually obtained from a genuine database. The sculpture then appeared on the screen, either in the same body proportion as the database (original condition) or in a modified proportion (deformed condition, unknown to subjects). In case of this panel, the lower half of the sculpture (Doryphoros by Polykleitos) was vertically extended, whereas the upper half was shortened (the long-leg and short-trunk deformation). The subjects provided an esthetic rating for the sculpture at the end of each trial using a scale from 1 (very unappealing) to 5 (very appealing). (B) Results of the rating in four conditions produced by a combination of the authenticity information ("genuine" or "fake") with proportions of sculptures (original or deformed). Two-way ANOVA indicated significant main effects of the authenticity information (contextual factor) and the proportions (visual factor), with no

significant interaction between these two factors (see Results). (C) Results of a questionnaire on experiences in art (see Methods for details about items in the questionnaire). Scores of subjects participating in the EEG measurements (non-experts) were generally lower than those of experts who underwent a formal training in art; this confirmed that the subjects in the present EEG study had no professional experience in art. In this and subsequent figures, error bars denote standard errors (SEs). ***p < 0.001.

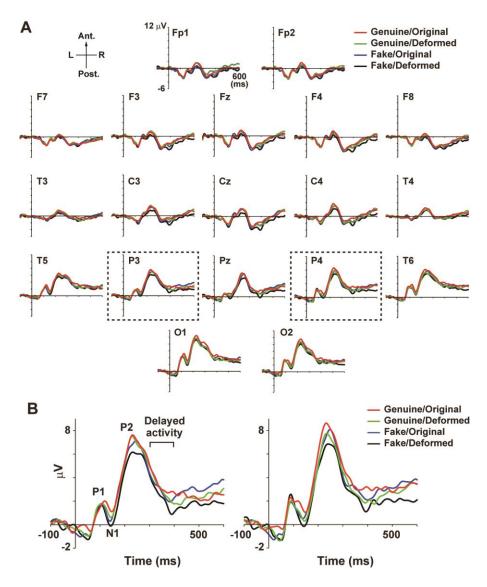


Figure 2. Visual-evoked potentials (VEPs) in response to a target image (sculpture). (**A**) VEPs at 19 electrodes over the scalp. Red: genuine-original condition, green: genuine-deformed condition, blue: fake-original condition, black: fake-deformed condition. (**B**) Enlarged displays of VEPs at P3 (left parietal) and P4 (right parietal) electrodes. Although no effect of contextual (genuine vs. fake) and visual (original vs. deformed) factors was observed in initial EEG components (P1 and N1), these factors strongly modulated amplitudes of later components, such as P2 (200–300 ms) and the delayed activity (300–400 ms).

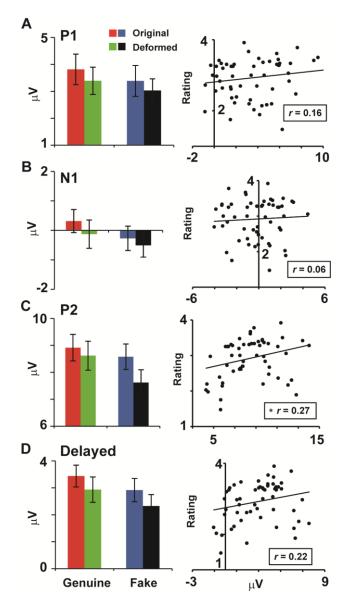


Figure 3. Amplitudes of each EEG component (left) and their correlation with the behavioral data of the esthetic rating (right). The data at P3 and P4 electrodes were pooled. In peak amplitudes of the P1 (90–144 ms, panel **A**) and N1 (146–200 ms, panel **B**) components, no effect of contextual ("genuine" vs. "fake") or visual (original vs. deformed) factors was observed. In contrast, amplitudes of the P2 (202–286 ms, panel **C**) component and the delayed activity (300–400 ms, panel **D**) showed a significant main effect of both the contextual (P2: p = 0.031, delayed activity: p = 0.007) and visual (P2: p = 0.041, delayed activity: p = 0.009) factors. The P2 component further showed a significant correlation with behavioral data (right panels), indicating a close relationship of this component with the

esthetic rating. Data of 14 subjects in the four conditions (56 points in total) were plotted in each correlation diagram. *p < 0.05.

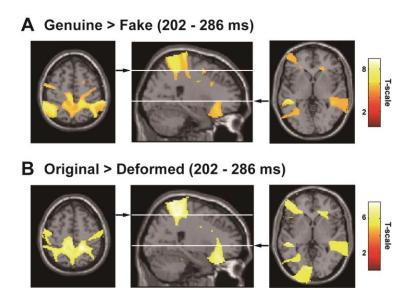


Figure 4. Results of source estimations for contextual and visual effects. (**A**) Contextual effect (genuine > fake) in the P2 time range (202–286 ms). Several regions, particularly those in the parietal cortex, showed increased activity in the genuine–original and genuine–deformed conditions compared with that in the fake–original and fake–deformed conditions. Left: axial slice at z = 54 in the template brain from the Montreal Neurological Institute. Middle: sagittal slice at z = 24. Right: axial slice at z = 0. (**B**) The effect of visual factor (genuine–original and fake–original > genuine–deformed and fake–deformed) in the P2 time range (202–286 ms). The parietal regions that showed a contextual effect (genuine > fake) in panel **A** also showed stronger responses to sculptures with original proportions than to those with deformed proportions (left), indicating that contextual and visual factors were integrated in these regions. We also found significant responses in the occipital cortex (right), which may reflect the neural processing for visual analyses of the sculpture images. Positions of axial and sagittal slices are identical to panel **A**.