Art for reward's sake: Visual art recruits the ventral striatum

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ABSTRACT

A recent study showed that people evaluate products more positively when they are physically associated with art images than similar non-art images. Neuroimaging studies of visual art have investigated artistic style and esthetic preference but not brain responses attributable specifically to the artistic status of images. Here we tested the hypothesis that the artistic status of images engages reward circuitry, using event-related functional magnetic resonance imaging (fMRI) during viewing of art and non-art images matched for content. Subjects made animacy judgments in response to each image. Relative to non-art images, art images activated, on both subject- and item-wise analyses, reward-related regions: the ventral striatum, hypothalamus and orbitofrontal cortex. Neither response times nor ratings of familiarity or esthetic preference for art images correlated significantly with activity that was selective for art images, suggesting that these variables were not responsible for the art-selective activations. Investigation of effective connectivity, using time-varying, wavelet-based, correlation-purged Granger causality analyses, further showed that the ventral striatum was driven by visual cortical regions when viewing art images but not non-art images, and was not driven by regions that correlated with esthetic preference for either art or non-art images. These findings are consistent with our hypothesis, leading us to propose that the appeal of visual art involves activation of reward circuitry based on artistic status alone and independently of its hedonic value.

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Introduction

Neuroesthetics, the study of brain responses to the perception of beauty, is a relatively new field which thus far has mainly concentrated on esthetic judgment and preference in relation to art stimuli (reviewed by Di Dio and Gallese, 2009). The experience of art in whatever form has long been characterized as pleasurable both to the senses and to the intellect (Dutton, 2009). It is therefore reasonable to expect that part of the neural response to art should reflect the rewarding aspects of this experience by activating the reward circuit. This circuit consists of the ventral striatum (VS), a region that includes the nucleus accumbens and extends into the

ventromedial putamen and caudate (Yacubian et al., 2007), along with the interconnected medial prefrontal and orbitofrontal cortex (OFC), the amygdala and dopaminergic midbrain nuclei (O'Doherty, 2004). The VS is considered a key node of the reward circuit (Yacubian et al., 2007; Heekeren et al., 2007; O'Doherty, 2004). Note that the commonly used term "reward circuit" does not necessarily imply that the associated pathways function exclusively to signal hedonic values; in fact, a key function of this circuit is reinforcement of particular behavioral outcomes under conditions of uncertainty (Schultz, 2006).

Previous neuroimaging studies of responses to visual art have reported activity in regions associated with reward processing: the medial OFC bilaterally (Kawabata and Zeki, 2004; Kirk, 2008; Kirk et al., 2009a, 2009b), the right amygdala (Di Dio et al., 2007) and the left VS (Kirk et al., 2009b). The OFC was activated by art images judged beautiful compared to those judged ugly (Kawabata and Zeki, 2004); its activation correlated with esthetic ratings (Kirk, 2008) and was modulated by context (Kirk et al., 2009b). Further, OFC activity during esthetic judgments of buildings was modulated by architectural

expertise (Kirk et al., 2009a). When images of sculptures were viewed by non-experts, images judged beautiful selectively activated the right amygdala, relative to those judged ugly (Di Dio et al., 2007). Left VS activity during viewing of buildings and faces showed a non-linear relationship, independent of architectural expertise, with maximal responses for extreme values of esthetic judgments regardless of valence (Kirk et al., 2009b). Activity in the right caudate nucleus decreased with decreasing esthetic preference for viewed art images (Vartanian and Goel, 2004); note that this activity was in the dorsal striatum, which is less consistently reported to be recruited during reward processing, though it may be involved in reward-associated learning (O'Doherty, 2004).

Esthetic preference is clearly an important aspect of the human response to visual art. Not surprisingly, then, it has been the primary focus of earlier neuroimaging studies of responses to visual art. These studies investigated the neural correlates of esthetic preference (Kawabata and Zeki, 2004; Cela-Conde et al., 2004; Vartanian and Goel, 2004; Di Dio et al., 2007), gender differences in esthetic preference (Cela-Conde et al., 2009), and contextual effects on esthetic experience (Lengger et al., 2007; Kirk, 2008; Kirk et al., 2009a). However, esthetic preference is not confined to art and can be expressed about a range of stimuli. Furthermore, it is perhaps not surprising that esthetically pleasing images activate reward circuitry. A related problem is how to define esthetic preference. Several studies use ratings of beauty as a proxy for it (Kawabata and Zeki, 2004; Cela-Conde et al., 2004, 2009), but esthetic preference is unlikely to be a unitary phenomenon and may involve sensorimotor, cognitive, and emotional elements (Di Dio and Gallese, 2009; Leder et al., 2004). Lengger et al. (2007), for example, had participants rate images for how interesting and pleasing they found them, their understanding of the images, and the images' ability to evoke emotions and associations, all of which were considered to contribute to esthetic experience. It is important to note that these elements may conflict and yet be consistent with identifying an image as art (Dutton, 2009). For instance, an atheist might appreciate the formal beauty of Dali's 'Crucifixion' but remain unmoved by its associations while a religious person might feel the reverse: both might nonetheless agree that it is a work of art. Thus, while studies of esthetic preference are clearly highly relevant to art, they may not reveal processes that are unique to art; indeed, the study implicating the left VS (Kirk et al., 2009b) did not actually use art images.

An alternative viewpoint is suggested by recent research describing the 'art infusion' effect, in which consumers evaluated products more favorably when associated with art images incorporated into packaging, advertisements, or the products themselves, than when associated with control images that depicted the same content but which were not classified as art (Hagtvedt and Patrick, 2008). Since the art and control images were matched for content, the 'art infusion' effect seems to depend on the perceived status of an image as art, rather than the content depicted. This suggests that recognition of an image as art is enough to influence behavior. The effect is posited to arise from a content-independent transfer of art-associated perceptions of luxury and intrinsic worth to the product with which the art is associated (Hagtvedt and Patrick, 2008). The neural basis for the 'art infusion' effect is unknown but a neuroeconomic perspective is helpful here: stimuli that signify wealth, such as sports and luxury cars, activate the VS (Erk et al., 2002; Schaefer and Rotte, 2007); VS activity correlates with product preference and predicts purchasing decisions (Knutson et al., 2007); and the rate of activity change over successive trials at some foci in the striatum (both dorsal and ventral) and midbrain correlates with the marginal utility (decrease in the subjective value of gains as one's assets increase) of monetary gain (Tobler et al., 2007). From the point of view of neural responses to art, we therefore hypothesized that art images would activate reward circuitry and, in particular the VS, simply by virtue of their status as art, independently of their content and particular style, which we

controlled for by comparing responses to matched art and non-art images, and by drawing art images from a number of periods and genres.

None of the prior studies reviewed above addressed neural responses that can be isolated to the perceived status of images as art. In some studies, the control stimuli were non-art images but were not matched to the art images in terms of content (Cela-Conde et al., 2004, 2009). Others employed only art images of varying genres: representational and abstract art (Vartanian and Goel, 2004; Lengger et al., 2007; Fairhall and Ishai, 2008); abstract art alone (Kirk et al., 2009a); photographs of sculptures (Di Dio et al., 2007); or portraits, landscapes, still-life and abstract art (Kawabata and Zeki, 2004). Yet another study compared esthetic judgments for buildings and faces (Kirk et al., 2009b). Two studies compared art images to modified versions of the same images: photographs of sculptures with altered proportions (Di Dio et al., 2007) and paintings in which a single element had been transposed (Vartanian and Goel, 2004). Although the control images in these last two studies were matched to the corresponding art images for content, the control images were still recognizable as art. Here, we performed an event-related functional magnetic resonance imaging (fMRI) study to test our hypothesis that viewing visual art is intrinsically rewarding. By contrasting neural responses to art images with responses to control non-art images that were matched for content, we aimed to isolate responses attributable to the status of the image as art. If visual art is intrinsically rewarding, we expected that this contrast would reveal activity in the reward centers of the brain and, in particular, the VS. This approach can be considered as orthogonal to prior approaches exploring the neural correlates of esthetic preference.

In addition to the usual analyses treating subjects as a random factor, which enable generalization of the findings to subjects not included in the study, we also conducted an analysis treating items as a random factor in order to permit generalization of the findings to items not included in the study (Bedny et al., 2007). Such item analysis is almost absent from fMRI research (Bedny et al., 2007) and this methodological step represents an advance on previous imaging studies of responses to art. In the present context, together with the matching of art images to their controls, it allowed us to test specifically whether the observed activations are attributable to the artistic status of images, regardless of their genre and content. In order to rule out alternative hypotheses for the occurrence of art-selective activations, we examined correlations between fMRI responses and a number of behavioral variables: response time, familiarity ratings and ratings of esthetic preference. Finally, we also conducted effective connectivity analyses to obtain converging evidence for the involvement of ventral striatal connectivity during viewing of art images, as opposed to non-art images. Such analyses have not previously been reported in neuroimaging studies of visual art. A preliminary report of some of the findings has been presented (Sathian et al., 2008).

Methods

Participants

Eight people (four male and four female; mean age 23 years, 1 month), naïve to the hypothesis and with no formal art education, took part. All were right-handed based on the validated subset of the Edinburgh handedness inventory (Raczkowski et al., 1974). Informed consent was obtained and all procedures were approved by the Emory University Institutional Review Board.

Stimuli

Fifty art images representing a variety of artistic styles and time periods were selected by one of the authors (HH), an art historian. Although there are numerous definitions of art (Wartenberg, 2006),

we relied on a conceptualization of art as that which viewers categorize as such (Dewey, 1989; Bourdieu and Darbel, 1997). While most of the images selected would not be familiar to a lay audience, they were all selected to be easily recognizable as works of art. The artworks chosen conformed to the guidelines that the works would be "perceived as skillful and creative expressions of human experience, in which the manner of creation is not primarily driven by any other function" (Hagtvedt and Patrick, 2008, p. 380). The final selection is listed in Appendix A. The next step was to identify non-art images that were matched for content with the art images. Through an iterative process of searching for suitable images in online photo-libraries, we identified multiple potential controls for each art image and selected the one that was the closest match to the art image in terms of content depicted and the spatial layout of the elements in the image (Fig. 1). The resulting non-art images were all photographs while all the art images were paintings or drawings. We were careful to select 'ordinary' photographs, i.e., not work by 'art' photographers and, as detailed later, we performed additional psychophysical testing to confirm that participants agreed with the experimenters' classification of these images as art or non-art. Since Cela-Conde et al. (2004) found no differences in activations for esthetic judgments between paintings and photographs (see also Zaidel, 2005), the critical difference between our art and non-art images was artistic status, rather than the medium (photographs vs. paintings/drawings).

We then carried out two pilot tests ($n = 10$), with different participants from those who took part in the main study, to verify that the images were easily classified as art or non-art and that the images were matched for content. In the first pilot test, images were centrally presented on a computer screen, in pseudorandom order so that an art image and its non-art counterpart were never presented consecutively, and participants answered the question 'Would you consider this image to be a work of art?', rating their responses on a five-point scale where 1 = 'not at all' and 5 = 'definitely'. Art images were rated significantly more highly than non-art images (art: $4.74 \pm .06$ (mean $\pm$ SEM); non-art: $1.57 \pm .08$; $t_9 = 29.9$, $p < .001$). In the second pilot test (with the same participants as the first), each art image and its non-art counterpart were presented side by side on a computer screen and participants answered the question 'How similar are these images?', again using a five-point scale where 1 = 'not at all' and 5 = 'extremely'. Participants were instructed to assess similarity in terms of *what* was depicted (i.e., content) rather than *how* it was depicted (i.e., painting, photograph, sketch, art or not art). Compared to the mid-point of the rating scale (2.5), the matched pairs were rated as highly similar ($4.39 \pm .14$) ($t_9 = 13.7$, $p < .001$). We tested against the mid-point of the scale because the mid-point represents a point at which images are not clearly similar/dissimilar, and thus serves as a suitable reference point to give meaning to the observed ratings. Thus, these pilot tests showed that the art images

were readily identified as works of art while the non-art images were classified as non-art, and that the matched art/non-art pairs were highly similar in content. In the final stimulus set for the main study, we classified 28 image pairs as depicting animate content and 22 pairs as depicting inanimate content (see below and Fig. 1).

Functional imaging and post-scan testing

Participants lay supine in the MR scanner, with foam blocks positioned around the head to minimize movement. A mirror angled over the head coil enabled participants to see the images and a centrally placed fixation cross projected on a screen placed in the rear magnet aperture. Participants were instructed to keep their eyes open, that they would see a series of images and that they were to decide whether the main content in each image was animate or inanimate; when no image was present they were instructed to fix their gaze on the cross. We chose this task as it was orthogonal to the art/non-art contrast. We specifically did not require participants to make esthetic judgments of each image (see below for rationale). A fiberoptic response box was held in the right hand; the second and third fingers were used to press buttons indicating animacy judgments. Participants wore headphones that attenuated external sounds by 20 dB to muffle scanner noise. Each participant completed 2 runs in a single scan session. Each run consisted of 50 trials of 2 s duration, with a fixed interval of 8 s between the end of one trial and the start of the next, in a 'slow' event-related design. In each trial, an image was presented for 1 s, followed by a 1 s response period; half the trials were art images and half were non-art images. The stimulus presentation time of 1 s is somewhat shorter than in other fMRI studies where presentation times have ranged from 2 s (Kawabata and Zeki, 2004) to 6 s (Vartanian and Goel, 2004). However, these earlier studies required participants to rate esthetic preference on a scale rather than the binary animate/inanimate decision required here. Since we were interested in the neural basis of the 'art infusion' effect, which is apparent with only brief or incidental exposure to art images (Hagtvedt and Patrick, 2008), our choice of stimulus parameters was intended to approximate the conditions under which the 'art infusion' effect was originally obtained. The two trial types were interleaved in a pseudorandom order within each run so that an art image and its non-art counterpart were never presented consecutively, and the order of the two runs was counterbalanced across participants. There were six 10 s baseline periods of fixation without stimulation, one at the beginning and end of each run and four at pseudorandom intervals during each run. The stimuli were presented, and responses recorded, using Presentation software (Neurobehavioral Systems Inc., Albany, CA).

Immediately after the scanning session, participants viewed the images again. As was done during pilot testing (in different subjects),
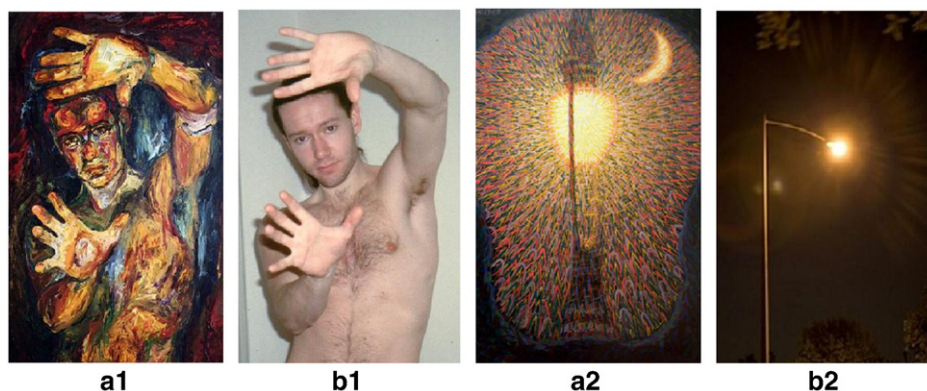

Fig. 1. Examples of animate (left pair) and inanimate (right pair) art (a1 and a2) and non-art (b1 and b2) images.

they were shown the images presented during scanning, but, instead of rating how strongly they classified each image as art, they classified each image as either art or non-art and answered the additional question 'How familiar are you with this *particular* image?' (rating responses on a five-point scale where 1 = not at all familiar and 5 = extremely familiar). They also carried out the similarity rating task for paired art and control images, just as in the pilot test. Both post-scan tests were presented in the same session, in counter-balanced order across participants. On later dates, participants completed three questionnaires that tested aspects of esthetic preference. The same images seen during scanning were presented again and participants answered one of the following questions 'How beautiful is this image?', 'How much do you like this image?' and 'How esthetically pleasing is this image?' (rating responses to each question on a five-point scale). The order in which these question-naires were completed was counterbalanced; each was completed on a different day with at least a day's separation between one questionnaire and another.

MR scanning

MR scans were performed on a 3 Tesla Siemens Trio whole body scanner (Siemens Medical Solutions, Malvern, PA), using a twelve-channel matrix head coil. T2*-weighted functional images were acquired using a single-shot gradient-recalled echoplanar imaging (EPI) sequence for blood oxygenation level-dependent (BOLD) contrast. These functional scans acquired 29 axial slices of 4 mm thickness using the following parameters: repetition time (TR) 2000 ms, echo time (TE) 30 ms, field of view (FOV) 220 mm, flip angle (FA) 90°, in-plane resolution 3.4 × 3.4 mm, and in-plane matrix 64 × 64. High-resolution 3D anatomic images were acquired using an MPRAGE sequence (TR 2300 ms, TE 3.9 ms, inversion time 1100 ms, FA 8°) comprising 176 sagittal slices of 1 mm thickness (FOV 256 mm, in-plane resolution 1 × 1 mm, and in-plane matrix 256 × 256). Once magnetic stabilization was achieved in each run, the scanner triggered the computer running the Presentation software so that the sequence of experimental trials was synchro-nized with scan acquisition.

Image processing and analysis

Image processing and analysis was performed using BrainVoyager QX v1.10.3 (Brain Innovation, Maastricht, The Netherlands). Each subject's functional runs were real-time motion-corrected utilizing Siemens 3D-PACE (prospective acquisition motion correction). Func-tional images were preprocessed utilizing sinc interpolation for slice scan time correction, trilinear-sinc interpolation for intra-session alignment of functional volumes, and high-pass temporal filtering to 3 cycles per run to remove slow drifts in the data. Anatomic 3D images were processed, co-registered with the functional data, and trans-formed into Talairach space (Talairach and Tournoux, 1988). Activa-tions were localized with respect to 3D cortical anatomy with the help of an MRI atlas (Duvernoy, 1999). For group analysis, the transformed data were spatially smoothed with an isotropic Gaussian kernel (full-width half-maximum 4 mm).

Statistical analyses of imaging data

For analysis of imaging data, runs were percent signal change normalized (i.e., the mean signal value for each voxel's time course was transformed to a value of 100, so that the individual values fluctuated around that mean as percent signal deviations.) Statistical analysis of group data used random-effects, general linear models (GLM) followed by pairwise contrasts (art > non-art).

In subject-wise analyses, "subject" was treated as a random factor, averaging responses across items of each class to arrive at a single

contrast estimate for each subject. This is now standard practice in neuroimaging, allowing generalization of the results to other individuals. However, in order to also allow generalization to items other than those used, it is necessary to conduct another analysis in which "item" is treated as a random factor (Clark, 1973). Implement-ing the technique described by Bedny et al. (2007), all stimuli (50 art images and 50 non-art images) were itemized by building a stimulation protocol in which each trial was identified as a discrete condition (art image 1, art image 2…art image 50; non-art image 1, non-art image 2…non-art image 50). Items were appropriately numbered to facilitate pairing of each art image to its non-art control image. A multi-subject random-effects general linear model (GLM) with z-transformation was employed to create "standardized" beta maps. Fifty "itemized-pair" (art > non-art) beta maps were specified, and a 1-sample t-test was performed on these "differences". This equates to performing a paired t-test on data averaged across subjects for each item. Activations were considered significant only if they were present on both the subject-wise and item-wise analyses, enabling generalization of the results beyond the specific subjects scanned and specific items used (Bedny et al., 2007).

In order to test our primary *a priori* hypothesis that viewing art images, relative to their non-art controls, activates the VS, we generated bilateral VS regions of interest (ROIs) based on the study of Yacubian et al. (2007) that examined activity during processing of reward probability and reward magnitude. We chose this study as it included 98 subjects: this was the largest number of subjects taking part in a single study of reward processing in the VS that we were able to find, and was thus likely to have yielded the most reliable localization. The ROIs were cubes of 20 mm side, centered halfway between the average coordinates of the peak voxels for reward probability and reward magnitude. The Talairach coordinates of these ROI centers were at 10, 12, −2 and −12, 9, −1. In addition to the ROIs, we also searched for activations in the whole brain. Corrections for multiple comparisons (corrected p<.05) were achieved by imposing a threshold for the volume of clusters comprising contig-uous voxels (anatomic dimensions, 1 × 1 × 1 mm) that passed a voxel-wise threshold of p<.05, using a 3D extension (implemented in BrainVoyager QX) of the 2D Monte Carlo simulation procedure described by Forman et al. (1995). The resulting cluster-size threshold was 28 voxels for the subject-wise analysis and 23 voxels for the item-wise analysis. Whole-brain corrections were performed within a functionally defined mask comprising all voxels active (p<.05, uncorrected, fixed-effects analysis) for either art or non-art images relative to baseline. For the VS, small-volume corrections were performed within the ROIs defined as above, with a cluster-size threshold of 13 voxels for both subject- and item-wise analyses.

Because differences emerged between art and non-art images for ratings of esthetic preference and familiarity, and response times on the animacy task, the ANCOVA option in BrainVoyager was used to test for voxels showing significant correlations between their activation magnitude and item familiarity/response time/esthetic preference ratings. These analyses were performed in an item-wise manner, analogous to that described for the item analysis above, separately for the sets of art and non-art images and also on the entire set of 100 images. We set a threshold r-value of .4, which is equivalent to a moderate correlation (Guilford, 1965). The resulting r-maps were corrected for multiple comparisons as above (corrected p<.05), but without application of a mask, in order to search for correlations in the whole brain. The rationale for this is that correlations could be found in regions with high enough variance between individuals that they do not show activations on the group map.

Effective connectivity

Effective connectivity was assessed using Granger causality analysis (GCA), which can be used to infer causality between two

time series by cross-prediction — if future values of time series $y(t)$ can be predicted from past values of time series $x(t)$, then $x(t)$ can be said to have a causal influence on $y(t)$ (Granger, 1969). This approach has been applied to the time series of BOLD signal intensities from selected ROIs in order to assess effective connectivity (Roebroeck et al., 2005; Stilla et al., 2007, 2008; Deshpande et al., 2008, 2010a,b; Chen et al., 2009; Marinazzo et al., in press). While GCA is often used in a bivariate manner using a given ROI as a seed to investigate its inputs and outputs (Roebroeck et al., 2005; Chen et al., 2009; Marinazzo et al., in press), our group has reported applications of a multivariate implementation of GCA to fMRI data (Stilla et al., 2007, 2008; Deshpande et al., 2008, 2010a), including task-specific analyses (Deshpande et al., 2010a). Where this multivariate approach requires a large number of candidate ROIs, e.g., when selected in a data-driven manner, the resulting connectivity network can be simplified using a recursive network reduction method that eliminates ROIs that do not contribute significantly to overall connectivity, thus aiding interpretation (Deshpande et al., 2008). Because the temporal resolution of BOLD time series data is poor, being constrained by the TR, such time-lagged analyses are susceptible to zero-lag correlations leaking into the connectivity estimates (Deshpande et al., 2010b,c). This can be resolved by modeling the zero-lag effects and excluding them from the computation of causal influences; we call this correlation-purged Granger causality (CPGC) (Deshpande et al., 2010a,c).

Our previous applications of GCA were all in block design studies (Stilla et al., 2007, 2008; Deshpande et al., 2008, 2010a). The use of an event-related design in the present study presents additional complications for GCA, owing to the limited number of time points for each event. Thus, we performed a temporally adaptive CPGC analysis for every run and every subject, using a first-order, multivariate, vector autoregressive (mVAR) model and discrete wavelet transforms (see Appendix B for details). Each run was modeled using a single-wavelet mVAR model, without any assumptions about timing or shape of responses on individual trials. It was verified that the number of functions in the wavelet expansion was large enough so that the smoothness of connectivity variation would match that of the HRF-convolved experimental paradigm, i.e., the frequency spectrum of the wavelet basis included the frequencies of interest in the evoked BOLD signal. The boxcar function corresponding to the experimental paradigm was smoothed by a standard hemodynamic response function (HRF) and entered into the design matrix. Using a fixed-effects general linear model, considering temporally-varying CPGC as the response variable and the HRF-convolved paradigm as the predictor variable, the paths which significantly ($p < .05$, Bonferroni-corrected) covaried with the experimental paradigm were determined, to yield task-specific patterns of effective connectivity (art and non-art). The advantage of this approach is that it does not suffer from the lack of sufficient time points per event that can limit application of traditional GCA to event-related paradigms. Also, this approach formulates connectivity investigation within the methodological framework used for "activity detection", which makes it easier to interpret the relationship between activity and connectivity.

Selection of ROIs

ROIs for GCA were selected in a data-driven manner to investigate interconnections between regions that were selectively active during the viewing of art images. To this end, regions significantly active on the art > non-art contrast were included. In order to rule out the hypothesis that the VS was driven by regions exhibiting correlations between their activity and ratings of esthetic preference, those regions were also included. Where there were multiple "hot spots" within an ROI, or when the same region was correlated with different ratings, the focus with the highest t-max was chosen. Because of the large number of ROIs, we analyzed the connectivity for each hemisphere separately and also ran the network reduction procedure cited above (Deshpande et al., 2008). ROIs were based on the center of

gravity of activations and restricted to be no larger than 125 mm^3 ($5 \times 5 \times 5$ mm cube). For each ROI, the time series was based on the t-weighted spatial average of activity over that ROI. The resulting data was normalized across runs and subjects before being entered into the GCA procedures.

Results

Behavior

Repeated-measures ANOVAs showed no significant differences in animacy judgments between either art ($90.0 \pm 3.5\%$ correct (mean $\pm$ SEM)) and non-art ($96.6 \pm 1.0\%$ correct) images ($F_{1,7} = 4.6$, $p = .07$), or animate ($91.3 \pm 3.2\%$ correct) and inanimate ($95.3 \pm 1.3\%$ correct) images ($F_{1,7} = 2.3$, $p = .17$). Participants were significantly slower in making animacy judgments ($t_7 = 5.9$, $p = .001$) for art images ($.97 \pm .08$ s) than non-art images ($.89 \pm .08$ s) but did not differ significantly in response times for animate and inanimate images ($t_7 = -1.7$, $p = .13$).

In immediate post-scan testing, participants showed good ($88.3 \pm 2.6\%$) agreement with the experimenters' classification of images as art or non-art, significantly higher than chance ($t_7 = 14.5$, $p < .001$). Similarity ratings for the matched art/non-art pairs were significantly higher than the mid-point of the scale (2.5) for both animate ($3.27 \pm .16$, $t_7 = 4.8$, $p = .002$) and inanimate ($3.53 \pm .24$, $t_7 = 4.4$, $p = .003$) pairs, without a significant difference between animate and inanimate pairs ($t_7 = -2.2$, $p = .06$). Compared to the mid-point of the scale (2.5), non-art images were rated as unfamiliar ($1.52 \pm .26$, $t_7 = -3.7$, $p = .007$). Art images were not rated as highly familiar, since their mean rating ($2.61 \pm .28$) was not significantly different from the mid-point of the scale ($t_7 = .4$, $p = .72$). However, art images were rated as more familiar than non-art images ($t_7 = 5.4$, $p = .001$). (As for the pilots, we tested against the mid-points of the scales, representing points at which images are not clearly familiar/unfamiliar or similar/dissimilar and thus suitable as reference points to give meaning to the observed ratings).

Participants liked art images more than non-art images (art $3.49 \pm .09$; non-art $2.91 \pm .07$; $t_7 = 4.9$, $p = .002$) and also rated them as more beautiful (art $3.51 \pm .1$; non-art $2.81 \pm .1$; $t_7 = 4.5$, $p = .003$). Ratings of esthetic pleasing were not significantly different between art and non-art (art $3.18 \pm .2$; $2.93 \pm .1$; $t_7 = .9$, $p = .4$). However, one participant's response on this last rating appeared to be an outlier; when this person's data was excluded, there was a significant effect of image type (art $3.38 \pm .1$, non-art $2.89 \pm .1$, $t_6 = 3.2$, $p = .02$). Correlations between the three rating scores for art and non-art images showed, unsurprisingly, that art images considered beautiful were also liked ($r = .8$, $p = .01$); however, there were no other significant correlations. This suggests that responses to one questionnaire did not necessarily influence responses to another and that these aspects of esthetic experience were independent for non-art images while, for art images, esthetic pleasure was independent of the other two ratings.

Activations

Our primary *a priori* hypothesis was that viewing art images, compared to non-art images, would activate the VS. Fig. 2a shows, in red and green respectively, voxels in the VS that were more strongly activated for art compared to non-art images, on the analyses treating subject and item, respectively, as random factors. Voxels identified as art-selective on both subject- and item-wise analyses are shown in tan; the VS ROIs are outlined in light blue. The subject-wise analyses survived small-volume corrections for multiple comparisons within these ROIs bilaterally; the item-wise analyses survived correction on the left but not the right.
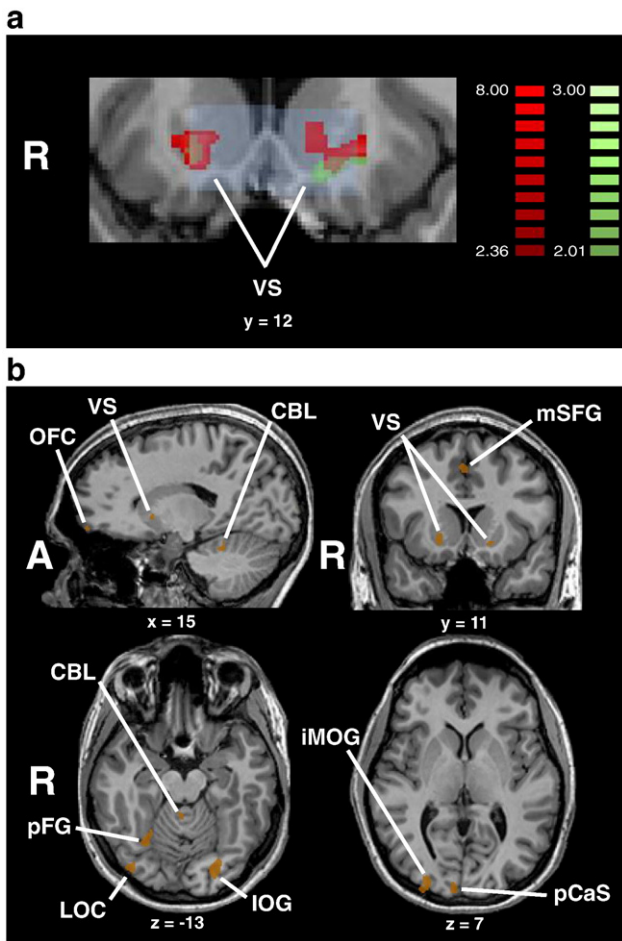
Fig. 2. (a) Art-selective activations in the ventral striatum (VS). VS regions of interest (ROIs) shown in light blue; voxels identified on subject-wise analysis shown in red (small-volume corrected for multiple comparisons within both VS ROIs); voxels identified on item-wise analysis shown in green (small-volume corrected for multiple comparisons within left VS ROI; activation in right VS ROI did not survive correction for multiple comparisons); overlap of subject- and item-wise analyses shown in tan. Color t scales on right of figure. (b) Activations common to both subject-wise and item-wise analyses of the art>non-art contrast shown in tan. Activations outside the VS are corrected for multiple comparisons. Talairach plane is given below each slice. See list for abbreviations.

Table 1

Activations common to both subject-wise and item-wise analyses on the art>non-art contrast. Activations outside the ventral striatum are corrected for multiple comparisons in both analyses; x, y, z = Talairach coordinates; t_{max} = peak t value. Cluster size = number of activated voxels in region. Verified = number of individual subjects (total = 8) in whom activation was verified (p<.05 uncorrected). See list for abbreviations.

Region	x	y	z	Subject-wise t_{max}	Item-wise t_{max}	Cluster size	Verified
R VS	17	12	1	3.8	2.6	131	7
L VS	−16	14	−2	4.2	2.6	103	8
L mSFG	0	16	44	5.1	3.0	883	7
R IFS	40	27	30	3.6	3.5	757	7
R OFC	16	56	−5	4.9	3.6	32	7
R hypoth	5	−21	−1	4.0	3.1	226	6
L hypoth	−5	−19	−1	5.2	3.4	659	7
R iMOG	27	−89	5	4.9	2.9	502	8
L IOG	−23	−78	−16	5.1	3.2	687	8
R pCaS	8	−93	7	2.8	3.2	185	8
L pCaS	−16	−87	−7	3.7	3.8	781	8
R FG	27	−59	−13	6.5	3.6	329	7
R LOC	38	−79	−12	3.7	2.5	219	6
R CBL	7	−42	−17	5.1	2.9	480	7
L CBL	−14	−49	−27	5.7	3.7	394	8

wise analyses, provides reasonable assurance that they are robust. Overall, these data support the hypothesis that art images selectively recruit VS activity.

Table 1 lists details of activations common to both the subject- and item-wise analyses. All the activations outside the VS survived correction for multiple comparisons. These additional activations selective for art images were located in right medial OFC, bilateral hypothalamus, prefrontal cortex, multiple regions of visual cortex, and bilateral cerebellum. The prefrontal activations were in the right inferior frontal sulcus (IFS) and medial superior frontal gyrus (mSFG). Fig. 2b illustrates some of the activations, while activation time-courses at selected foci, including those in the VS, are shown in Fig. 3. Because some of these cortical areas, particularly the OFC, are close to sinuses they are potentially susceptible to signal drop-out (Li et al., 1996). We therefore verified the existence of all activations in individual subjects. Table 1 shows that each of the activations, including those in the OFC, was present in 6 or more of our 8 participants.

Correlations with esthetic preference

To test the possibility that the art-selective activations arose from differential esthetic preference for art compared to non-art images, we computed r-maps reflecting the item-wise correlation of the 'esthetically pleasing', 'beauty' and 'like' ratings with voxel activation magnitudes (relative to baseline), for art and non-art conditions separately. The resulting regions, shown in Figs. 4 and 5 and listed in Table 2, were entirely independent of the art-selective regions in Table 1 with the exception of a minimal (3 voxels) overlap in the right lateral occipital complex for the correlation of 'like' ratings with activation magnitude for art images. When the r-maps were computed for these ratings across the entire set of 100 images, the correlated regions were reduced to three foci in the fusi-form gyrus that were independent of the art-selective activations (Supplementary Table 1). We also tested for correlations within the two VS ROIs with a small volume correction, i.e., at the same threshold that the main hypothesis was tested (see Activations section above). For the 'esthetically pleasing' and 'beauty' ratings, there were no correlated voxels for the art and non-art images separately, or for the complete 100 image set. For the 'like' ratings, there was a small correlated region (2 voxels) for art images in the right VS (x, y, z: 1, 21, 2; r-max = .5), overlapping with the subject-wise art-selective activation only and actually located in the inferior

Because of the small sample size, we carried out several checks to confirm that the VS activity was robust. Firstly, the primary analyses were conducted in a random-effects manner, treating subjects as a random factor for the subject-wise analyses and item as a random factor for the item-wise analyses. In addition, we verified VS activity on an individual basis and confirmed that this was present in all 8 subjects individually on the left, and in 7 of 8 on the right (Table 1). We also calculated the effect sizes and confidence intervals for the VS activations by extracting the baseline-referenced z-transformed beta weights for each VS ROI in each condition for each participant. This subject-wise analysis showed that Cohen's d was 1.18 (95% confidence interval [CI] .94–1.33) for the right VS and 1.08 (95% CI .81–1.37) for the left VS. On item-wise analysis, Cohen's d was .48 (95% CI .27–.7) for the right VS and .64 (95% CI .43–.86) for the left VS. Thus there is a large subject-wise effect and at least a medium item-wise effect in the VS, both with narrow confidence intervals that are clearly distinct from zero. A major concern with small samples is their association with wide confidence intervals that can result in spuriously large effect size estimates. Verifying that the effect sizes here were associated with relatively narrow confidence intervals that are clearly far from zero, on both subject- and item-
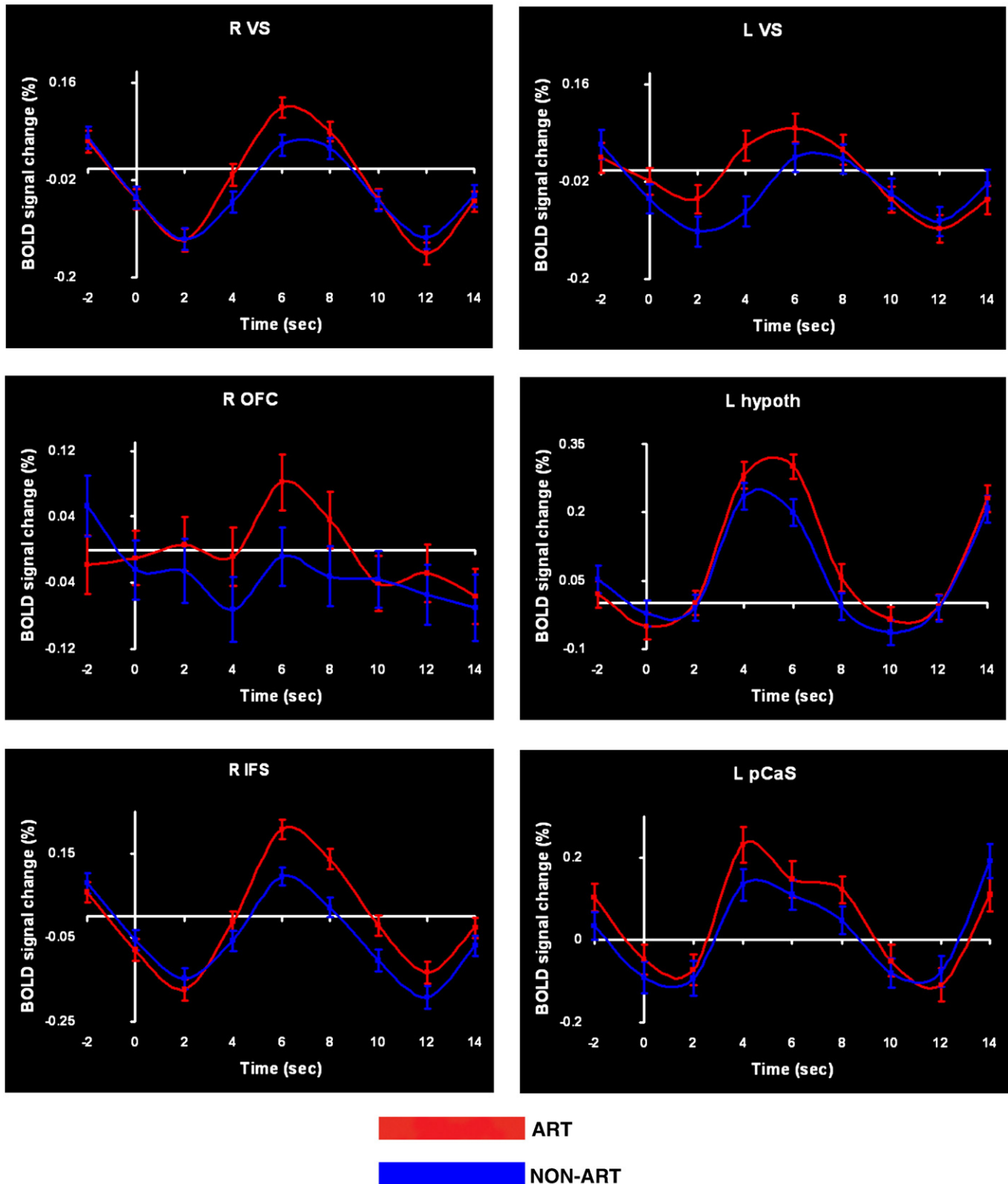
Fig. 3. Time-courses of BOLD signal change in representative regions common to the subject- and item-wise analyses for the art>non-art contrast. Error bars: SEM. See list for abbreviations.

part of the anterior cingulate gyrus rather than the VS *per se.* There were no correlated regions for non-art images or for the complete 100 image set. Thus we conclude that the art-selective activations did not reflect differences in participants' esthetic experience of the art and non-art images.

Familiarity effects

To rule out the possibility that the art-selective activations were due to the somewhat greater familiarity of art images compared to the non-art images, an r-map was computed, reflecting the item-wise
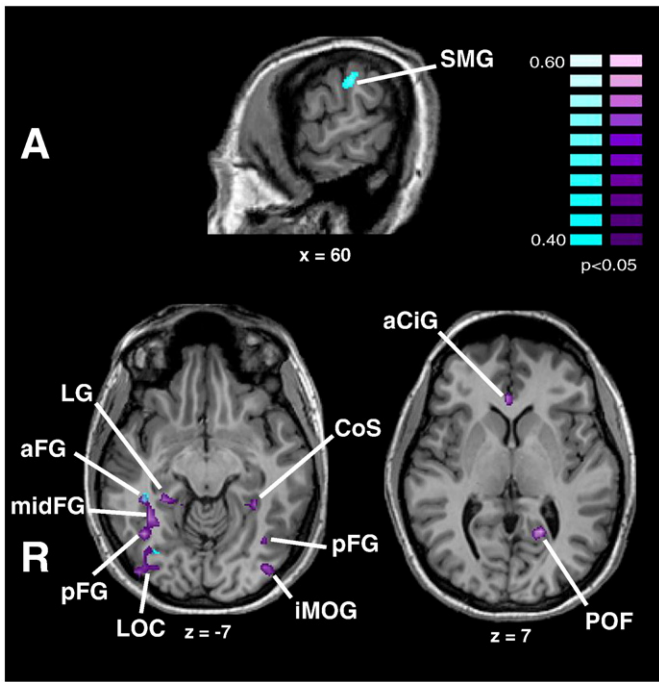
Fig. 4. r-map showing regions with item-wise correlation of activation magnitude with esthetic preference ratings (turquoise = "how beautiful is this image?", purple = "how much do you like this image?") for art images, corrected for multiple comparisons. See list for abbreviations.

correlation of voxel activation magnitudes in the art condition (relative to baseline) with familiarity ratings. These regions, all in left inferior frontal cortex, were completely independent of the activation map: there was no overlap between the activation map and
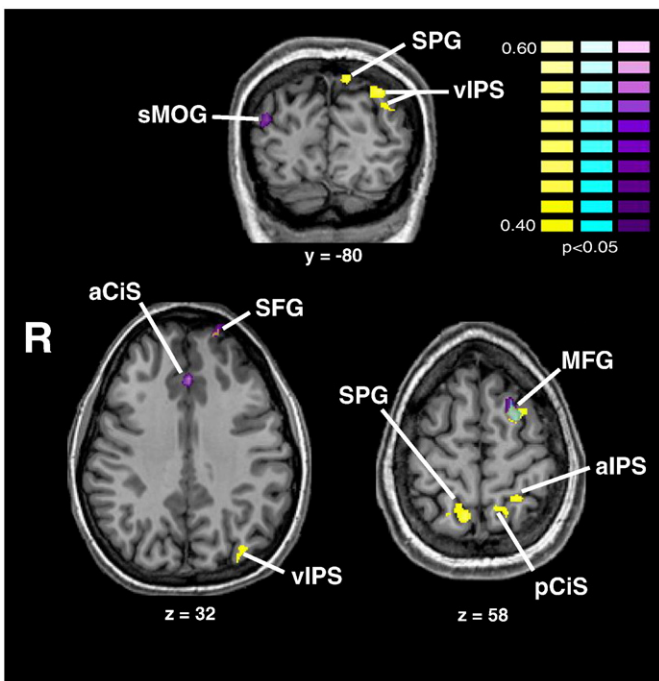

Fig. 5. r-map showing regions with item-wise correlation of activation magnitude with esthetic preference ratings (turquoise and purple as for Fig. 4, yellow = "how esthetically pleasing is this image?") for non-art images, corrected for multiple comparisons. See list for abbreviations.

the r-map (Supplementary Fig. 1 and Supplementary Table 2). This indicates that none of the art-selective activations was attributable to greater familiarity of the art images. There were no regions correlated with familiarity ratings for the non-art images, or when the r-map was computed for the entire set of 100 images. As above, we also tested for correlations in the VS ROIs with a small volume correction; there were no significant correlations for art, non-art, or the complete 100 image set. Therefore, we concluded that the art-selective activations did not reflect differential familiarity with the images.

Response time effects

To rule out the possibility that the art-selective activations were due to longer response times for art images, we computed r-maps reflecting the item-wise correlation of voxel activation magnitudes in the art condition (relative to baseline) with response times for art images. These regions were primarily in prefrontal and visual cortex and, again, constituted a network largely independent of the regions showing selectivity for art images (Supplementary Fig. 2 and Supplementary Table 3). The only exception was in the mSFG, where voxels showing significant correlations between activation magnitudes and response times to art images overlapped with art-selective activations. A similar correlational analysis for response times to non-art images revealed a substantially different network in parts of frontal, parietal and inferotemporal visual cortex, again without overlap with the art-selective activations (Supplementary Fig. 2 and Supplementary Table 4). Computing the r-map for all 100 images resulted in a smaller set of regions, also independent of the art-selective activations (Supplementary Table 1). As above, we also tested for correlations in the VS ROIs with a small volume correction. In the left VS, there were correlations for both art (Talairach coordinates: −12, 4, 7) and non-art (Talairach coordinates: −13, 11, −5) images; the former comprising 2 voxels that overlapped with the subject-wise activation (but not the item-wise activation or the common region listed in Table 1) while the latter overlapped with the common region in Table 1. In the right VS, there was a correlation for art images (Talairach coordinates: 13, 6, 6), part of which overlapped with the common region in Table 1 and part with the subject-wise activation only, but no correlation for non-art images. When considering the complete 100 image set, there were no correlations in either the right or left VS. Thus, any correlations with response times in the left VS were not specific to the art images; although those in the right VS were, the absence of correlations in the entire image set on either side in the VS suggests that response time effects did not explain art-selective activations in the VS. This is consistent with the fact that the response times were to the animacy task which is orthogonal to any art- or reward-related processing. Thus, even if response time correlations and art-selective activations in the VS are considered co-extensive, any potential response time confound is not necessarily attributable to processing of art or reward *per se*. We therefore conclude that the art-selective activations could not be explained by the longer response times to the art images.

Effective connectivity

Temporally adaptive CPGC analysis of effective connectivity showed that, when viewing art images, the VS was driven by art-selective visual cortex, particularly in the right hemisphere, but not by regions that were correlated with esthetic preference — these correlated regions did not show connectivity with the VS for either kind of image (Figs. 6 and 7: for the path weights see Supplementary Tables 5–8). When viewing non-art images, the VS was completely disengaged, with neither inputs nor outputs to any other region. Regions showing correlations between activation magnitude and esthetic preference ratings tended to drive visual cortical regions for

Table 2
Regions where activation magnitudes showed correlations with three esthetic preference ratings for art and non-art images; x, y, z = Talairach coordinates; r_{max} = peak r value. See list for abbreviations.

Questionnaire:	How esthetically pleasing is this image?					How beautiful is this image?					How much do you like this image?				
Image type	Region	x	y	z	r_{max}	Region	x	y	z	r_{max}	Region	x	y	z	r_{max}
Art	No correlated regions					R SMG	60	−33	34	.5	R aCiS	3	25	5	.51
						R LOC	34	−73	−4	.46	R LOC[a,b]	37	−76	−5	.51
						R CoS	32	−50	−11	.54	R aFG	38	−38	−9	.58
						R FG[b]	34	−41	−15	.56	R mid FG	34	−48	−8	.58
											R pFG	39	−57	−6	.53
											R LG	24	−36	−6	.5
											L POF	−16	−55	9	.56
											L CoS	−27	−42	−5	.53
											L aFG	−37	−43	−17	.51
											L pFG	−36	−61	−9	.48
											L iMOG	−38	−80	−10	.57
											L amyg	−23	2	−16	.52
Non-art	R SPG	12	−54	59	.51	L MFG	−20	7	56	.51	L aCiS	0	29	34	.53
	L MFG[b]	−21	7	55	.54						R sMOG	41	−78	22	.48
	L aIPS	−18	−50	62	.48						L MFG[b]	−19	8	56	.55
	L pCiS	−9	−50	55	.47						L SFG	−16	59	35	.57
	L SPG	−8	−73	48	.55										
	L vIPS	−29	−80	37	.54										
	L SFG[b]	−16	58	37	.56										

[a] 3 voxels in this region overlapped with the region common to subject- and item-wise analyses (Table 1).
[b] These regions were excluded from the effective connectivity analysis as they were duplicated in other ROI sets.

both art and non-art images. These results further reinforce our conclusion that individual differences in esthetic preference do not account for the art-selective activations.

Discussion

The present study is the first to report activity in reward-related regions of the brain, attributable to the artistic status of viewed images independently of the depicted content and of the particular genre or style. In accordance with our *a priori* hypothesis, viewing art images activated the VS. This was true in both subject and item analyses, indicating that this finding generalizes to other individuals and art images (Bedny et al., 2007). The VS activation was verified in all participants on the left and in all but one on the right. Effect sizes in bilateral VS were large with relatively narrow 95% confidence intervals that were distinctly separate from zero. Taken together, these results suggest that, despite the small sample size, the VS activity was robust. Since the content and other properties of the paired art and non-art images were chosen to be, and were also rated as, highly similar, the greater activations for art images can be attributed to their status as art. The VS is involved in coding both reward probability and magnitude (Heekeren et al., 2007; O'Doherty, 2004; Yacubian et al., 2007). Our VS ROIs were chosen without bias towards reward probability or magnitude, since they were centered on the mid-point between the probability and magnitude peaks identified by Yacubian et al. (2007). The VS foci that were preferentially active during viewing art images were located anteriorly, close to foci shown to encode reward probability, whereas more posterior foci encode reward magnitude (Yacubian et al., 2007). The VS is also involved in computing reward prediction errors (the difference between expected and actual outcomes) in tasks involving decision-making (Hare et al., 2008) or classical conditioning (O'Doherty et al., 2003). Our study involved no explicit gain/loss consequences to viewing art or non-art images, and the animacy task on which participants actually made decisions was orthogonal to the artistic status of the stimuli. These considerations tend to argue against the idea that VS activity in the present study reflected prediction error signals; however, we cannot rule out the possibility

that unpredictability of the timing of art/non-art images may have led to VS activation.

Art as a rewarding experience

Experiencing art, whether visual or otherwise, is a pleasurable, rewarding experience (Dutton, 2009). The finding that artistic status alone activates reward centers is interesting in the light of recent suggestions (e.g., Zaidel, 2005; Dutton, 2009) that production and appreciation of art may be related to the evolution in humans of mechanisms that were important for survival of the individual and species. It has been suggested that visual artists, consciously or otherwise, have learned to exploit the evolved characteristics of human visual perception (Ramachandran, 2004; Zaidel, 2005). On this account, visual art exploits perceptual processes such as grouping, attention, etc. in order to produce a visually appealing image. While visual appeal might thus be part of the basis for artistic status, it no doubt also contributes to esthetic preference. In this respect, it is interesting to note that the left VS focus observed here was previously reported to be active during esthetic judgments of both buildings and faces, regardless of the architectural expertise of the subjects (Kirk et al., 2009b). By contrast, the right OFC focus in the present study was somewhat lateral to the near-midline activity reported during judgments of beauty (Kawabata and Zeki, 2004) and foci found to be modulated by esthetic preference (Kirk, 2008; Kirk et al., 2009a). However, it still lies within the medial sector of the OFC and within the region associated with encoding predicted reward values (Hare et al., 2008).

Perhaps surprisingly, we did not find activity selective for viewing art images in the amygdala, which is also implicated in reward processing (O'Doherty, 2004). However, abstract reward-associated activity is reported less consistently in the amygdala than at other sites such as the VS and OFC (Elliott et al., 2003) and, as pointed out by Nadal et al. (2008), a number of other studies utilizing art images also failed to find amygdala activation (e.g., Kawabata and Zeki, 2004; Vartanian and Goel, 2004; Kirk, 2008; Kirk et al., 2009a). However, a study involving images of sculptures found selective activity in the right amygdala for images judged to be beautiful, compared to those judged to be ugly (Di Dio et al., 2007). By contrast, we did find art-
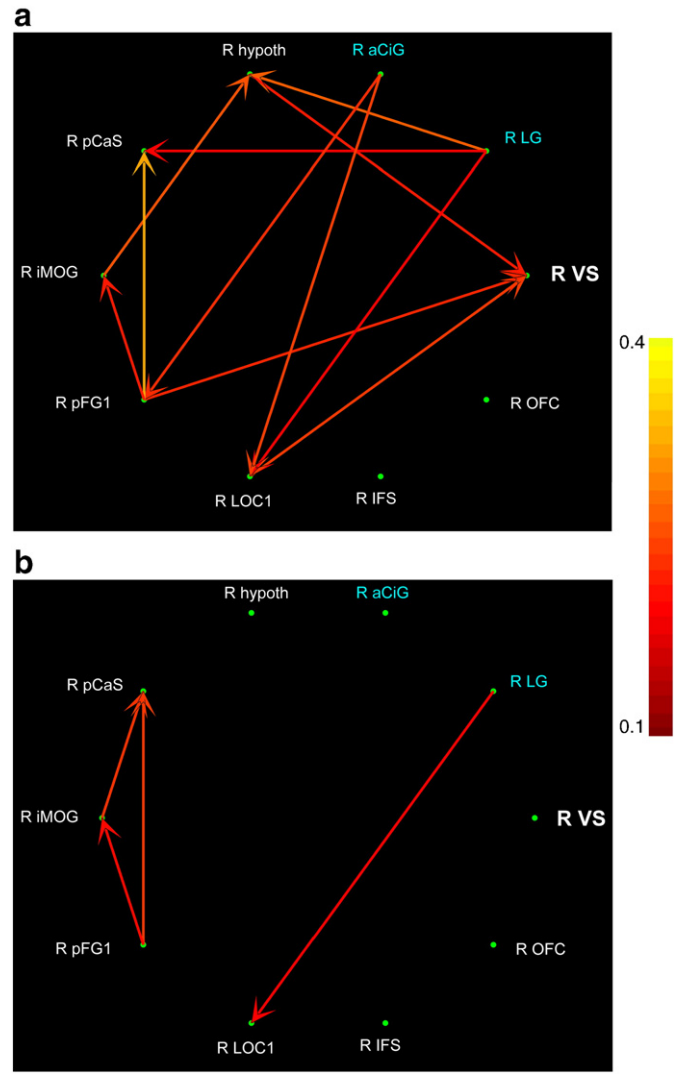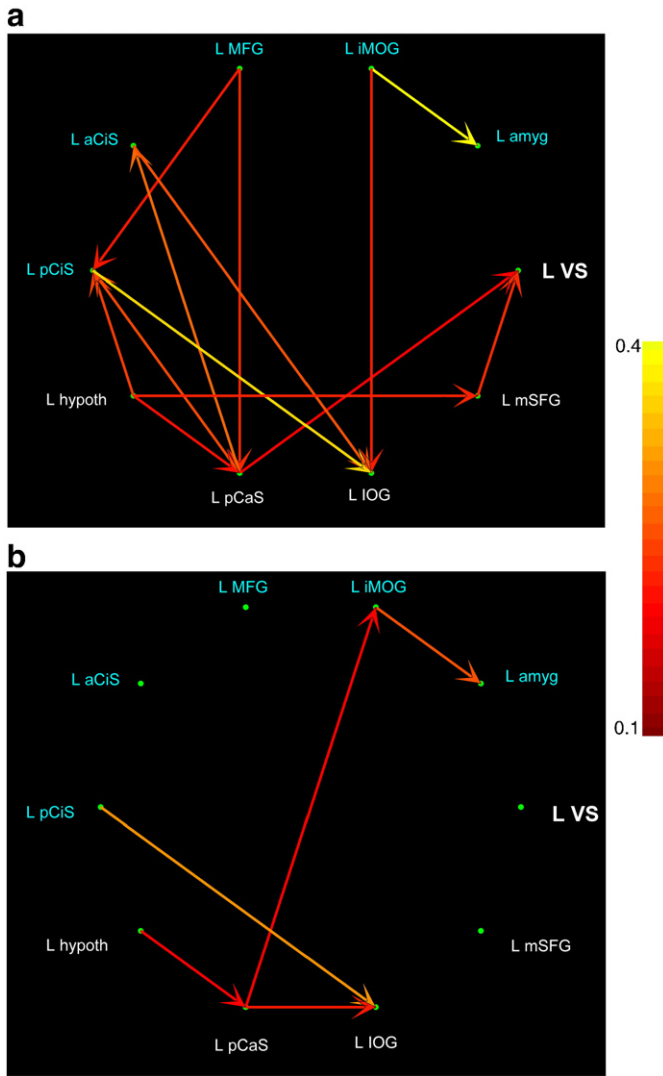
Fig. 6. Left hemisphere effective connectivity between ventral striatum, art-selective regions (white font) and regions correlated with esthetic preference ratings (blue font) for art (a) and non-art (b) images after network reduction. The pseudocolor code indexes task-specific path weights. See list for abbreviations.

Fig. 7. Right hemisphere effective connectivity between ventral striatum, art-selective regions (white font) and regions correlated with esthetic preference ratings (blue font) for art (a) and non-art (b) images after network reduction. The pseudocolor code indexes task-specific path weights. See list for abbreviations.

selective activity in the hypothalamus which is not typically considered part of the reward circuit (e.g., O'Doherty, 2004) although more recent evidence suggests that hypothalamic orexin neurons are involved in reward-related behavior (Ganjavi and Shapiro, 2007; Hikosaka et al., 2008). It is not clear why there was activation in the mSFG. This activation was in the pre-supplementary motor area; it is relevant to note that viewing art images that were deemed ugly selectively activated primary motor cortex, relative to images deemed beautiful, perhaps as a precursor to action avoiding aversive stimuli (Kawabata and Zeki, 2004). The mSFG also showed a significant correlation across subjects between activation magnitude and response time; this could reflect processing of potential actions that delayed response. Clearly, these ideas require further study.

Art images were rated higher than non-art images on all three esthetic preference questionnaires. However, none of the art-selective activations had an activation magnitude that was correlated with any of the three ratings. Instead, esthetic preference ratings were correlated in regions that were essentially independent of the art-selective activations. This, and the effective connectivity results (see below), reinforce our view that esthetic preference, while important

to the experience of art, is not unique to it and thus may not be the sole determinant of reward-related activity in processing of visual art. Esthetic preference is likely a complex phenomenon involving sensorimotor, cognitive and emotional processes (Di Dio and Gallese, 2009; Leder et al., 2004). This complexity is reflected in the nature of the regions exhibiting correlations with esthetic preference ratings. Interestingly, most regions where activity correlated with esthetic preference for art images were in extrastriate visual cortex, whereas those showing correlations with esthetic preference for non-art images were in frontoparietal cortex.

The present study is the first to examine effective connectivity in relation to processing of visual art. This analysis showed that the VS was driven by art-selective regions when viewing art images, was disengaged when non-art images were viewed, and was not driven by any region correlated with ratings of esthetic preference. These findings support our hypothesis that the VS responds specifically to the artistic status of the images and argue against the idea that the art-selective activations were associated with esthetic ratings. Further work is necessary to delineate the relationship between the activity and connectivity of the reward circuit reported here and learning, in the context of motivation (Camara et al., 2009).

Art as marketing tool — the 'art infusion' effect

The present study was originally motivated by the discovery of the 'art infusion' effect, in which consumers rate products more positively when associated with art images than when associated with non-art images depicting similar content (Hagtvedt and Patrick, 2008). The psychological basis for this was assumed to be a content-independent transfer of perceptions of luxury and intrinsic value from the art image to the product (Hagtvedt and Patrick, 2008). The reward-related activity observed in the present study supports the view that the neural basis of the 'art infusion' effect is a content-independent activation of reward circuitry, deriving from the status of images as art, that presumably induces more favorable evaluation of the product associated with the image. In the original experiments, consumers' attention was directed to the product that they were required to rate so that perception of the images associated with the product, whether art or not, was not explicit. It is interesting to note that similarly, in the present study, the reward circuit was activated in the absence of explicit rewards: participants made animacy, but not explicit value or affective, judgments. This contrasts with other studies in which participants rated the attractiveness of sports cars compared to ordinary cars during scanning (Erk et al., 2002), or imagined owning and driving luxury/sports cars (Schaefer and Rotte, 2007).

Our understanding of the neural bases of marketing phenomena is still at an early stage (Plassmann et al., 2007; Kenning and Plassmann, 2008). The present study examined responses evoked by images merely by virtue of being art, which is assumed to be the basis of the 'art infusion' effect, but did not explicitly investigate the 'art infusion' effect itself. This could be done in future studies by examining the neural response to art and non-art images when presented with images of products varying in such measures as cost, perceived luxury and so on. As noted in the Introduction, VS responses to financial reward scale with the marginal utility of the reward (Tobler et al., 2007). Our finding of VS activity evoked by visual art thus raises the possibility that the 'art infusion' effect could be used to modify perceived marginal utility.

Familiarity and response time effects

Art images were rated as generally unfamiliar, though somewhat more familiar than non-art images. However, activation magnitudes of the art-selective activations did not correlate significantly with familiarity ratings for either art or non-art images. Instead, familiarity with the art (but not non-art) images correlated with activation strength in a separate network that comprised left inferolateral frontal foci, some of which have previously been implicated in mediating the sense of familiarity in memory retrieval paradigms (Yonelinas et al., 2005). In a recent study, Fairhall and Ishai (2008) showed participants representational, abstract, and indeterminate paintings and asked them to indicate if they recognized any familiar objects within each image. In contrast to our findings, perceiving such familiar objects was associated with activity in the right temporoparietal junction but this no doubt reflected familiarity with the objects in the images rather than with the images themselves.

The analysis of response time/activation magnitude correlations similarly showed that response time drove a network largely independent of that involved in processing art images. Independent networks for response time and processing art images would be consistent with findings of a dissociation between perceptual and decision processes in other domains (e.g., Binder et al., 2004). The correlations with response times found in cingulate and motor-related regions could reflect the attentional demands of the animacy discrimination task and the use of button presses to record responses. The bilateral anterior insular regions showing response time correlations here were also found to show positive correlations with response times in auditory discrimination (Binder et al., 2004), while the correlations with response times in the anterior cingulate, middle and inferior frontal gyri found here are similar to those reported in a visual discrimination task (Thielscher and Pessoa, 2007).

Conclusions

The present study suggests that reward processing makes a specific contribution to the neural processing of visual art, that artistic status alone is enough to instantiate reward processing, and that the brain thus responds to 'art for art's sake'. The findings reported here complement earlier studies describing activity in reward-related regions during esthetic judgments (Kawabata and Zeki, 2004; Vartanian and Goel, 2004; Di Dio et al., 2007; Kirk, 2008; Kirk et al., 2009a,b). In the present study, esthetic preference was uncorrelated with activity in art-selective regions and did not drive reward-related activity. It remains for future research to delineate the relationship between neural processing of perceived artistic status and that of individual esthetic appeal, and how these neural processes relate to the function of reward circuitry.

Supplementary materials related to this article can be found online at doi: 10.1016/j.neuroimage.2010.11.027.

Abbreviations

amyg	amygdala
CaS	calcarine sulcus
CBL	cerebellum
CiS	cingulate sulcus
CoS	collateral sulcus
FG	fusiform gyrus
hypoth	hypothalamus
IFS	inferior frontal sulcus
IOG	inferior occipital gyrus
IPS	intraparietal sulcus
LG	lingual gyrus
LOC	lateral occipital complex
MFG	middle frontal gyrus
MOG	middle occipital gyrus
OFC	orbitofrontal cortex
POF	parieto-occipital fissure
SFG	superior frontal gyrus
SMG	supramarginal gyrus
SPG	superior parietal gyrus
VS	ventral striatum
L	left
R	right
a	anterior
i	inferior
m	medial
p	posterior
s	superior
v	ventral

Appendix A. Art images

Artist	Date of composition	Title
Anonymous	c200 CE	Fayum funerary portrait of adult male: Roman Egypt
	Unknown	Cave art (horses and bulls), origin unknown.
	Unknown	Venice, Grand Canal
Balla, Giacomo	1909	Street Light.
	1912	Dynamism of a Dog on a Leash
Chagall, Marc	1911	I and the Village
da Vinci, Leonardo	c1499–1500	The Virgin and Child with St. Anne and St. John the Baptist
Degas, Edgar	1872	Dance Studio at the Opera (detail)
de Vlaminck, Maurice	1906	Tugboat on the Seine, Chatou
Fragonard, Jean-Honoré	c1770–72	The Reader
Gordon, Jerry	2001	Vlaminck and Derain - Studio
Hagtvedt, Henrik	1996	Search
	1998	Search
	2000	Bjørnstjerne Bjørnson
	1996	Focus
	1996	Lost
	2002	Picasso
	1996	Evasion
	2000	Roald Amundsen
Heda, Willem Claesz	1631	Breakfast: Still Life with Blackberry Pie
Hokusai, Katsushika	c1829–32	The Great Wave off Kanagawa
Kandinsky, Wassiliy	1916	Moscow I
Klee, Paul	1922	Senecio
Klimt, Gustav	1907–08	The Kiss
Kokoschka, Oskar	1926	Mandrill
Manet, Edouard	1882	The House at Rueil
Millais, John Everett	1852	Ophelia
Monet, Claude	1899	The Japanese Bridge
	1897–99	Water Lilies
	1891	Haystacks at the End of Summer, Morning Effect
Munch, Edvard	1893	The Scream
O'Keeffe, Georgia	1924	Light Iris
Picasso, Pablo	1922	Still Life with Guitar
Renoir, Pierre-Auguste	1883	Dance at Bougival
	1881	The Doge's Palace, Venice
	1876	Girl with a Watering Can
Rouault, Georges	1937	The Old King
Seurat, Georges	1884–86	A Sunday Afternoon on the Island of La Grande Jatte
Titian	1510	Portrait of Ariosto
Turner, JMW	1835	The Burning of the Houses of Lords and Commons
	1838	The Fighting Temeraire
van Gogh, Vincent	1889	Landscape with House and Ploughman
	1888	Shoes
	1888	Chair
	1888	Café Terrace at Night
	1889	Irises
	1890	Road with Cypress and Star
Warhol, Andy	1962	Turquoise Marilyn
Wood, Grant	1930	American Gothic
Wyeth, Andrew	1948	Christina's World

Appendix B. Granger causality analysis methods

Correlation-purged Granger causality

Suppose x_m, $m = 1...k$ correspond to the k selected ROI time series and $\boldsymbol{X}(t) = (x_1(t), x_2(t)...x_k(t))^T$, then the traditional vector autoregressive (VAR) model with model parameters $\boldsymbol{A}(n)$ of order p is given by

$$X(t) = V + \sum_{n=1}^{p} A(n)X(t-n) + E(t) \tag{1}$$

where $\boldsymbol{V}$ is the intercept vector, $\boldsymbol{E}(t)$ is the vector corresponding to the residuals and t represents discrete time. Direct causal relationship between the k time series can be inferred from the VAR coefficients (Kaminski et al., 2001) as follows

$$D_{ij} = \sum_{n=1}^{p} a_{ij}^2(n) \tag{2}$$

where a_{ij} are the elements of the matrix $\boldsymbol{A}$. In order to model the effects of instantaneous correlation, we introduced the zero-lag terms into Eq. (1), thereby obtaining a modified VAR (or mVAR) (Deshpande et al., 2010c) as shown below

$$X(t) = V + \sum_{n=0}^{p} A'(n)X(t-n) + E'(t) \tag{3}$$

where the diagonal elements of $A'(0)$ are zero such that only the instantaneous cross-correlation, and not the zero-lag auto-correlation, between the time series are modeled. Accordingly, correlation-purged Granger causality (CPGC) is defined as follows

$$CPGC_{ij} = \sum_{n=1}^{p} \left[a'_{ij}(n) \right]^2. \tag{4}$$

It is noteworthy that $A'(1)...A'(p) \neq A(1)...A(p)$ and the causal relationship obtained from only $A'(1)...A'(p)$ (Eq. (4)) is purged of correlation leakage effects as shown before (Deshpande et al., 2010c).

Network reduction

The total number of paths obtained from 23 and 32 ROIs for the left and right hemispheric networks, respectively, was very large. We were deliberately inclusive in selecting ROIs in order to avoid the problem of circularity that can result from overly constraining ROI selection. To reduce the number of paths to be considered, we employed network reduction using a recursive procedure as previously reported by us (Deshpande et al., 2008). Accordingly, let the CPGC matrix of the original k ROIs be A. Upon removal of an ROI, a connectivity matrix B was determined using the remaining $k-1$ ROIs. A cost function, η, was then defined as follows

$$\eta = \frac{1}{N_k} \sum_{i=1}^{k} \sum_{j=1; \, i \neq j}^{k} A(i,j) - \frac{1}{N_{k-1}} \sum_{i=1}^{k-1} \sum_{j=1; \, i \neq j}^{k-1} B(i,j) \tag{5}$$

where $N_k = k(k-1)$ are the total number of possible paths. A null distribution of , i.e. n_{null}, was obtained by repeated calculation from phase randomized surrogate time series (Theiler et al., 1992; Deshpande et al., 2009) which were generated from the original data. Subsequently, n was compared with n_{null} and the ROI under consideration was retained if was found to be significantly positive (p<.05). The above procedure was started with $k = 23$ (for left hemisphere) or $k = 32$ (for right hemisphere) ROIs and successively repeated by dropping the least significant ROI at each stage where in the network was recalculated with the remaining ROIs. The procedure was terminated when the cost function of all the ROIs in the residual network was significant.

Temporally adaptive CPGC using wavelets

Let k' ($k' < k$) denote the number of ROIs surviving the reduction process. Then, $\boldsymbol{X}(t)$ was defined as $(x_1(t), x_2(t)...x_{k'}(t))^T$. A temporally adaptive mVAR using $\boldsymbol{X}(t)$ was defined such that its coefficients are a function of time

$$X(t) = V(t) + \sum_{n=0}^{p} A'(n,t)X(t-n) + E'(t). \tag{6}$$

In accordance with previous studies (Sato et al., 2006), the elements of $A'(n,t)$, i.e. $a'_{ij}(n,t)$, can be expanded using a wavelet basis as follows

$$a'_{ij}(n,t) = c^n_{-1,0}\phi(t) + \sum_{x=0}^{X}\sum_{y=0}^{2^x-1} c^n_{x,y}\psi_{x,y}(t) \qquad (7)$$

where $c^n_{x,y}$ ($x = -1, 0, 1...T-1$, $y = 0, 1, 2...2^x-1$ and $n = 1...p$) are the wavelet coefficients, $\varphi(t)$ is the scaling function and $\psi_{x,y}(t)$ are orthonormal basis functions derived from a mother wavelet. We chose the Daubechies wavelet as the mother wavelet owing to its regularity and compact support (Daubechies, 1988). The choice of the specific Daubechies wavelet (D2–D20) is dictated by the expected order of polynomial behavior in the data, given the fact that the number of vanishing moments of DN is N/2. For example, D4 is most suited for modeling a constant and linear component in the data (polynomial with two coefficients) because it has four wavelet filter coefficients and two vanishing moments. We chose the D8 Daubechies wavelet as the mother wavelet in this study because previous studies have indicated that fMRI activation data may be appropriately modeled by polynomials of order 3 to 5 (Gibbons et al., 2004; Clark, 2002). Both parameter T and maximum resolution parameter X must be a power of two. An iterative generalized least squares estimation procedure (Sato et al., 2006) was adopted to solve for the wavelet coefficients in order to obtain $A'(n,t)$ and $V(t)$. Temporally adaptive CPGC was then obtained as follows

$$CPGC_{ij}(t) = \sum_{n=1}^{p} a'_{ij}(n,t). \qquad (8)$$

References

Bedny, M., Aguirre, G.K., Thompson-Schill, S.L., 2007. Item analysis in functional magnetic resonance imaging. Neuroimage 35, 1093–1102.
Binder, J.R., Liebenthal, E., Possing, E.T., Medler, D.A., Ward, D., 2004. Neural correlates of sensory and decision processes in auditory object identification. Nat. Neurosci. 7, 295–301.
Bourdieu, P., Darbel, A., 1997. The Love of Art: European Art Museums and their Public. Blackwell, Oxford.
Camara, E., Rodriguez-Fornells, A., Ye, Z., Munte, T.F., 2009. Reward networks in the brain as captured by connectivity measures. Front. Neurosci. 3, 350–362. doi:10.3389/neuro.01.034.2009.
Cela-Conde, C.J., Marty, G., Maestu, F., Ortiz, T., Munar, E., Fernandez, A., Roca, M., Rossello, J., Quesney, F., 2004. Activation of the prefrontal cortex in the human visual aesthetic perception. Proc. Natl Acad. Sci. USA 101, 6321–6325.
Cela-Conde, C.J., Ayala, F.J., Munar, E., Maestu, F., Nadal, M., Capo, M.A., del Rio, D., Lopez-Ibor, J.J., Ortiz, T., Mirasso, C., Marty, G., 2009. Sex-related similarities and differences in the neural correlates of beauty. Proc. Natl Acad. Sci. USA 106, 3847–3852.
Chen, H., Yang, Q., Liao, W., Shen, S., 2009. Evaluation of the effective connectivity of supplementary motor areas during motor imagery using Granger causality mapping. Neuroimage 47, 1844–1853.
Clark, H., 1973. The language-as-a-fixed-effect fallacy: critique of language statistics in psychological research. J. Verbal Learn. Verbal Behav. 12, 335–359.
Clark, V.P., 2002. Orthogonal polynomial regression for the detection of response variability in event-related fMRI. Neuroimage 17, 344–363.
Daubechies, I., 1988. Orthonormal bases of compactly supported wavelets. Commun. Pure Appl. Math. 41, 909–996.
Deshpande, G., Hu, X., Lacey, S., Stilla, R., Sathian, K., 2010a. Object familiarity modulates effective connectivity during haptic shape perception. Neuroimage 49, 1991–2000.
Deshpande, G., Hu, X., Stilla, R., Sathian, K., 2008. Effective connectivity during haptic perception: a study using Granger causality of functional magnetic resonance imaging data. Neuroimage 40, 1807–1814.
Deshpande, G., LaConte, S., James, G.A., Peltier, S., Hu, X., 2009. Multivariate Granger causality analysis of brain networks. Hum. Brain Mapp. 30, 1361–1373.
Deshpande, G., Sathian, K., Hu, X., 2010b. Effect of hemodynamic variability on Granger causality analysis of fMRI. NeuroImage 52, 884–896.
Deshpande, G., Sathian, K., Hu, X., 2010c. Assessing and compensating for zero-lag correlation effects in time-lagged Granger causality analysis of fMRI. IEEE Transactions in Biomedical Engineering 57, 1446–1456.
Dewey, J., 1989. "Having an Experience", in John Dewey: The Later Works, 1925–1953, Vol 10: Art as Experience, pp 42–63 Jo Ann Boydston, ed. Southern Illinois University Press, Carbondale.
Di Dio, C., Gallese, V., 2009. Neuroaesthetics: a review. Curr. Opin. Neurobiol. 19, 682–687.
Di Dio, C., Macaluso, E., Rizzolatti, G., 2007. The golden beauty: brain responses to classical and renaissance sculptures. PLoS ONE 2, e1201.
Dutton, D., 2009. The Art Instinct: Beauty, Pleasure and Human Evolution. Bloomsbury Press, New York.
Duvernoy, H.M., 1999. The Human Brain. Surface, Blood Supply and Three-Dimensional Sectional Anatomy. Springer, New York.
Elliott, R., Newman, J.L., Longe, O.A., Deakin, J.F.W., 2003. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. J. Neurosci. 23, 303–307.
Erk, S., Spitzer, M., Wunderlich, A.P., Galley, L., Walter, H., 2002. Cultural objects modulate reward circuitry. NeuroReport 13, 2499–2503.
Fairhall, S.L., Ishai, A., 2008. Neural correlates of object indeterminacy in art compositions. Conscious. Cogn. 17, 923–932.
Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. Magn. Reson. Imaging Med. 33, 636–647.
Ganjavi, H., Shapiro, C.M., 2007. Hypocretin/orexin: a molecular link between sleep, energy regulation and pleasure. J. Neuropsychiatry Clin. Neurosci. 19, 413–419.
Gibbons, R.D., Lazar, N.A., Bhaumik, D.K., Sclove, S.L., Chen, H.Y., Thulborn, K.R., Sweeney, J.A., Hur, K., Patterson, D., 2004. Estimation and classification of fMRI hemodynamic response patterns. Neuroimage 22, 804–814.
Granger, C.W.J., 1969. Investigating causal relations by econometric models and cross-spectral methods. Econometrica 37, 424–438.
Guilford, J.P., 1965. Fundamental Statistics in Psychology and Education. McGraw Hill, New York.
Hagtvedt, H., Patrick, V.M., 2008. Art infusion: the influence of visual art on the perception and evaluation of consumer products. J. Mark. Res. 45, 379–389.
Hare, T.A., O'Doherty, J., Camerer, C.F., Schultz, W., Rangel, A., 2008. Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. J. Neurosci. 28, 5623–5630.
Heekeren, H.R., Wartenburger, I., Marschner, A., Mell, T., Villringer, A., Reischies, F.M., 2007. Role of ventral striatum in reward-based decision making. NeuroReport 18, 951–955.
Hikosaka, O., Bromberg-Martin, E., Hong, S., Matsumoto, M., 2008. New insights on the subcortical representation of reward. Curr. Opin. Neurobiol. 18, 203–208.
Kaminski, M., Ding, M., Truccolo, W.A., Bressler, S.L., 2001. Evaluating causal relations in neural systems: Granger causality, directed transfer function and statistical assessment of significance. Biol. Cybern. 85, 145–157.
Kawabata, H., Zeki, S.J., 2004. Neural correlates of beauty. J. Neurophysiol. 91, 1699–1705.
Kenning, P., Plassmann, H., 2008. How neuroscience can inform consumer research. IEEE Trans. Neural Syst. Rehabil. Eng. 16, 532–538.
Kirk, U., 2008. The neural basis of object-context relationships on aesthetic judgment. PLoS ONE 3, e3754. doi:10.1371/journal.pone.0003754.
Kirk, U., Skov, M., Hulme, O., Christensen, M.S., Zeki, S., 2009a. Modulation of aesthetic value by semantic context: an fMRI study. Neuroimage 44, 1125–1132.
Kirk, U., Skov, M., Christensen, M.S., Nygaard, N., 2009b. Brain correlates of aesthetic expertise: a parametric fMRI study. Brain Cogn. 69, 306–315.
Knutson, B., Rick, S., Wimmer, G.E., Prelec, D., Loewenstein, G., 2007. Neural predictors of purchases. Neuron 53, 147–156.
Leder, H., Belke, B., Oeberst, A., Augustin, D., 2004. A model of aesthetic appreciation and aesthetic judgments. Br. J. Psychol. 95, 489–508.
Lengger, P.G., Fischmeister, F.Ph.S., Leder, H., Bauer, H., 2007. Functional neuroanatomy of the perception of modern art: a DC-EEG study on the influence of stylistic information on aesthetic experience. Brain Res. 1158, 93–102.
Li, S., Dardzinski, B.J., Collins, C.M., Yang, Q.X., Smith, M.B., 1996. Three-dimensional mapping of the static magnetic field inside the human head. Magn. Reson. Med. 36, 705–714.
Marinazzo, D., Liao, W., Chen, H. and Stramaglia, S. (2010). Nonlinear connectivity by Granger causality. NeuroImage, in press. doi: 10.1016/j.neuroimage.2010.01.099.
Nadal, M., Munar, E., Capó, M.A., Rosselló, J., Cela-Conde, C.J., 2008. Towards a framework for the study of the neural correlates of aesthetic preference. Spat. Vis. 21, 379–396.
O'Doherty, J., 2004. Reward representations and reward-related learning in the human brain: insights from neuroimaging. Curr. Opin. Neurobiol. 14, 769–776.
O'Doherty, J., Dayan, P., Friston, K., Critchley, H., Dolan, R.J., 2003. Temporal difference models and reward-related learning in the human brain. Neuron 28, 329–337.
Plassmann, H., Ambler, T., Braeutigam, S., Kenning, P., 2007. What can advertisers learn from neuroscience? Int. J. Advert. 26, 151–175.
Raczkowski, D., Kalat, J.W., Nebes, R., 1974. Reliability and validity of some handedness questionnaire items. Neuropsychologia 12, 43–47.
Ramachandran, V.S., 2004. A Brief Tour of Human Consciousness. Pi Press, New York.
Roebroeck, A., Formisano, E., Goebel, R., 2005. Mapping directed influence over the brain using Granger causality and fMRI. Neuroimage 25, 230–242.
Sathian, K., Lacey, S., Anderson, A., Stilla, R., Hagtvedt, H., Patrick, V., Reddy, S., 2008. Viewing art images activates reward and affective circuitry. Soc. Neurosci. Abstr. 189, 10.
Sato, J.R., Junior, E.A., Takahashi, D.Y., de Maria Felix, M., Brammer, M.J., Morettin, P.A., 2006. A method to produce evolving functional connectivity maps during the course of an fMRI experiment using wavelet-based time-varying Granger causality. Neuroimage 31, 187–196.
Schaefer, M., Rotte, M., 2007. Favorite brands as cultural objects modulate reward circuit. NeuroReport 18, 141–145.

Schultz, W., 2006. Behavioral theories and the neurophysiology of reward. Annu. Rev. Psychol. 57, 87–115.

Stilla, R., Deshpande, G., LaConte, S., Hu, X., Sathian, K., 2007. Posteromedial parietal cortical activity and inputs predict tactile spatial acuity. J. Neurosci. 27, 11091–11102.

Stilla, R., Hanna, R., Hu, X., Deshpande, G., Sathian, K., 2008. Neural processing underlying tactile microspatial discrimination in the blind: a functional magnetic resonance imaging study. Journal of Vision 8(10) (13), 1–19.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Brain. Thieme Medical Publishers, New York.

Theiler, J., Eubank, S., Longtin, A., Galdrikian, B., Farmer, D., 1992. Testing for non-linearity in time series: the method of surrogate data. Phys. D 58, 77–94.

Thielscher, A., Pessoa, L., 2007. Neural correlates of perceptual choice and decision making during fear–disgust discrimination. J. Neurosci. 27, 2908–2917.

Tobler, P.N., Fletcher, P.C., Bullmore, E.T., Schultz, W., 2007. Learning-related human brain activations reflecting individual finances. Neuron 54, 167–175.

Vartanian, O., Goel, V., 2004. Neuroanatomical correlates of aesthetic preference for paintings. NeuroReport 15, 893–897.

Wartenberg, T.E., 2006. The Nature of Art: An Anthology, 2nd ed. Wadsworth, Belmont, CA.

Yacubian, J., Sommer, T., Schroeder, K., Gläscher, J., Braus, D.F., Büchel, C., 2007. Subregions of the ventral striatum show preferential coding of reward magnitude and probability. Neuroimage 38, 557–563.

Yonelinas, A.P., Otten, L.J., Shaw, K.N., Rugg, M.D., 2005. Separating the brain regions involved in recollection and familiarity in recognition memory. J. Neurosci. 25, 3002–3008.

Zaidel, D.W., 2005. Neuropsychology of Art: Neurological, Cognitive and Evolutionary Perspectives. Psychology Press, Hove, UK.