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Towards a sensorimotor aesthetics of performing art

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Abstract

The field of Neuroaesthetics attempts to identify the brain processes underlying aesthetic experience, including but not limited to beauty. Previous neuroaesthetic studies have focussed largely on paintings and music, while performing arts such as dance have been less studied. Nevertheless, increasing knowledge of the neural mechanisms that represent the bodies and actions of others, and which contribute to empathy, make a neuroaesthetics of dance timely. Here we present the first neuroscientific study of aesthetic perception in the context of the performing arts. We investigated brain areas whose activity during passive viewing of dance stimuli was related to later, independent aesthetic evaluation of the same stimuli. Brain activity of six naïve male subjects was measured using fMRI, while they watched 24 dance movements, and performed an irrelevant task. In a later session, participants rated each movement along a set of established aesthetic dimensions. The ratings were used to identify brain regions that were more active when viewing moves that received high average ratings than moves that received low average ratings. This contrast revealed bilateral activity in the occipital cortices and in right premotor cortex. Our results suggest a possible role of visual and sensorimotor brain areas in an automatic aesthetic response to dance. This sensorimotor response may explain why dance is widely appreciated in so many human cultures.

Keywords: neuroaesthetics, dance, visual, sensorimotor, fMRI, aesthetic dimensions, ballet, capoeira, mirror system.

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INTRODUCTION

Dance is a dynamic visual form of artistic expression that has accompanied mankind since ancient times. Many different dance styles and traditions exist, covering most human cultures. In dance performance, an observer watches the body movements of the dancer. The spatial and temporal features of the dancer's movement can induce aesthetic experience in the observer. Dance choreographers and performers exploit these influences to communicate their intentions to the viewer. Dance typically also involves several other elements, including but not limited to narrative, music, costume, and interaction between dancers. No single one of these additional elements is necessary, though the synergy between them undoubtedly increases the aesthetic impact of dance performance. How is this impact coded in the observer's mind and brain? Here we present a study that focuses on the neural mechanism underpinning the aesthetic experience of observers watching dance.

The term a*esthetic* is derived from the Greek word *Aesthesis*, and was re-defined by Baumgarten in the eighteen century as the gratification of the senses or sensuous delights (Goldman, 2001). A particular type of sensory stimulus, often but not exclusively a work or art, produces a psychological state usually termed a*esthetic experience*. The neural mechanisms that correlate with these internal processes associated to aesthetic experience have been a recent focus of several studies, and created a new field of "neuroaesthetics" (Cela-Conde et al., 2004; Kawabata & Zeki, 2004). Neuroaesthetics addresses the brain processes underlying aesthetic judgement, evaluation and interpretation. Evaluation is a particularly important element of aesthetic experience. Aesthetic experience can involve two kinds of evaluation: one attributes intrinsic perceptual properties to the stimulus (e.g. ‘it is beautiful’), and the second characterises the observer’s response attitude to the stimulus (e.g., “I like it”).

Two classical perspectives on aesthetics have led researchers to focus on different components of aesthetics. On the one hand, *objectivist* theories treat beauty and other aesthetic properties as attributes of stimuli, processed or perceived by the observer like other attributes. These theories often relied on psychophysical studies aiming to identify particular stimulus properties that induce aesthetic experience. Studies of the so-called ‘golden section’ in abstract geometrical figures provide one example (McManus & Weatherby, 1997), but similar approaches have been used with paintings (Jacobsen & Hofel 2002; Jacobsen, 2004; Jacobsen, Buchta, Kohler & Schroger, 2004; Whissell, 1980; McManus, 1980). Such studies generally suggest that aesthetic experience depends on *compositional* arrangement between parts of the stimulus, and between individual parts and the whole. Thus, symmetry, balance, complexity, and order of an image all contribute to its aesthetic impact (Leder, Belke, Oeberst & Augustin, 2004). Objectivist theories often claim some level of generality for these psychophysical regularities across individuals, since most individuals’ perceptual systems process stimulus patterns in the same way.

On the other hand, *subjectivist* theories maintain that ‘beauty is in the eye of the beholder’, and is largely a matter of attitudes, such as individual taste and preference.

This theory receives support from the strong effect of familiarity on aesthetic judgement. We tend to like what we know (Zajonc, 1968). Hence, individual differences in aesthetic judgement may arise from individual differences in prior experience, notably due to cultural environment. Because subjectivist theories focus on individuals, rather than on the generality of aesthetic experience, they often make rather few predictions that can be tested in traditional laboratory experiments. However, they have recently been reinforced by several neuroaesthetic studies identifying brain areas associated with specific aesthetic attitudes such as like / dislike, even though participants may have differed among themselves in which stimuli evoked these attitudes (Cela-Conde et al., 2004; Jacobsen, Schubotz, Hofel & Cramon, 2006; Kawabata & Zeki, 2004; Vartanian & Goel, 2004).

In general, subjects in these studies view several paintings, and give a rating of how much they like each one. Previous neuroaesthetic studies suggest that at least two broad brain networks may be involved in this process. One is primarily perceptual, centred on sensory and attentional regions. The second, centred on the prefrontal cortex, seems primarily cognitive and/or hedonic. More specifically, brain activity associated with viewing paintings that subjects liked, as opposed to disliked, was found in both visual and prefrontal brain areas (Cela-Conde et al., 2004; Kawabata et al., 2004; Vartanian et al., 2004). These included the occipital gyri and fusiform gyri bilaterally in the visual cortex. The same areas were shown to respond to the emotional significance of faces and pictures in other studies that did not focus on aesthetic experience (Paradiso et al., 1999; Iidaka et al., 2002; Vartanian et al., 2004). A prefrontal correlate of aesthetic evaluation has also been reported. This included the orbitofrontal cortex, which often reflects the reward value of a stimulus (Kawabata & Zeki, 2004; Rolls, 2000), and the prefrontal dorsolateral cortex, which plays a role as a centre of the perception-action interface and is critical for the monitoring and comparison of multiple events in working memory (Petrides et al., 2000; Cela-Conde et al., 2004). Such studies can reveal the neural correlates of liking or disliking aesthetically-relevant stimuli. However, they provide little information about the physical properties responsible for the aesthetic experience. In other words, they cannot project their conclusions back into stimulus space, to identify which parameters of a stimulus lead to its being liked or disliked. This limitation is a consequence of comparing different sets of stimuli according to the attitudes expressed by each subject (Kawabata et al., 2004; Cela-Conde et al., 2004).

Jacobsen and colleagues (Jacobsen et al., 2006) recently used a subjectivist approach to investigate the neural correlates of aesthetic judgments of abstract geometric forms, and found essentially similar results. Beauty judgments for these stimuli activated both temporoparietal regions, but also fronto-median and prefrontal regions. They then correlated aesthetic preference with symmetry judgments for the same stimuli, and found significant overlap. Psychophysical studies reached similar conclusions (Leder et al., 2004; McManus, 1980). Interestingly, some of these areas were previously shown to underlie other types of human judgement (i.e. social and moral judgement) (Cunningham, Johnson, Gatenby, Gore & Banaji, 2003).

Overall, previous neuroaesthetic studies demonstrate an important role of prefrontal areas in aesthetic evaluation. These areas are also involved in representing the reward value of stimuli, which would not be considered aesthetic (Aharon et al., 2001; Rolls, 2000; Small, Zatorre, Dagher, Evans & Jones-Gotman, 2001). Moreover, the aesthetic evaluation network partially overlaps with brain regions processing social and moral behaviour (Jacobsen et al., 2006). Interestingly, these frontal areas have also increased disproportionately in size and complexity during recent human evolution. They may contribute both to the large difference in sophistication of the social interactions between humans and other mammals, and to creation of art by humans, but not other species (Cela-Conde et al., 2004).

In summary, three main issues emerge from these studies. First, most studies have used *static* images such as paintings, photographs, or abstract forms. Second, most studies have investigated brain activity during explicit aesthetic *evaluation or appreciation*. Few studies have considered automatic effects of viewing stimuli that have aesthetic potential. Finally, studies have focused on aesthetic judgements of *individuals*, rather than the potential of stimuli to elicit similar aesthetic responses in a group of individuals. Here we extend previous neuroaesthetic work by using a new class of stimuli (dance), by using an implicit task during stimulus presentation, and by studying group-average rather than individual responses.

Dance is a dynamic, fluent and fugitive visual art form. To simplify our approach to the aesthetic appreciation of human dance, we have reduced dance to its core motor elements, as the key to its aesthetic value. For this, we studied the kinematics of dance movements while keeping all other features such as visual background constant. We therefore removed narrative, costume, and musical elements. We reasoned that any variation in neural activity related to aesthetic valuation could then be explained only by differences in the movements' kinematics. A disadvantage of this simplifying approach, however, is that the stimulus itself and the subject's aesthetic response to it may fall far short of the typical dance performance situation. On the other hand, simplified experiments allow any positive findings to be interpreted more clearly. For example, an experimenter can more confidently identify specific stimulus parameters that lead to particular aesthetic responses.

In addition, simplified dance stimuli allow aesthetic responses to be directly related to studies on selectivity of relevant brain areas. Two well-established brain systems appear to be specifically relevant to processing of dance kinematics. These are brain regions responsible for processing motion stimuli such as random dots or moving objects. These activate area MT/V5 (Sunaert, Van Hecke, Marchal, & Orban, 1999). A second system is concerned with processing a special class of stimulus motions, caused by the actions of other individuals. This system comprises areas in the premotor, and parietal cortices (so-called 'mirror neuron areas'), and also the superior temporal sulcus. To give one example, this latter area responds to observation of biological but not non-biological motion (Puce & Perrett, 2003; Vaina, Solomon, Chowdhury, Sinha & Belliveau, 2001; Grossman & Blake, 2002). The human mirror system is also known to be involved in action observation in general (Decety & Grèzes, 1999; Grafton, Arbib, Fadiga & Rizzolatti, 1996; Rizzolatti et al., 1996), and dance observation in particular (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton & Grafton, 2006). We hypothesised that variation in aesthetic responses to a set of dance movements might correlate with the extent to which the movements activated these specialised visual and motor brain systems.

We therefore recorded brain activity in naïve subjects with no dance experience while they watched video clips of two dance styles (classical ballet and capoeira). No explicit aesthetic or evaluative questions were asked at the time of viewing inside the scanner. A range of dance styles and kinematic parameters were chosen to probe general brain responses to dance movements, rather than recognition or association with individual culturally familiar stimuli. We then showed the same stimuli to the subjects again in a later testing session. This time, the subjects gave ratings to evaluate each stimulus along a number of standard aesthetic dimensions. The group average of all subjects' ratings was used to identify brain areas coding these aesthetic dimensions. Finally, we evaluated the characteristics of the dance movements that lead to most and least activation of any brain area thus identified. This allowed us to identify kinematic features encoded by that brain area, and related to its aesthetic coding.

MATERIALS AND METHODS

Participants:

Six right handed males, with normal or corrected vision participated in the study (mean age 26, SD=2). Subjects were naïve to the purpose of the study and were paid for their participation. None of them had previous experience with the dance styles used here, either as a performer or as a regular observer. None of the participants regularly performed any specific activity associated with dance during the interval between the two sessions.

Materials:

Ballet and capoeira movements were performed in front of a chromablue background by a professional ballet dancer and a capoeira dancer, respectively. Both dancers were matched for body shape, appearance and clothes. The dancers were naïve regarding the subsequent use of the videos. With the help of a choreographer, we selected a set of 24 videos (12 classical ballet movements, 12 capoeira movements). The classical ballet moves were selected to match specific capoeira movements according to four criteria: speed, part of the body involved, body location in space, and movement direction. These parameters can play an important role in the aesthetic experience of dance, so we attempted to match these kinematic characteristics across both dance styles as much as possible. We fixed the duration of each video at 3 seconds. And blured the faces of the dancers to avoid specific face processing.

Brain image acquisition:

Brain activity was recorded on a 1.5 T Magnetom VISION system (Siemens). Functional images were obtained with a gradient echo-planar sequence using blood oxygenation level-dependent (BOLD) contrast, each comprising 36 contiguous axial slices (2.5mm thickness). Volumes were acquired continuously with a repetition time (TR) of 3.24 s. A total of 280 scans were acquired for each participant in a single session (15 min). The first five volumes were discarded to allow for T1 equilibration effects.

Participants watched the dance videos while their brain activity was recorded in the scanner. In order to ensure subjects were paying attention to the stimuli, they were asked to indicate ‘how tiring’ they thought each movement was by pressing a keypad with their right hand. This was essentially a “dummy” task and the data were not analyzed. No instructions mentioning aesthetic responses or values were given at the time of the scanner. Videos were presented in randomized order on a screen situated outside the scanner which the subject viewed via a mirror (20 x 9 cm) located inside the scanner. During the experiment, each video was repeated four times. To avoid related motor preparation, assignment of buttons to response categories was randomized across trials and signalled after each video. Previous training with this response schedule was done outside the scanner with a second set of dance videos. The raw brain imaging data for the present study was collected in the context of a larger study with different hypotheses and analyses (Calvo-Merino et al., 2005). The analyses and research questions discussed here are independent of the previous study.

Psychophysical testing and scaling

In a second testing session, we used a questionnaire to measure aesthetic response to each dance stimulus. This session was performed long after scanning (approximately 1 year) so that aesthetic judgements were incidental to the initial presentation, and were based on current perception during the second presentation, rather than memory of the first presentation. Such delay is thought to favour the influence of the neural action observation system, rather than memory-based neural systems (cf. Grèzes et al., 2004).

The aesthetic questionnaire was constructed using five key aesthetic dimensions identified by Berlyne (1974). Each of these dimensions was taken as being an economical description of purportedly independent elements of aesthetic experience, and was therefore treated independently. The dimensions are characterised by the adjectival terms describing the poles of each dimension: 1) simple-complex, 2) dull-interesting; 3) tense-relaxed; 4) weak-powerful and 5) like-dislike. Participants were asked to rate each dance movement on each dimension using a 5-point Likert scale. The movements were presented in random order on a computer screen. After each stimulus, subjects responded within 4 seconds to a specific question related to one of the 5 dimensions. The dimension names were presented at random and only after the to-be-judged stimulus. During the experiment, each movie was presented once per dimension, i.e. 5 times in total. These ratings were used as subjective aesthetic evaluations of the dance movements.

The ratings for the 24 movies were first normalized within each subject and each dimension. Normalization removed differences between individuals and between dimensions in the portion of the Likert scale used. These normalized scores for each stimulus were then averaged across subjects to create a *consensus rating* for each stimulus on each dimension. Finally, we used the consensus ratings to divide the dance movements into two subsets of 12 movements each, using a median split. One subgroup contained the 12 movements with the highest scores, the other those with the lowest scores. This is a relatively conservative approach, and represents the importance of each of the five dimensions independently across the whole study.

If we assume that the ratings of our sample of subjects can generalize to the population, these consensus ratings represent the evaluation by a putative “average” observer (this assumption is revisited in the Discussion section). We note that this approach is quite different to most previous neuroaesthetic studies (e.g., (Cela-Conde et al., 2004; Kawabata et al., 2004)). Those studies focus on each individual participant’s responses, at the expense of information about the stimuli that caused the response. Our consensus approach quantifies the aesthetic status of each individual *stimulus* by focusing on the group average response to the stimulus, at the expense of information about the individual participants who contributed to the average.

Brain images and behavioural analysis:

fMRI data were analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB 6.5. Individual scans were realigned, slice time-corrected, normalized and spatially smoothed by a 6 mm full width at half maximum Gaussian kernel using standard SPM methods. The voxel dimensions of each reconstructed scan were 3x3x3 mm in the x, y and z dimensions, respectively.

We modelled the event-related activity for each voxel, subject and dance movement using a canonical haemodynamic response function. Statistical parametric maps of the t-statistic (SPM{t}) were generated for each subject. We then built second level models for each aesthetic dimension, using the t contrast created for each subject and movement.

The second level models were used to perform t- tests to identify brain areas whose activation differed between observation of dance movements that received higher or lower ratings on that dimension. We used the consensus rating rather than individual subject ratings as the basis for grouping the stimuli. Likewise, subjects were treated as a fixed effect, and dance movements as a random effect at the second level. Therefore, the results of this contrast show which brain areas showed aesthetic sensitivity in our sample of 6 subjects. In the language of inferential statistics, any results from this analysis can be generalised to the population of all dance movements, but are restricted to the participants in our study, and cannot be generalised to the population of all observers. An analogy for this style of analysis comes from psycholinguistics research, where a clear distinction is made between results which generalise across subjects, and results which generalise across stimulus items (Clark, 1973). Our analysis is of the latter kind. That is, the results may generalise across dance stimuli. However, we have not tested, and cannot comment on whether the results generalise to subjects other than those in our sample.

Activated voxels were superimposed on high-resolution magnetic resonance (MR) scans of a standard brain (Montreal Neurological Institute, MNI). In Table 1, we list clusters of activations where SPM{t} $p < 0.001$. Anatomical identification was performed on cross-sections with reference to the atlas of Duvernoy (Duvernoy, 1999).

The consensus approach allowed us to project functional imaging results back into stimulus space. That is, we identified the stimuli that maximally and minimally activated each aesthetically-relevant brain area, by plotting the 24 parameter estimates (one per dance movement) for each peak voxel of a priori specified areas of interest. This identifies the movements for which each voxel is preferentially tuned in the putative “average” brain generated by averaging the responses of our 6 subjects. We classified these movements according to their kinematic characteristic such as speed, part of body used, direction of the movement and vertical and horizontal displacement to define movements. Again, we emphasise that this method makes no claim to generalise such results to the wider population. According to classical inferential statistics, such a claim would involve showing that individual differences between subjects were small relative to differences between experimental conditions. However, our method eliminated individual differences between subjects when generating the consensus average. Rather, our method allows us to identify stimulus qualities that specifically modulated aesthetically-relevant areas of the group of brains studied here. A complementary analysis using a more classical approach based on modelling individual ratings and a random effect analysis over subjects, is also shown in supplementary material (Figure S1 and Table S1).

RESULTS

For each of the five aesthetic dimensions studied, we identified brain areas whose activation when viewing stimuli differed according to whether the stimuli had low or high consensus scores on that particular aesthetic dimension. Only the 'liking-disliking' dimension revealed significant neuroaesthetic tuning. Figure 1 shows the brain areas that were more activated when subjects viewed movements that (on average, in the consensus) they liked, than when they viewed movements that, on average, they disliked. These regions included bilateral activity in early visual cortex in the medial region (in the left hemisphere (*x/y/z* -6, -81, 18) and in the right hemisphere (*x/y/z* 15, -87, 33)), and in the premotor cortex of the right hemisphere (*x/y/z* 24, 0, 69), (all $p<0.001$). These areas can thus be considered neural correlates of positive aesthetic experience for dance, at least in our consensus data. No significant results were found during using the reverse comparison (disliked-liked).

For each of the aesthetically-responsive brain areas shown in Figure 1, we investigated which dance movements were responsible for maximal and minimal activation, as described in Methods. Figure 2a shows an example of the movements that achieve highest and lowest neural responses for the occipital area in the left hemisphere (-6, -81, 18). Figure 2b shows the equivalent stimuli for the right premotor activation (24, 0, 69). We also produced a physical description of those dance movements that preferentially target these aesthetically sensitive areas. We based this description on the four initial criteria used independently to select the movement stimuli for the scanning session. This allowed us to investigate the role of movement characteristics such as speed, part of body used, direction of movement and degree of vertical and horizontal displacement in aesthetic perception. This suggested that, on average, these areas of our subjects' brains preferred whole body movements, such as in jumping in place or with a significant displacement of the entire body in space (e.g. horizontal jump).

Figure 3 shows the movements that received highest and lowest consensus liking score in the subjective rating. The kinematic properties of these stimuli show clear correspondence with the moves that target the brain areas revealed as aesthetically relevant in the functional imaging analysis.

DISCUSSION

We investigated the neural correlates of implicit aesthetic responses to dance. Naïve subjects watched dance videos in an fMRI scanner without any instruction to evaluate them aesthetically. In a later session, they gave ratings to indicate their aesthetic response to the stimulus along a number of established aesthetic dimensions. Only the like-dislike dimension revealed significant neural correlates of aesthetic experience in our analysis. We show that brain activity increases in right premotor cortex and bilateral early visual cortices, during observation of movements having higher group-average aesthetic ratings. These results suggest the involvement of sensorimotor and visual cortices during the aesthetic experience of dance.

A physical description of the dance movements in each of the brain regions targeted by the liking-disliking aesthetic dimension showed that these areas prefer dance movements involving whole body movement with significant displacement of the body in space (e.g. jumping). Dance movements confined to a single limb, without significant displacement of the torso, and movement without vertical variation, produced least activation in the aesthetically-relevant areas. We found no obvious differences in aesthetic coding between occipital and sensorimotor areas. This suggests that the two areas together form part of a common aesthetic network for movement.

A very similar pattern of dance movement preference was identified by highest and lowest rated movements in the behavioural questionnaire. To summarize, in dance, a putative ‘average’ observer based on the consensus of our 6 subjects would prefer energetic jumping movements over simpler in-place movements. This group-average subjective response corresponds to the subjects’ visual and premotor cortex activations. In other words, description of the four movement criteria showed strong agreement between the subjective questionnaire responses and the quantitative analysis based on visual and sensorimotor cortical activations. Specific movement parameters such as vertical and horizontal displacement of the body may selectively target aesthetically relevant brain areas, and thus generate specific aesthetic responses, at least in our putative average observer. Choreographers could use this information to ‘neurotarget’ their choreography. Finally, although we can generalise our findings over the population of ballet and capoeira moves, and perhaps therefore to dance generally, we cannot be confident that all biological movements, including hand actions, running etc., would evoke aesthetic responses in the same way.

We were unable to find any reliable neuroaesthetic correlates of any of the other dimensions included in our questionnaire. There could be several reasons for this null finding. It could be merely a power problem, due to the small number of subjects tested. It could also be a by-product of our consensus approach. If our 6 subjects showed large individual differences in judgements of, say, tense-relaxed, then there might be little homogeneity between activations when viewing ‘consensus-tense’ or ‘consensus-relaxed’, and thus no consistent difference in brain activation across subjects between these categories. However, inspection of the variability across our 6 subjects in normalised ratings showed similar variability in all the aesthetic dimensions. More interestingly, it could be that the brain is more concerned with coding some parameters of action than with others.

We find it interesting that a relatively straightforward stimulus dimension, such as ‘simple-complex’ lacks a clear neural substrate, while an attitudinal, affective dimension such as ‘like-dislike’ has a clear link to specifying underlying brain processes. Our results suggest that ‘liking-disliking’ may be a fundamental dimension of aesthetic activation, with clear and consistent neural correlates. Similar uni-dimensional approaches have been suggested on the basis of factor analysis of aesthetic judgements (Eysenk, 1940; Marty et al., 2003). Those studies suggest a single ‘aesthetic impression’, often captured by the terms ‘liking’, ‘beauty’, accounts for a major part of aesthetic evaluation and experience in many individuals. Zeki (1999) has suggested that we may have a fundamental appreciation while discarding any underlying artistic theories of why our preferences are as they are (Zeki, 1999): ‘I might not know much about art but I know what I like’. Moreover, Zeki argues, the selectivity of visual perceptual processes in the brain may explain such liking.

Therefore, one might distinguish between three levels of aesthetic experience: 1) sensorial experience; 2) cognitive/semantic experience; 3) emotional / hedonic experience. Our results suggest that there is a neural activation corresponding to consensus liking. This activation was clearly located in sensory and motor brain areas, and not in the dopaminergic reward system (O'Doherty, Deichmann, Critchley & Dolan, 2002). Aesthetic experience is also often linked to the concept of pleasure. Emotional and hedonic brain regions have been reported to correlate with intense pleasurable experience associated with *pre-selected* artistic stimuli (e.g. favourite music; Blood & Zatorre, 2001). These activations presumably explain why many people choose to attend dance performances. Our fMRI study, in contrast, did not aim to produce hedonic responses. Indeed, aesthetic and hedonic responses were incidental to the subject's task during scanning. That is, we aimed to identify the neural correlates of *the perceptual experience of merely seeing* dance stimuli that are, on average, liked

According to Kant and followers, observers need to be in a certain state to have aesthetic experience, which Cupchik and Laszlo (1992) have called 'aesthetic attitude'. This attitude might be related to the aesthetic evaluation process of the stimuli.

In most neuroaesthetic experiments, brain activity has been measured during explicit aesthetic judgements (Cela-Conde et al., 2004; Kawabata et al., 2004). Here aesthetically-relevant brain activity was totally implicit, since brain activity was registered in a first session and aesthetic evaluation happened in a second presentation of the stimuli. This captures the ability of aesthetic content to surprise us: we may perceive and enjoy the aesthetic value of a stimulus even when we are not actively looking for beauty.

The brain network for implicit aesthetic perception of dance included the occipital and premotor cortices. The premotor cortex forms part of the 'mirror system' for perceiving and executing actions (Decety et al., 1999; Grafton et al., 1996; Rizzolatti et al., 1996). In a previous study using the same stimuli and additional expert dancer participants, we showed that activity in this area is modulated by the motor experience that the observer has with the action (Calvo-Merino et al., 2005; Calvo-Merino et al., 2006). Premotor areas showed stronger activations when dancers watched dance movements that they could themselves perform, compared to movements which they had not attempted. These studies suggest that when we watch an action, we simulate the movement using the same brain network that we use to execute it. Most action observation studies report bilateral activations, though these are typically stronger in the left hemisphere. Some studies have suggested that the left and right premotor cortices might code for different aspects of the observed movement. On one views the left premotor cortex would perform an initial analysis of the movement, while a more detailed analysis occurs in the right hemisphere (Grèzes, Costes & Decety., 1998). A related theory suggests that a categorical representation of goals is made in the left hemisphere, while the right hemisphere is more interested in detailed movement parameters (Manthey et al., 2003; Kosslyn et al., 1989). Our result is broadly consistent with the later interpretation. Since our subjects were naïve, and the dance movements were meaningless, categorical processing of action was presumably minimal. We suggest, instead, that the aesthetic response was driven by the specific kinematic details of the movements observed, leading to a right premotor dominance.

Here we show that a key area within the mirror system is also specifically activated when observing movements which are preferred, on average, by untrained observers. More specifically, we suggest that premotor cortex showed an additional epiphenomenological reaction that correlated with subjective liking. Since this area is also tuned by observations of large movements such as jumps and body displacement, there could be a correlation between the degree of liking, the degree of movement in a stimulus and, the activity induced in the premotor cortex.

The observer's liking might depend on the performer's ability. That is, beauty could reduce simply to skill. However, we might then expect other aesthetic dimensions, such as simple-complex, to have similar neuroaesthetic correlates to liking; yet this was not found. In addition, it is a commonplace in many arts, including dance, that a very simple stimulus can nevertheless seem beautiful. Finally, our participants were specifically selected as naïve observers with no dance experience. They should therefore have only a very general sensitivity to the specific motor skills required to perform the movements that they saw.

A previous study by Kawabata et al. (2004) reported activity in the nearby primary motor cortex during observation of pictures previously classified as ugly, in comparisons to those considered beautiful (Kawabata et al., 2004). Our study used dance movements, in contrast to the paintings used by Kawabata et al.. Moreover, we found a different direction of activation (liked>unliked) in *pre*motor cortex. We speculate that the brain's motor systems may be involved in two different levels of aesthetic response. First, primary motor areas may code for basic orienting behaviours such as approach and retreat, to aesthetically pleasing or unpleasant stimuli respectively. These responses would be independent of the specific form and content of the stimulus. Second, specific kinds of aesthetic content which involve motor performance, may induce a form of 'motor resonance' (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) in premotor areas, and other structures of the so-called ‘mirror system’ (Calvo-Merino et al., 2006). Kawabata et al.’s result might involve the first mechanism, while our present result might involve the second.

A network of visual cortical areas independently process multiple features of stimuli, such as colour, form, motion and depth independently (Zeki & Lamb, 1994). Here we were careful to control for as many of these factors as possible. For example, we used only two performers, with neutral clothing and background, and blurred facial features. Therefore, differences between the dance movements can only be attributed to essential kinematic aspects of the movements, such as speed, and movement direction. Previous studies have shown activation in several visual areas during aesthetic evaluation of paintings (Vartanian et al., 2004). Interestingly, Jacobsen and collaborators (Jacobsen et al., 2006) found greater activity in extrastriate visual cortex during symmetry judgement compared to aesthetic judgment. It is know that symmetry is a visual property often associated with beauty (Leder et al., 2004). Our results suggest that dance movements which were on average liked by observers, evoked greater activity in early visual cortex than those less liked. Moreover, this difference correlates with specific visual attributes of the movement, notably the amount of visual motion. Our results from dance therefore agree with Zeki and Lamb’s assertion that *‘All visual art must obey the laws of the visual system’* (Zeki et al., 1994).

Final conclusions

Dance is a performing art based on aesthetic experiences being induced by observing others’ actions. The neuroscientific basis of this cultural and artistic form has been relatively little studied. We show that bilateral occipital cortex and right premotor cortex are involved in the aesthetic response to dance. Specifically, when a group of naïve subjects viewed dance movements, activation of these areas was related to later group-average aesthetic evaluations of the stimuli. Knowledge of how aesthetically pleasing actions are coded in the human brain could be applied in dance teaching and choreography. We found that the degree of whole-body movement is a major driver of aesthetic evaluation of dance, and also has reliable consensus correlates in sensorimotor and visual form processing areas of the human brain. Therefore, our results give rise to the possibility of a ‘menu’ of dance moves, from which artists could choose those which target aesthetically sensitive areas. We believe this is the first neuroscientific study of aesthetic perception in the context of the performing arts.

Figure 1: Areas with activations correlating with consensus aesthetic evaluation. The highlights indicate areas whose activations correlate (p<0.001 uncorrected) with the group consensus aesthetic ratings on a scale between ‘like’ and ‘dislike’. Projections of the activation foci on the surface of a standard brain (Montreal Neurological Institute) show (**A**) posterior view showing bilateral activations in medial visual cortices: in the left hemisphere (-6, -81, 18) and in the right hemisphere (15, -87, 33), (**B**) lateral view showing right premotor activation (24, 0, 69).

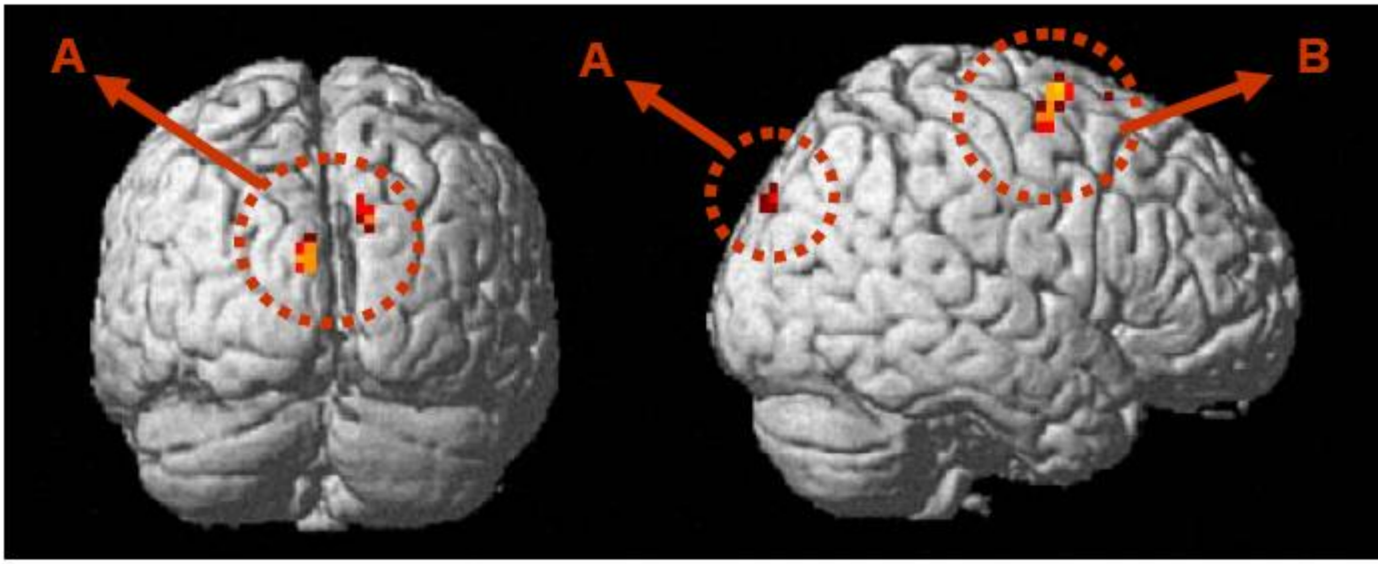

Figure 2. Dance movements associated with activation in premotor and visual areas. The top row shows still images of the 3 s movements associated with strongest brain responses in (**A**) visual regions (medial visual cortex in the left hemisphere; -6, -81, 18) and (**B**) premotor regions (right premotor cortex; 24, 0, 69). The bottom row shows the movements that evoked the weakest activity in the same brain areas. Note that the movements in the top row (stronger activation) include horizontal and vertical displacement (jumping), while those in the bottom row (weaker activity) involve mainly one limb and little displacement.

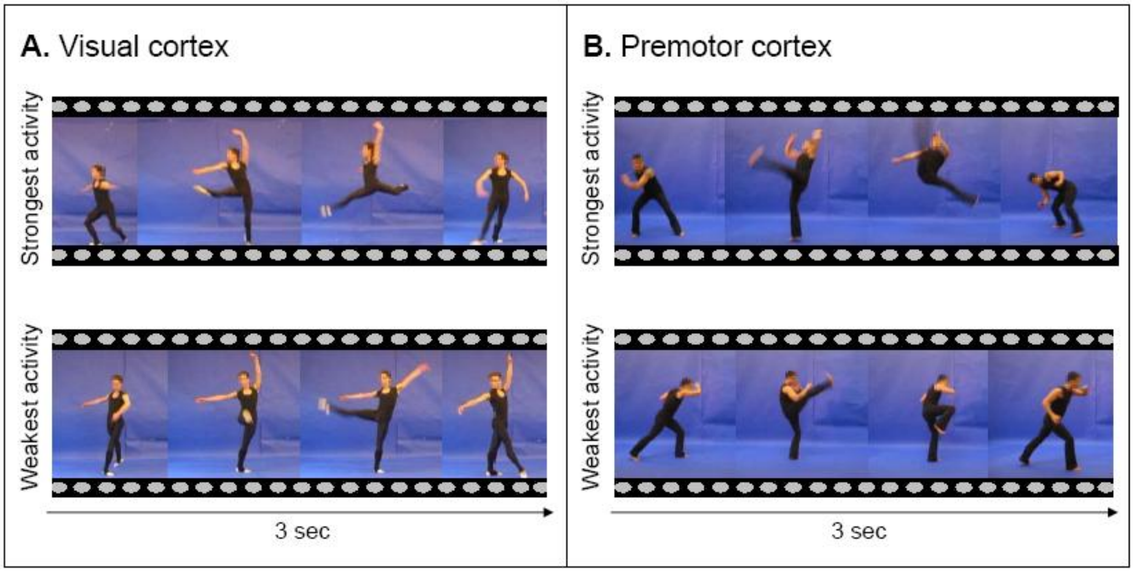

Figure 3: Example of dance movements that achieved highest and lowest scores on the aesthetic questionnaire. Movements that achieved the highest (A) and lowest (B) consensus rating in the like-dislike scale. Note that the movements with higher scores include vertical displacement/jumping, while the movements with lower scores involve minimal horizontal displacement.

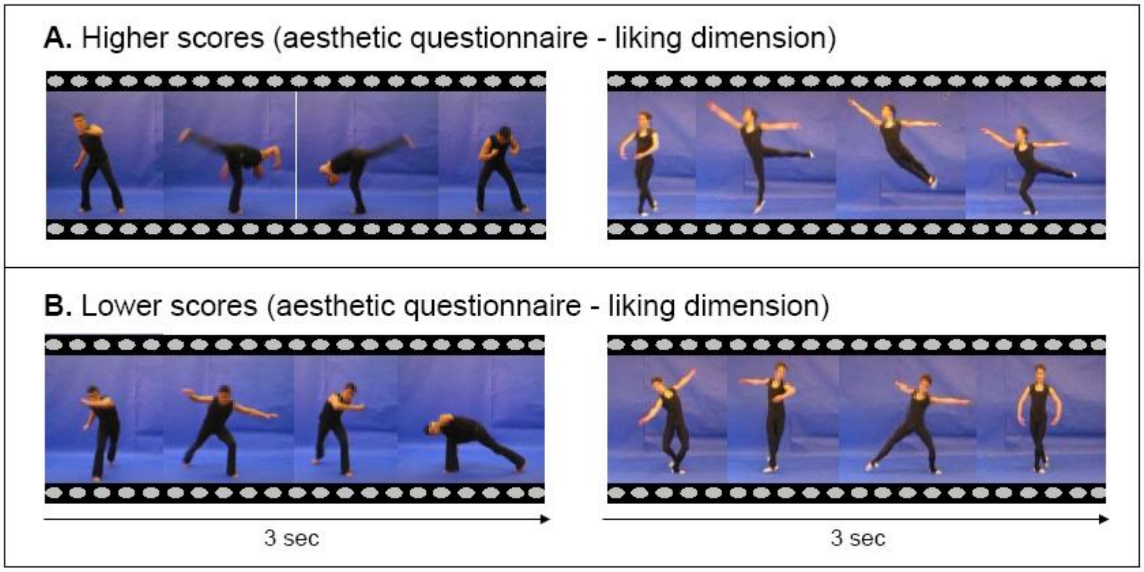

Table 1: Transformed Z scores from an SPM{t} map for those brain areas whose activation differed between observation of dance movements that received higher or lower ratings on the liking dimension. L, left hemisphere; R, right hemisphere; p<.0001 uncorrected. Only activations in excess of 10 voxels are listed.

Brain regions	**MNI coordinates**			***Z*-score**
	x	***y***	***z***	
R Superior frontal gyrus	**24**	**0**	**69**	**4.16**
R Superior precentral sulcus	**30**	**-3**	**36**	**3.85**
R precuneus/ superior occipital gyrus	**15**	**87**	**33**	**3.44**
L cuneus/superior occipital gyrus	**-6**	**-81**	**18**	**3.71**

References

Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron, 32,* 537-551.

Berlyne, D. E. (1974). *Studies in the new experimental aesthetics: steps toward an objective psychology of aesthetic appreciation*. (vols. Washington, D.C.: Hemisphere Publishing).

Blood, A. J. & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences of the United States of America, 98,* 11818-11823.

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cereb.Cortex, 15,* 1243-1249.

Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr.Biol., 16,* 1905-1910.

Cela-Conde, C. J., Marty, G., Maestu, F., Ortiz, T., Munar, E., Fernandez, A. et al. (2004). Activation of the prefrontal cortex in the human visual aesthetic perception. *Proc.Natl.Acad.Sci.U.S.A, 101,* 6321-6325.

Cross, E. S., Hamilton, A. F. D. C., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *Neuroimage, 31,* 1257-1267.

Cunningham, W. A., Johnson, M. K., Gatenby, J. C., Gore, J. C., & Banaji, M. R. (2003). Neural components of social evaluation. *J Pers.Soc.Psychol, 85,* 639-649.

Cupchik, G. C. & László, J. (1992). Emerging visions of the aesthetic process : psychology, semiology, and philosophy. Cambridge University Press, Cambridge, New York, USA.

Decety, J. & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends Cogn Sci., 3,* 172-178.

Duvernoy HM (1999). *The human Brain. Surface, blood supply and three-dimensional sectional anatomy.*

Goldman, A. (2001). The Routledge companion to aesthetics. In B.Gaut and D.McIver Lopes (Ed.), *The Aesthetic* (pp. 181-192). London: Routledge..

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp.Brain Res., 112,* 103-111.

Grèzes, J., Costes, N., & Decety L. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology, 15,* 553-582.

Grèzes, J., Frith, C. D., & Passingham, R. E. (2004). Inferring false beliefs from the actions of oneself and others: an fMRI study. *Neuroimage, 21,* 744-750.

Grossman, E. D. & Blake, R. (2002). Brain Areas Active during Visual Perception of Biological Motion. *Neuron, 35,* 1167-1175.

Iidaka, T., Okada, T., Murata, T., Omori, M., Kosaka, H., Sadato, N. et al. (2002). Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. *Hippocampus, 12,* 352-362.

Jacobsen, T. (2004). Individual and group modelling of aesthetic judgment strategies. *Br.J Psychol, 95,* 41-56.

Jacobsen, T., Buchta, K., Kohler, M., & Schroger, E. (2004). The primacy of beauty in judging the aesthetics of objects. *Psychol Rep., 94,* 1253-1260.

Jacobsen, T. & Hofel, L. (2002). Aesthetic judgments of novel graphic patterns: analyses of individual judgments. *Percept.Mot.Skills, 95,* 755-766.

Jacobsen, T., Schubotz, R. I., Hofel, L., & Cramon, D. Y. (2006). Brain correlates of aesthetic judgment of beauty. *Neuroimage., 29,* 276-285.

Kawabata, H. & Zeki, S. (2004). Neural correlates of beauty. *J Neurophysiol., 91,* 1699-1705.

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. E. (1989). Evidence for 2 Types of Spatial Representations - Hemispheric-Specialization for Categorical and Coordinate Relations

650. *Journal of Experimental Psychology-Human Perception and Performance, 15,* 723-735.

Leder, H., Belke, B., Oeberst, A., & Augustin, D. (2004). A model of aesthetic appreciation and aesthetic judgments. *Br.J Psychol, 95,* 489-508.

Manthey, S., Schubotz, R. I., & von Cramon, D. Y. (2003). Premotor cortex in observing erroneous action: an fMRI study. *Cognitive Brain Research, 15,* 296-307.

Marty, G., Conde, C. J. C., Munar, E., Rossello, J., Roca, M., & Excudero, J. T. (2003). Factorial dimension of aesthetic experience. *Psicothema, 15,* 478-483.

McManus, I. C. (1980). The aesthetics of simple figures. *Br.J Psychol, 71,* 505-524.

McManus, I. C. & Weatherby, P. (1997). The Golden Section and the aesthetics of form and composition: A cognitive model. *Empirical Studies of the Arts, 15*.

O'Doherty, J. P., Deichmann, R., Critchley, H. D., & Dolan, R. J. (2002). Neural responses during anticipation of a primary taste reward. *Neuron, 33,* 815-826.

Paradiso, S., Johnson, D. L., Andreasen, N. C., O'Leary, D. S., Watkins, G. L., Ponto, L. L. et al. (1999). Cerebral blood flow changes associated with attribution of emotional valence to pleasant, unpleasant, and neutral visual stimuli in a PET study of normal subjects. *Am.J Psychiatry, 156,* 1618-1629.

Petrides, M. (2000). The role of the mid-dorsolateral prefrontal cortex in working memory.. *Exp.Brain Res., 133,* 44-54.

Puce, A. & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philos.Trans.R.Soc.Lond B Biol.Sci., 358,* 435-445.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D. et al. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp.Brain Res., 111,* 246-252.

Rolls, E. T. (2000a). Precis of The brain and emotion. *Behav.Brain Sci., 23,* 177-191.

Rolls, E. T. (2000b). The orbitofrontal cortex and reward. *Cereb.Cortex, 10,* 284-294.

Small, D. M., Zatorre, R. J., Dagher, A., Evans, A. C., & Jones-Gotman, M. (2001). Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain, 124,* 1720-1733.

Sunaert, S., Van Hecke, P., Marchal, G., & Orban, G. A. (1999). Motion-responsive regions of the human brain. *Exp.Brain Res., 127,* 355-370.

Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proc.Natl.Acad.Sci.U.S.A, 98,* 11656-11661.

Vartanian, O. & Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport, 15,* 893-897.

Whissell, C. M. (1980). Aesthetic judgment of shapes: eye color, complexity, and first- and second-order symmetry as predictors. *Percept.Mot.Skills, 51,* 395-401.

Zajonc, R. B. (1968). Attitudinal Effects of Mere Exposure. *Journal of Personality and Social Psychology, 9,* 1-&.

Zeki, S. (1999). Inner Vision. Oxford: Oxford University Press .

Zeki, S. & Lamb, M. (1994). The neurology of kinetic art. *Brain, 117 (Pt 3),* 607-636.