The influence of sensorimotor experience on the aesthetic evaluation of dance across the life span

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Abstract

Understanding how action perception, embodiment, and emotion interact is essential for advancing knowledge about how we perceive and interact with each other in a social world. One tool that has proved particularly useful in the past decade for exploring the relationship between perception, action, and affect is dance. Dance is, in its essence, a rich and multisensory art form that can be used to help answer not only basic questions about social cognition but also questions concerning how aging shapes the relationship between action perception, and the role played by affect, emotion, and aesthetics in social perception. In the present study, we used a 1-week physical and visual dance training paradigm to instill varying degrees of sensorimotor experience among non-dancers from three distinct age groups (early adolescents, young adults, and older adults). Our aim was to begin to build an understanding of how aging influences the relationship between action embodiment and affective (or aesthetic) value, at both brain and behavioral levels. On balance, our results point toward a similar positive effect of sensorimotor training on aesthetic evaluations across the life span on a behavioral level, but to rather different neural substrates supporting implicit aesthetic judgment of dance movements at different life stages. Taken together, the present study contributes valuable first insights into the relationship between sensorimotor experience and affective evaluations across ages, and underscores the utility of dance as a stimulus and training intervention for addressing key questions relevant to human neuroscience as well as the arts and humanities.

Keywords

Dance, Embodiment, Affective judgment, Neuroaesthetics, Sensorimotor experience, Aging, Life span

1 INTRODUCTION

Humans are intensely social creatures, and as such, many of our waking hours are filled with watching and interacting with each other. Our ability to understand other peoples' behavior from their actions is essential not just for forming friendships and achieving mutual goals but also for the very survival of our species (Frith and Frith, 2012). Neuroscience research probing the biological substrates of social action perception has grown exponentially in the last two decades, with a PubMed search performed in January 2018 revealing over 1000 papers published on this topic in the past 5 years alone. This surge in recent research activity on social action perception means that our understanding of the underlying cognitive and neural mechanisms that support complex action perception and learning is developing and advancing at a rapid rate.

However, an often-overlooked feature of action perception is the influence of affect or emotion on how we perceive others' movements. It is uncontroversial that affective evaluations influence myriad of our everyday choices, such as choosing one object over another (Bayliss et al., 2006; Constable et al., 2014; Flavell et al., 2017), and it is also well known that our emotional state modulates how we empathize with and understand other people (Silani et al., 2013; Singer and Lamm, 2009; Steinbeis, 2016). However, while many studies have explored the relationship between facial expressions and a perceiver's affect, only a small number of recent studies have begun to explore how body movements might influence an observers' affective state, and which factors modulate the relationship between action perception and affective processing (Christensen et al., 2016; Grèzes et al., 2013; Kirsch et al., 2016a).

One research avenue that is proving to be particularly fruitful for identifying the relationship between action perception and affective processing involves exploring aesthetic evaluations of performing arts that feature the human body in motion. More broadly speaking, the relationship between aesthetic experience, art, and science has generated great interest in recent years. Art both contributes to and defines human culture, thus cementing its importance in human society. Over the past several decades, an increasing volume of research seeking to characterize aesthetic experiences at brain and behavioral levels has given rise to the burgeoning field of neuroaesthetics. As a field, neuroaesthetics seeks to quantify and characterize the relationship between neurobiology and aesthetic judgment (Chatterjee, 2011, 2013; Chatterjee and Vartanian, 2014; Kawabata and Zeki, 2004; Leder and Nadal, 2014; Leder et al., 2004; Rolls, 2014). Nadal et al. (2012) describe aesthetic judgment as a fully embodied and enactive process in which expertise plays an

important role. Authors note distinct neural substrates subserving positive aesthetic judgments, including somatosensory cortical regions (Calvo-Merino et al., 2008, 2010), subcortical reward circuitry (Bohrn et al., 2013; Kawabata and Zeki, 2004; Vartanian and Goel, 2004), and areas of prefrontal cortex involved in top-down processing and evaluative judgments (Cela-Conde et al., 2004; see Chatterjee and Vartanian, 2014 and Kirsch et al., 2016b for reviews). However, most of the neuroaesthetics research to date has focused on how we perceive paintings or geometrical shapes (e.g., Berlyne, 1974; Ishizu and Zeki, 2013; Jacobsen et al., 2006). Fewer studies have explored aesthetic appreciation of dynamic stimuli, such as those that typify the performing arts. The relative paucity of research attention on the performing arts in general, and dance in particular, is noteworthy due to the fact that the human body in motion is a stimulus with incomparable biological relevance, and has widely been the object and the instrument of art creation (Calvo-Merino et al., 2010; Cazzato et al., 2014; Di Dio et al., 2007). Taken together, a deeper understanding of how we cognitively, perceptually, and emotionally respond to artworks that feature the human body in motion should advance understanding not only of affective perception but also of the artifacts and performances that serve as hallmarks of a civilized society.

A growing number of studies document how prior experience with an action shapes the brain's response during action observation (Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009; Gardner et al., 2015; Kirsch and Cross, 2015; Liew et al., 2013). Similarly, an observer's aesthetic experience of an action can also change depending on his or her prior experience with the stimulus being observed (Calvo-Merino et al., 2010; Cross et al., 2011; Kirsch et al., 2013, 2015; Ticini et al., 2014). Activation of sensorimotor cortex during the aesthetic judgment of any kind of stimulus was originally speculated to relate to preparing the observer for action, either to avoid an unpleasant (ugly) stimulus or approach a pleasant (beautiful) stimulus (Armory and Dolan, 2002; Kawabata and Zeki, 2004). The role played by the motor cortex in aesthetic experience has been reconsidered, however, by a theoretical framework proposed by Freedberg and Gallese (2007). According to this framework, the simulation of actions, emotions, and corporeal sensations provoked by a particular art form brings about an aesthetic experience in an observer. This theory, called the embodied simulation account of aesthetics, is largely based on the notion that a tight link exists between perception and action (Coello and Fischer, 2015; Prinz, 1997; Schütz-Bosbach and Prinz, 2007). By allowing embodiment of the actions depicted on a canvas or performed by an actor or dancer on stage, or in any other way elicited by an artist via an artistic medium, sensorimotor brain regions contribute to the aesthetic evaluation of a given artwork and underpin a spectator's empathic response toward the art (Kirsch et al., 2015; Ticini et al., 2015). In a review paper, Nadal et al. (2012) add further support to Freedberg and Gallese's proposal (2007) by describing the aesthetic experience as one that is fully embodied and enactive, in which an observer's prior experience or expertise plays a role.

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Several studies have demonstrated that acquired expertise influences aesthetic judgments. A consistent finding is that individuals tend to like objects, paintings, text, and even abstract visual stimuli more when they are familiar with them (Bohrn et al., 2013; Hekkert et al., 2003; Jacobsen et al., 2006; Sluckin et al., 1982). Behavioral studies have shown that the level of an observer's expertise modulates his or her aesthetic evaluation of artworks (Hekkert and van Wiering, 1996; Schmidt et al., 1989; Sluckin et al., 1982; Zajonc, 1968), and brain imaging experiments confirm that acquired expertise is associated with changes in brain structures underlying perceptual and memory processes (Bangert et al., 2006). Moreover, our group has shown that accumulating experience with a movement across a number of sensorimotor modalities (such as the visual, auditory, and sensorimotor domains) leads to a greater enjoyment during subsequent viewing of this movement (Kirsch et al., 2013, 2015). Together, these studies suggest that an observer's expertise, whether embodied or conceptual, changes how artworks are perceived and judged.

In the present study, our aim was to begin to build a more holistic picture of the impact of sensorimotor experience on aesthetic evaluation of dance by examining the relationship between embodiment and aesthetics throughout the life span. As with several of our previous studies (e.g., Cross et al., 2011; Kirsch et al., 2015), we are interested in examining this relationship at both behavioral and brain levels. The current work builds upon our previous investigations in two main ways: (1) we aim to focus on "pure," distilled motor representations related to sensorimotor training experience, and achieve this by using silhouettes of individual movements (cf. Sumanapala et al., 2017); and (2) we aim to take the first steps in building understanding of the impact of development and aging on aesthetic appreciation of dance, which we achieve by testing three age groups on our experimental measures.

As the discipline of neuroaesthetics itself is still in its naissance, and research attention examining neuroaesthetic questions in the performing arts is even more limited, it is perhaps not surprising that the small number of studies published in this domain to date has primarily focused on young adults (Calvo-Merino et al., 2010; Kirsch et al., 2015). However, as we begin to more fully understand the role played by affective processing during social action perception, greater knowledge about how implicit and explicit emotional responses evolve across the life span will be beneficial, both in terms of advancing understanding of the basic neurocognitive mechanisms that support social perception, and also to help foster a deeper appreciation of the value of art from childhood through to advanced age. To date, and to our knowledge, only a handful of studies have looked at questions concerning the relationship between age and the aesthetic appreciation of art. For example, Savazzi et al. (2014) examined the visual explorative behavior of adolescents while looking at paintings, during aesthetic and movement judgment tasks, and Pugach et al. (2017) examined the stability of aesthetic preferences for faces and landscapes across the life span. Importantly, this latter study used a cross-sectional design with the primary focus of evaluating the stability of aesthetic judgment across the life span. Thus, an understanding on how life span development and an observer's bespoke experience with a given stimulus shapes and changes aesthetic appreciation is still an area ripe for exploration.

In the present study, our aim is to take the next steps toward characterizing life span changes in aesthetic perception by adapting a similar approach to one we used previously (Kirsch et al., 2015). This paradigm makes use of a whole-body dance training paradigm, with subjective ratings and fMRI scans collected before and after different types of sensorimotor training. To address the life span development question, we carried out our experimental procedures with three age groups: young adolescents (12-14 years), young adults (18-23 years), and older adults (55–69 years). It is important to note that we designed this study to ask a number of different questions (several of which are examined in other papers, for example, Kirsch et al., 2018; chapter "Neurodevelopmental perspectives on dance learning: insights from early adolescence and young adulthood" by Sumanapala et al., in this volume). The questions examined in the present paper are by definition exploratory in nature, given the modest sample size composing each age group. However, given the novelty and relevance of questions concerning the relationship between embodiment, aesthetic evaluation, and the role of life span development to individuals from both art and science domains, the present study should nonetheless provide a useful point of departure for future work to replicate and extend.

2 METHODS

2.1 PARTICIPANTS

Seventeen neurologically and physically healthy adolescents aged between 12 and 14 years were recruited through advertisements shared through internal mailing lists within Bangor University, 23 physically and neurologically healthy young adults were recruited from the Bangor University student population, and 19 physically and neurologically healthy older adults were recruited from the local community. Older adults were screened for any past medical history, and we excluded any participants who reported any prior neurological diseases or use of medication that might alter their performance during the task or fMRI scanning. Only dance-naïve participants were selected to take part. Two adolescents and five young adult participants were excluded from the final sample due to excessive motion artifacts while undergoing fMRI scanning, and one young adult dropped out of the study halfway through the training phase, and thus had to be excluded due to having an incomplete data set. Four older adults were excluded, as they did not complete all ratings collected during the pre-training phase. The final sample thus comprised 15 young adolescents (6 females; mean age = 12.80 years, SD = 0.77, range 12-14 years), 18 young adult participants (12 females; mean age = 19.5 years, SD = 1.54, range 18–23 years), and 15 older adult participants (11 females; mean age = 63.6 years, SD = 4.4, range 55–69 years). All participants provided written, informed consent prior to taking part in any study procedures, and were reimbursed for their involvement with either cash or course credit. For adolescent participants, parents/legal guardians provided informed consent before participation. The Bangor University School of Psychology Research Ethics Committee approved all components of this study (protocol number 2014-13123-A12806).

2.2 STIMULI AND APPARATUS

Six dance sequences from the dance game "Dance Central 2" (Harmonix Music Systems, 2011) for the XBox 360 KinectTM console were chosen that featured gender-neutral dance movements. The six chosen dance sequences were specifically selected so as to contain no overlapping dance moves between songs (i.e., each move was uniquely associated to one song/dance sequence). Each dance sequence was set to a popular song (for example, Like a G6 by Far East Movement or What is Love by Haddaway; average length = $2.22 \,\mathrm{min}$, SD = $10 \,\mathrm{s}$; average tempo = $118.83 \,\mathrm{bpm}$, SD = 11.21). To focus participants' attention on the avatar whose moves they were learning, the same background setting was selected for all dance videos, which had a minimal amount of extraneous movement. The difficulty of the dance sequences (complexity and amplitude of dance movements) was set to a minimum level to ensure participants across both age groups could perform them to some degree from the very first training day, but would still have ample room for improvement. The six dance sequences were paired to create three groups whose composition was matched for number and complexity of specific dance movements, as well as tempo. Each pair of sequences was assigned to one of the three training conditions; physical training, visual training, and no experience/untrained. A total of three different training groups were assembled, meaning that each pair of dance sequences was trained in all three training conditions across participants.

Animated silhouettes from the game depicting individual movements from the preselected dance sequences were captured and used as stimuli during both preand post-training fMRI sessions. The use of silhouettes, instead of original game footage, was specifically chosen to reduce visual cues associated with the original training context and to focus attention on the movements alone (Sumanapala et al., 2017). In this way, brain activity recorded when observing these pared-down dance movements should be more attributable to sensorimotor experience. Eighteen short animated silhouettes dance segments without music were extracted using iMovie '11 (Apple Inc.) and edited using Adobe Premiere Pro (Version 7.1 for Microsoft Windows 7), three sequences from each full dance sequence. The resultant 18 stimuli were matched for length to all be 1.95 s long. Each stimulus was edited so that it featured one complete, coherent dance move involving whole-body motion and significant spatial displacement of the limbs (cf. Calvo-Merino et al., 2008). All stimuli were novel to participants during the pre-training fMRI scan.

2.3 BEHAVIORAL TRAINING PROCEDURE AND ANALYSIS

Participants were randomly assigned to one of three training groups in which they experienced the same pairs of sequences assigned to the two training conditions (this took place between the pre- and post-training fMRI scanning sessions, see Fig. 1). For each training session, participants completed physical and visual training on the sets of sequences to which they had been randomly assigned. Participants physically practiced the same two sequences twice (once with a female and once

A Example of one trial seen in the scanner 500 ms 1.95 s 400 ms 1.95 s 3 s + One dance movement stimulus = 4.3 s

Time

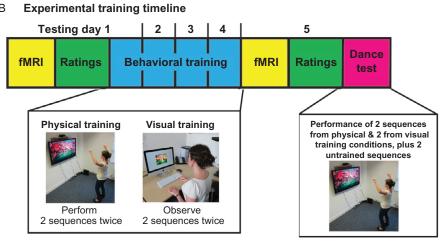


FIG. 1

(A) Schematic of a single fMRI trial. Each typical fMRI trial consisted of a 500 ms fixation cross, one dance movement stimuli lasting for 4.3 s, and an intertrial interval (ITI) of 3 s. (B) Overview of experimental procedures across the 5 days of the experiment. Participants of the 3 age groups underwent the exact same procedure. First they underwent a scanning session on Day 1, then rated the same stimuli outside the scanner, and then started the behavioural training on that same day and the following 3 days. During each training day (Days 1–4), participants physically trained with 2 long sequences, and visually trained with other long sequences. 2 other long sequences remained untrained. On Day 5, participants underwent the same scanning session as on Day 1. After scanning on Day 5, participants had to first rate again all the stimuli observed in the scanner, and then to physically perform all the long sequences (physically, visually trained, and untrained).

with a male avatar), and observed two additional sequences twice. The order in which participants completed the training conditions was counterbalanced within and across participants across training days. Each training session lasted approximately 30 min.

2.3.1 Physical training

For sequences participants physically practiced, they stood approximately 2 m away from a 52" Sharp flat screen television mounted on the wall in front of them. Participants' task was to mirror the dance movements of the avatar in the *Dance Central 2* Xbox 360 KinectTM game as closely as possible and concentrate on improving their performance during subsequent sessions. Similar procedures using this system have been successfully applied in previous studies measuring the neural effects of dance training in young adults (see also chapter "Neurodevelopmental perspectives on dance learning: insights from early adolescence and young adulthood" by Sumanapala et al., in this volumefor more details; Karpati et al., 2017; Kirsch and Cross, 2015; Kirsch et al., 2013, 2015, 2018; Sumanapala et al., 2017). Participants' dance scores were recorded by the researcher and used as an objective measure of dance performance ability for the behavioral analyses.

The four dance scores participants received each day for the dance sequences in the physical training condition were averaged so that each participant had a single score representing dance performance for each training day. A mixed ANOVA with training day assigned as a within-subjects factor with four levels (training days 1–4), and age group as between-subject factor (adolescents, young adults, older adults), was conducted on these scores in order to determine how performance across consecutive days of training compared between age groups.

2.3.2 Visual training

For the sequences for which participants acquired visual experience, they sat comfortably in front of a computer running Psychophysics Toolbox 3 in MATLAB[®] R2010a (MathWorks Inc.), which presented the full dance videos, with the associated audio soundtrack. Each video was shown twice, once for each avatar (male, female), in a random order. Participants were instructed to pay close attention to the dance sequences, and were told that they would have to perform the sequences at the end of the week, so they should try to learn the movements as best as they could by watching. To test that participants paid close attention, at the end of each music video, 10 short dance segments (five from the videos they had just watched) were displayed, without music, each followed by the question "Did you see this movement in the video you just watched?." Participants had to respond "yes" or "no" using the keyboard arrow keys. Test videos were presented silently as the task would have been too easy if the accompanying soundtracks were also presented. An accuracy score for each participant for each of the 4 days of training was calculated based on their performance on this task. The same ANOVA described earlier for the physical training scores was repeated for the visual accuracy scores.

2.3.3 Post-training performance assessment

On the final day of the study (day 5), after all other experimental procedures had been completed (including the post-training fMRI session), participants returned to the dance training laboratory to perform the four full dance sequences used in training (two physically trained sequences and two visually trained sequences), as well as

the two untrained sequences (segments that they had observed during both fMRI sessions only). The test followed the same procedures as the physical training phase of the study: participants physically performed the dance sequences from all six songs, mirroring the avatar's dance movements as closely as possible while the KinectTM system captured and scored their movements. The six sequences were randomized and balanced for the gender of the avatar. Objective performance scores were obtained in the same way as for the physical training condition.

Raw scores from both exemplars from each training category were averaged within training conditions to produce an average score per participant for each of the three test conditions. We first performed a mixed-design ANOVA using age group as a between-groups factor to compare dance performance among adolescents, young adults, and older adults on day 5. To further investigate performance in each age group independently, we then performed repeated-measures ANOVAs on these scores to investigate the impact of different kinds of experience on physical performance. Pairwise comparisons (Bonferroni corrected for multiple comparisons, with adjusted alpha levels of 0.025) were subsequently evaluated to investigate differences between conditions in more detail. Degrees of freedom reflect the Greenhouse–Geisser correction where assumptions of sphericity have been violated.

2.3.4 Liking ratings

On days 1 and 5, immediately following the pre- and post-training scanning sessions, participants were asked to watch again each dance sequence seen during scanning (18 in total), and to answer the question "How much did you like the movement you just watched?," on a 1–8 scale, with 1 corresponding to "not at all" and 8 corresponding to "extremely." By collecting these ratings on both day 1 (before any training took place) and day 5 (following all training procedures), this enabled us to have clear measures of pre- and post-training self-report aesthetic evaluation (as measured by liking; see Calvo-Merino et al., 2008; Cross et al., 2011). Moreover, in a separate block, participants watched again the 18 sequences and answered on the same 1–8 scale the question "How well do you think you can reproduce the movement you just watched?." These ratings were used as a parameter of noninterest in the fMRI design matrix, to control for individual differences in perceived physical ability to reproduce the movements.

Differences between post- and pre-training liking scores were calculated for each sequence, and then averaged by training condition. Repeated-measures ANOVAs were conducted on average liking ratings from the pre-training session (day 1) and the post-training session (day 5), as well as on the difference between post- and pre-training averaged liking ratings, with training type as a within-subjects factor and age group as a between-subjects factor.

2.4 NEUROIMAGING PROCEDURE AND fMRI DATA PROCESSING

Each participant completed one fMRI session prior to the training procedures and an identical session immediately following the 4 days of training (Fig. 1B). Participants completed 6 runs within each scanning session, lasting an average of 9 min and

while in the scanner.

containing 60 trials each. In each run, participants watched three times 18 stimuli featuring short dance segments taken from the three training conditions (physically trained, visually trained, and untrained; 6 stimuli per training condition). Unlike the video footage used during training, the videos used during scanning featured the silhouette of an avatar performing each dance movement, which lasted 1.95 s. Each individual dance movement was presented twice in a row with a 400 ms black screen between each presentation (see Fig. 1A). Each stimulus was preceded by a green fixation cross presented for 500 ms, to announce the next trial. Each dance stimulus was followed by a fixation cross presented for a fixed duration of 3 s. After this, the next trial started. Finally, six additional video stimuli (featuring dance movements that were not part of the full set of 18 videos taken from the training conditions—these dance movements were never encountered outside of scanning) were included for attentional control questions. After each of these six test trials, participants were asked a question that required a yes or no response (button responses were counterbalanced across participants, with an index finger press corresponding to a yes response and a middle finger press corresponding to a no response for half of the participants and the inverse response schedule for the other half of participants). Participants had 4 s to provide a response via a four-button fiber-optic response box placed on their lap on which they rested the index finger and middle finger of both hands over the buttons. The question that appeared was randomly selected to be one of the following four: "Did the dancer place at least one arm above his head?"; or "Did the dancer reproduced the same movement on the left and on the right?"; or "Did the dancer take a step forward?"; or "Did the dancer move his legs?." These questions appeared in a random order and were designed to ensure participants paid full attention to the dancer's movement in each stimulus. Each test trial was followed by a 12s fixation cross that served as implicit baseline. Participants were familiarized outside the scanner prior to the pretraining scan with all features of the experiment and what they would be asked to do

Stimulus presentation and response recording was done via a Mac desktop computer running MATLAB® R2013a (MathWorks, Natick, MA) and Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). The video stimuli were presented on a 24" LCD BOLDscreen (Cambridge Research Systems), which was visible to participants via a mirror mounted on the head coil. The experiment was carried out in a 3T Philips MRI scanner using a SENSE phased-array 32-channel head coil. For functional imaging, a single-shot echo planar imaging sequence was used (T2*-weighted, gradient echo sequence; echo time TE = 30 ms; flip angle, 90 degree). The scanning parameters were set as follows: repetition time TR = 2500 ms; 38 transverse slices; voxel dimensions, 2.3×2.3 mm with voxel slice thickness = 3 mm; slice gap = 0.1 mm; field of view, $224 \times 224 \times 118$ mm; matrix size, 96×95 mm \times 38 slices; anterior–posterior phase encoding. Parameters for T1-weighted anatomical scans were: $240 \times 224 \times 175$ mm; voxel dimensions, $1 \times 1 \times 1$ mm; TR = 12 ms; TE = 3.5 ms; flip angle = 8 degree. All the scans were collected in an ascending order. For each run of each scanning session, the first

two brain volumes were discarded to reduce saturation effects. 224 volumes per functional run were collected for each participant.

Anatomical localization of all activations was assigned based on consultation of the Anatomy Toolbox in SPM v. 2.2. (Eickhoff et al., 2005a,b), in combination with the Yale online search tool (http://sprout022.sprout.yale.edu/mni2tal/mni2tal.html).

2.5 fMRI DATA ANALYSIS

Neuroimaging data from each scanning session (before and after training) were preprocessed separately. Using SPM12 (Wellcome Department of Imaging Neuroscience, London, United Kingdom), data were realigned and unwarped, coregistered to the individual participants' T1 scans, and normalized to the Montreal Neurological Institute (MNI) template. Slice timing correction was performed after realignment and all images were finally spatially smoothed using an 8 mm FWHM Gaussian kernel. A design matrix was fitted for each participant with a high-pass filter cutoff of 128 s, with each type of dance video (physical training, visual training, and untrained conditions), as well as attentional control videos and button presses associated, modeled together as a boxcar function convolved with the hemodynamic response function with temporal and dispersion derivatives. Two additional parametric modulators were included: participants' individual ratings of how much they liked each dance sequence and participants' individual ratings of how well they thought they could reproduce each dance sequence. Additionally, participant-specific movement parameters were modeled as separate regressors of no interest.

Group-level analyses were evaluated at the P < 0.005, k = 10 voxels threshold (Lieberman and Cunningham, 2009). As only few results survived cluster-corrected thresholds for multiple comparisons, all results should be considered preliminary at this stage (Eklund et al., 2016). Group-level analyses were designed to achieve two main objectives:

- 1. Aesthetic evaluation of novel dance movements. For each age group, a parametric analysis was run on the pre-training data, including individual participants' liking ratings for each movement sequence as a parametric regressor. All conditions are considered together in this analysis, as they were yet to be trained and were equally novel or unfamiliar at this stage.
- 2. Interaction between amount of experience and liking. For each age group, we next ran the same analysis on the post-training data. In this analysis stimuli of all conditions were also collapsed in a one-column matrix, as behavioral results showed a gradual increase of physical performance from untrained to visually trained to physically trained conditions, and a similar pattern was reflected in liking scores. This analysis should therefore reveal how increases in sensorimotor experience and liking modulate brain activity and to some extent reveals how experience and liking interact.

3 RESULTS

3.1 EFFECT OF TRAINING ON LIKING RATINGS ACROSS AGE GROUPS

To investigate the effect of training on liking ratings, we first assessed the effect of training on physical and visual performance across age. All participants increased their physical performance across days during physical training ($F_{(2.056,94.562)} = 114.502$, P < 0.001, $\eta_p^2 = 0.713$), as well as improved their recognition accuracy during visual training ($F_{(3.138)} = 27.039$, P < 0.001, $\eta_p^2 = 0.370$). Physical performance improvement interacted with age groups ($F_{(4.111,94.562)} = 7.080$, P < 0.001, $\eta_p^2 = 0.235$), with both adolescents and young adults performing better than older adults (AD vs OA: P = 0.010; YA vs OA: P = 0.004; AD vs YA: P = 1); however, in the visual accuracy task, no effect of age group on performance emerged (Fig. 2A and B).

On day 5 after 4 days of training, we assessed physical performance of all participants on all dance sequences (Fig. 2C). A main effect of training type was found across groups ($F_{(2,92)} = 67.140$, P < 0.001, $\eta_p^2 = 0.593$), with physically trained sequences being performed better than visually trained and untrained sequences (physically vs visually trained: P < 0.001; physically trained vs untrained: P < 0.001); but also visually trained sequences being better performed than untrained sequences (P = 0.024). Moreover, a main effect of age group on physical performance was observed ($F_{(2,46)} = 8.554$, P = 0.001, $\eta_p^2 = 0.271$), with adolescents

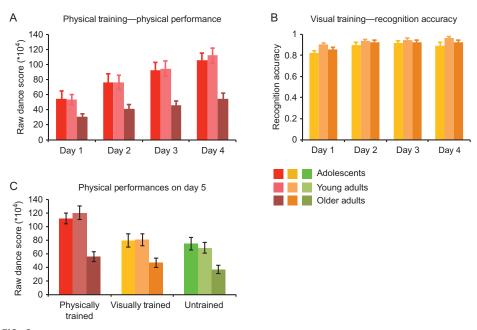


FIG. 2

Behavioral results across age groups. (A) Physical performance across days of training and age groups. (B) Recognition accuracy during visual training across age groups. (C) Physical performances on day 5 after different trainings across age groups.

and young adults performing similarly but better than older adults overall (AD vs YA: P = 1; AD vs OA: P = 0.004; YA vs OA: P = 0.001).

Before any training, participants rated how much they liked a series of individual dance movements (same as seen in the scanner) that were to be subsequently physically trained, visually trained, or were to remain untrained. On day 5, after the scanning session, participants rated again the same sequences. We observed no general effect of age on liking ratings ($F_{(2,46)} = 0.219$, P = 0.804, $\eta_p^2 = 0.082$), with all age groups ratings similarly the movement sequences (Fig. 3A). However, there was a main effect of day, with ratings being higher on day 5 than day 1 ($F_{(1,46)} = 42.990$, P < 0.001, $\eta_p^2 = 0.483$), but with no interaction with age groups ($F_{(2,46)} = 1.844$, P = 0.170, $\eta_p^2 = 0.074$).

To further assess the effect of training on liking ratings between age groups, the average difference between liking ratings on day 1 before training and liking ratings on day 5 after training for each training category (physically trained, visually trained, untrained) for each age group, was computed (Fig. 3B). A repeated-measures ANOVA evaluating these pre- and post-training difference liking scores, with age as a betweengroup factor, revealed a main effect of training type ($F_{(2,92)} = 16.393$, P < 0.001, $\eta_p^2 = 0.263$), but no main effect of age ($F_{(2,46)} = 1.844$, P = 0.170, $\eta_p^2 = 0.074$), nor an interaction between training type and age group ($F_{(4,92)} = 1.470$, P = 0.218, $\eta_p^2 = 0.060$). This suggests that participants' age does not lead to major differences on the effect of training on liking ratings. However, even if not statistically significant, it is of note that older adults were the only age group that preferred the untrained sequences on day 5, suggesting a training effect generalization to all dance sequences, regardless of actual experience, in advanced age. Across all age groups, we observe that physically and visually trained sequences were liked more after training, whereas untrained sequences were liked to a similar degree pre- and post-training.

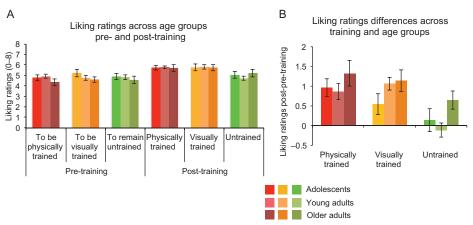


FIG. 3

Liking ratings across age groups. (A) Average liking ratings for each condition pre- and post-training for each age group. (B) Liking ratings difference between post- and pre-training depending on the type of training, across age groups.

3.2 EFFECTS OF TRAINING AND LIKING AT THE BRAIN LEVEL

3.2.1 Aesthetic evaluation of novel dance sequences, across the life span

To explore the impact of positive affective evaluation on brain activity while watching dance, we ran a parametric analysis on the day 1 (pre-training) scans, taking individual participants' ratings of how much they liked each movement as parametric regressor.

In adolescents, this contrast revealed a unique cluster in the left caudate (Fig. 4A; Table 1a), whereas in young adults, only the right inferior frontal gyrus emerged (Fig. 4B; Table 1b). Among older adults, more regions were more activated the more older adults liked the observed movement, thus including the right fusiform gyrus and bilateral middle occipital gyrus (Fig. 4C; Table 1c).

3.2.2 Aesthetic evaluation of trained dance sequence: Interaction between experience and aesthetic evaluation of an observed movement

To explore the effect of liking experienced dance movements via different modalities, we ran a similar parametric analysis on the post-training fMRI data. As behavioral results revealed a gradual increase of physical performance from untrained to physically trained sequences (Fig. 2A), as well as for liking (Fig. 4B), this analysis should inform how modulation of physical ability and liking by different kinds of experience is related to brain activity. Among adolescents, no regions survived the threshold. Among young adults, this contrast revealed activity in several brain regions, including the bilateral middle frontal gyrus and angular gyrus (Fig. 4E; Table 1e). Among older adults, the parametric analysis of liking ratings from the post-training scan revealed engagement of the left lingual gyrus, bilateral posterior cingulate cortex, and the precuneus (Fig. 4F; Table 1f).

4 DISCUSSION

4.1 IMPACT OF DEVELOPMENT AND AGING ON AESTHETIC APPRECIATION OF DANCE AT THE BEHAVIORAL LEVEL

In the present study, our aim was to contribute to constructing a more complete picture of the relationship between perception, embodiment, and affect by examining the relationship between sensorimotor experience and aesthetic appraisals at three distinct points in the life span. At the behavioral level, we observed broadly consistent findings across all three age groups in terms of the relationship between sensorimotor training and aesthetic preferences: regardless of age, all participants reported increased aesthetic evaluations of movements after 4 days of training, with physical training resulting in the largest increases in affective ratings of dance movements, followed by visual experience and no training experience. These results are in line with previous findings using similar training measures with young adult samples (Kirsch et al., 2013, 2015), and provide the first evidence that sensorimotor

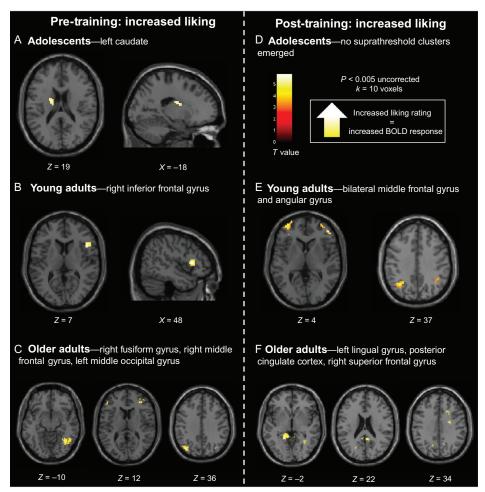


FIG. 4

Parametric analyses of all training conditions with increasing liking ratings, by age group. (A–C) Pre-training parametric analyses of all training conditions with increasing liking ratings for adolescents (A), young adults (B), and older adults (C). Regions more activated the more participants enjoyed watching movements after the 4 days of training (from all four training conditions) included the left caudate in adolescents (A), the right inferior frontal gyrus in young adults (B), and the right fusiform gyrus and right middle occipital gyrus in older adults (C). (D–F) Post-training parametric analyses of all training conditions with increasing liking after training, by age group. Regions more activated the more a participant reported liking an observed movement that s/he had either physical, visual, or untrained experience with. All regions are shown at a threshold of $P_{\text{uncorrected}} < 0.005$, k = 10 voxels.

	5 - - - - -	₩ 	MNI Coordinates	tes	MNI Coordinates	dpoint age of the	
Region	BA	*	>	z	T value	Cluster Size	P FWE _{corr.} Value
(a) Pre-training in adolescents Left caudate		138	4-	0	4.08	22	0.985
(b) Pre-training in vound adults							
R inferior frontal gyrus	44	48	17	10	4.70	39	0.895
(c) Pre-training in older adults							
Anterior cingulate gyrus	32	-16	16	30	5.13	51	0.971
Anterior cingulate gyrus	24	-12	9	30	4.63		
Dorsolateral prefrontal cortex	6	-24	16	32	3.13		
L middle occipital gyrus	39	-38	-72	36	4.88	120	0.332
R fusiform gyrus	37	36	-58	-10	4.73	330	0.003
R inferior temporal gyrus	37	48	09-	9-	4.37		
R inferior temporal gyrus	37	44	-56	-14	4.07		
R middle frontal gyrus	10	32	40	12	4.09	63	0.901
R middle frontal gyrus	10	40	44	∞	4.03		
R inferior frontal gyrus	46	40	36	10	3.11		
R middle temporal gyrus	21	64	-34	0	3.99	24	1.000
L inferior frontal gyrus	46	-46	38	14	3.67	20	1.000
R middle occipital gyrus	19	36	-68	24	3.67	13	1.000
R middle occipital gyrus	39	34	-72	36	3.54	10	1.000
L fusiform gyrus	37	-30	-54	-14	3.53	10	1.000
L middle occipital gyrus	18	-22	-86	9	3.40	11	1.000
L middle frontal gyrus	10	-38	40	22	3.28	12	1.000
L inferior frontal gyrus	46	-42	34	18	3.16		

Table 1 Regions Associated With an Increase in Liking, Depending on the Experience, by Age Group—cont'd

igner 1 regions Associated With all inclease in thing, Depending on the Experience, by Age Gloup County	יו מון ווכוע	ממסב ווו בוע	പു, നാധാ	ung on u	c Experience	, by Age aroup	OIL d
		M	MNI Coordinates	ies			
Region	ВА	*	>	N	7 value	Cluster Size	P FWE _{corr.} Value
(d) Post-training in adolescents No cluster survived the threshold							
(e) Post-training in young adults							
R middle frontal gyrus	46	48	44	4	5.88	94	0.446
R middle frontal gyrus	10	39	26	7	4.25		
R middle frontal gyrus	10	33	26	-	3.72		
R thalamus		9	-16	-2	5.11	55	0.776
R thalamus		0	-19	8-	3.96		
R thalamus		15	-13	-2	3.51		
L middle frontal gyrus	10	-36	26	-	4.83	104	0.379
L inferior frontal gyrus	10	-36	41	-2	3.43		
L angular gyrus	7	-33	-58	37	4.46	26	0.425
L angular gyrus	39	-42	-64	49	3.79		
L inferior frontal gyrus	44	-51	26	22	4.26	18	0.991
L pallidum		-15	4-	9-	3.78	12	0.997
L inferior occipital gyrus	19	-39	-82	1-1	3.76	47	0.844
L fusiform gyrus	19	-39	-70	-14	3.71		
L inferior parietal cortex	39	-39	-61	17	3.39		
R middle frontal gyrus	∞	36	=	55	3.35	11	0.998
L cerebellum		-3	-52	1-1	3.31	10	0.999
Cerebellar vermis		က	-58	-1	3.18		
R angular gyrus	39	42	-49	37	3.18	11	0.998
R angular gyrus	39	41	-61	40	2.99		

Table 1 Regions Associated With an Increase in Liking. Depending on the Experience. by Age Group—cont'd

		Z	MNI Coordinates	tes			
Region	ВА	*	٨	Z	7 value	Cluster Size	P FWE _{corr.} Value
(f) Post-training in older adults	_						
L lingual gyrus	18	-18	-44	-2	4.98	410	0.002
L cerebellum		-14	-46	-12	4.72		
L precuneus		-20	-48	∞	4.12		
R superior frontal gyrus	9	28	8-	36	4.98	26	1.000
R posterior cingulate cortex	23	∞	-46	22	4.77	83	0.796
R precuneus	23	12	-54	16	3.73		
R calcarine gyrus		2	09-	10	3.52		
R parahippocampus	36	14	-24	-16	4.75	10	1.000
R fusiform gyrus	37	26	-38	-14	4.31	11	1.000
R superior frontal gyrus	∞	20	18	34	4.25	39	0.998
R superior frontal gyrus	∞	28	12	38	3.60		
R superior frontal gyrus	_∞	26	16	28	3.37		
L hippocampus		-36	-40	9-	4.19	38	0.998
L hippocampus		-36	-30	-12	3.25		
L posterior cingulate cortex	23	9-	-46	22	4.08	15	1.000
R retrosplenial cortex	30	26	-46	2	3.73	69	0.960
R retrosplenial cortex	19	34	-54	-2	3.63		
L superior occipital gyrus	19	-20	89-	24	3.44	45	0.994
L precuneus	7	-14	99-	32	3.36		
L precuneus	31	-20	09-	28	3.32		
R precuneus	31	20	-62	30	3.33	21	1.000
R lingual gyrus	36	8	-34	4-	3.30	20	1.000
R lingual gyrus	36	80	-44	9-	3.22		
K linguai gyrus	30	α	-44	0	3.22		

BA: Brodmann's area; R: right; L: left; P < 0.005, uncorrected; K = 10 voxels. Bold regions are FWE-cluster corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8mm apart.

experience has a similar effect on aesthetic evaluations (measured here by liking ratings) of dance movements from early adolescence through to advanced age.

It is worth noting that liking ratings of dance movements that remained untrained did not reliably change before and after training among adolescents or young adults, thus reflecting the specificity of physical and visual training in increasing liking. However, older adults' liking ratings show that these individuals report an increased preference for all movements after training compared to before training (with changes in liking ratings being most pronounced for visuomotor experience, then visual experience only, followed by no training experience). This pattern likely reflects generalization or carryover effects from visual and/or motor training experience among the group of individuals who were arguably most unfamiliar with this type of dance before the experiment began. These preliminary behavioral results open myriad new questions, including to what extent might liking ratings change with experience and across the life span for other kinds of artistic and naturalistic stimuli, including landscapes, abstract art, and music?

Even though we did not find major differences in liking ratings for movements across age groups in the present study, a number of other studies suggest that brain mechanisms supporting affective processing of bodies and faces change with advancing age. For example, Ruffman et al. (2008) demonstrate that older adults are less accurate than young adults at identifying facial displays of emotion, and a number of studies document that older adults tend to show a positive bias in their ratings of facial expressions compared to younger adults (Ready et al., 2017), including neutral and negative expressions (Czerwon et al., 2011). The fact that we do not find strong evidence for a positive bias among older adults' aesthetic ratings (with perhaps the small exception of untrained movements being rated more positively post-training among this age group compared to the two younger groups) suggests that aesthetic evaluations are tapping into additional cognitive processes beyond emotion identification. However, little remains known about how aesthetic preferences are shaped and expressed as we age.

4.2 IMPACT OF DEVELOPMENT AND AGING ON AESTHETIC APPRECIATION OF DANCE AT THE NEURAL LEVEL

At the neural level, the fMRI findings in the present study were subtle and must be considered exploratory in nature, due to small sample sizes and a lack of cluster-corrected regions (except among the older adults). Among adolescents, the pre-training scan revealed that the left caudate showed a more robust response the more they reported liking an observed movement. Interestingly, after training, no brain regions showed parametric increases in response amplitude with liking ratings among this group. As the caudate is reliably implicated in reward processing (Balleine et al., 2007), and its engagement is often linked to dopamine release (Arias-Carrión et al., 2010), it is possible that the novelty of enjoyed dance movements observed during the first scanning session is associated with increased reward processing in the caudate, in adolescents. This finding resonates with those reported by Vartanian and Goel (2004), who showed decreased activity in the caudate in response to decreasing

preference ratings, with minimal activation for paintings with very low preference ratings (although it should be noted that they found more robust activity in the right caudate).

Among young adults, during the pre-training scan, only the right inferior frontal gyrus showed subtle evidence for increasing engagement with higher liking ratings. After training, several regions showed increasing activation with increasing liking of an observed move, including the middle frontal gyrus and angular gyrus. Activity within the middle frontal gyrus has been linked to decision making (e.g., Dricu and Frühholz, 2016; Ruff et al., 2010), while angular gyrus activity has been linked to a number of cognitive functions, ranging from language to numerical processing to attention (Gottlieb, 2007; Seghier, 2013). In the present study, it is possible that among the young adult participants, after training, implicit affective judgment processing shifts from more of a motor/premotor processing hub to brain regions more heavily involved in decision making and visual attention. Finally, among older adults, before training, increased liking ratings were associated with more activity in later visual regions, including the middle occipital and fusiform gyri, as well as the right middle frontal gyrus, associated with decision making (e.g., Ruff et al., 2010; Shamosh et al., 2008). Among this group, we see a shift after training to engagement of subcortical brain regions, including the left lingual gyrus and putamen, posterior cingulate cortex, and also the right superior frontal gyrus. While these findings remain preliminary at this stage, it is possibly of interest that a recent study shows putamen engagement when participants observe images that were previously associated with a reward (Koster et al., 2015), suggesting a link between memory, reward, and basal ganglia engagement.

It is important to remember that liking ratings were taken outside the scanner, after each scanning session (on days 1 and 5), and added to the design matrix during analyses. Participants' task during scanning was to closely but passively observe all movements, so they were not directly engaging in any aesthetic or affective appraisal. As such, any brain regions that emerge from parametric analyses of liking ratings should relate solely to implicit affective appreciation, and not conscious or overt liking judgments of movements. This is a crucial difference with several previous studies reported by our group (Cross et al., 2011; Kirsch et al., 2015), which could explain some discrepancies found between the results reported with young adults across these different studies. However, this approach is similar to the one taken by Calvo-Merino et al. (2008), who investigated brain activity during passive viewing of dance stimuli that was related to later, independent aesthetic evaluations of the same stimuli (although these ratings were averaged at the group level, whereas in the present study, each individual's ratings are retained in their first-level design matrix).

4.3 LIMITATIONS

In addition to the modest sample sizes used in the present study, several other limitations must be considered in order to contextualize the present findings more fully, and also to improve any follow-up studies that might stem from this work.

Speaking to the small sample sizes across the three groups, our research group supports initiatives to improve the rigor and reproducibility of research in the psychological and brain sciences (Cumming, 2014), and an unquestionable aspect of this is powering studies appropriately to detect predicted effects. This can be raised as a particularly difficult challenge in training studies (not to mention training studies that involve three age groups and fMRI), but this does not mean that such studies are without value (Lakens et al., 2018). In the meantime, researchers can contribute to increased transparency and ultimately rigor by reporting all results transparently and completely, even if they are null or mixed (Cumming, 2014; Simmons et al., 2011). For this reason, we believe the present imaging findings, though not uniformly statistically robust, are still of value to the research community, so long as important caveats about their preliminary nature are considered. Another caveat to consider is that the number of sequences learned and rated was limited (in part due to design constraints enforced by other research questions being evaluated by this same study; cf. Kirsch et al., 2018; chapter "Neurodevelopmental perspectives on dance learning: insights from early adolescence and young adulthood" by Sumanapala et al., in this volume). This could have limited the variability of liking ratings across all the sequences, thus diminishing chances of finding brain regions sensitive to the differences between stimuli. Finally, due to limited numbers of sequences and participants, it was not possible to run correlations between performance scores and liking ratings (in contrast to Cross et al., 2011; Kirsch et al., 2015), These limitations naturally present a number of opportunities for future work to advance upon, and we will be interested to see how this work is replicated and extended in the future.

4.4 IMPLICATIONS AND FUTURE DIRECTIONS

To date, only a small number of studies have looked at the possibility of using training paradigms to provide participants with augmented or additional types of knowledge to shape and enhance their aesthetic experience (Kirsch et al., 2015; Ticini et al., 2014). But why training? Training is a unique way to instill de novo experience, and compare how participants behave, how their brains respond, and how their preferences change before compared to after training. What this research demonstrates is the utility of learning or new experiences to enhance and inform the way the general public interacts with the arts.

In the context of art more broadly, public consumption of art is becoming less and less only a visual and 2D experience. This augmentation of how people experience art is being advanced with the development of immersive or interactive artworks, sometimes requiring an observer to directly act on the artwork (such as the "Musical Sculptures" of Jean Tinguely, which require observers to push a button to get the artwork to move), while others involve interaction between the spectator and the artwork, where the art evolves depending on the action or choices of the spectator (such as Ragnar Kjartansson's immersive film installation *The Visitors*). As such, a better understanding of the role played by multisensory experience will undoubtedly inform our appreciation of aesthetics. Keeping in mind the importance of action and motor components in perception (Prinz, 1997; Schütz-Bosbach and Prinz, 2007), more

and more research is now acknowledging the impact of these components on aesthetic experience (Freedberg and Gallese, 2007; Kirsch et al., 2016b; Ticini et al., 2014). To move forward toward a holistic understanding of affective action perception, what is required now is an integrative framework that brings together research from action perception, emotion/affect processing, multisensory experience, and perhaps empirical aesthetic as well. Moreover, different methodologies (electrophysiological recordings, neuroimaging, and psychophysiological techniques) should be combined to answer not only what areas correlate with affective perceptual processing but also how these brain regions interact and are modulated by different kinds of experience (emotional/sensorial; see Kirsch et al., 2016b). Taken together, the present study helps to establish a foundation for examining affective judgment and aesthetic preferences across the life span by using dance training and observation as a model. The findings have potential to inform researchers and practitioners beyond human neuroscience, including arts education, choreographic practice, and marketing.

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