Neurodevelopmental perspectives on dance learning: Insights from early adolescence and young adulthood

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Abstract

Studies investigating human motor learning and movement perception have shown that similar sensorimotor brain regions are engaged when we observe or perform action sequences. However, the way these networks enable translation of complex observed actions into motor commands—such as in the context of dance—remains poorly understood. Emerging evidence suggests that the ability to encode specific visuospatial and kinematic movement properties encountered via different routes of sensorimotor experience may be an integral component of action learning throughout development. Using a video game-based dance training paradigm, we demonstrate that patterns of voxel activity in visual and sensorimotor brain regions when perceiving movements following training are related to the sensory modalities through which these movements were encountered during whole-body dance training. Compared to adolescents, young adults in this study demonstrated more distinctive patterns of voxel activity in visual cortices in relation to different types of sensorimotor experience. This finding suggests that cortical maturity might influence the extent to which prior sensorimotor experiences shape brain activity when watching others in action, and potentially impact how we acquire new motor skills.

Keywords

Over the past several decades, an increasing number of scholars from domains beyond the arts, such as psychology and neuroscience (e.g., Brow and Dissanayake, 2009; Bullot and Reber, 2013; Kawabata and Zeki, 2004), have joined the ranks of artists, historians, and philosophers (e.g., Becker, 1982; Carroll, 1988, 2012; Tolstoy, 1899) in investigating the value and utility of art in contemporary society. While scholars working within behavioral and brain sciences predominantly focus on the neuropsychological antecedents and consequences of art appreciation (Chatterjee and Vartanian, 2014; Leder et al., 2004; Pelowski et al., 2017), artistic objects or processes can also be used as tools to investigate fundamental questions about the human brain and behavior (Christensen et al., 2017; Kirsch et al., 2016; Orgs et al., 2011). Within our work, we have utilized the art form of dance to study basic cognitive neuroscience questions related to expertise (Cross et al., 2006; Kirsch et al., 2016), multisensory integration (Kirsch et al., 2015), memory (Sumanapala et al., 2017), perception of human and nonhuman agents (Cross et al., 2009, 2012), and observational learning (Cross et al., 2009; Kirsch and Cross, 2015). In this study, we have again turned to dance to help us address a basic cognitive neuroscience question. Specifically, here we are interested in examining how the ability to learn complex action sequences by visual experience or physical practice changes from early adolescence to early adulthood, and how representations of these kinds of learning compare in the teenage and young adult brain. We chose to use a dance video game paradigm as our training manipulation, due to the fact that dance is engaging, challenging, and allows us to explore the observation and performance of "movement for movement's sake."

1 LEARNING VIA WATCHING VERSUS DOING

Observing skilled performers is an integral part of learning complex motor skills throughout one's lifespan (Blandin et al., 1999; Brandone, 2015; Carroll and Bandura, 1985, 1987; Marshall and Meltzoff, 2014). Although the development of basic motor skills through observational learning has been extensively examined during infancy (Grossmann et al., 2013; Hunnius and Bekkering, 2014; Koterba and Iverson, 2009; Marshall and Meltzoff, 2014; Southgate et al., 2010), the mechanisms involved in acquiring more complex motor repertoires through observation during later development remain relatively unknown. In performance art settings, motor sequences such as intricate dance choreography often require exact reproduction of complex movements performed by a skilled model. However, the way that the human brain and body are able to translate these visual cues to precisely executed

motor commands, and how this ability matures from adolescence to early adulthood remains to be investigated.

Among adult populations, studies that have specifically investigated brain activity when watching others in action reveal a link between action observation and action execution. A network of frontal, parietal, and temporal brain regions, collectively referred to as the Action Observation Network, has been broadly implicated during action observation (Alaerts et al., 2015; Molinari et al., 2013; Ricciardi et al., 2013; Turella et al., 2012). Several of the brain regions that compose the AON, including premotor cortex and the inferior parietal lobule, also respond to executed actions in a similar manner to observed actions (Bremmer et al., 2001; Chong et al., 2008; Coull et al., 1996; Kilner et al., 2009; Krüger et al., 2014). Similarities in activity when observing and performing actions have been attributed to motor resonance processes, which enable the mapping of observed actions onto one's own motor repertoire. However, a detailed understanding of how physical and visual experience with actions shape this motor resonance process, and the extent to which information about specific action representations might be stored within these sensorimotor brain regions is lacking. Examining how brain regions associated with the AON contribute to complex motor skill learning in the physical and visual domains, and how this learning is manifest at two developmental time points should advance our understanding of how we learn new motor skills, as well as inform training strategies that involve complex motor learning via observation or physical practice.

Similarities in cortical engagement when observing as well as performing actions have been linked to "mirror neuron"-like activity in the human brain (Iacoboni et al., 1999; Kilner et al., 2009). However, overlapping patterns of cortical engagement across action observation and execution may be driven by the simplicity of the hand actions that are encountered in most paradigms used to study such questions. Work demonstrating how physical experience shapes perception using more complex, full-body movements could help to address how complex and intransitive movements are learnt over time. In a study that investigated how dance experts perceive complex movement Calvo-Merino et al. (2005) found widespread increases in activity across premotor, parietal, and temporal AON regions when ballet dancers observed ballet movements compared to highly unfamiliar capoeira movements. A related longitudinal study by Cross et al. (2006) demonstrated parametric increases in AON engagement when dancers watched dance movements they were learning to perfect over 5 weeks of rehearsing. Together these findings suggest that an observer's prior motor repertoire shapes how he or she perceives others' actions, and that physical experience actively shapes and changes how sensorimotor brain regions respond to action observation.

While most work has studied the impact of motor (or visuomotor) experience on the engagement of sensorimotor brain regions, a small but growing number of studies have examined how visual experience alone might impact brain activity as well as behavioral performance. In one such study, Calvo-Merino et al. (2006) scanned the brains of male and female ballet dancers while they watched male- and female-specific ballet movements. This meant that participants would be watching one

set of movements they were extremely familiar with physically performing, and another set of movements they never physically performed, but with which they had a very high level of visual familiarity. They found that ballet dancers showed the greatest AON engagement when watching their own-gendered movements, compared to movements that were specific to the other gender. The authors interpret this as visuomotor experience leading to greatest AON engagement compared to visual experience alone, regardless of overall movement familiarity (Calvo-Merino et al., 2006). A similar relationship between sensorimotor experience and AON engagement has been demonstrated among dance-naïve individuals following only 1 week of sensorimotor training. Kirsch and Cross (2015) found that the number of sensory modalities through which one encountered a dance music video during training was positively correlated with AON response amplitude when observing these movements following training. The condition associated with the greatest degree of sensorimotor engagement consisted of motor, visual, and auditory experience, followed by visual and auditory experience, then auditory experience alone. Finally, viewing untrained videos during testing resulted in the least engagement of sensorimotor brain regions. These findings suggest that even with limited training, AON engagement already reflects the richness of an observer's own history of sensorimotor experience, and could possibly be used as an index for learning aptitude.

2 DEVELOPMENTAL PERSPECTIVES ON SENSORIMOTOR LEARNING

Currently, the ways in which visual and visuomotor experience influence brain and behavior at different stages in development remain underinvestigated. Frontal brain regions undergo continued growth and development through adolescence and into early adulthood (Burnett et al., 2011; Simmonds et al., 2014; Spear, 2000), which may affect the nature of how actions are perceived during this period. For instance, internal models of actions, which may be encoded within premotor regions according to prior studies in adults (Kilner, 2011; Kilner et al., 2007b), might still be undergoing development at this stage, proving to be less informative in anticipating the visuospatial and kinematic features of observed actions. Additionally, changes in gray matter volume within frontal, temporal, and parietal regions during adolescence (Blakemore and Choudhury, 2006; Gogtay et al., 2004) could potentially affect the ability to use one's own action experiences to anticipate the actions of others during this developmental period, given that reduced gray matter volume has been associated with impairments in social perception (Ota et al., 2017; Syal et al., 2012). Within an adolescent AON, these regions may instead drive action perception in a bottom-up fashion by visual and somatosensory regions that experience a loss in gray matter early in adolescence, progressively followed by losses in parietal, temporal, and frontal brain regions (Gogtay et al., 2004). If lower-level visual and somatosensory cortices are some of the first to undergo maturational changes, these regions may facilitate processes related to action perception while other regions of the adolescent AON continue to develop.

3 THIS STUDY

To explore the possibility that the ability to perceive actions may be influenced by maturity as well as sensorimotor experience, we developed a week-long dance training paradigm with pre- and post-training fMRI sessions to investigate whether different degrees of visuomotor experience with whole-body movements were associated with different magnitudes of AON engagement. Moreover, this engagement was examined when participants viewed pared-down visual depictions of movements during scanning that were otherwise experienced in a visually rich training environment (Fig. 1).

In accordance with the studies that demonstrate changes in AON response amplitude with increasing sensorimotor experience (Balser et al., 2014; Cross et al., 2009; Kirsch and Cross, 2015; Liew et al., 2013a), we also examined the extent to which the AON is influenced by the increasing richness of sensorimotor experience. By using a combination of univariate and multivariate pattern analysis techniques, we aimed to investigate the extent to which both the *amplitude* and *patterns* of sensorimotor engagement reflect prior experience with an observed movement. Although several prior studies highlighted in this introduction have examined similar questions, we aimed to isolate cortical indices of action experience when observing generalized representations of movements in a context containing limited extraneous visual information, such as visual perspective or action goals.

For the purposes of univariate analyses, regional voxel activity is typically averaged across multiple trials and subjects to measure the average engagement of brain regions associated with a specific task (Aguirre et al., 1997, 1998). However, these approaches do not correct well for activity that covaries across neighboring voxels, potentially leading to poor discrimination of activity associated with varying degrees of movement experience. In contrast, multivariate approaches can be used to exploit this covariance by identifying patterns of voxel activity characteristic to a condition of

FIG. 1

Still frames of movement stimuli. The *left panel* depicts movements as encountered during training, and the *right panel* depicts movement silhouettes encountered during scanning.

interest (Haynes and Rees, 2005; Kamitani and Tong, 2005, 2006). Overlapping regions of cortical engagement in the motor cortex have been demonstrated to show distinct patterns of voxel activity associated with the experience of learning individual sequences of key presses (Wiestler and Diedrichsen, 2013). Although this finding measured action experience in the context of fine-motor skill learning, similar indices of sensorimotor experience may underlie overlapping regions of AON engagement associated with different kinds of training experience. As such, in addition to univariate analyses, a multivariate decoding procedure (Hebart et al., 2014) was used to determine if distributed voxel activity could be used to discriminate between patterns associated with viewing physically experienced, observed, and untrained movements.

By analyzing differences in voxel patterns that occur when perceiving intransitive whole-body movements, we predicted that premotor and parietal regions would encode differences between physically experienced and observed actions due to differences in visuomotor engagement acquired during training that might influence how actions are subsequently anticipated. In addition, we predicted that temporal regions would encode differences between observed and untrained actions due to changes in encoding visuospatial movement information through visual experience. Finally, we predicted that differences between physically experienced and untrained actions may be reflected in voxel pattern differences across premotor, parietal, and temporal regions of the AON, due to an overall difference in acquired experience affecting perception. Identifying such indices could serve as a crucial step toward identifying how engagement of sensorimotor brain regions is differentially shaped by an observer's prior action experience in a more generalized sense. Such findings could potentially help inform training strategies that cater to different developmental periods by acknowledging the plasticity of visuomotor learning.

4 METHOD
4.1 PARTICIPANTS

Following completion of a dance experience questionnaire, only participants with less than 3 years of dance experience were screened for MRI compatibility, as per procedures set forth by the Bangor University Brain Imaging Unit.

4.2 YOUNG ADULTS

Twenty-three neurologically and physically healthy young adults aged 18–25 were recruited from Bangor University's undergraduate student population. Data from four participants were excluded due to excessive motion artifacts, while one participant discontinued participation on the fourth day of training due to personal reasons. The final young adult sample consisted of 18 right-handed individuals (mean Edinburgh Handedness Inventory total = 60.78; SD = 22.20; range = 20–100) comprising 7 males and 11 females (mean age = 19.44; SD = 1.62; range = 26.32–100). All participants provided written informed consent before beginning any experimental procedures, and were reimbursed with cash or course credit for their participation.

4.3 ADOLESCENTS

Seventeen neurologically and physically healthy adolescents aged between 12 and 14 years were recruited via Bangor University's internal mailing lists. Parents/legal guardians of all adolescent participants provided written informed consent before participation. Parents/legal guardians of 11 participants also agreed to complete the Child Behavior Checklist (Achenbach & Ruffle, 2000) assessing behavioral development. As defined by the checklist, these participants fell within typical ranges of behavioral development for this age group. Prior to participating, adolescents received a detailed verbal and written briefing from the experimenter regarding the requirements of the study, and potential risks associated with participation. Adolescents were only recruited if they provided written proof of assent. Of the initial sample recruited, two participants were excluded due to technical problems. The final sample consisted of 15 right-handed individuals (mean Edinburgh Handedness Inventory total = 66.26; SD = 19.43) comprising 9 males and 6 females (mean age = 12.80; SD = 0.77). Participants were reimbursed in cash upon completing participation.

All experimental protocols for both participant samples were approved by the Bangor University School of Psychology Research Ethics Committee (ethics protocol: 2014-13125).

4.4 STIMULI AND APPARATUS

Six dance sequences from the XBOX 360 game "Dance Central 2" (Harmonix Music Systems 2011) were selected for observational and physical training. These sequences were selected based on gender-neutral choreography with each song associated with a unique set of dance movements. All sequences were set to popular songs (such as "Like a G6" by Far East Movement and "What is Love" by Haddaway), ranging from 2 min and 20 s to 2 min and 29 s in length (average length = 2 min, 22 s; SD = 10 s), and varying in tempo from 105 to 129 bpm (average bpm = 118.83; SD = 11.21). Game difficulty settings were set to "Easy" mode to encourage performance gains for a dance-naïve sample. A single visual backdrop and dance character were selected across all training periods to maintain visual consistency across physical and observational training conditions. Dance sequences were divided into three pairs (see Section 4.5), matched for movement complexity, bpm, and song duration.

Animated silhouettes from the game featuring individual movements from these preselected sequences were captured and used as stimuli during pre- and post-training fMRI sessions (see Sumanapala et al., 2017 for more details). These silhouettes were extracted and edited using iMovie '11 (Version 9.0 for Apple Inc.) and Adobe Premiere Pro (Version 7.1 for Microsoft Windows 7). The duration for all stimuli was set to 4.3 s. Each stimulus featured one coherent whole body movement that was repeated twice across an interval of 400 ms (see Fig. 4). Subsets of three short movements per dance sequence were presented during scanning, equaling a total of 18 stimuli (3 movements × 2 dance sequences × 3 training categories), devoid of the accompanying audio soundtrack.

4.5 BEHAVIORAL TRAINING

For each participant, each sequence pair was assigned to one of three training categories (physically experienced = "Physical," observed = "Observe," and untrained = "Untrained"). Participants were trained on physically experienced and observed sequences across four consecutive days, with training order counterbalanced per day. Dance movements from the untrained condition were encountered only during pre- and post-training scan sessions and during the post-training dance test when participants were asked to perform all sequences from all training categories.

Details for the physical training procedures are as reported by Kirsch and Cross (2015) and Sumanapala et al. (2017). Briefly, participants' task was to imitate an avatar's dance movements as accurately as possible, in real time, in the context of the video gameplay (Fig. 2). Participants' movements were captured by the XBOX 360 Kinect motion tracking device and compared with the avatar's movements in order to generate an accuracy score. A repeated-measures ANOVA was conducted to determine whether predicted performance improvements were observed for physical training across the 4 days of the training intervention.

During observational training, participants were instructed to observe two separate sequences (repeated twice) on a computer running MATLAB® R2010a
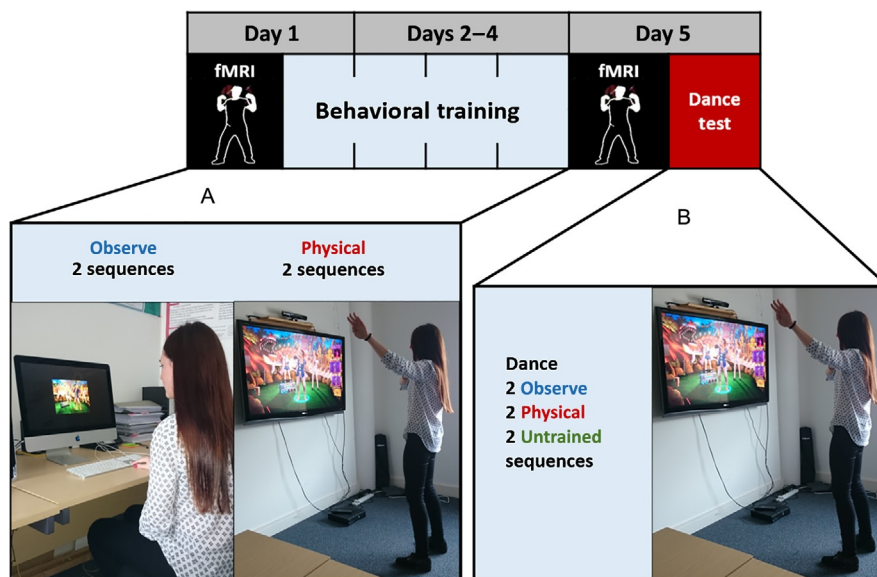

FIG. 2

Training setup. (A) Overview of behavioral training, involving four consecutive days of observing one set of sequences, and physically experiencing a different set. (B) Performance test for two observed sequences (Observe), two physically experienced sequences (Physical), and two untrained sequences (Untrained) on Day 5.

(MathWorks, Inc.). Participants were instructed to pay close attention to the movements of the central avatar to determine whether these movements were featured in short movement clips that were presented following the main video (see Kirsch and Cross, 2015; Sumanapala et al., 2017). A general accuracy score for this task was then calculated as a percent for each day of training as a measure of attention. A repeated-measures ANOVA was conducted to determine whether performance differences on this task were observed across the 4-day intervention.

Following the post-training scanning session, participants were asked to perform all six of the physically experienced, observed, and untrained dance sequences in randomized order. Raw scores for each category were averaged to reflect performance ability specific to each training category. A repeated-measures ANOVA with three levels (physically experienced, observed, and untrained) was conducted to investigate the impact of training experience performance of all sequences. Pairwise comparisons for all ANOVAS were examined using Tukey's HSD.

4.6 NEUROIMAGING PROCEDURE

To obtain a pre-training profile of brain activity while observing all stimuli in an untrained state, participants completed one fMRI session featuring the movement silhouettes they would subsequently encounter in the dance video game during the training phase. An identical fMRI session was conducted following 4 days of training to examine the effects of the three different kinds of training experience on perceiving simplified action representations (Fig. 3).

Assignment of stimuli into three different training categories was not discussed with participants before either scanning session to avoid any brain responses driven by explicit awareness of training contexts associated with each movement. Each scanning session comprised six runs, each approximately 9 min in length. Each of the 18 stimuli was presented three times, appearing in random order to ensure that movements across each category were evenly distributed within a run. A fixation cross was presented for 500 ms to announce the start of each trial. An additional fixation cross was presented during intertrial intervals for a duration of 3 s (Fig. 4).

Additionally, six separate dance silhouettes (not derived from any of the training sequences) were embedded within each run as attentional controls to ensure that participants were focused on the movements throughout the entire session. Each control silhouette was followed by one of four questions regarding the depicted movement. These questions were: "Did the dancer raise an arm above his head?", "Did the dancer take a step forward?", "Did the dancer repeat the movement on both sides?", and "Did the dancer move his legs?". Participants responded using a four-button fiber-optic response box held in both hands, using the left thumb to press Button 1 (Yes) and the right thumb to press Button 4 (No). Participants were given task instructions prior to the pre-training scan and were reminded of these again before undergoing the post-training scan.

A computer running MATLAB® R2010a (MathWorks, Inc.) using Windows 7 (Microsoft, Inc.) operating software was used to present stimuli and record
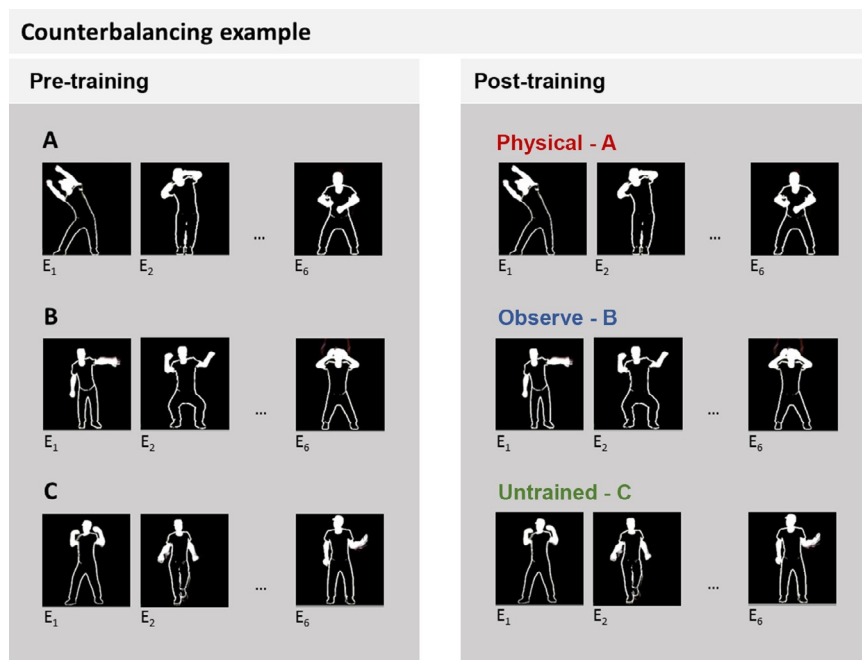
FIG. 3

Each category of stimuli (A–C) is comprised of six unique dance movements. The three categories were counterbalanced for every participant as movements to be physically experienced (Physical), to be observed (Observe), and to be left untrained (Untrained). During the pre-training scan, these movements would not have been associated with any specific form of experience, unlike the post-training scan.
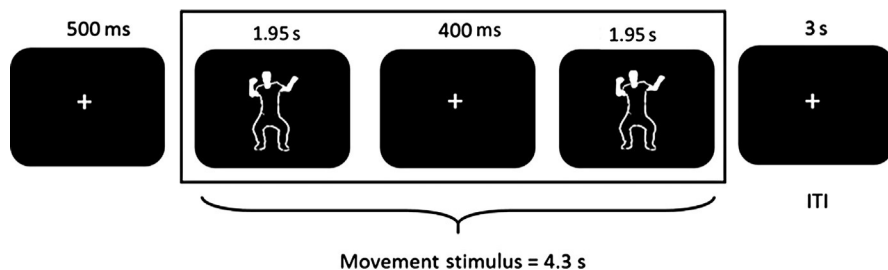

FIG. 4

Illustration of fMRI setup. During both pre- and post-training scanning sessions, participants observed movement silhouettes. Prior to training, these silhouettes would not have been associated with any differentiated sensorimotor experience.

participants' responses. Stimuli were projected onto a display monitor located at the rear of the scanner, which participants could view via a mirror suspended from a head coil. Scanning sessions were conducted within a 3-T Philips MRI scanner using a SENSE phased-array 32-channel head coil. Functional images were obtained using a single-shot echo-planar imaging sequence (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^2 $\times 38$ slices; anterior–posterior phase encoding. Parameters for T1-weighted anatomical scans were: $240 \times 224 \times 175$ slices; voxel dimensions, $1 \times 1 \times 1$ mm; TR $=12$ ms; TE $= 3.5$ ms; flip angle $= 8$ degrees. The first two volumes of each run were discarded to reduce saturation effects. All scans were acquired in ascending order. A design matrix was fitted for each participant featuring separate regressors for control videos, button presses in response to questions that followed each control video, and videos from each training category, convolved with the standard hemodynamic response function.

4.7 fMRI DATA ANALYSIS

Neuroimaging data from each scanning session were separately analyzed before conducting univariate or multivariate group-level statistics. These analyses included realignment, unwarping, and slice-timing correction in SPM12. Each participant's functional imaging data were normalized to their own anatomical scan (resolution: 3 mm^3) before being normalized to the standard Montreal Neurological Institute template. These data were subsequently smoothed using a 7 mm Gaussian smoothing kernel (FWHM) for univariate analyses, while multivariate analyses were performed on unsmoothed data. Only whole runs with less than 3 mm of motion were used across both types of analyses.

4.7.1 Univariate Analyses Examining the Additive Impact of Sensorimotor Engagement

For each subject group, univariate analyses were conducted to determine whether increasing sensorimotor engagement during training (Physical > Observe > Untrained) was associated with corresponding increases in activity within the AON. A group-level mask was created per group to constrain these analyses to voxels that were active above rest during movement observation on either day of scanning (Figs. 5 and 6).

Specifically, to investigate increases in AON amplitude in response to increasingly rich training experience, we conducted the following three contrasts for each day of training: (1) Physical > Observe, (2) Observe > Untrained, and (3) Physical > Untrained. Contrast maps generated for each of these tests were compared between training sessions using paired *t*-tests to determine which regions showed differences in engagement associated with training.

12 Dance learning in adolescence and young adulthood
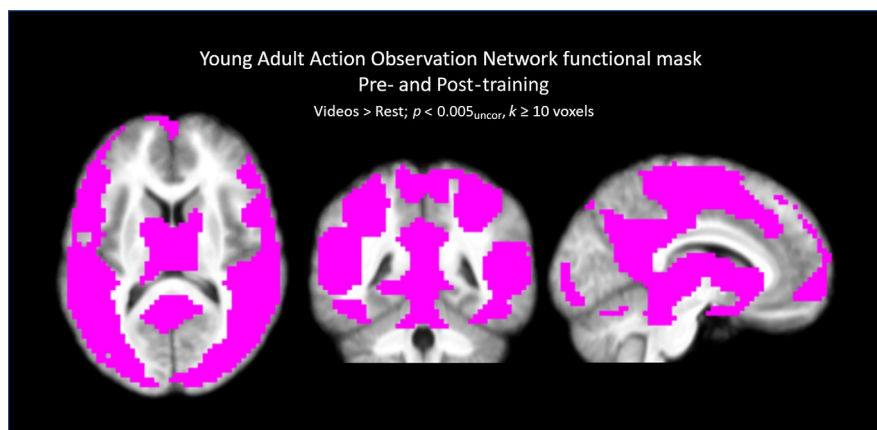
FIG. 5

Young adult group-level mask. *Pink voxels* indicate regions active above baseline during movement observation across either day of scanning ($p < 0.005_{uncor}$, $k \geq 10$ voxels). From *left* to *right*: coronal, sagittal, and axial cross-sections depicted. Mask superimposed on averaged structural T1 images of young adults.
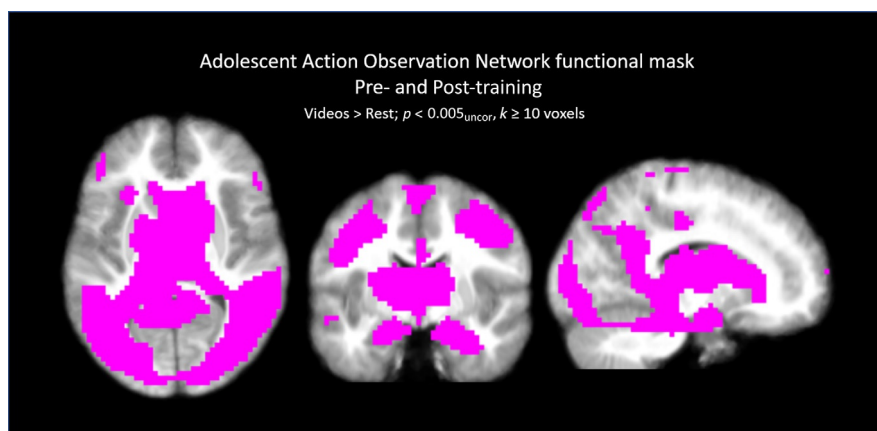
FIG. 6

Adolescent group-level mask. *Pink voxels* indicate regions active above baseline during movement observation across either day of scanning for adolescents ($p < 0.005_{uncor}$, $k \geq 10$ voxels). From *left* to *right*: axial, coronal, and sagittal cross-sections depicted. Mask superimposed on averaged structural T1 images of adolescents.

4.7.2 Multivariate Analysis

Next, we applied a multivariate decoding procedure to determine whether distributed voxel activity could be used to classify activity patterns associated with viewing physically experienced, observed, and untrained movements.

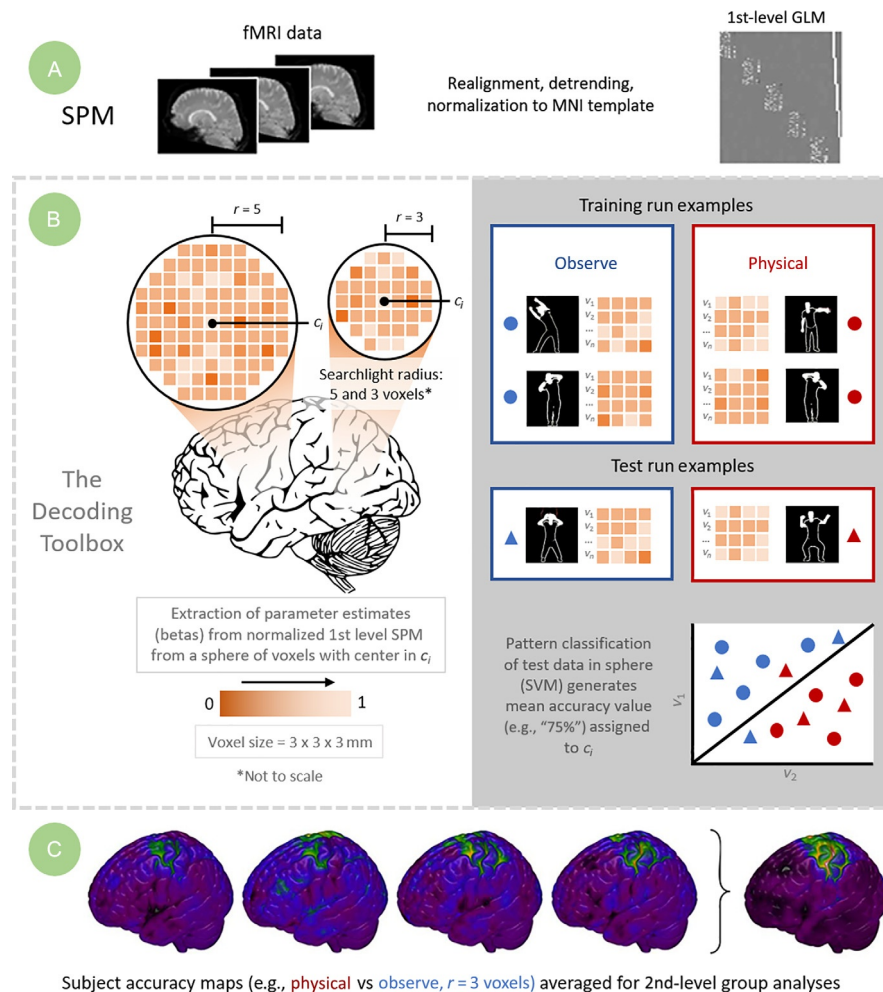#### 4.7.2.1 Searchlight Procedure

Since all dance movements should be equally unfamiliar to participants prior to training, the three categories of stimuli featured during scanning should only be distinguishable based on visual features that define each movement, and not based on any other prior motor knowledge. Following training, stimuli from each of these categories should now be associated with a specific kind of training experience for each participant, as depicted in Fig. 3. To decode this differentiated experience, a searchlight procedure was used to identify patterns of voxel activity associated with viewing each movement category, both before and after training.

A searchlight is defined as a volume with a specified radius that can be used to analyze patterns of activity surrounding a central voxel. This procedure can be repeated for every voxel of interest and is used to train an algorithm to identify patterns of voxel activity associated with each group (Fig. 7).

In a standard leave-one-run-out cross-validation procedure, a set of algorithms decode voxel patterns in an unknown "test" run using category-specific pattern information derived from all other similarly structured runs (Müller et al., 2001). This study adopts this approach, whereby each run was used five times as a "training" set and once as a "test" set for each category as depicted in Fig. 8.

Scripts within The Decoding Toolbox (Hebart et al., 2014) were then used to generate three pairs of classification accuracy maps for each participant (Fig. 7) both before and after training, indicating the rate with which regional activity around each voxel could be used to decode whether a viewed movement was physically experienced, observed, or untrained. For each age group, a group-level mask created for the univariate analyses was also used to constrain each classification accuracy map to voxels that were only active above rest during movement observation on either day of scanning (Figs. 5 and 6). As recommended by Hebart et al. (2014), these classification maps were used to conduct group-level analyses. Specifically, paired t-tests between pre- and post-training sessions were conducted to determine which voxels were most informative of category membership before and after training by assessing how voxel classification accuracy within this mask changed with training. Classification accuracy maps were also compared between age groups using a combined group-level post-training mask (Fig. 9) to determine whether young adults demonstrated higher degrees of sensitivity to sensorimotor experience when perceiving actions compared to adolescents.

Since accuracy maps generated from searchlight procedures can be affected by different searchlight volumes (Etzel et al., 2013; Stelzer et al., 2013), the entire cross-validation procedure was conducted twice using two separate searchlight volumes (radii of 3 and 5 voxels). Specifically, these volumes were chosen to avoid biased classification results related to the spacing of highly informative voxels and weakly informative voxels within different searchlight volumes. A detailed discussion of

14   Dance learning in adolescence and young adulthood

FIG. 7

Stream of searchlight-decoding analysis using The Decoding Toolbox. (A) SPM was used to perform typical preprocessing of functional fMRI runs prior to running TDT. (B) A searchlight-decoding procedure was used to constrain spheres of voxels (with center c_i) to discriminate patterns of voxel activity for movement silhouettes based on prior sensorimotor experience. Patterns for viewed movements were discriminated between category pairs (e.g., Physical versus Observe, as shown) by training a Support Vector Machine (SVM) classifier to associate voxel parameter estimates (betas) in training runs with corresponding category labels. The classifier was then tested on its ability to label voxel patterns for trials within an unknown "test" run (see Fig. 8 for cross-validation of runs). The classifier boundary between categories is only shown between two voxels (v_1 and v_2) for visual simplicity. The classifier's overall accuracy as a percentage of correctly labeled patterns is then assigned to the center of the searchlight sphere, c_i. (C) This process is repeated for

(Continued)
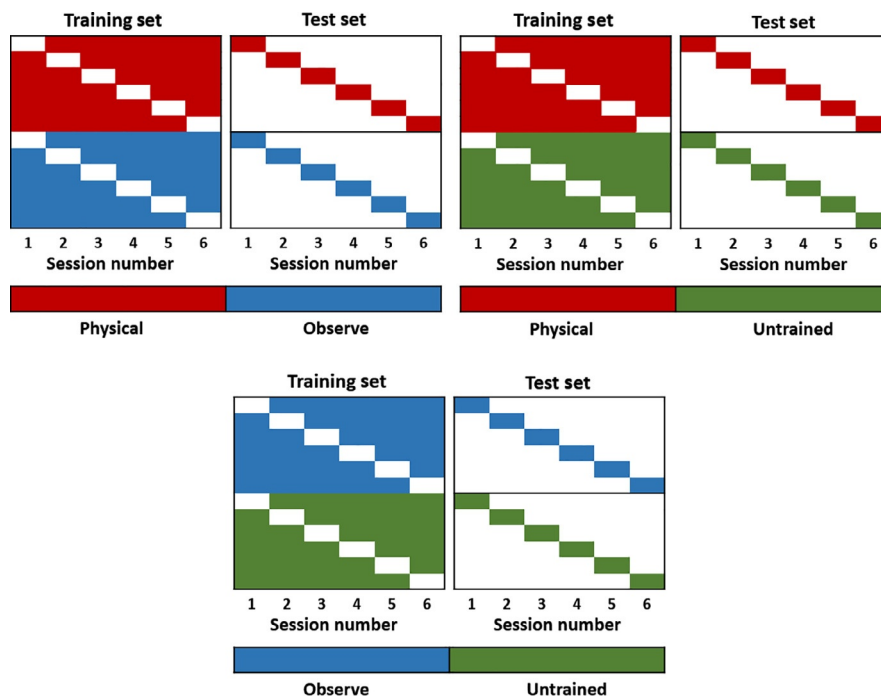
FIG. 8

Decoding procedure for classification accuracy maps. To generate classification maps for each pair of movement training categories (i.e., Physical versus Untrained, Observe versus Untrained, and Physical versus Observe), the decoding procedure used a leave-one-run-out cross-validation scheme to identify patterns associated with each category of movement, both before and after training. Each run serves once as a "test" run, where voxel patterns for each category are discriminated using SVM based on "trained" patterns in all other five runs. Although the above figure depicts these differences according to sensorimotor experience, note that before training, these categories would only differ from each other based on the specific movements that form each category (Fig. 3).

FIG. 7—Cont'd

every voxel of interest to generate a classification accuracy map, e.g., Physical versus Observe. For each subject group, the procedure was constrained using a functional group-level mask to voxels that were active above rest when viewing movements on either day of scanning (Figs. 5 and 6). For each participant, two accuracy maps were created using two searchlight volumes (radius 3 and 5 voxels), generated per day of scanning (pre- and post-training) equaling four maps in total. Per subject group, these maps were then averaged to conduct standard second-level analyses in SPM.

Adapted from Hebart, M.N., Görgen, K., Haynes, J.-D., 2014. The Decoding Toolbox (TDT): a versatile software package for multivariate analyses of functional imaging data. Front. Neuroinform. 8, 88. doi:10.3389/fninf.2014.00088.
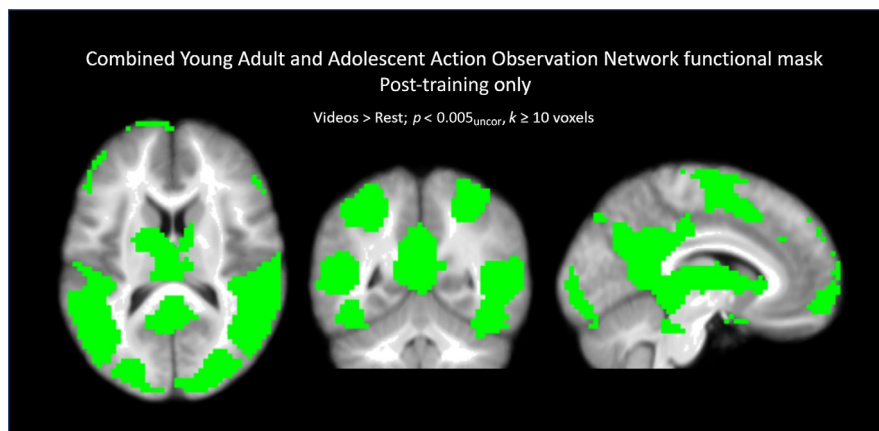
FIG. 9

Combined young adult and adolescent mask. *Green voxels* indicate voxels active above baseline for both adolescents and young adults when observing movements following training ($p < 0.005_{uncor}$, $k \geq 10$ voxels). From *left to right*: axial, coronal, and sagittal cross-sections depicted. Mask superimposed on averaged structural T1 images of all participants.

searchlight volumes and their impact on classification accuracy is featured in a recent review by Etzel et al. (2013).

5 RESULTS
5.1 TRAINING PERFORMANCE
5.1.1 Physical training

For each participant (both young adult and adolescent), physical performance was assessed per day by averaging raw performance scores across both dance sequences assigned to physical training. A 2×4 repeated-measures ANOVA incorporating both age groups and all four training days indicated that Mauchly's test of sphericity had been violated ($p < 0.001$); therefore, a Greenhouse–Geisser correction was used ($\varepsilon = 0.66$). Physical performance significantly improved across the 4 days as indicated by a main effect of training day, $F(1.98, 61.38) = 86.17$, $p < 0.001$, $\eta_p^2 = 0.74$. Pairwise comparisons across days indicate that significant differences were observed between all possible pairs of days (Fig. 10A). Overall, no significant difference in performance was found between young adults and adolescents.

5.1.2 Observational training

Both young adult and adolescent participants' attention during observational training was measured by recording response accuracy on the observation task. A 2×4 repeated-measures ANOVA was used to assess changes in attention during the observation task across both age groups and all four training days. This analysis indicated that Mauchly's test of sphericity had been violated ($p = 0.03$); therefore,
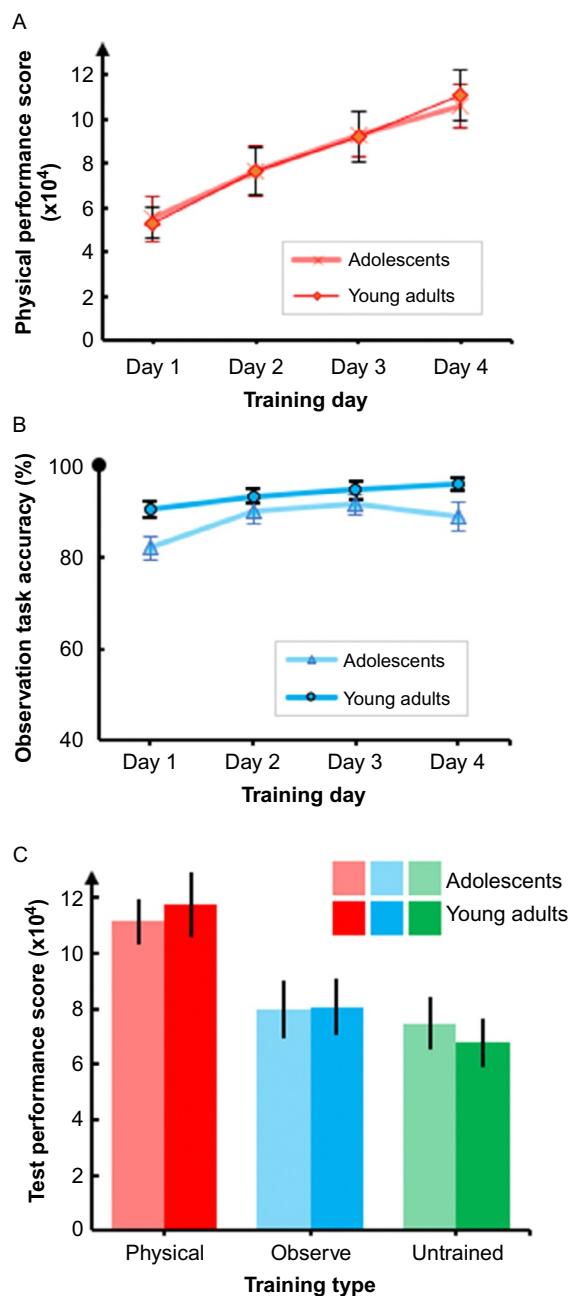
FIG. 10

Behavioral training and test day performance for young adults and adolescents. (A) Physical performance scores recorded from XBOX-based video game (Dance Central 2). *Error bars* indicate standard error of the mean. (B) Observation task accuracy scores depict average accuracy for selecting seen versus unseen movements during observational training across each training day. *Error bars* indicate standard error of the mean. (C) Test day physical performance scores for all sequences. *Error bars* indicate standard error of the mean.

a Greenhouse–Geisser correction was used ($\varepsilon = 0.78$). A main effect of increasing response accuracy across the 4 days of training indicated that participants were consistently able to recognize movements that had appeared in the observed videos, $F(2.36, 73.10) = 16.92$, $p < 0.001$, $\eta_p^2 = 0.35$. A marginally significant interaction was also found between age group and training day, such that young adults demonstrated greater improvement than adolescents on this task, $F(2.36, 73.10) = 2.97$, $p = 0.049$, $\eta_p^2 = 0.09$. Pairwise comparisons across days indicate significant differences between Day 1 and all other training days (Fig. 10B).

5.2 TEST DAY PERFORMANCE

On the final day of testing, all participants were required to perform all six dance sequences (two each from the physically trained, observed, and untrained conditions) to assess the impact of differentiated sensorimotor experience on motor performance. A 2×3 ANOVA was used to assess differences in performance gains across both age groups and differences in performance gains between the three categories of training. This analysis revealed a main effect of training type on dance performance, $F(2, 93) = 10.34$, $p < 0.001$, $\eta_p^2 = 0.18$. Pairwise comparisons indicate that physically trained sequences were performed significantly better than observed or untrained sequences. No significant differences in performance were found between observed and untrained sequences, or more generally between young adults and adolescents (Fig. 10C).

6 NEUROIMAGING RESULTS
6.1 UNIVARIATE ANALYSES

Prior to examining differences in spatiotemporal activity patterns, univariate analyses were used to investigate an interaction between training session (pre or post) and type of sensorimotor engagement (physically experienced, observed, or untrained) on the degree of cortical engagement when perceiving movements. As illustrated in Table 1, these within-subject contrasts did not reveal any significant clusters, indicating that sensitivity to sensorimotor experience when perceiving movements did not emerge as a difference in the magnitude of engagement within a functionally defined AON mask per sample.

7 MULTIVARIATE RESULTS
7.1 WITHIN AGE GROUPS

Within the young adult sample, differences in spatiotemporal voxel activity patterns for physically experienced versus observed actions appeared to increase within the left inferior parietal lobe when evaluating an interaction between training session and sensorimotor engagement (Table 2 and Fig. 11).

Table 1 Univariate Analyses Within Age Groups: Post-training $>$ Pre-training ($p < 0.005_{uncor}$, $k \geq 10$)

		MNI Coordinates				Cluster Level			Peak Level
	Region	**x**	**y**	**z**	**t-Value**	**Size (k)**	**p_{uncor}**	**FDR**	**p_{uncor}**
Young adults									
Physical $>$ Observe	R caudate nucleus	9	17	7	5.07	37	0.189	0.663	<0.001
	R caudate nucleus	−3	20	7	4.06				<0.001
	L superior frontal gyrus	−21	−16	46	4.55	73	0.073	0.663	<0.001
	L superior frontal gyrus	−15	−16	58	4.35				<0.001
	L superior frontal gyrus	−21	−4	67	3.56				0.001
	R superior parietal lobule	18	−58	61	4.45	41	0.168	0.633	<0.001
	L superior parietal lobule	−15	−64	61	4.06	38	0.184	0.663	<0.001
	L superior parietal lobule	−24	−55	64	3.81				0.001
	L precentral gyrus	−39	−7	49	3.65	21	0.320	0.861	0.001
Observe $>$ Untrained	No clusters	—	—	—	—	—	—	—	
Physical $>$ Untrained	L posterior cingulate gyrus	−18	−22	37	4.20	21	0.299	0.853	<0.001
	L inferior parietal lobule	−36	−55	46	3.71	10	0.478	0.853	0.001
Adolescents									
Physical $>$ Observe	L basal forebrain	−6	−1	−14	4.99	12	0.525	0.884	<0.001
	L subiculum	3	−37	−8	4.13	64	0.140	0.884	0.001
	L parahippocampal gyrus	−6	−34	−11	3.84				0.001
	L parahippocampal gyrus	−18	−37	−11	3.76				0.001
Observe $>$ Untrained	No clusters	—	—	—	—	—	—	—	
Physical $>$ Untrained	R posterior cingulate gyrus	3	−25	25	3.39	10	0.554	0.881	0.002
	L parahippocampal gyrus	−18	−40	−8	3.38	14	0.477	0.881	0.002

Table 2 Classification Accuracy Within Age Groups: Post-training $>$ Pre-training ($p < 0.005_{uncor}$, $k \geq 10$)

	Region	MNI Coordinates				Cluster Level			Peak Level
		x	y	z	t-Value	Size (k)	p_{uncor}	FDR	p_{uncor}
Young adults									
Physical versus Observe									
3-voxel radius	L inferior parietal lobule	−42	−52	55	4.77	34	0.000	0.002	<0.001
	L inferior parietal sulcus	−42	−49	46	4.24				<0.001
	L inferior parietal sulcus	−36	−43	49	3.96				0.001
5-voxel radius	L inferior parietal lobule	−48	−49	52	5.36	55	0.000	0.009	<0.001
	L inferior parietal sulcus	−42	−40	55	4.59				<0.001
	L superior parietal lobule	−36	−49	58	3.91				0.001
	L thalamus (parietal)	−18	−28	10	4.79	29	0.004	0.088	<0.001
	L thalamus (prefrontal)	−9	−25	4	3.64				<0.001
	L hippocampus	−21	−37	7	3.38				<0.001
Observe versus Untrained									
3-voxel radius	No clusters	—	—	—	—	—	—	—	—
5-voxel radius	L superior temporal gyrus	−51	−28	13	3.57	12	0.047	0.559	0.001
Physical versus Untrained									
3-voxel radius	No clusters	—	—	—	—	—	—	—	
5-voxel radius	L superior frontal gyrus	−15	44	37	4.19	13	0.040	0.560	<0.001
Adolescents									
Physical versus Observe									
3-voxel radius	R superior temporal gyrus	63	−31	13	4.31	26	0.000	0.012	<0.001
	R superior temporal gyrus	66	−37	19	4.05				0.001
	R higher auditory cortex	66	−28	4	3.34				0.002

5-voxel radius	L inferior occipital gyrus	−39	−76	−5	5.41	24	0.010	0.576	<0.001
	L lateral occipital cortex	−36	−85	−2	4.43				<0.001
	R superior temporal gyrus	48	−40	10	5.19	15	0.035	0.576	<0.001
	R fusiform gyrus	45	−49	10	3.43				0.002
	L hippocampus	−21	−31	−5	4.16	10	0.077	0.576	<0.001
	L fusiform gyrus	−27	−37	−11	3.28				0.003
	L parahippocampal gyrus	−24	−31	−14	4.11	13	0.048	0.576	0.001
	L parahippocampal gyrus	−18	−22	−14	3.64				0.001
Observe versus Untrained									
3-voxel radius	L superior temporal gyrus	−54	−40	22	3.69	10	0.008	0.233	
5-voxel radius	No clusters	—	—	—	—	—	—	—	
Physical versus Untrained									
3-voxel radius	No clusters	—	—	—	—	—	—	—	
5-voxel radius	No clusters	—	—	—	—	—	—	—	
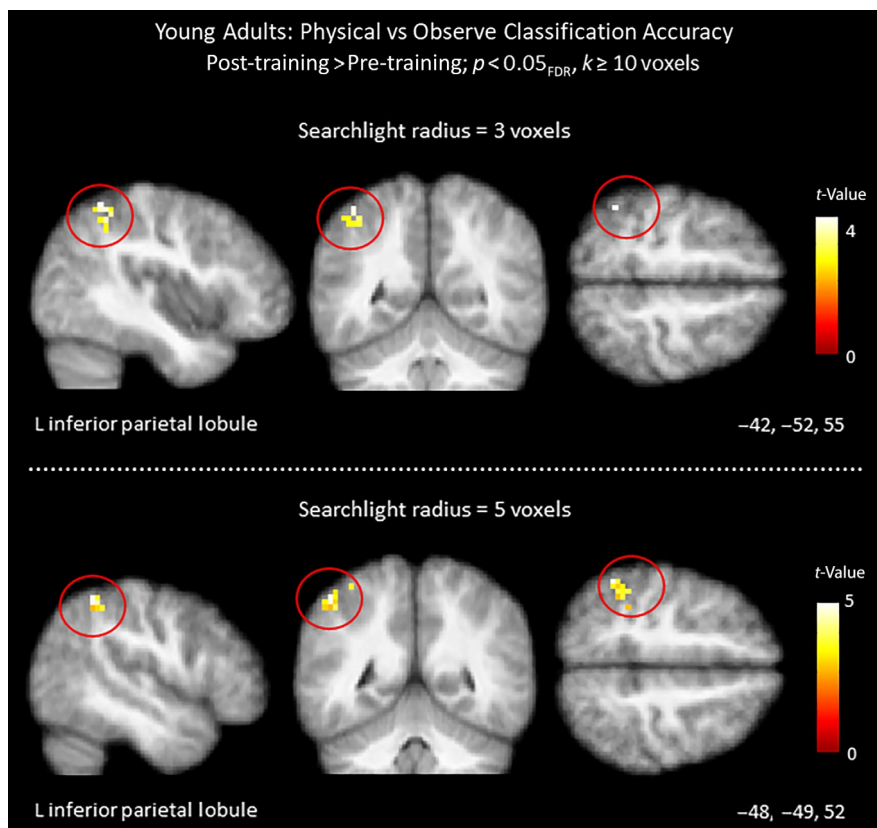
FIG. 11

Post-training > Pre-training classification accuracy for Physical versus Observe movement categories in young adults (searchlight radii = 3 and 5 voxels). Results from paired *t*-tests depicting increased classification accuracy between physically experienced and observed movements from pre- to post-training. *t*-Tests depicted per searchlight volume. Analysis was constrained to regions that fell within the group-level mask (Fig. 5). Results superimposed on averaged structural T1 images of young adult participants.

However, among adolescents, the same interaction revealed that patterns of voxel activity within the right superior temporal gyrus appeared to increase in dissimilarity between these two movement categories (Table 2 and Fig. 12). These findings suggest that within each age group, different regions of the AON appeared to be sensitive to differences in prior visual versus visuomotor experience with movements. However, no other interactions revealed regions of spatiotemporal voxel activity that differed between physically experienced versus untrained, or observed versus untrained movements within either age group.
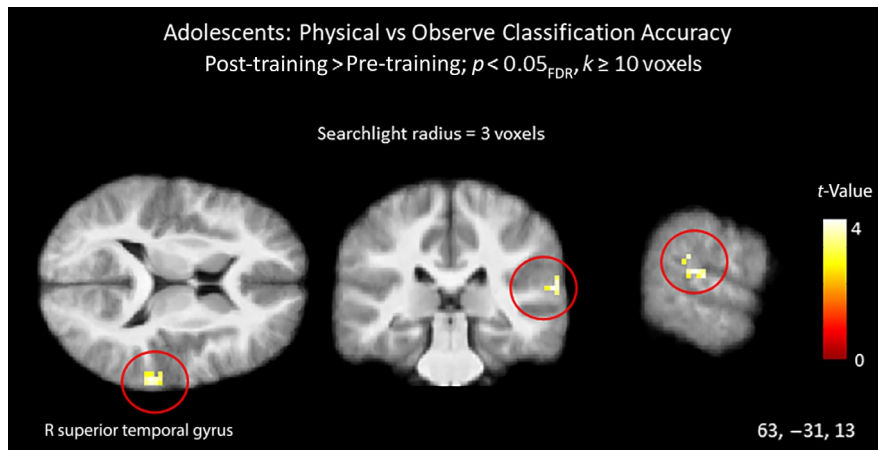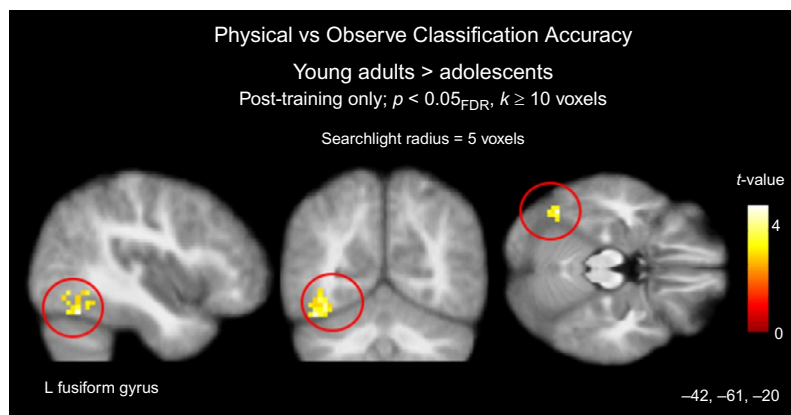
FIG. 12

Post-training > Pre-training classification accuracy for Physical versus Observe movement categories in adolescents (searchlight radii = 3 voxels). Results from paired *t*-tests depicting increased classification accuracy between physically experienced and observed movements from pre- to post-training. Analysis contained within group-level mask (Fig. 6). Results superimposed on averaged structural T1 images of adolescent participants.

7.2 BETWEEN AGE GROUPS

Overall, canonical AON regions in young adults did not appear to be more sensitive to differences in sensorimotor experience than these regions among adolescents when examining differences in spatiotemporal voxel activity patterns following training. These between-group analyses incorporated a functional AON mask that was limited to voxels across both age groups that were active ($p < 0.005_{uncor}$, $k \geq 10$) when participants were viewing movements during the post-training scan (Fig. 9).

However, primary visual regions that were incorporated within this mask did appear to be more sensitive to differences in sensorimotor experience among young adults compared to adolescents. When comparing activity patterns for physically experienced versus observed movements, the 5-voxel radius searchlight revealed heightened dissimilarity for these movement categories among young adults compared to the adolescents within the left fusiform gyrus (Fig. 13 and Table 3). This dissimilarity suggests that this region encodes information relating to visual versus visuomotor engagement with greater accuracy among young adults compared to adolescents when perceiving movements following training.

Differences in voxel activity patterns between observed and untrained movements were also heightened in young adults compared to adolescents in the left fusiform gyrus, left superior parietal lobule, right calcarine gyrus, and the right lingual gyrus when viewing these movements post-training (Figs. 14 and 15 and Table 3).

FIG. 13

Young Adults > Adolescents classification accuracy for Physical versus Observe movement categories (searchlight radii = 5 voxels). Results from paired t-tests depicting greater classification accuracy between physically experienced and observed movements in young adults compared to adolescents following training. Analysis contained within combined group-level mask for young adults and adolescents (Fig. 9). Results superimposed on averaged structural T1 images of all participants.

Such differences suggest that these regions encode information related to the presence or absence of prior visual engagement with movements.

Finally, the left fusiform gyrus and left middle occipital gyrus also appeared to demonstrate greater sensitivity to visuomotor experience with movements (physical experience versus untrained) to a greater extent in young adults compared to adolescents (Fig. 16 and Table 3).

8 DISCUSSION

The primary goal of this study was to investigate how activity within premotor, parietal, and temporal brain regions facilitates complex and intransitive movement learning (such as choreographed dance sequences) through sensorimotor experience. In addition, we aimed to examine whether these brain regions encode sensorimotor experience within an adolescent population in a manner that could inform observational learning while these regions are still undergoing development (Blakemore, 2012; Grosbras and Paus, 2006; Paus, 2010; Ross et al., 2014; Shaw et al., 2012).

Although previous work has demonstrated a link between the number of sensory modalities used to experience a movement and the *degree* of cortical engagement within temporal, parietal, and premotor (AON) regions when subsequently observing a movement (Kirsch and Cross, 2015; Liew et al., 2013a,b), this study failed to replicate these results. An alternative explanation for the correspondence between the
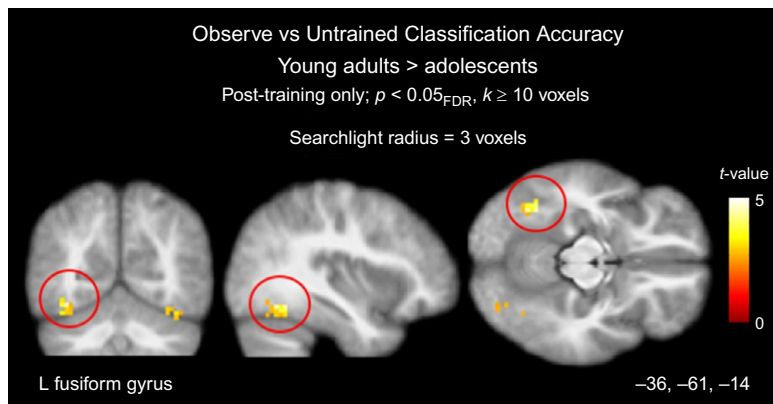
Table 3 Classification Accuracy Between Age Groups: Post-training Only ($p < 0.005_{uncor}$, $k \geq 10$)

		MNI Coordinates				Cluster Level			Peak Level
	Region	x	y	z	t-Value	Size (k)	P_{uncor}	FDR	P_{uncor}
Young Adults > Adolescents									
Physical versus Observe									
3-voxel radius	L posterior medial frontal area	−3	−13	58	4.44	16	0.005	0.325	<0.001
	L paracentral lobule	0	−19	64	4.18				<0.001
	L superior parietal lobule	−18	−64	49	3.95	11	0.016	0.431	<0.001
5-voxel radius	L fusiform gyrus	−42	−61	−20	4.64	56	0.001	0.043	<0.001
	L fusiform gyrus	−39	−52	−8	4.09				<0.001
	L fusiform gyrus	−36	−61	−14	4.07				<0.001
	L paracentral lobule	−9	−22	73	3.75	17	0.049	0.633	<0.001
Observe versus Untrained									
3-voxel radius	R posterior medial frontal area	3	−16	64	5.34	19	0.002	0.076	<0.001
	L posterior medial frontal	−6	−13	58	2.86				0.004
	L fusiform gyrus	−36	−61	−14	4.87	35	0.000	0.006	<0.001
	L fusiform gyrus	−45	−55	−17	3.79				<0.001
	R fusiform gyrus	30	−79	−11	3.73	10	0.016	0.310	<0.001
	R fusiform gyrus	39	−61	−20	3.42	11	0.012	0.310	0.001
5-voxel radius	L fusiform gyrus	−33	−61	−14	4.47	68	0.000	0.007	<0.001
	L cerebellum (VI)	−36	−67	−20	4.23				<0.001
	L fusiform gyrus	−39	−52	−20	3.85				<0.001
	R calcarine gyrus	12	−97	4	4.47	49	0.001	0.025	<0.001
	R calcarine gyrus	12	−91	10	3.88				<0.001
	R ventral extrastriate cortex	24	−97	1	3.45				0.001
	L superior parietal lobule	−24	−55	46	4.10	71	0.000	0.007	<0.001
	L angular gyrus	−42	−55	43	3.70				<0.001
	L inferior parietal lobule	−33	−55	46	3.66				<0.001

Continued

Table 3 Classification Accuracy Between Age Groups: Post-training Only ($p < 0.005_{uncor}$, $k \geq 10$)—cont'd

|		MNI Coordinates				Cluster Level			Peak Level
	Region	x	y	z	t-Value	Size (k)	P_{uncor}	FDR	P_{uncor}
	R lingual gyrus	12	−85	−14	4.05	43	0.002	0.033	<0.001
	R lingual gyrus	21	−85	14	3.76				<0.001
	R lingual gyrus	21	−76	−14	3.38				0.001
Physical versus Untrained									
3-voxel radius	L middle occipital gyrus	−18	−85	13	4.92	13	0.008	0.260	<0.001
	L superior occipital gyrus	−21	−85	22	4.06				<0.001
	L fusiform gyrus	−24	−73	−11	4.49	42	0.000	0.002	<0.001
	L fusiform gyrus	−24	−85	−5	4.40				<0.001
	L middle occipital gyrus	−30	−79	4	4.07				<0.001
	R lingual gyrus	18	−94	−8	4.00	11	0.013	0.288	<0.001
5-voxel radius	L middle occipital gyrus	−36	−85	−2	4.26	76	0.000	0.007	<0.001
	L primary visual cortex	−18	−82	7	4.03				<0.001
	L middle occipital gyrus	−30	−76	−2	3.94				<0.001
	L middle temporal gyrus	−48	−67	1	3.53	10	0.107	0.618	0.001
	L middle occipital gyrus	−39	−61	1	3.26				0.001

FIG. 14

Young Adults > Adolescents classification accuracy for Observe versus Untrained movement categories (searchlight radius = 3 voxels). Results from paired *t*-tests depicting greater classification accuracy between observed and untrained movements in young adults compared to adolescents following training. Analysis contained within combined group-level mask for young adults and adolescents (Fig. 9). Results superimposed on averaged structural T1 images of all participants.
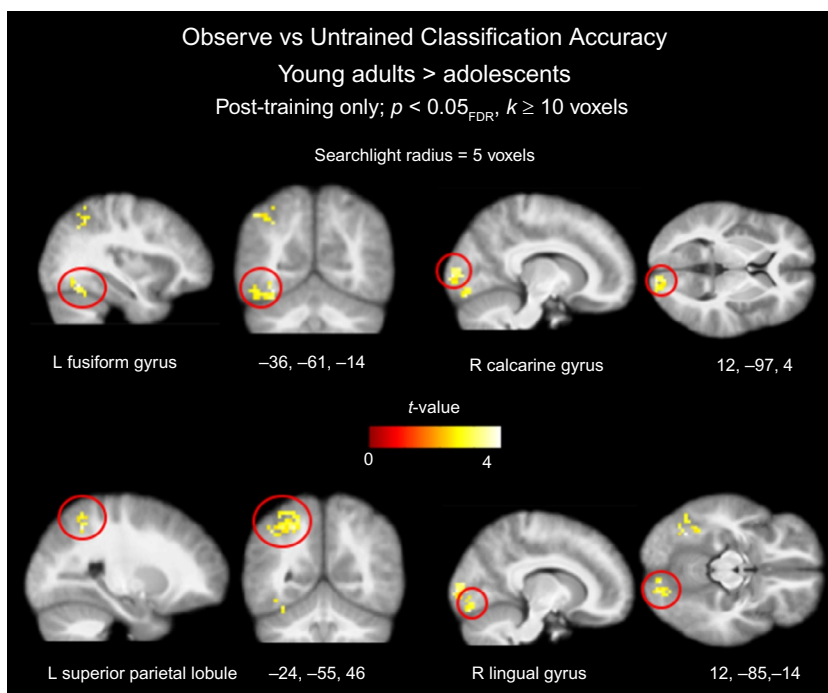
FIG. 15

Young Adults > Adolescents classification accuracy for Observe versus Untrained movement categories (searchlight radius = 5 voxels). Results from paired *t*-tests depicting greater classification accuracy between observed and untrained movements in young adults compared to adolescents following training. Analysis contained within combined group-level mask for young adults and adolescents (Fig. 9). Results superimposed on averaged structural T1 images of all participants.
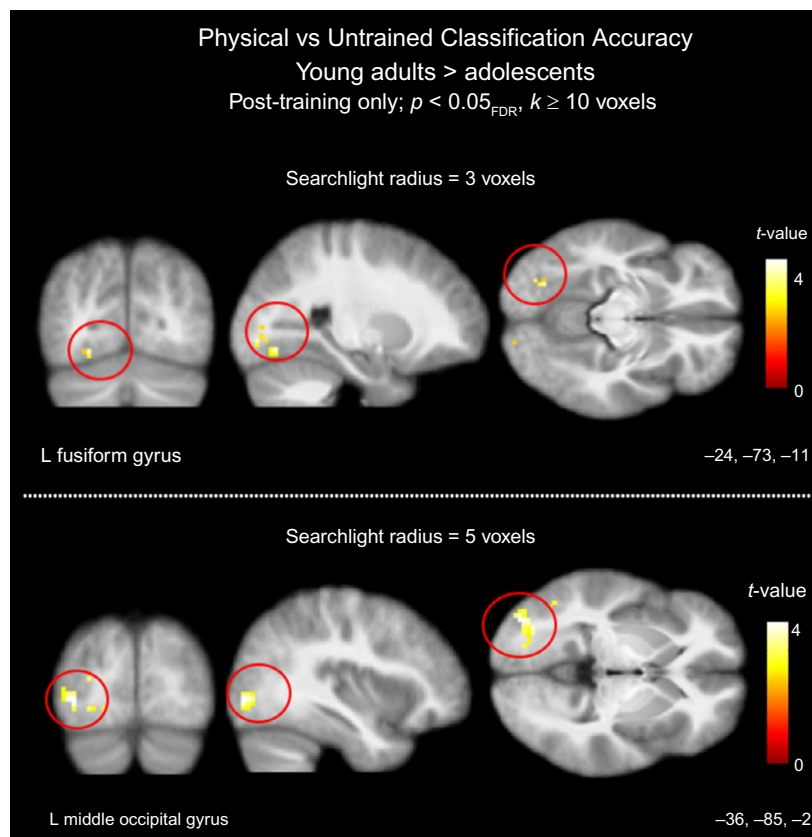
FIG. 16

Young Adults > Adolescents classification accuracy for Physical versus Untrained movement categories (searchlight radii = 3 and 5 voxels). Results from paired t-tests depicting greater classification accuracy between physically experienced and untrained movements in young adults compared to adolescents following training. t-Tests depicted per searchlight volume. Analysis contained within combined group-level mask for young adults and adolescents (Fig. 9). Results superimposed on averaged structural T1 images of all participants.

magnitude of AON engagement and degree of sensorimotor engagement may be related to the rich contextual, social, and emotional detail of the stimuli used to probe movement perception in these paradigms. A number of previous studies demonstrate that social, emotional, and contextual processing is closely linked to AON engagement during action perception (Carlin et al., 2012; Cross et al., 2012; Pelphrey et al., 2004). Here, we wanted to remove as many of these kinds of cues as possible to examine the extent to which these regions demonstrated specific encoding of visuospatial and kinematic movement properties based on prior experience. In doing so, we aimed to isolate how AON regions may be involved in incorporating an observer's own history of sensorimotor experience when viewing stripped-down action cues.

Although the magnitude of AON engagement in this study was not associated with differences in sensorimotor experience, physically experienced and exclusively observed movements could be discriminated from each other based on spatiotemporal voxel activity patterns in both young adults and adolescents. Young adults appeared to demonstrate this sensitivity to sensorimotor engagement in the left inferior parietal lobule, while adolescents exhibited it within the right superior temporal gyrus. However, in the latter case, only the 3-voxel radius searchlight procedure appeared to reveal this pattern discriminability, suggesting that the superior temporal gyrus might only encode differences in visual versus visuomotor engagement within a limited cortical region. Overall, these findings suggest that depending on age, regions within the AON might differ according to how visuospatial and kinematic properties of movements are encoded. While young adults could encode differences in the spatial representations of experienced movements, adolescents may access bottom-up knowledge of body motion through sensorimotor experience, given that the superior temporal gyrus has been linked to perception of human form in adolescents as well as adults (Allison et al., 2000; Avenanti et al., 2013; Giese and Poggio, 2003; Servos et al., 2002). As such, cortical development could differentially impact the extent to which different sensorimotor cues are integrated during action learning and subsequent perception of these actions, particularly in the context of intransitive movements that often lack identifiable action goals.

When directly comparing both age groups, we additionally found that primary visual cortices in young adults appeared more sensitive to differences in sensorimotor experience compared to adolescents as evidenced by spatiotemporal voxel patterns that were more distinguishable according to training experience. However, this comparison did not reveal any regions of voxel activity within canonical AON regions that demonstrated the same age difference in sensitivity to visual and visuomotor engagement. These findings suggest that maturity of primary visual cortices could also influence how sensorimotor experience is encoded when perceiving others perform complex movement. Previous work has already demonstrated that in adults compared to adolescents, extrastriate body area, fusiform body area, and posterior superior temporal sulcus appear to be more engaged compared to adolescents when observing human bodies as point-light stimuli (Ross et al., 2012, 2014), suggesting that increased maturity does indeed impact how body motion is perceived.

Overall, the current findings suggest that both sensorimotor experience and cortical development influence how complex, intransitive actions are perceived. By using an engaging dance learning paradigm that allows us to examine experience-dependent changes in behavioral performance and brain activity, we can advance our understanding of the role played by sensorimotor experience in learning and perception. By using a multivariate analytical approach to identify indices of visual and motor engagement in overlapping brain regions, we report data that challenge some aspects of motor resonance theories of action perception. These theories, which suggest that we perceive movements by mapping them onto our own motor repertoires (Aglioti et al., 2008; Calvo-Merino et al., 2005, 2006; Cross et al., 2006), do not specifically address how the perceptual system negotiates differences in skill level between a model performer and an observer. Within this study, the ability to link perception of specific

movements with their corresponding training context suggests that parietal regions (in young adults) and temporal regions (in adolescents) do encode differences in visually experienced versus performed actions. In contrast, theories of strict correspondence between representations of observed and performed actions (Jeannerod, 2001; Rizzolatti and Sinigaglia, 2010; Umiltà et al., 2001) would suggest that neural engagement for observed and performed actions ought to be identical in nature, if observed actions are directly mapped onto the observer's body in order to be understood.

By decoding patterns of voxel activity, we have demonstrated that differences in visual and visuomotor engagement are decipherable during movement perception even in the absence of overall differences in the magnitude of cortical engagement. As such, we suggest that cognitive mechanisms responsible for discriminating between perceived actions on the basis of experience could provide a pathway for learning complex movements by observation (see related work by Wiestler and Diedrichsen, 2013 on learning via physical practice). Such mechanisms also provide support for predictive coding accounts of action perception (Kilner, 2011; Kilner et al., 2007a,b) which describe how actions can be encoded according to higher-order features (such as an actor's intent and goals) as well as lower-order properties (such as the exact kinematics and visual features) of a movement. Despite our focus on intransitive actions, our findings could be indicative of lower-level visuospatial and kinematic encoding, driven by differences in sensorimotor experience. Given that our evidence suggests adolescents and young adults encode these differences in the superior temporal gyrus and inferior parietal lobule, respectively, this suggests brain maturation influences how complex movements are *perceived* during learning. While the adult AON is able to anticipate movements using acquired spatial information, potentially decoded within the parietal cortex, adolescents appear to rely more heavily on visual body information decoded within superior temporal regions. Nevertheless, additional investigations that combine multivariate decoding paradigms with visual and/or motor experience should help to paint a more detailed picture of the development of action knowledge and motor skill.

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