

Exploring collective experience in watching dance through intersubject correlation and functional connectivity of fMRI brain activity

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Frank E. Pollick^{*,1}, Staci Vicary^{†,‡}, Katie Noble^{*}, Naree Kim[§],
Seonhee Jang[§], Catherine J. Stevens[†]

^{*}*School of Psychology, University of Glasgow, Glasgow, United Kingdom*

[†]*MARCS Institute for Brain, Behaviour & Development and School of Social Sciences & Psychology, Western Sydney University, Penrith, NSW, Australia*

[‡]*Psychological Sciences, Australian College of Applied Psychology, Sydney, NSW, Australia*

[§]*Dance Department, Sejong University, Seoul, Republic of Korea*

¹*Corresponding author: Tel.: +44-141-330-3945, e-mail address: frank.pollick@glasgow.ac.uk*

Abstract

How the brain contends with naturalistic viewing conditions when it must cope with concurrent streams of diverse sensory inputs and internally generated thoughts is still largely an open question. In this study, we used fMRI to record brain activity while a group of 18 participants watched an edited dance duet accompanied by a soundtrack. After scanning, participants performed a short behavioral task to identify neural correlates of dance segments that could later be recalled. Intersubject correlation (ISC) analysis was used to identify the brain regions correlated among observers, and the results of this ISC map were used to define a set of regions for subsequent analysis of functional connectivity. The resulting network was found to be composed of eight subnetworks and the significance of these subnetworks is discussed. While most subnetworks could be explained by sensory and motor processes, two subnetworks appeared related more to complex cognition. These results inform our understanding of the neural basis of common experience in watching dance and open new directions for the study of complex cognition.

Keywords

Dance, fMRI, Intersubject correlation, Network, Brain, Default mode network, Functional connectivity, Cognitive neuroscience, Neuroaesthetics

A question that persists within both philosophical and scientific enquiry regards the possibility of collective experience: do you and I perceive and experience the environment in the same way? Investigations into the neural responses of many people observing the same extended audiovisual stimulus have provided some insight into such collective experiences (Bartels and Zeki, 2004; Hasson et al., 2004; Kauppi et al., 2010; Nishimoto et al., 2011; Zacks et al., 2001). Typically, these studies have involved intersubject correlation (ISC) analysis of blood oxygen level dependent (BOLD) responses acquired from a number of participants passively observing a feature film. For example, Hasson et al. (2004) acquired a significant map of synchronized BOLD activity across participants who watched an uninterrupted 30-min segment of a popular film. The fact that highly significant patterns of neural response occurred across participants even though they were “free viewing” and not completing any specific experimental task suggests that elements within the film “drove” a collective response among otherwise noncollective set of observers. This line of research has been extended to demonstrate ISC not only to low-level visual and auditory stimulation but also to higher order components of the movie, such as social relationships (Kauppi et al., 2010).

One particular domain in which the collective response of observers may be paramount is in the performance arts, in particular dance. As a scientific tool, dance provides an extremely rich and easily accessible source of stimuli for the study of human perception and cognition (Bläsing et al., 2012; Cross et al., 2014). For example, experimental research has made use of dance in the study of action observation (Calvo-Merino et al., 2006; Cross et al., 2009; Orgs et al., 2008), visual memory (Cortese and Rossi-Arnaud, 2010; Smyth and Pendleton, 2018; Stevens et al., 2011; Vicary et al., 2014; Vicary and Stevens, 2014), sequence learning (Ille and Cadopi, 1999; Opacic et al., 2009; Starkes et al., 1987), motor learning and proprioception (Jola et al., 2011), neuroaesthetics (Calvo-Merino et al., 2008; Christensen and Calvo-Merino, 2013; Cross et al., 2011), and social cognition (Zimmermann et al., 2018). However, in much of this research, dance is necessarily reduced to its elements with a focus on just the body, particular body parts or, in the most extreme cases, a set of point light markers. While this enables strict experimental control, the reduction of dance to its elements limits the degree to which collective responses to dance as a whole can be inferred. In particular, during a controlled experiment it is typical that a movement dance clip is seen interposed between a neutral image and these movements are random in their presentation order. This has the advantage of bringing brain activity back to a “baseline” at the beginning of each presentation so that comparison of events is more equitable. However, the great disadvantage is that watching dance is a dynamic and fluid experience where we would expect brain activity to concurrently be (a) moved away from “baseline” by what was just seen, (b) processing what is currently being viewed, and (c) in a state of expectation or prediction of what might appear next. Addressing how to measure this concurrent activity in a systematic way that could illuminate more of the nature of the complex cognition surrounding this perceptual experience is the goal of this research.

Here, we seek not only to use dance as a “tool” for scientific enquiry but also rather as an art form that is engaged with and enjoyed in its own right. Part of a choreographer’s role in creating dance is to design performance elements in a way that will engage the audience on an emotional, intellectual, and psychological level. Therefore, it is of interest to determine the neural correlates of dance observation and whether the movement sequences that the choreographer has planned are later recognized by the audience. Further, it is intriguing to determine the ways in which a group of otherwise unconnected individuals might collectively respond to the same stimulus on a neural level. Doing so will not only promote greater understanding of the neural underpinnings of naturalistic dance observation, but more generally add to the growing body of literature describing the nature of collective experience.

Therefore, this study aimed to determine the patterns of correlated neural activity arising from the observation of a naturalistic dance performance over a few minutes. It also examined what pattern of brain activity arose when observers experienced a portion of the dance that could later be recalled. The dance film to be observed was not created for this research, but rather was a performance piece involved in a previous study considering the eye movements made by novice and expert audience members as they watch dance (Stevens et al., 2010). Therefore, this piece is naturalistic in the sense that it has not been specifically manipulated in any way to tease out collective responses or allow specific comparisons across experimental conditions. The piece involves two performers, with minimal use of props, staging, or different camera angles, and is characteristic of modern or contemporary dance styles.

Previous dance research has obtained ISC maps of the brain activity of observers watching dance to examine the effects of different soundscapes (Reason et al., 2016), video editing (Herbec et al., 2015), and audiovisual integration (Jola et al., 2013). While these studies have revealed where in the brain activity is synchronized between observers there is a growing interest in understanding how these regions of synchronization organize into separate networks (Kauppi et al., 2017; Simony et al., 2016). To address this topic, we use methods of functional connectivity (Behrens and Sporns, 2012; Sporns, 2012) to explore the network organization of regions revealed by ISC when watching video of a dance performance. The purpose of such a network analysis is to reveal how the different brain regions relate to one another and if this provides insight into how sensory, perceptual, and cognitive processes interact with one another.

1 METHOD

1.1 PARTICIPANTS

Eighteen participants (10 female and 8 male, right-handed, healthy) participated in the study. Average age was 27.77 years (± 4.46). Participants were recruited from the list of registered participants of the Centre for Cognitive Neuroimaging (CCNi) at University of Glasgow, as well as from among student volunteers recruited via email. None of the participants had experience in practicing or watching classical

ballet or contemporary dance. Before participating participants underwent safety checks and gave written consent to take part in the study. Ethical approval for the study was granted by the ethics committee of the Glasgow University, College of Science and Engineering.

1.2 STIMULI

While in the scanner participants were shown the dance film titled “13 & 32” choreographed by Sue Healey and performed by dancers James Batchelor and Tom Hodgson, with music composed by Darrin Verhagen (13 & 32, 2006). The film had an overall duration of 308 s, of which 268 s entailed the dance performance (with a black screen showing the title and credits before after the dance). The dance was filmed from a single camera placed at the center front and contained minimal editing (at times the camera zooms in to focus on the dancers at the back or in the middle of the stage). White partitions placed on the side of the stage were used by the choreographer to create depth and varied entry/exit points for the dancers. At differing times within the film either one or both of the dancers were visible on the stage. When on the stage together, the dancers either danced together with physical contact, danced together without physical contact, or danced separately, without directly acknowledging the others presence. Screenshots of the dance are shown in Fig. 1.

Rehearsal footage of the same dancers performing an extended version of the same choreography was used to obtain short 6-s clips for a behavioral memory task. This task enabled a posttest measure of attentiveness (i.e., participants who could not identify a majority of the clips as “old” could be removed from analyses) and also



FIG. 1

Representative screenshots from the dance “13 & 32,” directed by Sue Healey and music by Darrin Verhagen, which was viewed by participants while being scanned. The camera maintained a view down the center line of the stage and between cuts varied from wider to closer shots of the dancers James Batchelor and Tom Hodgson.

allowed investigation of neural correlates of dance memory. Twelve clips taken from the rehearsal footage showed the dancers performing choreography that was either included in the final performance (six clips) or was not included but matched to the overall style of the final performance (six clips). Note that all the clips for the recognition task were taken from the rehearsal footage and so were matched in terms of background, lighting, and costuming of the dancers.

1.3 fMRI DATA ACQUISITION AND PREPROCESSING

All fMRI data were collected using a 3T Tim Trio Siemens scanner (Erlangen, Germany) during one scanning session. A functional T2*-weighted MRI was acquired while participants observed the dance film (EPI, TR 2000ms; TE 30ms; 32 slices; 3-mm cube isovoxel; 70×70 matrix; 175 volumes). The dance film was presented using Presentation software (Neurobehavioral Systems, Inc.) and using a LCD projector was back projected on a translucent screen while participants watched via an angled mirror in the scanner. The soundtrack was played using in-ear headphones (model S14 by Sensimetrics, Malden, USA). During the scanning session, participants were instructed to relax, enjoy, stay still, and watch the movies passively. Participants were not aware of the nature of any additional behavioral tasks to be performed outside of the scanner. At the end of the scanning session, a high-resolution T1-weighted anatomical scan was performed (192 slices; 1-mm cube isovoxel; sagittal slice; TR = 1900ms; TE = 2.52; 256×256 image resolution). Participants were in the scanner for up to 80min, during which time additional functional runs not related to that which is reported here were also obtained.

Standard preprocessing of the functional data was performed for each participant (Goebel et al., 2006). For preprocessing and data analysis we used Brain Voyager QX (Version 2.4 Brain Innovation B.V., Maastricht, The Netherlands). The first two functional scans were excluded to eliminate any potential effects of filtering artifacts. Slice scan time correction was performed using cubic spline interpolation. Additionally, 3D motion correction was performed to detect and correct for small head movements by spatially aligning all the volumes of a participant to the volume closest to the anatomical scan using rigid body transformations with trilinear/sinc interpolation. This processing was followed by normalization of the functional scans into the common Talairach space (Talairach and Tournoux, 1988) and coregistration of functional and anatomical data. In addition, linear trend removal and spatial smoothing with a FWHM Gaussian kernel of 6 mm were applied to each participant's functional data. Finally, the functional data corresponding to the 134 volumes (268s) of each dance were selected. These volumes only included the time corresponding to presentation of the dance (excluding title and credit screens).

1.4 BEHAVIORAL DATA

After all scanning sessions, participants completed the short recognition task. Participants were shown the 12 6-s clips that did or did not show choreography present in the dance film. Participants were asked to observe each clip and indicate whether

they remembered seeing the choreography by labeling each clip as “old” or “new.” Presentation of the clips was counterbalanced across participants. Two practice trials with feedback were shown before the recognition task. Behavioral data were scored using signal detection theory whereby an old item correctly identified as old equaled a “Hit” and an old item incorrectly identified as new equaled a “Miss.” False alarms (new labeled as old) and Correct Rejections (new labeled as new) were scored but did not count into the analysis, as participants did not view these items in the original scanning session.

The six “old” events used in the recognition task were fit back into the timeline of the original film. This timeline was synchronized with the volume-based time course of the scanning session and the structural analysis from the choreographer detailing the timing of prominent events (Spiers and Maguire, 2007). Of the six “old” events used in the recognition task, events four, five, and six occurred too close in time such that any observed differences in BOLD response could not be separated due to the fact that the hemodynamic response function limiting temporal resolution of the BOLD signal. To remove this issue, item number 5 was excluded from further analysis. This resulted in five unique events across the time course of the film. One additional participant with no “missed” events (after removal of item 5) was excluded from the analysis, leaving $n = 16$.

2 ANALYSIS

2.1 GENERAL LINEAR MODEL ANALYSIS OF RECOGNITION PERFORMANCE

For the first level general linear model (GLM) analysis, individual protocol files were derived for each participant’s data, capturing the onset and offset of the events classed as hits or misses. The time course of each predictor (Hit, Miss) was convolved with a hemodynamic response function. Additionally, data were normalized with z -score transformations and corrected for serial correlations. For the second level analysis we performed a random effects analysis, with Recognition (Hit, Miss) used as a within subject predictor. Activations are reported at a threshold of $P < 0.001$ (uncorrected) and were corrected for multiple comparisons using a cluster size threshold iterative Monte Carlo simulation procedure that estimates and corrects for cluster-level false-positive rates (Forman et al., 1995; Goebel et al., 2006). After 1000 iterations, the minimum cluster size that yielded a cluster-level false-positive rate of 5% was used to threshold the statistical map.

2.2 ISC ANALYSIS

The ISC analysis examined which brain regions showed correlated activity among the 18 observers while viewing the dance. This analysis followed the principles presented by Kauppi et al. (2010) that have been detailed in previous studies of dance

(Herbec et al., 2015; Reason et al., 2016). It produced an ISC map showing the brain regions where there was significant correlation. To deal with the issue of multiple comparisons we applied a threshold of $q(\text{FDR})=0.001$, voxel-wise FDR, with positive dependence corrected over the entire brain. In addition, we applied a cluster threshold of 108mm^3 to eliminate consideration of small clusters.

2.3 NETWORK ANALYSIS

To analyze how the brain regions revealed by the ISC map interact as a network, we examined the functional connectivity of these brain regions. To deal with the issue that the ISC analysis can return very large clusters that extend broadly across the brain, we examined large clusters for local maxima of the ISC map using the MATLAB[®] function *imdilate*. The locations of these local ISC maxima, along with the locations of peak ISC in the smaller clusters defined the nodes of our functional connectivity analysis. For the location of each node, we extracted the time course of BOLD activity for each participant and used these signals to assess the network structure.

From defining the nodes and extracting the brain activity signal, the analysis of networks structure proceeded with finding the partial correlation matrix for each participant, which showed the degree of functional connectivity between all combinations of node pairs. This allowed analysis with a GLM to find those links where there was correlation greater than chance, using a FDR corrected value of $P=0.0042$ ($q(\text{FDR})=0.05$) to deal with multiple comparisons (Kruschwitz et al., 2015). These statistically significant links included both positive and negative correlations and produced a mean association matrix defining network behavior. This mean association matrix was further examined for its community structure by use of the Louvain algorithm as implemented by the Brain Connectivity Toolbox (Rubinov and Sporns, 2010). The negative asymmetric option was chosen to reflect the fact that there were a smaller number of negative correlations (Rubinov and Sporns, 2011). The resulting community structure provides an idea of how the entire set of nodes subdivides into subnetworks of common activity.

3 RESULTS

3.1 RESULTS OF GLM ANALYSIS OF RECOGNITION TASK

Results of the random effects analysis are shown in Table 1. Two clusters survived corrections for multiple comparisons, including a cluster of voxels in the left superior parietal lobe corresponding to the precuneus (BA 7) that showed significantly greater activation for remembered events (hits) compared to forgotten events (misses). The opposite pattern of activity was shown by a cluster of voxels in the right cerebellum, with significantly greater activation for forgotten compared to remembered events.

3.2 RESULTS OF ISC

The resulting ISC maps showing the brain areas where correlated brain activity was found among the 18 participants are visualized in Fig. 2 and the location of the peak ISC of the cluster and its anatomic label is presented in Table 2. It is worth noting that the anatomic labels provided for clusters with large volumes should be interpreted with care. For example, the most extensive cluster had peak activity in the right inferior temporal gyrus (ITG) but extended bilaterally over occipital, temporal, and parietal cortex. Additional clusters were found in parietal and frontal cortices.

The ISC map obtained for the dance “13 & 32” is similar in many ways to that found in previous studies looking at brain activity during dance (Herbec et al., 2015; Jola et al., 2013; Reason et al., 2016). It has been proposed by Hasson et al. (2008)

Table 1 Results of Random Effects GLM Analysis of the Recognition Task

Anatomical Region	Hemisphere	Talairach Coordinates (x, y, z)			Number of Voxels (mm ³)	P-Value	BA
		x	y	z			
Superior parietal lobe (precuneus)	Left	-22	-56	42	484	0.00012	7
Cerebellum	Right	5	-47	-15	82	0.00002	—

BA—Brodmann's area.

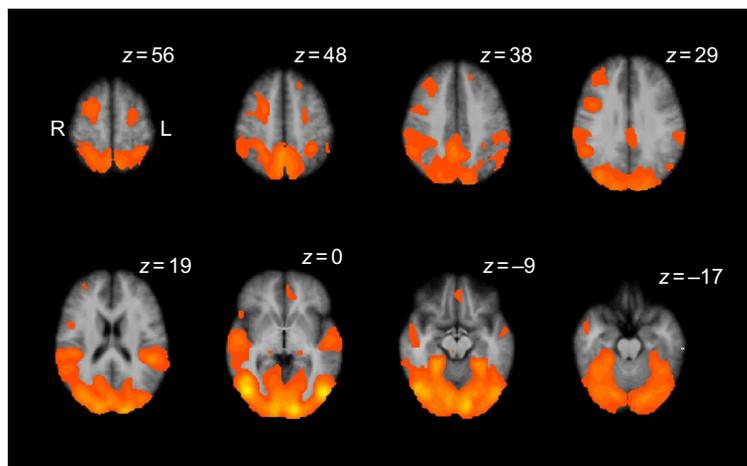


FIG. 2

Results of the intersubject correlation (ISC) analysis across the 18 participants viewing the dance video “13 & 32.” The regions where the ISC map was significant are shown in orange and superimposed on axial slices of the average anatomical structure. Brighter shades indicate higher amounts of correlation. The z-values indicate the Talairach coordinate used to define the axial slice.

Table 2 Results of ISC Analysis for Watching the Dance “13 & 32”

Anatomical Region	Hemisphere	Talairach Coordinates (x, y, z)			Number of Voxels (mm ³)	Peak Statistic	BA
		x	y	z			
Inferior temporal gyrus	Right	44	-71	0	326,872	0.534	37
Middle frontal gyrus	Right	26	1	57	19,937	0.172	6
Superior temporal gyrus	Right	51	13	-3	348	0.078	22
Brainstem	Right	4	-26	-6	374	0.096	—
Anterior cingulate	Left	-1	40	-9	1394	0.087	32
Middle frontal gyrus	Left	-22	-5	57	4380	0.118	6
Superior frontal gyrus	Left	-16	37	42	825	0.084	8
Cerebellum	Left	-16	-68	-30	223	0.074	—
Thalamus	Left	-19	-26	-3	328	0.094	—
Angular gyrus	Left	-46	-65	30	3073	0.091	39
Middle frontal gyrus	Left	-37	49	15	224	0.072	10
Precentral gyrus	Left	-41	-8	42	112	0.072	6

BA—Brodmann's area; Peak statistic is modified r-value.

that one way to further understand the ISC map is to compare it to ISC maps obtained from other related stimuli, as was the case, for example, in the analysis of various Hollywood style movies. Following this lead, we can compare the ISC map obtained for “13 & 32” to previously obtained results that used an identical analysis. In order to make this comparison more meaningful, it is helpful to deal systematically with the situation that the previous results have been obtained under varied audio and visual conditions. These differences include the presence or absence of sound and the presence or absence of video editing and are shown in [Table 3](#) for eight available ISC maps. From the conditions of video, audio, and video editing, we can examine what brain regions were obtained in the conjunction of all the conditions (1–8) where the only common stimulus property to all stimuli is vision (V), the conjunction of conditions 1, 2, 6, 7, 8 that included both dance and sound (VA), and the conjunction of only conditions 2 and 8 that contained dance, sound, and video editing (VAE). While the eight conditions examined here do not cover all possible dance, sound, and video-editing scenarios possible, the results of these conjunctions still

Table 3 Summary of Dance Scenarios Explored in Other Studies Using ISC

Condition	Style	Duration (s)	Dance	Sound	Video Edits	Number of Dancers	Number of Participants Scanned
1	Ballet	320	Sleeping beauty	Tchaikovsky Op. 66	No	1	$n = 16$
2		320	Sleeping beauty	Tchaikovsky Op. 66	Yes	1	
3	Ballet	90	Giselle	No	No	1	$n = 18$
4		90	Swan lake	No	No	1	
5		90	Agon	No	No	1	
6	Contemporary	304	Double points: 3X	Bach Concerto in A minor	No	2	$n = 21$
7		304	Double points: 3X	Breath	No	2	
8	Contemporary	308	13 & 32	Rhythmic	Yes	2	$n = 18$

provide us with an idea of how the brain areas found in ISC maps are sensitive to these conditions. The results are shown in Fig. 3 and indicate that the ISC map increases from V to VA to VAE. Although this increase is expected by the addition of auditory regions in VA and eye movement regions in VAE, there appears to be also a general increase in the volume of the ISC maps that goes beyond simply the addition of audio and eye movement regions. These results support the idea that the obtained ISC map for “13 & 32” is consistent with previous ISC findings.

A final analysis of the ISC map involved finding local maxima within the large clusters. This was necessary to define the brain regions to be used as the nodes for the network analysis. The results of this analysis are presented in Table 4, which provides the Talairach coordinates of these 59 locations and their anatomic and Brodmann areas.

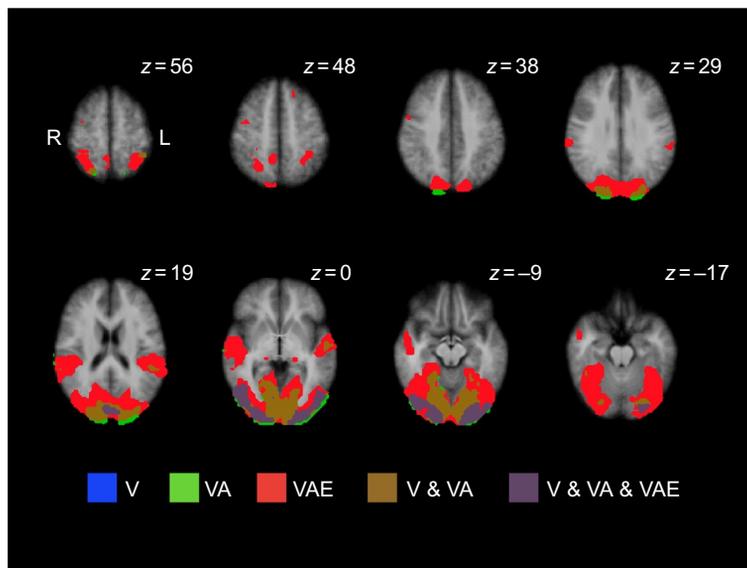


FIG. 3

Results of the comparison between previously obtained ISC maps of watching dance obtained under different audio and visual conditions. V denotes the brain mask obtained by the conjunction of the eight ISC maps that included visual presentation and thus shows the regions sensitive to visual presentation. VA denotes the brain mask obtained by the conjunction of the five ISC maps that included both visual and audio presentation and thus shows the regions sensitive to audiovisual presentation. VAE denotes the brain mask obtained by the conjunction of the two ISC maps that included visual and audio presentation and had edited cuts in the video. This VAE condition includes the ISC map of “13 & 32” discussed in the present study. The *additional colors* and conditions are obtained by the overlap of separate masks. The figure demonstrates the general consistency between ISC maps of different dances and the increase in volume of the ISC map as audio and video editing are added to visual presentation.

Table 4 Local Maxima Derived From ISC Map and Their Subnetwork Assignment

Subnetwork	Anatomical Region	Abbreviation	Talairach Coordinates (x, y, z)			Statistic	BA
1	Parahippocampal gyrus	rPHG	23	-38	-12	0.302	35
	Brainstem	rBrstm	4	-26	-6	0.096	—
	Posterior cingulate	rPCin	14	-59	15	0.186	30
	Lingual gyrus	rLG	11	-56	3	0.154	18
	Posterior cingulate	IPCin	-19	-65	15	0.129	31
	Thalamus	rTh	-19	-26	-3	0.094	—
	Parahippocampal gyrus	IPHG	-25	-41	-9	0.273	36
2	Superior temporal gyrus	rSTG	59	-29	12	0.232	42
	Superior temporal gyrus	rSTG	56	-17	6	0.302	41
	Superior temporal gyrus	rSTG	50	-44	15	0.191	13
	Superior temporal gyrus	rSTG	50	-5	-12	0.120	21
	Superior temporal gyrus	rSTG	44	-20	6	0.314	13
	Superior temporal gyrus	rSTG	44	-25	1	0.125	22
	Insula	rIns	41	-29	18	0.196	13
	Superior temporal gyrus	ISTG	-40	-29	9	0.387	41
	Superior temporal gyrus	ISTG	-55	-2	-6	0.125	22
	3	Inferior temporal gyrus	rITG	44	-71	0	0.534
Fusiform gyrus		rFuG	38	-47	-15	0.234	37
Inferior occipital gyrus		rIOG	23	-89	-9	0.222	18
Cerebellum		ICb	-16	-68	-30	0.074	—
Fusiform gyrus		IFuG	-40	-47	-15	0.206	37
Inferior temporal gyrus		IITG	-46	-71	0	0.508	37

4	Postcentral gyrus	rPoG	29	-44	57	0.169	40
	Paracentral lobule	rPCL	26	-41	45	0.171	—
5	Precuneus	rPCun	20	-53	54	0.181	7
	Inferior parietal lobule	IIPL	-31	-47	54	0.174	40
	Lingual gyrus	rLgG	20	-71	-12	0.296	18
	Lingual gyrus	rLgG	14	-92	9	0.427	17
6	Lingual gyrus	lLgG	-13	-89	-3	0.496	17
	Lingual gyrus	lLgG	-22	-74	-12	0.285	19
	Superior occipital gyrus	rSOG	32	-77	24	0.279	19
	Precuneus	rPCun	23	-62	36	0.109	7
	Precuneus	rPCun	20	-74	42	0.149	7
	Precuneus	rPCun	5	-62	45	0.253	7
	Precuneus	rPCun	2	-50	45	0.282	7
	Precuneus	IPCun	-7	-68	48	0.198	7
	Cuneus	lCun	-19	-83	33	0.211	19
	Middle occipital gyrus	lMOG	-34	-80	18	0.191	19
7	Supramarginal gyrus	rSMG	47	-47	33	0.163	40
	Anterior cingulate	lACin	-1	40	-9	0.087	32
	Cingulate gyrus	lCin	-4	-32	30	0.095	31
	Cingulate gyrus	lCin	-16	37	42	0.084	8
	Superior frontal gyrus	lSFG	-16	28	51	0.073	6
	Precuneus	IPCun	-25	-62	35	0.071	7
	Inferior parietal lobule	IIPL	-37	-56	39	0.069	40
	Middle frontal gyrus	lMFG	-37	49	15	0.072	10
	Angular gyrus	lAG	-46	-65	30	0.091	39
	Inferior parietal lobule	IIPL	-55	-47	42	0.083	40

Continued

Table 4 Local Maxima Derived From ISC Map and Their Subnetwork Assignment—cont'd

Subnetwork	Anatomical Region	Abbreviation	Talairach Coordinates (x, y, z)			Statistic	BA
8	Postcentral gyrus	rPoG	50	-26	36	0.120	2
	Precentral gyrus	rPrG	41	-5	45	0.086	6
	Superior temporal gyrus	rSTG	51	13	-3	0.078	22
	Inferior frontal gyrus	rIFG	41	4	30	0.147	9
	Middle frontal gyrus	rMFG	32	40	30	0.099	9
	Middle frontal gyrus	rMFG	26	1	57	0.172	6
	Middle frontal gyrus	rMFG	5	-11	63	0.088	6
	Precentral gyrus	IPrG	-16	-14	66	0.095	6
	Precuneus	IPCun	-22	-5	57	0.118	6
	Precentral gyrus	IPrG	-41	-8	42	0.072	6
	Inferior parietal lobule	IIPL	-52	-26	33	0.095	40

BA—Brodmann's area; Peak statistic is modified *r*-value.

3.3 RESULTS OF NETWORK ANALYSIS

The results of the functional connectivity network analysis are shown in Fig. 4, which shows the eight different subnetworks found by the community detection analysis. A schematic diagram of the connectivity is shown in Fig. 4A, where colors indicate the different communities and lines indicate that a significant correlation was found between the nodes; the thickness of the node indicates the degree of correlation, with thicker lines indicating more correlation. Red lines indicate positive correlations, while blue lines indicate negative correlations. Subnetwork 1 is located at the 12 o'clock position and the nodes move clockwise using the order shown in Table 4. The locations of these nodes in the brain are indicated in Fig. 4B using Brainnet Viewer (Sohn et al., 2015). The same color scheme is used to indicate community and sign of correlation, and magnitude of correlation is indicated by thickness of the line connecting the nodes.

Overall, the network analysis shows that the majority of correlations between brain areas were positive and the largest values of correlation were obtained by bilateral links between the same brain region in the left and right hemispheres. For example, between right and left parahippocampal gyrus (PHG) or left and right ITG. Connections were found both within nodes of the same subnetwork and between nodes of different subnetworks, and the degree of connectivity varied from subnetwork to subnetwork. The nodes of the network originated from regions that ISC revealed were highly correlated between observers viewing the dance performance. Assuming that the brain activity is time locked to the performance (Hasson et al., 2004), it is possible that the activity seen is unique to this performance. Certainly, from our examination of ISC maps across different performance conditions we would expect differences. However, if the community structure reveals subnetworks of a modular nature then it is possible that this subnetwork structure might generalize for use in analysis of dance performance. For this reason, we examined the eight subnetworks using reverse inference for evidence of specialized function within each subnetwork. The following contains a putative function for the eight subnetworks.

Subnetwork 1—Visuospatial and scene processing. This subnetwork shown in red consists of bilateral pathways that include the medial regions of the posterior cingulate and retrosplenial cortex, as well as the PHG. Both the retrosplenial cortex and the PHG have been implicated in mediating processes between visual processing and memory. Further, the retrosplenial cortex has been reported previously in the perception of dance (Jang and Pollick, 2011). The parahippocampal regions found are close to a brain area known as the parahippocampal place area (PPA) that was found to be sensitive to the perception of scenes (Epstein et al., 1999). However, further examination has revealed that PPA also encodes the context of a scene (Park and Park, 2017) and is divided into different subregions that on the one hand are closely related to visual areas that process low-level features and on the other hand are related to default mode regions that involve memory and scene context (Baldassano et al., 2013). For the present case, due to the large

magnitude of correlation found in the parahippocampal gyri, we conjecture that the activity is more due to visual scene processing since we would assume memory to be idiosyncratic across participants, while visual processing would be able to be driven directly by stimulus properties. Interestingly, this region has six of its seven between-subnetwork links to subnetwork 6, which we attribute to the hub and default mode network processing.

Subnetwork 2—Auditory feature and complex sound processing. This subnetwork shown in brown includes bilateral activation of auditory cortex, along with several nodes in the right superior temporal gyrus that are associated with more complex sound processing. Although these findings of auditory and sound processing regions are consistent with expectations and previous exploration of music listening using ISC (Abrams et al., 2013), it is unclear why this subnetwork is more prevalent on the right hemisphere. This subnetwork is richly connected with other networks such as subnetwork 6 (hub/default mode) and subnetwork 7 (attention and frontoparietal control).

Subnetwork 3—Body motion and form processing. This subnetwork shown in dark green involves strong bilateral connections between right and left ITG and fusiform gyrus (FuG). This particular region of ITG at Brodmann area 37 is frequently reported in ISC studies of dance (Herbec et al., 2015; Jola et al., 2013; Noble et al., 2014; Reason et al., 2016), and it has been noted that this area is in the vicinity of the overlapping regions of the motion processing region of middle temporal cortex and the extrastriate body area (Peelen et al., 2006). The FuG region is significant as this area has been implicated in being selective for processing the human body (Peelen and Downing, 2005). A notable aspect of this subnetwork is its lack of connectivity with other regions, which is consistent with the view that these regions provide perceptually rich but cognitively unelaborated information about the human body (Downing and Peelen, 2011).

Subnetwork 4—Somatosensory associated processing. This subnetwork shown in light blue includes three regions in Brodmann areas 7 and 40 of the parietal cortex. While these brain areas have been implicated in a variety of other cognitive processes their proximity to somatosensory cortex has implicated them broadly in association with somatosensory processing.

Subnetwork 5—Visual feature processing. This subnetwork shown in dark blue includes four regions in Brodmann areas 17, 18, and 19 of the occipital cortex. These Brodmann areas are known as primary, secondary, and associative visual regions, respectively.

Subnetwork 6—Hub processing and default mode. This subnetwork shown in yellow is composed primarily of brain regions in both the left and right precuneus (PCun). The precuneus is a complex brain area that has been implicated as a part of the default mode network (Buckner et al., 2008; Raichle, 2015), which shows the property of increasing activity when a person is not performing a task and decreasing activity when a person is performing a task. Thus, in the simple view default mode processing is thought to be antagonistic

with brain processing that occurs when a person is involved in a task. It has been proposed that the precuneus has a unique role in connecting between default and frontoparietal networks (Utevsky et al., 2014) and more broadly as a hub region that is connected to multiple other large scale brain networks (van den Heuvel and Sporns, 2013). The idea of a hub is consistent with the pattern of connectivity seen in this subnetwork in Fig. 4A, with numerous connections with other subnetworks as well as the presence of both positive and negative correlations. A final important note is that previous examination of brain activity while observing human motion has revealed involvement of default mode network in differentiating between biological and nonbiological motion (Dayan et al., 2016).

Subnetwork 7—Attention and frontoparietal control. This subnetwork shown in purple is composed of brain areas in both the parietal and frontal cortices and was almost exclusively found in the left hemisphere. These areas include those found in the frontoparietal control network and the dorsal and ventral attention networks (Yeo et al., 2011). These regions are largely consistent with the idea of top-down attention and task control as has been discussed in the attention literature (Dosenbach et al., 2008; Petersen and Posner, 2012). Previous studies examining ISC maps revealed by participants when listening to music have found evidence for a right hemisphere dominant attentional network (Abrams et al., 2013; Sridharan et al., 2007). Given our finding in the left hemisphere these previous results argue against the activation in this network corresponding to attention to the sound, although there are links between nodes in this subnetwork and the sound processing subnetwork 2.

Subnetwork 8—Motor cognition. This subnetwork shown in light green is composed primarily of bilateral brain regions in frontal cortex such as Brodmann area 6, which includes premotor cortex and supplementary motor area; all regions that are associated with motor cognition. However, this subnetwork also included a region of primary somatosensory cortex in the postcentral gyrus and this node has a positive link to subnetwork 2, which we attributed to somatosensory associated processing. While the audiovisual task of watching the dance movie did not require motor or somatosensory processing, the existence of mirror neurons (Rizzolatti et al., 2014) argues for a duality of movement perception and production that can explain how motor systems become involved in action perception (Vogt et al., 2013).

In summary, the subnetwork structure that emerged from analysis of the 59 brain locations revealed by ISC provides a framework in which to view the brain activity involved while watching the dance performance. The different subnetworks appear to separate into a complex cognition domain as well as different basic sensorimotor domains (audio, visual, somatosensory, and motor), with visual processing being further elaborated into visuospatial and human body motion processing domains. One possible limitation of the present subnetwork decomposition is that the programming and execution of eye movements are not clearly ascribed to any particular

network. Previous results (Herbec et al., 2015) have shown that video editing substantially increases ISC and this was attributed to how the process of editing synchronizes participants viewing of dance; further study is needed to refine how eye movements contribute to network activity. Finally, the hub aspect of subnetwork 6 that was based primarily in the precuneus provides a window into the dynamic nature of how these different networks interact with one another.

4 DISCUSSION

This research used fMRI to examine how the experience of observing an edited video of a dance duet performance leads to synchronized brain activity among a group of novice observers. Results showed that the areas revealed in the ISC map are consistent with previous findings of synchronized brain activity when watching dance. Moreover, these areas go beyond primary sensory regions to include regions throughout the brain. A network analysis of the functional connectivity of these brain regions indicated several large-scale brain networks that correspond to established perceptual and cognitive functions. A novel finding here was network activity found in the precuneus, which is associated with the default mode network, and extensive connectivity of this region with other brain areas. We also performed an additional memory task after scanning with the purpose of identifying whether there was brain activity that differentiated between later recognized vs nonrecognized dance sequences. These results showed a cluster in the precuneus region of the left parietal cortex that was more active during watching dance sequences that were subsequently recognized.

The responses to our memory task were made outside of the scanner after viewing the video, so the precuneus region observed corresponds to activity during “study phase” that was higher for recollected dance segments than dance segments that were not recollected. This finding is consistent with the idea that the precuneus is involved in “familiarity” memory rather than confident recollection (Yonelinas, 2005). This higher activation while viewing the later recollected dance movement could also possibly be related to indirect processes involved with encoding the movements such as attention. It is noteworthy that this region of the precuneus did not overlap with regions in the ISC map. This is probably because the pattern of which movement was later recalled and which movement was not later recalled varied between participants, and from such an idiosyncratic pattern of responses we would not expect it to be found in the ISC map. This further supports the idea that the ISC map indicates regions related to aspects of experience that are common to the group of observers.

Eight subnetworks were found among the 59 nodes defined by the ISC map, and given the data-driven approach used to obtain the nodes of the subnetworks, and that they might be unique to this performance video; it is important to consider how we would expect these subnetworks to generalize for cases found during observation of other activities. We would expect basic sensory processing to generalize

across task and thus the involvement of visual (subnetworks 1 and 5) and sound (subnetwork 2) processing should generalize to other audiovisual tasks. However, subnetwork 3 appears related specifically to the visual processing of human form in motion and subnetworks 4 and 8 further involved in the somatomotor interpretation of the viewed actions. Thus, we would expect the pattern of activity of these three regions to be due to the viewing of human actions and that they would engage differently when nonanimate activities are observed. In summary, the activity of these six subnetworks (1, 2, 3, 4, 5, and 8) can be attributed to general stimulus properties related to the dance performance and are broadly supported by the action understanding literature (Cross et al., 2006; Grafton, 2009). The remaining two subnetworks (6 and 7) do not seem to map directly into physical properties of the dance performance or action understanding and appear involved in emotional or complex cognitive processing activity such as allocation of attention and access of internal information.

The processes subtended by subnetworks 6 and 7 could also be dynamically reconfigured as the task demands change (Cole et al., 2013). For example, evidence for the reconfiguration of connectivity of the default mode network (subnetwork 6) when listening to a narrative has been revealed by Simony et al. (2016). Similarly, data from MEG studying the brain response to beautiful and not beautiful images revealed activity from 250 to 750 ms after stimulus onset related to an initial aesthetic evaluation that is followed in the time window 1000–1500 ms by brain activity in the default mode network related to a late aesthetic evaluation (Cela-Conde et al., 2013). Evidence that this parietal region found in subnetwork 6 could be involved in the balance between emotional and cognitive processing of watching dance videos comes from a repetitive transcranial magnetic stimulation (rTMS) study. In this study, brain activity at Talairach coordinates (27, -53, 39), which is near to a node of subnetwork 6 located in right precuneus, were temporarily perturbed and while this perturbation was in effect participants reported increased positive emotional response for a specific segment of the viewed dance video (Grosbras et al., 2012). It was argued that this brain location is involved in cognitive control that is inversely related to emotional responding. This conclusion is consistent with the finding that subnetwork 6 has negative correlations with other brain areas and provides further insight into how this brain region and network might contribute to evaluation of watching dance.

An additional observation regarding subnetworks 6 and 7 is that activity within these networks should be critical for the evaluation and interpretation of the viewed dance. This is because these networks include areas involved in the control of attention through frontoparietal connections as well as access to internal states through default mode activity. Indeed, recent evidence suggests that these attention, control, and default mode networks are interlinked in their function (Dixon et al., 2018). One important aspect that brain activity in these subnetworks could subservise is in the depth or creativity of the interpretation given the incoming sensory information. Support for this view comes from results showing that the default mode network is involved in creativity (Beaty et al., 2014, 2016) to the extent that individual

differences in default mode activity can be related to creativity (Beaty et al., 2018). While the current analysis focused on brain activity common to a group of observers, future research can explore whether individual differences in these brain areas relate to the creative interpretation of dance.

In conclusion, although brain imaging studies where individuals view short segments of dance video have revealed much about how the brain processes dance, there is still little known about how the brain contends with naturalistic viewing conditions when it must cope with a continuous stream of audiovisual input. We examined how brain activity varied with watching a dance performance over several minutes and were able to find neural correlates of later recalled dance segments, as well as how brain regions that correlate among observers form into a network that reflects the brain activity common to the experience. Decomposing this network into subnetworks revealed eight subnetworks, six of which are consistent with processing sensory and motor aspects of human action observation. The remaining two networks appear to be involved more with processing complex cognitive activities and included a subnetwork that overlaps largely with the default mode network, which is thought to play an important role in the access of internal information. These findings help to pave the way toward future experiments exploring complex cognitive processes such as recognition as well as the important question in aesthetic experience of how incoming sensory information about dance and music are interpreted within the context of previous experience.

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