REFERENCES

Experience Influences Brain Mechanisms of Watching Dance

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The study of dance has been helpful to advance our understanding of how human brain networks of action observation are influenced by experience. However previous studies have not examined the effect of extensive visual experience alone: for example, an art critic or dance fan who has a rich experience of watching dance but negligible experience performing dance. To explore the effect of pure visual experience we performed a single experiment using functional Magnetic Resonance Imaging (fMRI) to compare the neural processing of dance actions in 3 groups: a) 14 ballet dancers, b) 10 experienced viewers, c) 12 novices without any extensive dance or viewing experience.

Each of the 36 participants viewed short 2-second displays of ballet derived from motion capture of a professional ballerina. These displays represented the ballerina as only points of light at the major joints. We wished to study the action observation network broadly and thus included two different types of display and two different tasks for participants to perform. The two different displays were: a) brief movies of a ballet action and b) frames from the ballet movies with the points of lights connected by lines to show a ballet posture. The two different tasks were: a) passively observe the display and b) imagine performing the action depicted in the display. The two levels of display and task were combined factorially to produce four experimental conditions (observe movie, observe posture, motor imagery of movie, motor imagery of posture). The set of stimuli used in the experiment are available for download after this paper.

A random effects ANOVA was performed on brain activity and an effect of experience was obtained in seven different brain areas including: right Temporoparietal Junction (TPJ), left Retrosplenial Cortex (RSC), right Primary Somatosensory Cortex (S1), bilateral Primary Motor Cortex (M1), right Orbitofrontal Cortex (OFC), right Temporal Pole (TP). The

patterns of activation were plotted in each of these areas (TPJ, RSC, S1, M1, OFC, TP) to investigate more closely how the effect of experience changed across these areas. For this analysis, novices were treated as baseline and the relative effect of experience examined in the dancer and experienced viewer groups.

Interpretation of these results suggests that both visual and motor experience appear equivalent in producing more extensive early processing of dance actions in early stages of representation (TPJ and RSC) and we hypothesise that this could be due to the involvement of autobiographical memory processes. The pattern of results found for dancers in S1 and M1 suggest that their perception of dance actions are enhanced by embodied processes. For example, the S1 results are consistent with claims that this brain area shows mirror properties. The pattern of results found for the experienced viewers in OFC and TP suggests that their perception of dance actions are enhanced by cognitive processes. For example, involving aspects of social cognition and hedonic processing – the experienced viewers find the motor imagery task more pleasant and have richer connections of dance to social memory. While aspects of our interpretation are speculative the core results clearly show common and distinct aspects of how viewing experience and physical experience shape brain responses to watching dance.

INTRODUCTION

An essential theme in psychology is how experience shapes our mental processes, and in this paper we use functional Magnetic Resonance Imaging (fMRI) to explore how experience shapes our neural responses to watching dance. It is obvious that visual experience would be influential. However, the rise of embodied views of perception and cognition (Gomila & Calvo, 2008; Wilson, 2002) and the discovery of mirror neurons (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992) demonstrate the importance of considering how bodily experience would also shape our neural responses of watching dance. We thus attempt to examine the effects of physical experience and visual experience by exploring the neural processes of a group of dancers, a group of experienced viewers and a group of novices with negligible experience in either viewing or producing dance movements.

How the body or the perception of bodily senses might accompany the observation of dance is not a question isolated to neuroscience. The dance scholar Susan Leigh Foster asks the same question: 'What do you feel, physically, when you watch another body performing? How and why do you respond to the motions of another body? What do you sense? How does your physical experience of what you are seeing help you understand what you are watching?' (Foster, 2008). Neuroscience can try to answer this question by examining the brain mechanisms involved in observing dance and defining the roles different components play in the process. By its reductionist framework it is difficult for neuroscience to describe the subjective and conscious experience of watching dance. However, it provides a framework for understanding what is possible, and how different components in the system might interact with each other. This in turn is useful for creating general theories of action understanding, and for providing insight into how and why we see what we do.

The neurosciences do not currently have a unitary, all-encompassing theory of how we understand viewed actions. Instead, there appear to be at least two general descriptive frameworks that relate to each other in complex ways. These include: a) Theory of Mind (ToM) which tries to find what neural processes serve the function of understanding the mental states of others (Frith & Frith, 1999); and b) Simulation Theory which is based on mirror neurons that are involved in both the production and perception of movement (Rizzolatti & Fabbri-Destro, 2008), and thus provide a neural mechanism to simulate the actions of others as a basis for uncovering movement meaning. Both Simulation theory and ToM have substantial bases of scientific evidence, but the terms are also related to previous philosophical discussions and a more neutral term to discuss the related neural activities has been termed Action Observation Networks (Grafton, 2009). An important question related to these theories is the role of experience in understanding the movements of others. Studies of dance and dancers have been influential in informing how experience shapes the neural processes that underpin our understanding of others (Calvo-Merino, et al., 2005, 2006; Cross, Hamilton & Grafton, 2006).

These previous dance studies have examined experience in participants with sophisticated movement production experience. Calvo-Merino et al (2005) contrasted experienced ballet dancers with experienced capoeira practitioners watching movements in and out of their repertoire, and Calvo-Merino et al (2006) contrasted male and female ballet dancers watching movements that, due to gender stereotyping, were in and out of their repertoire. In addition, Cross et al. (2006) studied the development of movement perception in trained dancers. In the current work we examine the effects of pure visual experience by using fMRI to study brain responses in ballet dancers, novices and experienced viewers. These experienced viewers were selected on the basis of their extensive experience of watching ballet with negligible experience of performing ballet movements. These observers could, like the dancers, be expected to have a rich vocabulary in discussing dance and a rich history of observing dance. From this experiment we hope to understand how these individuals with purely observational experience compare to dancers and novices with no experience.

To examine the action understanding network in our different experience groups we needed tasks that would broadly involve processes of action understanding. Based on our previous research (Lestou, Pollick, Kourtzi, 2008), we decided to use a combination of different displays and different tasks, broadly to engage action-understanding mechanisms. The different displays included point-light displays (Johannson, 1973) of either a moving ballerina or a static stick-figure (the point-lights connected by lines along the major joints). This was chosen since both motion (Grossman, Donelli, Price, Pickens, Morgan, Neighbor & Blake, 2000) and form (Jastorff & Orban, 2009; Downing et al., 2001, 2006) are known to contribute uniquely to the perception of human actions. At the same time, the point-light displays subtract many aspects of the form of a person which are potentially distracting to the current question. We also included task conditions of passive observation and mentally performing the viewed action

to examine how the neural response might change when observers were asked explicitly to internally simulate what they were observing. Action simulation has been shown to include brain activations that are consistent with motor cognition associated with actually performing actions (Grèzes and Decety, 2001).

MATERIALS AND METHODS

Participants

The responses of three groups of observers – 12 ballet novices, 14 ballet dancers and 10 experienced ballet observers were examined. Ballet novices (mean age 24) were all current or previous undergraduate students without any experience in dance and who had no prior experience of ballet dancing. The ballet dancers (mean age 24) all had at least 8 years of ballet experience in either a ballet dancing or teaching capacity. The experienced observers (mean age 31) had expertise in either dance theory, reporting dance events for the media, other related dance activities, or were fans with extensive ballet viewing but no experience of ballet dancing. All had a minimum of 6 to 15 years of experience as a viewer. All participants had no knowledge of the purpose of the experiment and had normal or corrected-to-normal vision.

Dance Stimuli: from motion-capture of dance to point-light display presentation

The stimuli were based on motion recordings of a professional ballerina from Seoul National Ballet performing ballet movements. These motion recordings were edited to two-second segments for use as point-light displays (Johansson, 1973). The following section discusses this procedure in more detail.

The ballet movements were captured at a professional motion capture studio. A whole-body marker set was attached to the ballerina and the 3D positions of these markers were recorded at 60 Hz. The original motion recordings consisted of 24 ballet sequences of between six and 24 seconds. The first step was to visualize these longer ballet sequences and produce 52 clips of two seconds each that consisted of basic movement elements. Of these original 52 clips, 35 two-second movements were selected by the first author, a professional dancer and choreographer, to produce a set of movements that ballet experts would consider to be unique exemplars of skilled ballet movements. The criteria for this selection process included factors such as removal of similar movements, elimination of 'connecting' movements, and general aesthetic considerations of the quality of the movement.

These original movement files were in Hierarchical Translation-Rotation (HTR) format and some processing was required to convert these files to point-light stimuli. The HTR files were converted into Character Studio Max format (Dekeyser, Verfaillie and Vanrie, 2002) and using techniques discussed by Ma, Paterson & Pollick (2006), 3D coordinate files were produced that represented 17

points on the dancer. The last step was to convert the 3D coordinates of these 17 points into visual displays. This was done with Matlab using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and the Showtime toolbox (Watson and Hu, 1999) for the creation of QuickTime movies. The markers were displayed as white points on a black background; the movies were 256×256 pixels with a frame rate of 60 Hz. In addition to the movies displaying dance we needed images to represent static ballet postures. To achieve this we selected random frames from our set of movies and connected the points of light to make stick figures. Examples of a motion sequence and a static posture are shown in Figure 1. Examples of the movies are shown in Videos 1–4 and the entire set of movies and static images used in the experiment are available in the Supporting Material.

Stimulus presentation was obtained using Matlab and the Psychophysics Toolbox on a Macintosh Powerbook G3 running OS9. From this computer, visual clips were projected through the MRI scanner's control room window onto a screen at the participant's feet using a video projector. The participant lay supine in the MRI scanner and viewed the display through a mirror mounted on the head coil.

fMRI experimental design and procedure

Each experiment consisted of three scans, each of which lasted 6 minutes and 32 seconds. Before each scanning session began, the participants were familiarized with the stimuli during a short practice session. Each scan consisted of 16, sixteen-second stimulus epochs with fixation and task instruction periods interleaved. Ten different images of static ballet posture or five movies were presented in each epoch. Each static ballet posture display was presented for 500 msec with a blank interval of 1100 msec between items. Each movement-type stimulus was presented for 2 secs with a blank interval of 1200 msec between items. All of the stimulus types were presented in all epochs within each scan. For all the scans, subjects were instructed (written instruction on the screen for 2 sec before each block) either to 'observe' or 'imagine to imitate' the displays, while fixating on a cross in the middle of the screen. That is, each of the four conditions (observe movements, observe static postures, imagine to imitate movements, imagine to imitate static postures) was repeated four times in each scan.

fMRI Data Acquisition

Some readers who do not have a background in neuroscience may wish to proceed to the 'Results' section at this point.

For all experiments scanning was performed on the 3T ISOL Technology scanner at KAIST (Daejon, Republic of Korea). A gradient echo pulse sequence (TR = 2000 msec, TE = 35 msec) was used to collect the functional imaging data. Twenty (3.44×3.44×5 mm) slices covering the whole brain volume were collected with a head coil and were obtained for 196 volumes per experimental run. Anatomical images were acquired with a T1-weighted
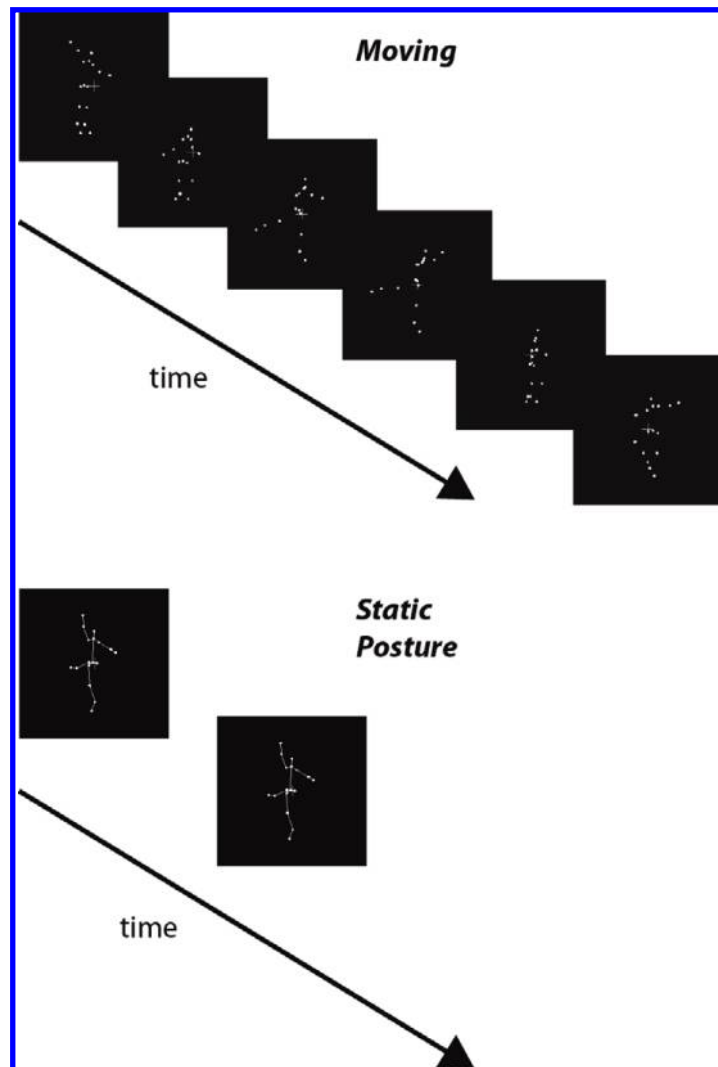
Fig. 1. Examples of frames from a point-light motion sequence are shown on the top and for static posture of a line figure are shown on the bottom. Note, this diagram illustrates the visual nature of the displays and not the times used in the actual experiment. (An example movie is available in Videos 1–4 and the entire set of movies and static images used in the experiment are available in the Supporting Material).

anatomical scan to obtain a whole-brain high-resolution anatomical volume (1.5 mm×0.859375 mm×0.859375 mm, FOV = 220, matrix 256×256, 128 slices).

fMRI Data Analysis

The functional and anatomical images were analysed using Brain Voyager QX 2.1 (Brain Innovation, Maastricht, The Netherlands).

Pre-processing of functional data: Functional imaging data (ANALYZE format) were pre-processed by performing a slice scan time correction. Slice scan time correction was performed and 3-D motion correction (6df) was performed to detect and correct for small head movements by spatial alignment of all volumes of a subject to the reference volume by rigid body transformations. Estimated translation and rotation parameters were inspected and never exceeded 3 mm or 2°. A linear trend removal and temporal high-pass filtering were then applied to remove low frequency non-linear drifts of 3 or fewer cycles per time course. The functional MR images were smoothed using a Gaussian filter with full-width at half-maximum (FWHM) equal to 8 mm.

Pre-processing of anatomical data: The anatomical data (ANALYZE format) of each subject was loaded and converted into BrainVoyager's internal 'VMR' data format. The data were then resampled to 1-mm resolution and transformed into anterior commissure-posterior commissure (AC-PC) and Talairach standard space. The three spatial transformations were combined and applied backward in one step to avoid quality loss due to successive data sampling. The two affine transformations, iso-voxel scaling and AC-PC transformation, were concatenated to form a single 4×4 transformation matrix.

Normalization of functional data: To transform the functional data into Talairach space, the functional time series data of each subject was first coregistered with the subject's 3-D anatomical dataset, followed by the application of the same transformation steps as performed for the 3-D anatomical dataset (see above). This step results in normalized 4-D volume time course ('VTC') data. In order to avoid quality loss due to successive data sampling, normalization was performed in a single step combining a functional-anatomical affine transformation matrix, a rigid-body AC-PC transformation matrix, and a piecewise affine Talairach grid scaling step. As described for the anatomical normalization procedure, these steps were performed backwards, starting with a voxel in Talairach space and sampling the corresponding data in the original functional space. The functional slices were coregistered to the anatomical volume using manual alignment to obtain optimal fit and reduce as much as possible the geometrical distortions of the echo-planar images. The necessary scaling adjustment was done interactively using appropriate transformation and visualization tools of BrainVoyager QX.

Analysis

First level analysis: Analyses were performed on the data of individual participants using multiple linear regression of the BOLD-response time course in each voxel using two predictors Task (observe, motor imagery) and Display (moving, static posture). For each run of each participant's event-related data, a BrainVoyager protocol file (PRT) was derived representing the onset and duration of the events for the different conditions. Predictors' time courses were adjusted for the haemodynamic response delay by convolution with a haemodynamic response function.

Second level analysis: Statistical evaluation of group data was based on a second-level GLM random effects analysis. We carried out a 3 (Experience: novices,

dancers, experienced viewers) X 2 (Task: observe and motor imagery) X 2 (Display: moving, static posture) analysis of variance with Experience as between-participants factor and Task and Display as within-participants factors. The activations are reported after applying an uncorrected threshold of $P < 0.001$ plus an extent threshold of a number of contiguous voxels equivalent to a corrected threshold of $P < 0.05$ defined by using the cluster-size threshold plug-in of Brain Voyager QX (for details see Goebel, Esposito, and Formisano, 2006). This procedure is based on a 3D extension of the randomization procedure described in Forman et al. (1995).

RESULTS

We present a statistical analysis of how brain activity differed in relation to the type of participant (novice, ballerina, experienced viewer), type of Task (observe, imagine) and type of Display (moving, static posture). Our presentation will emphasize the effect of participant since we were primarily interested in how experience shapes the brain networks for action understanding and watching dance.

A three-way Analysis of Variance (ANOVA) was conducted incorporating the factors Task and Display as within group variables and Experience as a between group variable. Results revealed 1) no main effect of Experience, 2) a main effect of Task, 3) a main effect of Display, 4) an interaction of Task on Display and 5) interactions of Experience with Task and Display (Experience X Task, Experience X Display and Experience X Task X Display). Discussion of the results can be divided into points 2–4 which are independent of the factor Experience and point 5 that involves Experience. In this paper we are primarily interested in how experience modulates the brain response to watching dance and thus we will concentrate our analysis on point 5 and discussion of how Experience interacts with Task and Display. However, it is also important to appreciate how the variables of Task and Display modulated the brain response and thus we will begin with a graphical summary of the effects of Task and Display that help to put the interactions with Experience into context.

Effects of Task and Display: Figure 2 shows, projected on transverse slices of the average anatomical structure, all the brain areas revealed by the main effects of Task and Display and their interaction (Results 2–4). The main effect of Task is given in red, the main effect of Display is given in green and their interaction is given in blue. For the sake of comparison, the interactions with Experience are shown in white and circled to facilitate viewing when overlapping. As can be seen in Figure 2 the brain regions revealed by Task and Display are distributed throughout the brain and greatly overlapping. These areas include anterior regions of frontal cortex, large portions of dorsal premotor cortex (BA6), parietal cortex, posterior regions of temporal cortex and much of primary and secondary visual cortex. The large extent of activations is consistent with the relatively lenient statistical threshold of $p < 0.001$ uncorrected for multiple comparisons. It is also consistent with the large variety of brain regions revealed in a recent
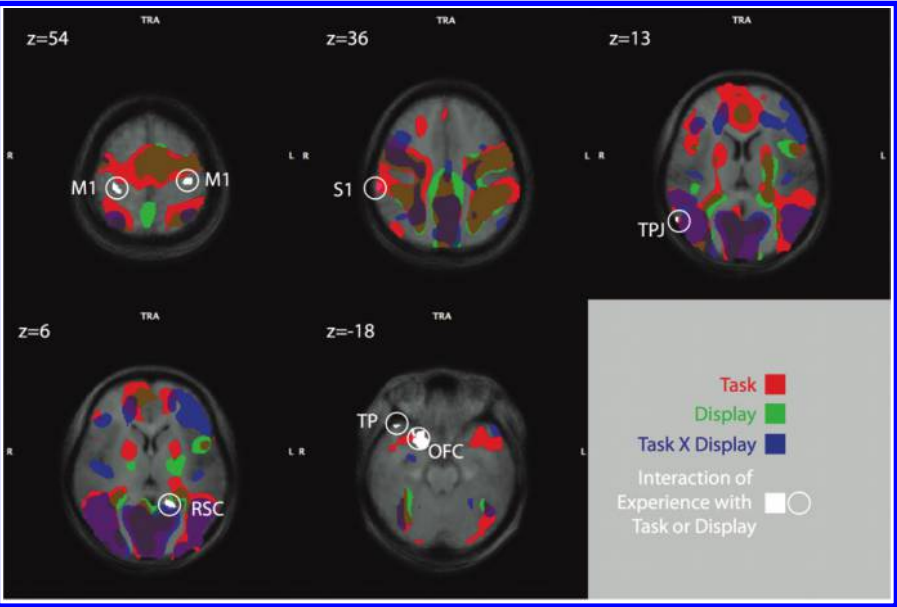
Fig. 2. Areas of brain activation projected on transverse slices of the average anatomical structure (z coordinate refers to Talairach coordinate for that slice). The main effect of Task (Observe versus Imagine) is given in red, the main effect of Display (Posture versus Movement) is given in green and their interaction is given in blue. Additional colors reflect overlapping activations. For example, if an area was activated both for Task and Display it is shown in brown. The areas involved in interactions with Experience are shown in white and circled with an adjacent label of the name of the brain area.

meta-analysis of action observation (Grosbras, et al., 2011) and studies using point light displays (Saygin, Wilson, Hagler, Bates & Sereno, 2004). This result is consistent with a view that our experimental design involving Task and Display was successful in broadly involving action understanding circuits.

Interactions of Experience with other factors: The activations arising from all interactions with Experience are given in Table 1 and shown in Figure 3 on coronal slices of the average brain anatomy of participants. These regions are identical to the white areas shown in Figure 2 but now include colour-coding to reveal the probability of the activation. The brain regions indicated in Table 1 were provided from lookup of the Talairach coordinates using the Talairach Daemon (Lancaster, Rainey, Summerlin, Freitas, Fox, Evans, Toga & Mazziotta 1997; Lancaster, Woldorff, Parsons, Liotti, Freitas, Rainey, Kochunov, Nickerson, Mikiten & Fox, 2000) to indicate the brain region consistent with the coordinates. This localization of activity was straightforward except for the activations revealed by the interaction of Experience and Task. For example, the activation at (17, 13, −18) that we report as orbitofrontal cortex (BA47) extended into the Uncus (BA34). In addition, the activation found at Talairach coordinates (41, 26, −15) proved problematic. The closest gray matter indicated by the Talairach Daemon was the orbitofrontal cortex.

Table 1. Experiment 1 clusters of activation from a 2×2×3 ANOVA with 'Experience' as between-participants factor and 'Task' and 'Display' as within-participants factors.

Anatomical region	Hemi-sphere	Talairach–coordinate (x,y,z)	Number of voxels	Effect size[a] F(2, 33)	p	BA
Experience X Task						
Temporal Pole (TP)	Right	41, 26, −15	88	9.34	0.00064	38
Orbito-Frontal Cortex (OFC)	Right	17, 13, −18	609	9.76	0.00054	47
Experience X Display						
Primary Motor Cortex (M1)	Right	29, −29, 54	121	8.82	0.00086	4
Retrosplenial Cortex (RSC)	Left	−16, −47, 6	317	10.24	0.00045	30
Primary Motor Cortex (M1)	Left	−31, −20, 54	322	9.49	0.00060	4
Experience X Task X Display						
Primary Somatosensory Cortex (S1)	Right	60, −26, 36	105	9.31	0.00066	2
Temporo-parietal Junction (TPJ)	Right	56, −57, 9	138	9.54	0.00060	39

[a]Effect size = average F and p value for all voxels in the ROI.
BA – Brodmann's area

However, visual inspection of this activation on the average anatomy suggested this activation was at the pole of the temporal cortex on the superior temporal gyrus. Since the orbital aspects of the frontal cortex (OFC) and the superior aspects of the temporal cortex are extremely close in physical proximity and the Talairach Daemon also placed this region as an anatomical landmark within 5 mm of the activation, we have denoted this region as the temporal pole (TP) due to its anterior location on temporal cortex. However, we suggest care is used for interpreting this anatomical localisation.

For each region found to be involved in an interaction with experience we obtained the contrast estimate of the region for individual participants and plotted the average value for each group (Figures 4–6). These plots of contrast estimates provide us with a view for each group of the level of activity in that brain region. By comparing the different groups we can see whether that group had enhanced or diminished activity in that brain region for a particular comparison. To better understand these graphs it is useful to know that these plots provide a measure of activity relative to an arbitrary baseline (baseline is defined as the zero level of the graph). That is to say that if the dancers show activation above baseline and novices show activation below baseline then we can conclude that dancers are greater than novices but we *cannot* conclude that
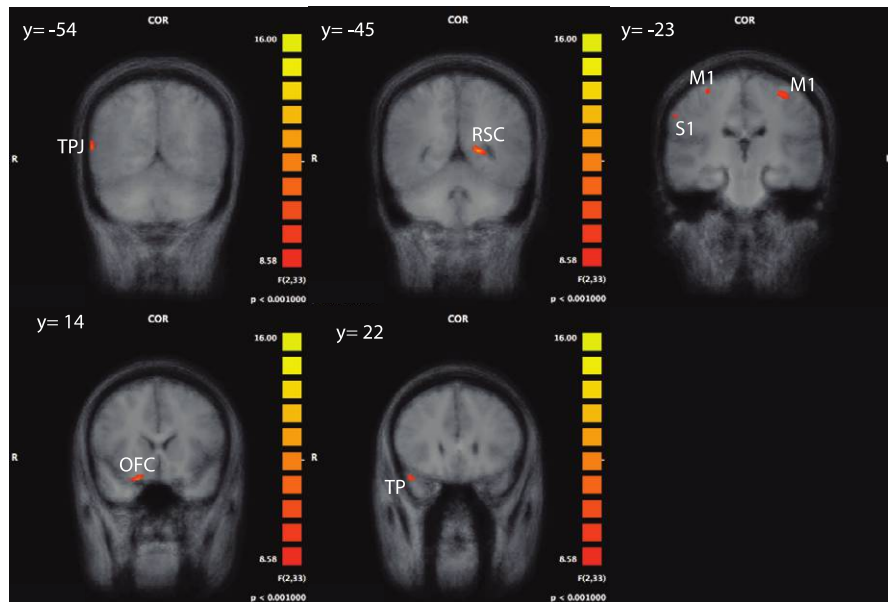
Fig. 3. Areas of brain activation projected on coronal slices of the average anatomical structure (y coordinate refers to Talairach coordinate for that slice). The color intensity is proportional to the test-statistic. The interaction of Experience with Task gave OFC and TP activations. The interaction of Experience with Display gave bilateral M1 and RSC activations. The interaction of Experience with Task and with Display gave the S1 and TPJ activations.

experts activate and novices deactivate this particular brain region. This is a common issue in the interpretation of fMRI brain imaging data. To address this issue we find it useful, therefore, to use the novice group as a reference group with which to compare other results. The performance of the novices informs us of what to expect when an observer has negligible visual or motor experience of dance and thus changes relative to it inform us of how experience changes brain activity. To facilitate the use of these graphs for comparing the different mean contrast estimates we adopt the convention of Moses (1987) to use error bars of 1.5 times the Standard Error. In using this convention to compare two means, if the error bars overlap then they are not significantly different from one another, if they do not overlap then the means are different. Note, however this does not take into account the issue of multiple comparisons which would provide longer error bars.

Interaction of Experience X Task. Figure 4 shows the contrast estimates for the Observe and Imagine conditions derived from the right TP and right OFC regions for the three groups. Since this is an interaction of Experience and Task we expect to see that either the effect of Task was not the same for all three experience groups or the effect of Experience was not the same for both tasks. We see that for right TP there was no difference among groups for the Observe condition but that dancers and novices were both lower than experienced viewers
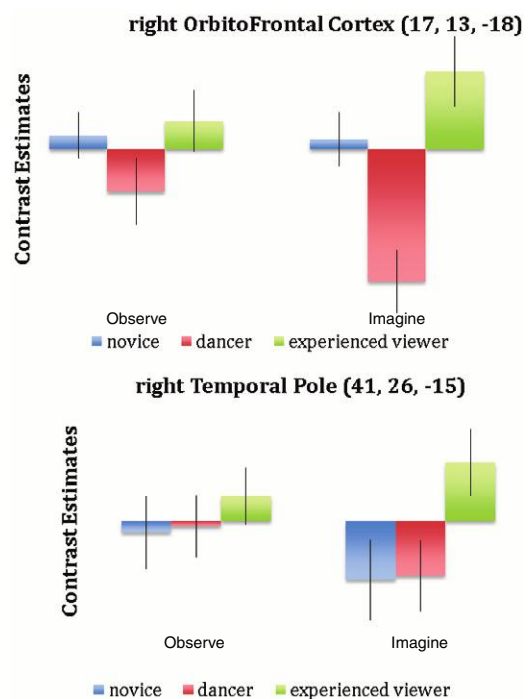
Fig. 4. Average contrast estimates are shown for the interaction of Experience and Task. Error bars indicate 1.5 times the Standard Error so that using the convention of Moses (1987) if two error bars do not overlap then their respective means are significantly different from each other.

in the Imagine condition. For right OFC, relative to the novices, we see that for the Observe condition dancers were different from experienced viewers but not from novices. This difference between dancers and experienced viewers increased for the Imagine condition, with both groups being different from the novices. If we take the novices as our baseline then we see that for right TP the primary differences found in this interaction are the increased activation of the experienced viewers. For the right OFC we see decreased activation for the dancers in the Imagine condition and increased activation for the experienced viewers.

Interaction of Experience X Display. Figure 5 shows the contrast estimates for the Posture and Moving conditions derived from the right and left motor cortices (M1) and the left retrosplenial cortex (RSP) for the three groups. Since this is an interaction of Experience and Display we expect to see that either the effect of Display was not the same for all three experience groups or the effect of Experience was not the same for both displays. The left and right activations in M1 appeared to be bilateral activations of arm/hand regions (Meier, Aflalo, Kastner & Graziano, 2008; Puce, Constable, Luby, McCarthy, Nobre, Spencer, Gore & Allison, 1995) and had similar patterns of results across the three groups. Taking novices as our baseline we can see that in the Posture condition there
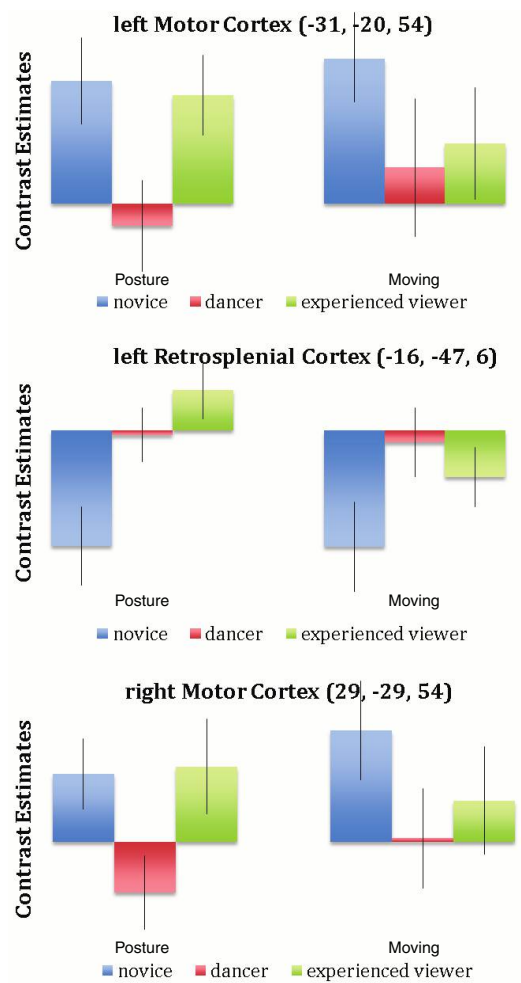
Fig. 5. Average contrast estimates are shown for the interaction of Experience and Display. Error bars indicate 1.5 times the Standard Error so that using the convention of Moses (1987) if two error bars do not overlap then their respective means are significantly different from each other.

was decreased bilateral M1 activation in the dancers. For the left RSP we can see that, taking novices as our baseline, there was increased activation for the dancers and experienced viewers in the Posture condition and for the dancers in the Moving condition. In addition, while the novices and dancers did not change between the Posture and Moving conditions, the experienced viewers decreased their activation.

Interaction of Experience X Task X Display. Figure 6 shows the four possible combinations of the contrast estimates for the Task and Display conditions derived from the right somatosensory cortex and the right temporoparietal junction (TPJ) for the three groups. Since this is an interaction of Experience
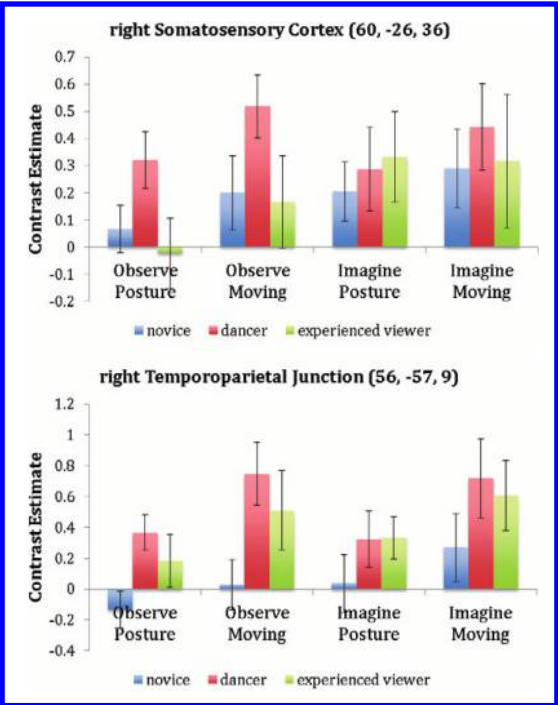
Fig. 6. Average contrast estimates are shown for the interaction of Experience, Task and Display. Error bars indicate 1.5 times the Standard Error so that using the convention of Moses (1987) if two error bars do not overlap then their respective means are significantly different from each other.

with both Task and Display we expect to see a complex pattern of results. In the right somatosensory cortex (S1) around approximately the arm/hand region (Puce, Constable, Luby, McCarthy, Nobre, Spencer, Gore & Allison, 1995) there did not appear to be any substantial differences between the groups for the conditions combining Imagine with either Posture or Moving. However, for the Observe condition combined with Posture and Moving there was higher activation for the dancer group. Other trends were visible in the data but due to the large variability these did not appear significant. In the right TPJ there appeared a general trend for dancers and experienced viewers to show greater activations but this did not fall into a consistent pattern. For the combination of Observe with both Posture and Moving conditions there was greater activation for dancers and experienced viewers that was not obtained for the Imagine conditions.

DISCUSSION

The results of our experiment demonstrated how the brain response to watching dance is modified by experience. Differences involving experience were seen in temporoparietal cortex (TPJ), primary somatosensory cortex (S1), bilateral

primary motor cortex (M1), left retrosplenial cortex (RSC), right orbitofrontal cortex (OFC) and right temporal pole (TP). Taking our novice observers as a standard baseline we can see that both visual-only (experienced viewers) and visuomotor (dancers) experience appear to have distinct effects. To interpret these effects better, we will structure this discussion into three parts. The first part of the discussion will review essential concepts and move on to present relevant neuroscience of the areas identified by our analysis and how this impacts our interpretation of the differences reported. In this first part we do not intend to be comprehensive in our review but instead wish to offer simplified summaries that will provide a reference to the reader unaccustomed with the neuroscience literature. The second part of the discussion will relate our findings to previous published results from the dance neuroscience literature. The final section of the discussion will synthesize across the different contrasts to make conclusions about how experience modulates the brain response and its implications.

Essential Neuroscience Concepts and Review of Identified Brain Areas

A starting point for the discussion is to review our basic design and analysis. We designed our experiment to examine the brain response of different experience groups of observers for different conditions and analyzed our data to see if differences in brain response could be accounted for by group or condition. We were particularly interested in what brain areas were influenced by experience and how experience modulated performance in the different conditions. The results plotted in Figures 4–6 reveal these differences. The pattern of results is complex with both positive and negative results present. However, by taking novices as our baseline we are able to say with some confidence how visual-only experience differed from dance training experience. It is important to note that the standard logic of contrasts in fMRI suggests that if a particular task shows greater activity this implicates involvement of this brain area. However, there is one notable exception to this that involves the effect of practice and we discuss this in the following paragraph.

A recent review by Kelly and Garavan (2005) discusses the neuroimaging changes associated with practice. They point out that activations could either increase or decrease with practice and that decreases of activation are common to the majority of studies examining task practice. The mechanism proposed for this decrease is increased neural efficiency where a sharpened response leads to only a minority of the originally-firing neurons to fire. Such a sharpening would certainly be of advantage in motor processes since it is known that signal-dependent noise places a limit on movement accuracy (Harris & Wolpert, 1998). Increases in activation have still been reported and these can be due to expansion of local cortical circuitry. Kelly and Garavan (2005) argue that changes in neural circuitry with experience could either arise from *redistribution* of processing within an existing network or *reorganization* of the network. The potential for reorganization provides a more radical path for the brain to adopt and provides substantial challenges for imaging, since practice and task overlearning could

lead to entirely different brain areas being used to accomplish a task. The implications for our results are that for every comparison involving experience we must consider whether the relative decrease in activation might occur due to efficient processing. Examples of deactivations that have been associated with practice and overlearning are provided by Petrini et al. (2011) in multisensory integration in drumming, Parsons et al. (2005) in piano playing, Imamizu et al. (2000) for learning tool use, and Lehericy et al. (2005) for sequence learning.

Given that the human brain is doing a multitude of tasks simultaneously it is useful to consider our basic assumption of what theories are relevant and what networks of brain areas these theories have proposed. A basic assumption is that the neural basis of social cognition is our starting point (Frith & Frith, 2010; Adolphs, 2009; Saxe, 2006). Dance is generally a social activity and so is watching dance, and although we might only show an isolated time segment of an isolated dancer in our experiment, we can expect the mechanisms of social perception and cognition to be what are shaped by dance experience. Several different brain networks have been proposed in social cognition as to how we interpret the actions of others (whether a dancer or a person we see on the street); and these theories are under constant development and change so any summary will not agree with all the published literature. Still, for those unaware of the different proposed networks, it is essential background before proceeding to description of the individual areas.

From social cognition there are two basic approaches as to how we might understand the actions of others. One of these is simulation theory and the other is theory of mind (ToM). Simulation theory, as its name indicates suggests we understand the actions of others by covertly simulating their behaviour. Strong empirical support for simulation theory comes from the discovery of mirror neurons (Rizzolatti, et al. 1996; Rizzolatti & Fabbri-Destro, 2008). This theory holds that particular neurons in the brain are involved in both producing movements and perceiving them, and this dual function makes them uniquely suited to 'invert' processes of movement production for the purpose of understanding actions. Results from Calvo-Merino and colleagues (2005, 2006) were influential in using dance experts to demonstrate human brain areas with the mirror neuron property of enhanced processing of movements in the dancer's repertoire. The proposed core mirror neuron areas in the brain include the *pars opercularis* of the premotor cortex and the inferior parietal lobule (Iacoboni & Dapretto, 2006). The posterior Superior Temporal Sulcus (pSTS) is thought to provide the sensory input to this system. The ToM system arises from a vast number of studies that have examined which brain areas are active when we make judgments about the mental states and intentions of others from either visual observation or narrative (Carrington & Bailey, 2009; Mar, 2011). Recently, notions of ToM have been enhanced to distinguish between 'cognitive' ToM where the propositional state of another is considered and 'empathic' ToM where the feelings of another is considered (Saxe, 2006; Shamay-Tsoory, et al., 2004). Although the neuroanatomical distinction between these cognitive and empathic theories appears beyond the scope of our current results, the core ToM

areas are central to our findings. The TPJ, OFC and TP have all been implicated in ToM studies and the TPJ is considered a core area of ToM processing along with the medial prefrontal cortex and STS.

Below we will briefly review the proposed function of the different areas revealed by the interaction with experience and relate this to our results. These include in the right hemisphere the areas TPJ, S1, M1, TP and in the left hemisphere areas M1 and RSC.

Temporoparietal Junction (TPJ). As a definable brain region, the temporoparietal junction is unique among the other terms adopted in this paper. The other terms arise from relating function to a location in the cortex that has some historical anatomical distinction. The TPJ on the other hand blurs across the major anatomical boundaries of the temporal, parietal and occipital lobes of the brain. As a region, the term has come about as the result of numerous studies revealing activations in the supramarginal gyrus of parietal cortex, posterior parts of the superior temporal gyrus and sulcus, and neighboring parts of the occipital gyri (Blake and Shiffrar, 2007; Decety & Lamm, 2007). Although sometimes activations are bilateral, responses are typically stronger in the right TPJ for perception of point light displays of biological motion as used in the current experiment and the right TPJ has been emphasized in social interactions. TPJ has commonly been found in ToM tasks and is considered a core area for ToM (Carrington & Bailey, 2009). It is also one of the few regions involved in ToM that is found regardless of whether the task was visual or story based (Mar, 2011).

The right TPJ was revealed in the 3-way interaction of Experience, Task and Display. Results (Figure 6) generally showed both the dancers and the experienced viewers exhibited greater activation than novices and this was most significant for observation of both moving and posture displays. Since the TPJ appears active in a broad range of ToM activities, including basic action representation in biological motion perception, we can take this increase of activity to be consistent with an expansion of local circuitry in order to represent the visual properties of the dance stimuli. This would be consistent with a redistribution of processing in the action-understanding networks of dancers and experienced viewers to increase representational power in the TPJ.

Retrosplenial Cortex (RSC). A recent review of the function of the retrosplenial cortex (Vann, Aggleton, Maguire, 2009) reveals that although a decade ago the only proposed function of the RSC was in the regulation of emotion, this has given way to an increasing variety of other functions. Its central anatomical location between the limbic system, the memory system and sensory areas, gives it clear potential to be involved in numerous functions. The RSC is often found to be activated by spatial navigation tasks and additional evidence for this comes from data showing that the RSC plays a role in converting information about scene layout from an allocentric frame of reference (location indexed according to external landmarks) to scene layout in an egocentric frame of reference (location indexed according to the self). It has also been found to be activated by tasks involving autobiographical memory.

The left RSC was revealed in the two-way interaction of Experience and Display. Results (Figure 5) showed both the dancers and the experienced viewers exhibited greater activation than novices for both moving and posture displays. Of note was the low activition for the novices which can be predicted if this activity is arising from autobiographical experience. It is also interesting to note that the RSC does not seem to distinguish between doing or seeing the dance movement, thus it might simply signal personal experience in relation to a kind of event. We have already mentioned that the increased activity in TPJ could be due to increased representational power of these brain areas. Another, somewhat related possibility is that this increased activity within the TPJ is related to the RSC activity, where access to memory is fed back to the TPJ and we see enhanced activity due to the influences of this higher level information further shaping the neural response. This involvement of the RSC would thus conceptually form a reorganization of the watching dance network with experience.

Primary Somatosensory Cortex (S1). The primary somatosensory cortex has long been known to be the brain region specialized for processing information about touch and body position. The right S1 represents the left side of the body and the left S1 represents the right side of the body. However, a recent review of the function of the somatosensory cortex (Keysers, Kaas, Gazzola, 2009) found evidence that this brain region is also heavily involved in how we process viewing other people being touched. This vicarious somatosensation, as the authors called it, involves the dual use of somatosensory cortex for processing being touched as well as observing someone else being touched. A key aspect of any region proposed to be involved in the dual function of representing both self and other, is how to distinguish between the two. It is argued that one part of somatosensory cortex is only involved in self-generated postures and touch, while Brodmann Area 2, the region found in our study, is involved in representing both self and other.

The right S1 was revealed in the three-way interaction of Experience, Task and Display. Results (Figure 6) generally showed the dancers had greater activity both when observing postures or moving displays. This activity in the somatosensory cortex is consistent with the proposals of Keysers et al (2009) that the somatosensory cortex has the additional ability of being sensitive to the visual properties of viewed actions. However, if this was a common function of S1 then it is not readily apparent why the effect was found only for the dancers. Possibly the revealed activation forms the basis of the reorganization of a network for watching dance. The activation in S1, like that in M1, was found approximately in a hand/arm area and there is possibly some relationship between these two activities due either to neurological constraints, or task constraints of how dancers develop their use of these limbs. However, since we only have data acquired from watching dance movements it is not possible to conclude whether the effect is unique to watching dance.

Primary Motor Cortex (M1). The primary motor cortex has long been known to be the final stage in planning movements and key to the execution of all

limb movements (Kandel, Schwartz & Jessell, 2000). It is a broad strip of cortex occupying the central gyrus that has output nerve fibres that send signals down the spinal cord to stimulate muscles. The right M1 is responsible for executing movements on the left side of the body and the left M1 is responsible for executing movements on the right side of the body. The motor cortex is organized such that specific regions correspond to specific body parts, and the activations reported correspond approximately to arm/hand regions (Meier, Aflalo, Kastner & Graziano, 2008; Puce, Constable, Luby, McCarthy, Nobre, Spencer, Gore & Allison, 1995).

These results of bilateral activations in M1 (Figure 5) show most prominently that when the dancers either observed or imagined adopting the postures, they had lower activation than the novices and experienced observers. A consistent explanation is that this lower activation arises from overlearning in the dancers. We know from studies of cortical excitability that movement observation causes motor cortex activity. Therefore it is reasonable to assume that the refined motor representations of the dancers show smaller activations due to extensive practice. Why the result is only evident for postures and only in the hand regions is open for speculation. However, they suggest that the dancers have a more consistent strategy for obtaining arm/hand postures than for other body parts. An important point to mention is that the experimental design used does not allow us to infer that the reduced activity in the dancers is due to them viewing dance movements. This is primarily due to the fact that we do not have data on their observation of any other movement. If this effect in M1 could be isolated to only the observation of movements in the repertoire of the dancers, then this would demonstrate a kind of mirror neuron region within M1.

Orbitofrontal Cortex (OFC). The orbitofrontal cortex has been linked to the signaling of expected outcomes and adaptive behavior (Schoenbaum,et al, 2009). These mechanisms, seen in both humans and lower animals, promote behaviours that provide essential resources (food, water, etc). However, the OFC in humans has been hypothesized to expand this basic capacity to the uniquely human characteristic of hedonic experience (Kringelbach, 2005), where humans appear to engage in pleasant behaviours independent of the physical resources they provide. The OFC includes both Brodmann areas 11 and 47 and receives sensory input from different modalities in its posterior aspects. These sensory inputs are thought to combine with each other, and with representations of reward value, to provide correlates of hedonic experience as well as to provide memory, learning and monitoring functions and evaluations that lead to change. The OFC is consistently found to be activated in tasks involving ToM (Carrington & Bailey, 2009), which suggests that the processes linking behaviour to predicted outcome and hedonic value can be applied not only to driving ones own behaviour, but also towards understanding the actions of others.

The right OFC was revealed in the two-way interaction of Experience and Task. Results (Figure 4) showed that for the Observe condition there was a small difference between dancers and experienced observers, but neither were significantly different from the novices. For the Imagine condition this difference

between dancers and experienced viewers increased, and both were different from novices. Interestingly, the direction of this difference was that the dancers showed less activation whilst imagining, and the experienced viewers showed more. It would seem appropriate to account for the decrease shown by dancers, similar to that seen in M1, as due to simple overlearning. However, such an explanation needs to be reconciled with the increase found in the experienced viewers and the ToM and evaluative functions of OFC described above. One possible explanation is that the dancers did not find observing or imagining the performance of these dance movements as pleasant as did the experienced viewers (or novices). In particular, the dancers might have a sharpened sense of which dance movements they enjoy watching or imagine performing.

Temporal Pole (TP). A recent review of the role of the temporal pole in social and emotional processing (Olson, Plotzker & Ezzyat, 2007) is relevant to discussing how this area might be involved in watching dance. These authors point out that, although the function of this anterior portion of the temporal cortex is not well understood, anatomical studies have linked it closely with the limbic system and systems of emotional regulation. Damage of the right anterior pole of the temporal lobe, which can occur in certain diseases, is known to cause a constellation of social and emotional deficits including poor production and recognition of facial expression, loss of empathy and loss of extraversion. The TP has also been implicated in ToM on a variety of tasks (Carrington & Bailey, 2009) and specific mechanisms have been suggested for how it might support ToM. However, a general formulation of the role of the TP is that it functions to link high-level sensory representations with emotional responses and social memory.

The right TP was revealed in the two-way interaction of Experience and Task. Results (Figure 4) showed there was no difference among groups for the Observe condition, but that dancers and novices were both lower than experienced viewers in the Imagine condition. A basic explanation for this result is that when the experienced viewers imagine producing these movements, they are activating richer emotional responses that connect more extensively with social memory.

Relationship to Previous Dance Research

Our results can be compared to three fMRI papers that have investigated how experience modulates the brain activity while watching dance. Two papers by Calvo-Merino and colleagues (2005, 2006) investigated the perception of short clips of ballet video and used a crossover design to control for experience. In the first paper ballet experts were compared to capoeira experts, and in the second paper male ballet experts were compared to female ballet experts using a set of movements that are gender stereotyped. The crossover design meant that in the 2005 paper the ballet dancers were unfamiliar with performing the capoeira movements and vice versa and in the 2006 paper the male ballet dancers were unfamiliar with performing the female ballet movements and vice versa. This design, unlike the current experiment, allows one to see whether

reported activations are specific to the particular movement repertoire of an observer. However, since for this design both groups are motor experts in some movement art, it does not include a group of viewers that has no extensive motor experience. Calvo-Merino et al. (2005, 2006) were successful in showing brain regions involved in the simulation of observed action in premotor, parietal and cerebellar regions. These results are similar to our findings showing S1 activity during action observation in dancers, and thus are consistent with the claims of Keysers et al. (2010) that we can extend regions involved in the simulation of dance to the somatosensory cortex. There are other similarities between our results and those reported by Calvo-Merino et al. (2005). For example, they also reported effects of experience in motor cortex and retrosplenial cortex and enhanced activation in STS regions with experience. Our finding of activations in OFC and TP, were not obtained by Calvo-Merino and colleagues, however this is possibly not surprising, since these areas were only found in our experienced viewers with no motor experience and this type of group was not used by them. In summary, our results are generally consistent with the previous reports of Calvo-Merino and colleagues (2005, 2006) and further support that somatosensory cortex contains simulation areas.

Another study that looked at experience in viewing dance was the study of Cross and colleagues who examined how dance training modified brain networks of action understanding (Cross, Hamilton & Grafton, 2006). Experienced dancers learned new movements across five weeks while being scanned weekly using fMRI. While being scanned they had the task of either observing or imagining performing the movements presented to them. Half of these presented movements had been previously rehearsed, and half were control movements to which they had not previously been exposed. The results of this experiment revealed simulation activity in several areas including inferior parietal lobule, cingulate, supplementary motor areas, ventral premotor cortex, superior temporal cortex and M1. This set of areas is consistent with the regions we found for the effects of Task and Display, though we did not show as great an effect of experience as Cross and colleagues. However, since they were looking at the effects of increasing experience of particular movements in individuals who had general dance expertise, direct comparison with our novice and experienced viewer is not appropriate. Still, if we take their contrasts of rehearsed movements versus control movements as equivalent to dancers versus novices then we do find additional similarities. In particular, activation was reported by Cross and colleagues in right S1 (BA 2) which is similar to what we found. In addition, similar to our results in the region we defined as TPJ and those of Calvo-Merino et al. (2005) for STS, Cross and colleagues found increased activations with experience in the STS region.

Interpreting the Differences across Groups

In this section we will provide a coherent view of all the results from the individual brain areas in which an effect of experience was found. It is instructive

to begin with the reminder that the effects of Task, Display and their interaction, had large effects on brain activation in all groups showing that there is much in common between the three groups. Consistent with our use of the novice group as baseline, we will organize our discussion by factors that were (a) unique to the dancers (b) unique to the experienced viewers and (c) common to both the dancers and the experienced viewers.

Brain Response of Dancers. The dancers were distinctive in their activations of right primary somatosensory cortex (S1) and bilateral primary motor cortex (M1). In S1 they had increased activations when observing postures or moving stimuli and in M1 they showed decreased activity when presented with postures and asked to observe or imagine doing the action; this suggests that, at the very least, the observation of body postures has an impact on processing in S1 and M1. It is known that static postures signal implied motion (Kourtzi and Kaniwisher, 2000) and that certain brain areas in humans (Downing et al., 2001, 2006) and monkeys (Vangeneugden, Pollick, Vogels, 2009) are sensitive to postures. It is possible that these regions might be more effective in driving responses to viewed stimuli, but why this would be, can only be speculated. One possibility is that viewing postures is in a sense the simplest task and that as complexity is added, the variability of the brain response increases as different dancers have different ways of achieving the task. Another possibility is that for the static postures, the brain would need to 'fill in' or simulate more of the action (e.g. what was the previous posture and what might be the next posture), whilst for the movements, the brain would be engaged in monitoring the changes of body posture as the movement evolved. Regardless of the mechanisms, what we can conclude is that dancers appear to be specialized in forming an embodied response to watching the movements.

Brain Response of Experienced Viewers. The Experienced viewers showed greater activity for imagining movement in the right orbitofrontal cortex (OFC) and the right temporal pole (TP), while the dancers had lower activation for the Imagine condition. Somewhat unexpectedly the novices appeared similar to the dancers in the Imagine condition in the TP. Both the OFC and TP have been implicated in cognitive activities including ToM. These types of activities can be typically thought of as higher order representations of the internal state of another and as driven by social cognition. These processes seemed to be enhanced when the experienced observers were asked to imagine performing the movements. This in turn suggests that they more extensively represent the social context and personal meaning of the movements, rather than any particular insight into the movements themselves. This can be considered an enhanced disembodied representation of dance. Interestingly, the two results seem complementary, to the extent that dancers have an enhanced embodied representation of viewing a static posture, while experienced viewers have an enhanced disembodied representation of imagining performing a movement.

Common Responses of Dancers & Experienced Viewers. The results which were common to both the Dancers and the Experienced Viewers were the higher activations in the right temporoparietal junction (TPJ) for observing all stimuli

and the left retrosplenial cortex (RSC) for both observing and imagining to perform all stimuli. Both of these areas are outside primary sensory receiving areas and involve higher order sensory representations of the stimuli. Although we might expect there to be differences between the dancers and the experienced viewers in these higher order sensory representations due to different task demands – dancers more often watch in order to undertake movement practically, while our experienced viewers primarily watch to enjoy – such a result was not obtained. One possibility is that both the dancers and the experienced viewers see abundant amounts of dance stimuli and that these effects in TPJ and RSC are dominated by mechanisms that provide enhanced visual representations for both dancers and experienced viewers.

Conclusion. Taken together we propose that the results suggest the following model for how experience influences the neural network for watching dance. At the earliest stage of processing action, the RSC and TPJ act together to enhance the processing of these familiar movements. We take the involvement of the TPJ to involve a reorganization of the core network. Past this preliminary stage the results reveal two types of enhanced processing, with the dancers having enhanced somatic processing evidenced by activation patterns in S1 and M1, while the experienced viewers have enhanced social processing evidenced by activation patterns in OFC and TP, potentially through mechanisms related to networks involving social cognition and ToM. Although the specific details of which function these different areas are involved with is unclear, there remains a basic distinction. The dancers show differences in motor-sensory processing when observing dance, and the experienced observers show differences in areas of higher cognitive processing. What they share is enhanced initial processing in early stages of processing that combine sensory information, as well as autobiographical memory.

In summary, these results further show that dancers and experienced viewers share aspects of enhanced encoding of movements, while dancers show unique embodied mechanisms of dance perception and experienced viewers show unique disembodied mechanisms of dance perception. In other words, dancers viewing a static posture can use their motor experience to elaborate a view of this posture while experienced viewers can bring their social and narrative experience to elaborate imagining the performance of the movement. This interpretation of the results does not push the boundaries of what might have been expected. However, the current results do open many avenues of research into how these mechanisms work and ways further to test the present interpretation. It is hoped that this body of research will develop over time and be used not only to understand social cognition but also to advance our knowledge of the unique challenges of dancers, choreographers and dance professionals.

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SUPPORTING MATERIAL

The single zip file decompresses into a folder with 40 quicktime movies of point-light dance movements with a duration of two-seconds and 80 image files of point-lights connected with lines in bmp format. The filenames can be considered arbitrary, but provide a unique identifier to the different actions and were generated through an index into the original motion capture recordings.