Neuronal bases of structural coherence in contemporary dance observation

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ABSTRACT

The neuronal processes underlying dance observation have been the focus of an increasing number of brain imaging studies over the past decade. However, the existing literature mainly dealt with effects of motor and visual expertise, whereas the neural and cognitive mechanisms that underlie the interpretation of dance choreographies remained unexplored. Hence, much attention has been given to the action observation network (AON) whereas the role of other potentially relevant neuro-cognitive mechanisms such as mentalizing (theory of mind) or language (narrative comprehension) in dance understanding is yet to be elucidated. We report the results of an fMRI study where the structural coherence of short contemporary dance choreographies was manipulated parametrically using the same taped movement material. Our participants were all trained dancers. The whole-brain analysis argues that the interpretation of structurally coherent dance phrases involves a subpart (superior parietal) of the AON as well as mentalizing regions in the dorsomedial prefrontal cortex. An ROI analysis based on a similar study using linguistic materials (Pallier et al., 2011) suggests that structural processing in language and dance might share certain neural mechanisms.

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Introduction

Dance, and in particular choreographed dance, is a communicative, nonverbal behavior, which requires the production and/or the perception of a complex, temporally extended chain of movements or gestures that form together, not unlike language, a coherent whole out of which emerges the aesthetic/communicative experience of both the dancer and the spectator. We present the results of a brain imaging study that highlight the brain networks specifically implicated in the perception or interpretation of choreographic sequences. The question of how a perceiver puts together and interprets a choreographed sequence of observed movements is relevant not only to the study of dance but more generally to the study of nonverbal (and eventually verbal) communication.

A large body of research has investigated the neuronal basis of nonverbal social interaction (Hari and Kujala, 2009). One of the central themes in this field has been the neural and cognitive basis of action observation. The action observation network (AON, Cross et al., 2009) encompasses a network of regions found to be active specifically during passive observation of another's actions: the inferior frontal gyrus (BA44/45), the superior parietal cortex (SPL), the inferior parietal sulcus (IPS), the posterior medio-temporal gyrus (pMTG), the fusiform face/

body area (FFA/FBA), the visual area V5 as well as the cerebellum (Caspers et al., 2010; Molenberghs et al., 2012). The AON also covers a set of regions active during both action observation and execution: the premotor cortex (PM), the supplementary motor area (SMA), the primary somatosensory cortex (SMA/SI), and the inferior parietal lobe (IPL).

One limitation of many studies of the AON is the use of decontextualized, isolated actions as stimuli, with little attention to the social and/or temporal context (e.g. Rosa et al., 2014). Clearly, however, movement is always embedded in an action sequence (e.g. Giese and Poggio, 2003) and its observation takes place in a social context.

Dance represents a particularly suitable area for the study of the observation of complex, temporally extended actions or sequences thereof. Early AON studies used dance (for a review see Sevdalis and Keller, 2011; Bläsing et al., 2012) to study the role of expertise in action perception and the observation of object- or goal-independent actions. These studies predominantly used short sections of moving images or static images with no temporal structure. They showed evidence for enhanced activity in spectators' AON for dance movements for which they had either physical (Calvo-Merino, 2005; Calvo-Merino et al., 2006; Cross et al., 2006; Orgs et al., 2008) or visual expertise (Jola et al., 2012). Yet dance is a fluent combination of movements extending over time and potentially coded as a specifically choreographed chain of actions. More recent research on dance has started to make use of longer and more naturalistic stimuli (Jola et al., 2012, 2013; Jola and

Grosbras, 2013; Noble et al., 2014; Grosbras et al., 2012b; Herbec et al., 2015) however the question of how single movements or gestures are combined into a coherent whole has been largely left unstudied.

Similar to language, the possibilities of how specific movements can be combined into a contemporary dance choreography seem unlimited, yet the selection of the dance actions and the combinations of these not only define the type of a dance (or its syntax) but also its esthetic appreciation (Orgs et al., 2013). For example, expert dancers and choreographers can make instantaneous judgments on the fluency or coherence of a sequence of dance steps (Amoruso et al., 2014).However, to our knowledge, no study has shown yet the neuronal activity underlying the emergence of the percept of a coherent choreographic whole.

In this paper we ask in which brain regions is the neural activity correlated with the degree of coherence of observed sequence of movements. Which, if any, of the regions, found in studies using single action observation, underlie the emergence of the percept of a coherent whole, and to what extent do other regions, or neurocognitive networks, not identified by studies of single action or dance observation, come into play?

We propose that at least two other cognitive domains are of particular pertinence when interpreting another's communicative actions (such as when watching a dance performance). These are our capacities to mentalize and to understand language. As with the AON, the neural networks underlying these capacities have been extensively studied. These three neurocognitive networks only partially overlap, with respect both to the associated neural tissue and to the presumed cognitive mechanisms (cf. Schwartz et al., 2012; Mar, 2011; Brass et al., 2007, among many others).

The observation of another's action implicates not only the recognition (or embodiment) of the observed motor sequence but also the identification (or induction) of the agent's intentions, as well as their specific perspective and information state: in other words, the construction of a theory of mind. Brass et al. (2007), for example, found that the mentalizing network, but not the mirror network, was sensitive to a manipulation of the affordance (to the agent) of an observed action. We wanted to assess to what extent the mentalizing network (or subparts of it) is also sensitive to the structural coherence of a short dance choreography, which is, albeit not a typical goal-directed-action (as the ones often studied in the context of the AON or mentalizing), nonetheless intentional, and whose goal could be defined in terms of an esthetic communication.

Language comprehension shares many features with dance spectating. Both activities are relational and situated. Both require the integration of multi-sensorial information over time and arguably both involve the decoding of a message or meaning given to that information. To what extent do brain regions or networks previously shown to subserve combinatorial or compositional processes in the domain of language have a role in the perception of choreographic structure? Structural coherence in the case of language is thought of as the extent of unity in a text or a discourse that stems from the links among its underlying ideas and from the logical organization of its thematic content or sub-parts. Indeed, this (abstract) understanding of coherence is not so far from the way coherence is thought of in the context of dance choreography (Foster, 2011).

In practice, coherence in language comprehension has been studied under a variety of different guises (or at different levels of granularity). In discourse analysis, coherence is usually measured at the level of entire texts or whole paragraphs and is primarily concerned with the ideas or conceptual representations evoked in these texts. In neuroimaging studies of text comprehension one common paradigm consists in comparing brain activation during the reading of a (naturalistic, coherent) text to brain activation during the reading of scrambled or unrelated sentences (that do not constitute a coherent text; cf. Yarkoni et al., 2008; Xu et al., 2005; Siebörger et al., 2007).

In theoretical linguistics, coherence has been studied in terms of sentence structure, or syntax. In that sense the sequence "dog the barked" is not a coherent linguistic utterance since it does not respect the structure of English syntax. One method to study the neural correlates of syntactic structures consists in comparing fully formed sentences to lists of words scrambled in a random order (e.g., Mazoyer et al., 1993). Pallier et al. (2011) have elaborated a more fine-grained version of this idea, starting from sentences and creating lists of words that contained progressively smaller and smaller syntactic constituents forming coherent units. In practice, a set of sentences were first sliced into smaller constituents, and constituents of a given size—from different sentences—were concatenated to generate new experimental stimuli. This allowed the authors to look at the brain responses to a parametric manipulation of constituent size, or syntactic coherence.

Here we apply the logic of Pallier et al.'s paradigm to short choreographed sequences of contemporary dance. In this experiment, the analog of fully formed sentences were excerpts from choreographed contemporary dance solos, specifically created by a professional choreographer. Each excerpt was then segmented into 8 snippets, which were parametrically scrambled (combining snippets from different solos) to form 3 additional conditions. Scrambling segments of a continuous movement video, while undoing the coherence of the global movement sequence, also produces local kinematic discontinuities not present in the original sequence, generating a possible confound for the interpretation of the results. Notably, Herbec et al. (2015) used both edited and non-edited video sequences of the same dances (with no temporal or other form of scrambling) and found important differences in inter-subject-correlations between spectators for the two versions. In order to address this issue we created local discontinuities also in the presentation of the original sequence.

The choice of the destructuring paradigm was motivated by a number of factors. First and foremost, unlike in the case of language, we do not have formal tools to evaluate or explicate the underlying structure of a dance choreography (no theorized 'dance syntax'). As a consequence we cannot simply compare two dance choreographies that differ in the complexity of their structure. The scrambling approach is specifically appropriate for the dance/language comparison since it has been used both at the sentence and discourse levels for language. This allows us to remain agnostic as to the mapping between linguistic units and dance or gestural units.

Materials and methods

Participants

We measured the brain responses of 22 professional contemporary dancers (5 males). In order to be included in the study, participants had to have at least 4 years of dance training. Their level of expertise was further measured by indexing the average hours of deliberate practice in the form of dance classes (including somatic practices) per week for each individual year from their first dance class up until the year of the study. Two participants had to be excluded, due to excessive motion (1 male, 38 years, 16 years of deliberate dance practice) and consistent errors in one block (1 female, 21 years, 7 years of deliberate practice). The average age of the remaining participants was 27.65 (SD = 6.07). The average accumulated total hours of deliberate practice of the participants included in the study was 20'416 hours; SD = 16,531 and an average of years of training of 17.85 (SD = 5.82)

We thus consider our group participants as dance experts (e.g. Ericsson, 2008). The study was approved by the regional ethical committee, and all participants gave informed consent prior to scanning. Participation was reimbursed with €80.00. Each participant had normal or corrected to normal vision. All but one of the participants were right handed. The participants were recruited through mailing lists of established educational dance centers in and around Paris (e.g. Centre National de la Danse, Université Paris 8, Studio Keller), and by word of mouth through the professional dance contacts of the authors.

Stimulus construction

The stimuli consisted of dance videos, each of 16 s duration. The dance movements were performed by two professional contemporary dancers in front of a white backdrop, recorded with an XD Camera HD422 (1920 × 1080 interleaved, 25 fps). First, we commissioned ten choreographed phrases of 1 min each, from the French choreographer Amandine Bajou. Notably, a choreographed sequence with a clear beginning and ending in dance is called a "phrase". Each phrase was then performed and recorded 4 times by two dancers. Post-recording, the most continuous, matching, and smoothly performed version of the four runs was chosen for editing. As described in more detail below, 22 s excerpts from these taped phrases were used to create 64 stimuli (16 in each level of coherence).

Coherence was manipulated by different combinations of 8 snippets of 2 s from the original excerpts (cf. Table 1). The identity of the dancer was kept constant across all levels of coherence (there was no change in dancer within a single stimulus).

As we already signaled in the introduction, concatenating two snippets from different choreographies not only reduces the interpretative coherence but also introduces low level visual discontinuities, not present in the original videos. Our solution to this possible confound was to introduce low level discontinuities also in the coherent chunks.

First, we overlaid blanks over each transition (both continuous and discontinuous). The blank interval replaced a segment of the original video (forming an apparent occlusion). Moreover, the actual length of the replaced segment varied, forming a 'jitter' (length of removed section — length of blank). This jitter was inserted to disrupt the predictions of the visual system regarding the location of the moving body after occlusion (Saunier et al., 2013).

After pre-testing of different jitter and blank duration values, we chose to insert a blank duration of 550 ms and jitter values ranging in 7 steps from 600 to 900 ms. For the continuous transitions, jitter within this range seemed to disrupt low level predictions while conserving the sense of coherence or continuity.

Finally, we created 8 additional probe trials (11% of all trials, 1 per dancer per coherence level), in which one of the snippets was speeded up (×4) and vertically inverted. The participants' task was to press a response button when they noticed an inversion. We thus had a total of 72 trials (2 dancers × 4 conditions × 8 variants plus 8 probes).

Procedure

A slow event-related design was used. Each trial started with the presentation of a white fixation cross on black background for 1.5 s. The screen was then cleared for 750 ms and a video stimulus was played for 16 s, after which the screen was cleared again and remained so until the next trial began. The interstimulus interval, between two successive videos' onsets, was fixed at 14 s. The stimuli were presented via a video projector with a native resolution of 1024 x 768 pixels on a screen visible under a visual angle of 30° through a mirror attached to the head coil. A response button placed in the dominant hand of the participants

Table 1
The structure of the experimental stimuli, by condition. Each stimuli was constructed from 8 snippets of 2 s. The 7 transitions were overlaid by blanks of 550 ms. Coherence was manipulated by varying the size of chunks (a sequence of snippets from the original taped phrases).

Condition	Structure of the stimulus
c8 (most coherent)	A single coherent chunk of 8 video snippets
c4	Concatenation of 2 coherent chunks of 4 video snippets
c2	Concatenation of 4 coherent chunks of 2 video snippets
c1 (Least coherent)	Concatenation of 8 video snippets

Examples of stimuli are provided at http://www.pallier.org/dancestruct

allowed them to signal the detection of accelerated video frames within the probe stimuli.

The experiment was split in three 12-min sessions containing 24 trials each. Each participant therefore received a total of 72 trials, that is, 16 trials from each of the 4 coherence levels (8 from dancer 1 and 8 from dancer 2) and 8 probe trials. The trials within a given condition were distributed as evenly as possible across the three runs (each run contained 5 or 6 trials per coherence level, and 2 or 3 probe trials). The order of conditions and stimuli was randomized for each participant. Stimulus presentation was controlled by the Eprime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

The acquisition was performed with a 3 Tesla Siemens magnetom Tim Trio scanner equipped with a 32 channels coil. An MPRAGE T1-weighted scan (Time of echo = 2.98 ms; voxel size = $1 \times 1 \times 1.1$ mm; field of view = 256 mm) was first acquired. Then, functional scans were acquired using a rapid Echo-Planar sequence developed at the Center for Magnetic Resonance Research of the University of Minnesota (Feinberg et al., 2010; Xu et al., 2013), with the following parameters: Time of repetition (TR) = 2.3 s; TE = 23 ms; voxel size = $1,5 \times 1,5 \times 1,5$ mm; 82 axial slices Grappa = 3 and multiband parallel acquisition = 3).

Data analysis

MRI data were processed using SPM8 (Wellcome Department of Cognitive Neurology). Functional volumes were motion-corrected, coregistered with the anatomical scan, and spatially normalized using the transformation obtained from the normalization of the anatomical scan onto the avg152 T1-weighted brain template defined by the Montreal Neurological Institute using spm8's default parameters. Finally, the functional images were smoothed with an isotropic Gaussian kernel with a full width at half maximum set to 5 mm.

Experimental effects at each voxel were estimated using a multi-session design matrix with regressors modeling the 4 types of stimuli, corresponding to the conditions c1 (fully coherent), c2 (2 coherent segments of 8 s each), c4 (4 coherent segments of 4 s each) and c8 (8 coherent segments of 2 s each) as well as the probe condition. Each stimulus was modeled as an epoch lasting 16 s, convolved by the standard SPM hemodynamic response function. The 6 movement parameters computed at the realignment stage were included as additional regressors of non-interest.

Individual contrasts averaging the regression coefficients associated with each condition across sessions were smoothed with an $8 \times 8 \times 8$ mm Gaussian kernel and were entered in a second-level group analysis. A "one way ANOVA — within subject" model was used, with the factors subject and coherence level. The model was estimated using the restricted maximum likelihood algorithm that did not assume equal variance, or independence across levels of coherence.

An additional analysis was performed focusing on six regions of interest (ROI) previously shown to be sensitive to linguistic coherence in the study by Pallier et al. (2011). These ROIs were defined in the Pallier et al. study as spheres of 2 cm diameter intersected with the linear contrast for constituent size thresholded at $p < .001$ voxel wise uncorrected. For each of these a-priori ROI and each participant, the coherence effect (linear contrast with weights -3; -1; 1; 3 respectively associated to conditions c1, c2, c4, c8) was extracted and averaged over all the voxels in the ROI, using MarsBar (http://marsbar.sourceforge.net/).

Results

The participants detected the speeded up inverted video frame 95% of the time and made 3 false alarms (0.2%).

Fig. 1 shows the global network of regions which were activated while participants viewed the dance excerpts, in contrast to fixating a
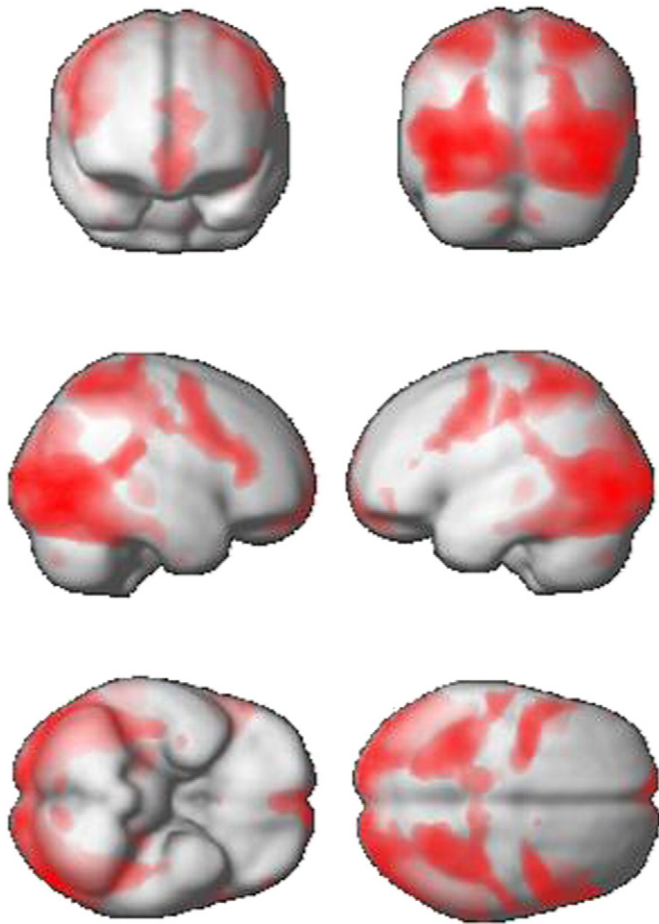
Fig. 1. Regions activated while watching dance. SPM t map of the contrast averaging all levels of coherence against the dot fixation condition (thresholded $p < .001$ voxelwise and uncorrected for multiple comparisons). The activations are overlaid on a smooth rendering of the MNI152 template provided by SPM8.

dot (activations were averaged over the four levels of coherence). The main regions implicated are the visual regions of the occipital lobe extending into the basal temporal lobe, the superior parietal regions, the premotor area and the medial prefrontal cortex.

To identify regions where activation increased with coherence, a positive linear contrast (with weights set to $-3; -1; 1; 3$) was used. The results are shown on Fig. 2. Two clusters reached significance ($p < .001$ voxel-wise and $p < .05$ on cluster size), one located in the left dorsomedial prefrontal cortex (peak at -14 48 24, MNI coordinates; cluster size = 3780 mm^3) and the other one in the left superior parietal region (peak at $-24 -48$ 73, cluster size = 1650mm^3). Homologous regions of the right hemisphere also contained suprathreshold ($p < .001$ voxelwise) voxels but with cluster sizes which did not reach significance (right prefrontal cortex: 14 50 25 cluster size = 900 mm^3; Right superior parietal cortex; 16 -44 74, size = 490 mm^3). Finally, an additional cluster was noticeable in the dorsal superior frontal region (peak at $-21 -4$ 48), but its size (1260 mm^3) was only marginally significant ($p = 0.06$).

We also searched for regions showing a decrease in activation with coherence level or, in other words, a stronger response to less coherent videos than to more coherent ones. The inverse linear contrast (with weights 3; 1; -1; -3) detected two clusters located in the occipital cortex (clusters: peak at 20 -94 16 size = 9790 mm^3 and -20 -100 18, size = 9500 mm^3) and extending into the basal temporal regions, in the lingual and fusiform gyri (the most anterior local maxima were at $-39 -36 -17$ on the left and 38 -44 30 on the right).

A priori regions-of-interest

Finally, we examined the effect of coherence in regions of interest that were sensitive to structure in linguistic stimuli by Pallier et al. (2011). The results are reported in Fig. 3. Significant effects of coherence were detected in three regions: the pars-triangularis and pars-orbitalis of the inferior frontal gyrus, and the posterior superior temporal sulcus. In the other regions (temporal pole, anterior STS and temporo-parietal junction), the effect was positive but did not reach the $p < .05$ significance level.

Additional dmPFC ROI analysis

In the whole brain analysis, we observed an effect of dance coherence in the dorso medial prefrontal cortex (dmPFC). Pallier et al. (2011), also reported an increase of activation with constituent size within this area although the cluster was not included in the a priori ROIs because of its relatively small extent (see Table S1 and Section 4 of the supporting material of that paper). To examine the overlap between the two studies, we defined a dmPFC ROI of 2 cm radius centered at the peak of the language constituent size effect (MNI coordinates -6 53 36; see table S1 of Pallier et al, 2011). The effect of coherence in dance in this dmPFC ROI was significant (linear contrast: (19) = 2.9; $p < .001$).

Discussion

We report the results of an experiment manipulating parametrically the degree of coherence, or structure, in a sequence of taped excerpts of short contemporary dance choreographies. Our participants were all experts in contemporary dance. The whole-brain analysis (dance observation − baseline) revealed extensive activations in the visual, somatosensory and motor networks as well as in the medial and lateral frontal regions. This extensive activation is in line with previous research on dance and human movement observation (Calvo-Merino, 2005; Caspers et al., 2010), but by itself does not provide particular insights into the mechanisms underlying this cognitive activity/state. We will not discuss these results in any further details. We now turn to the discussion of the effect of the parametric modulation of coherence.

Parametric modulation of coherence

The whole-brain analysis of this parametric manipulation detected a negative effect of coherence—more activity when the sequence is less coherent, or more scrambled—in a sizable bilateral cluster situated in the occipital and ventral temporal lobes. Increase in activation in these (early and secondary) visual regions could be related to larger 'low level' discontinuities in the sequence of scrambled dance choreographies that were not totally eliminated by the jittering of the coherent sequences. It is noteworthy that this disruption effect was confined to the visual system and did not produce activation in attention or executive control networks.

More relevant to the aim of this study, the positive effect of coherence, that is, an increased activity when the sequence is more coherent or less scrambled, was associated with significant increase in activation in two clusters, one in the dorsomedial prefrontal cortex, and the other in the superior parietal lobe. The ROI analysis, based on an analogous coherence manipulation of linguistic stimuli (Pallier et al., 2011), found significant effect of the parametric manipulation of dance stimuli in 3 out of the 6 regions: the pars orbitalis and pars triangularis of the left IFG, and the left posterior superior temporal sulcus (pSTS).

The dorsomedial prefrontal cortex (dmPFC)

The dmPFC region whose activity increased with coherence is not part of the canonical action observation network (AON, Caspers et al.,
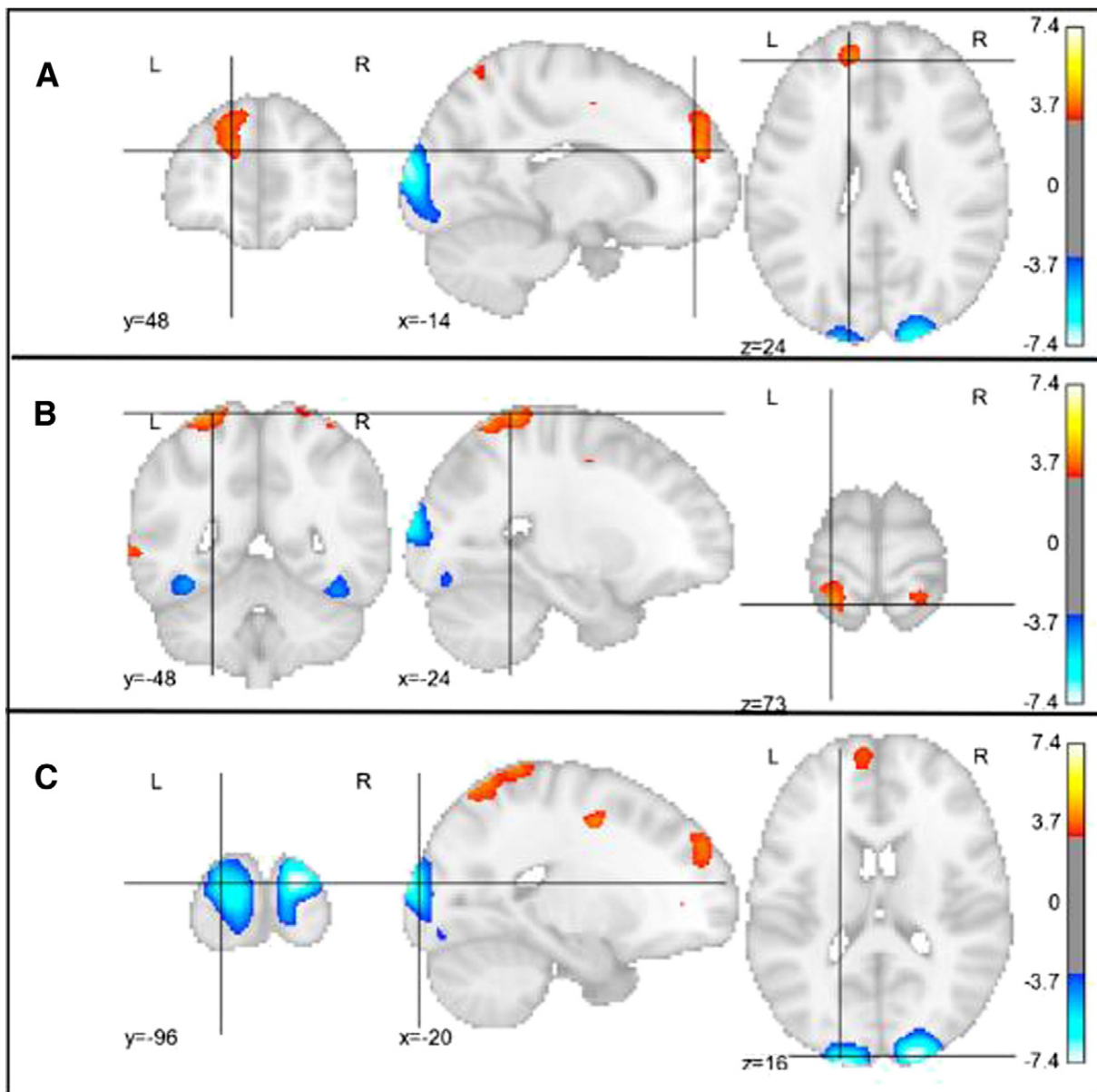
Fig. 2. Regions showing a significant increase (red) or decrease (blue) in activation as a function of level of coherence (SPM t maps thresholded *p* < .001 voxelwise, uncorrected for multiple comparisons). Axial, sagittal and coronal sections centered around A) the dmPFC cluster, B) the superior parietal cluster and C) the occipital cluster (deactivation with increased coherence).

2010) and has not been previously identified by fMRI studies of dance observation (which mostly focused on the physical dimension of specific dance gestures). Activation in the dmPFC has been detected in studies of language processing (see Mar, 2011). For example, it is activated both during production and comprehension of narratives (e.g. AbdulSabur et al., 2014, Silbert et al. 2014). Moreover, manipulating the coherence of pairs of sentences presented to participants, Siebörger et al. (2007) reported the very same region of the dmPFC observed in our study, to be more active for coherent pairs compared to less or in-coherent pairs. As mentioned in the results section, a subregion of the dmPFC was also sensitive to the size of constituents in the Pallier et al (2011) study, and our additional ROI analysis shows that the same region was sensitive to coherence in dance.

Narratives (and language use more generally) involve inherently pragmatic processes that implicate mentalizing. Indeed, a number of studies have demonstrated the role of the dmPFC in pragmatic reasoning such as communicative intent (Willems et al., 2010), conversational implicatures (Bašnáková et al. 2014), and pragmatic plausibility (Ye and

Zhou, 2009). Neither Ye and Zho (2009), nor Willems et al. (2010), did an orthogonal manipulation of syntactic complexity that had an effect on activation in this region, reinforcing the role of this region in pragmatic reasoning rather than in the computation of the linguistic structure/propositional meaning per-se. More generally, this region has been identified by multiple studies concerning the Theory of Mind (TOM) or mentalizing (cf. Mar, 2011; Bzdok et al., 2013; Denny et al., 2012). For example, Spunt and Adolphs (2014) showed that the dmPFC was engaged during a task requiring making an inference regarding a person's intention (see Schurz et al., 2014, for a review).

One perspective on the specific role of the dmPFC that brings together these different findings is Mason and Just's (2011) protagonist perspective network, which they propose the MPFC is a part of. Constructing a protagonist perspective implies (minimally) inferring (abductively or probabilistically) using a variety of cues, the visual perspective, state of mind, intentions and motivations of a person situationally in the focus of attention (a co-actor in an interaction or the protagonist of an ongoing narrative). The characterization of the role
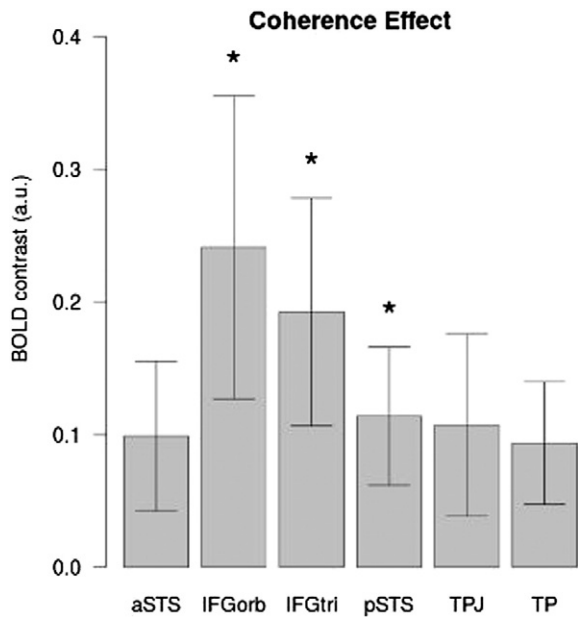
Coherence Effect

Fig. 3. Analyses in regions of interest for language. Linear change in BOLD signals when coherence increased from the less coherent to the most coherent dance pieces. Stars indicate regions where the amplitude of the effect was significant ($p < .05$) according to a one-sample *t*-test. The error bars indicate the standard errors of the means. aSTS = anterior superior temporal sulcus, IFGorb = inferior frontal gyrus pars orbitalis, IFGtri = inferior frontal gyrus pars triangularis, pSTS = posterior superior temporal sulcus, TPJ = temporal parietal junction, TP = temporal pole.

of the dmPFC in terms of protagonist perspective ties nicely with our results. Once dance choreography rather than isolated dance gestures is considered, the dancer is a natural protagonist, even if the narrative itself might be less explicit or linear than in theater or cinema (Foster, 2011). As a consequence, the more coherent the observed movement is, the more it supports (and affords) the mental construction of a protagonist's perspective. The role of the dmPFC in protagonist perspective representation rather than in the representation of dance movement explains the overlap between our results and the results from studies of linguistic narratives (e.g. Pallier et al., 2011; Siebörger et al., 2007), but also the absence of reported activation in this region in studies of dance that did not manipulate choreographic or structural complexity or otherwise varied the affordability of a protagonist (e.g. Calvo-Merino, 2005; Cross et al., 2006).

Our results and the interpretation thereof suggests that the observation of other (than dance) complex actions involving an intentional protagonist should potentially also activate the dmPFC. Indeed, Kim et al. (2011) have found activation in the dmPFC in expert archers compared to novices when watching short videos of an archer. Arching is a complex goal oriented action (however the goal was not shown in the video). The authors suggest that this out-of-AON activity might reflect the recruiting of the TOM network for the representation of the internal state of the archer.

The superior parietal region

Dance spectating has been argued to involve kinesthetic empathy, the sensation of one's own (still) body participating in the observed dance movement (Martin, 1965; Foster, 2011). The superior parietal region seems to be specifically involved in the representation of one's own kinesthesia and the perception of movement of one's own body (Lacquaniti et al., 1995; Romaiguère et al., 2003; Kavounoudias et al., 2008; Hagura et al., 2007). Dance focuses the attention of the dancer on her kinesthetic experience and the temporal and spatial organization of her body and movement. Brown et al., (2006), using PET, found the superior parietal region to be the only cortical region activated more when the subject performed tango dance steps (while in supine

position) compared to leg muscle contraction without displacement. In both conditions subjects were following a musical beat but only in the dance condition did the dancers have to organize their body in time and space.

The superior parietal region has been consistently implicated also in the representation of another's movement, as part of the AON network (Caspers et al., 2010). Relevant to our discussion of dance, it appears that activity in this region is specifically associated with whole-body, non-object oriented actions or gestures. That is, actions whose frame of reference is the body or the body's organization in space and so rely principally on kinesthetic awareness through visuomotor integration of body movement information (Iseki et al., 2008; Filimon et al., 2007; Meister and Iacoboni, 2007; Szameitat et al., 2007).

Putting together these two literatures, we propose that the superior parietal region plays a role in the emergence of kinesthetic empathy (in dance and more generally). Indeed a number fMRI studies of dance observation have found activation in the superior parietal region (e.g. Calvo-Merino, 2005; Cross et al., 2006, Miura et al., 2010). Calvo-Merino et al. found this region to be more active during the observation of very short video sequences in familiar compared to non-familiar dance style. Cross et al. found this region to be more active during dance observation and simulation (compared to a baseline). The authors report activation peak that is slightly ventral to the one found here (mni −30 −49 52), when the observation of short sequences of dance was contrasted with the observation of a video of a person standing still. Miura et al. (2010) compared the observation of a dance performed by a human, the same dance performed by a humanoid robot and a more awkward or stiffer version of the same dance performed by the robot. Activation in the superior parietal lobe distinguished between the natural and awkward dance (both by a robot), but did not distinguish between a human and a robot version of the same (natural) dance.

However, more needs to be said about what it is about dance that engages this region.

In our study, activation in this region increased with the coherence of the choreography, while in all conditions subjects observe (the same) dance movements. In addition, this region has not been implicated in all aspects or all studies of dance observation. Calvo-Merino et al. (2006), studying the observation of ballet movements that were gender-specific, did not find greater activation in this region when observing gender congruent compared to gender incongruent movements. Cross et al. (2009) did not find activation in this region to distinguish between observation of previously rehearsed and control dance choreographies (both of the same style).

In order to explain this pattern of results, we propose that the superior parietal lobe plays a specific role in the syntax of dance, underlying the perception of the gesture's where and when (in analogy to language syntax that represents the words when and where). Dance is an expressive practice whose principal medium is the kinesthetic experience of the organization of the human body in space and time. In a sense, this body/movement organization can be considered as the syntax of dance. By syntax we mean the form or structure which allows for meaning (in language) or affect (in dance or music) to arise. Pushing further the analogy with language, we can suggest that different dance styles are distinguished by different grammars (of temporal–spatial organization), explaining why the superior parietal region was found to be sensitive to a change in dance style (Calvo-Merino, 2005; Miura et al., 2010) but not sensitive to differences between sequences of dance pertaining to the same style (Cross et al. 2009, Calvo-Merino et al., 2006).

The central role for this region in the representation of dance syntax is motivated by our results here. Activity in this region increased with the increase in structural coherence of the observed dance. This is analog to the increase in activation in brain regions subserving language syntax (e.g. the IFG) observed by Pallier et al. (2011) in response to the same manipulation. The superior parietal region was not implicated by that study in the representation of language syntax (and is generally

not considered a 'language' area). Indeed, there is no reason to think that kinesthesia is relevant to language syntax. In our ROI analysis based on Pallier et al.'s results for language syntax, we wanted then to find out to what extent activity in regions who showed sensitivity to size of the linguistic structure is also sensitive to dance structure.

The inferior frontal and pSTS ROIs

The analysis in regions of interest revealed three additional areas where activity was modulated by the parametric modulation of dance stimuli: the pars orbitalis, the pars triangularis and the pSTS. This corresponds to the same subset of regions that showed sensitivity to structure once open class words were replaced by pseudo-words (the Jabberwocky condition) in the language stimuli of Pallier et al. (2011). The same regions were detected by a similar manipulation with musical stimuli (Cauvet et al., in preparation). Professional musicians were scanned while listening to musical stimuli in which the size of coherent chunks was manipulated. Activity increased with chunk size in the inferior frontal regions and the posterior STS (and, additionally, in the temporal pole). These converging results from three different domains (and modalities) provide preliminary evidence for shared representations or processes underlying structural coherence in language, music and dance and for the role of the IFG and the pSTS in the underlying, shared, neural computation. What would be the nature of the shared computations?

The inferior frontal gyrus has been long implicated in linguistic syntax and in particular the representation of manipulation of linguistic hierarchical structure (e.g. non local dependencies and recursion, Grodzinsky and Friederici, 2006; Opitz and Friederici, 2007). This region was also found to be active in a number of studies manipulating hierarchical structure in non-linguistic domains (artificial grammars: Bahlmann et al., 2009, action plans: Clerget et al., 2013). These combined evidence from multiple domains and methodologies convincingly argue for a critical role for the left IFG in the manipulation of hierarchical structure (whether in production or perception). Our results suggest that the observation of coherent dance choreographies induces hierarchical representations that are at least partially shared with other domains (such as language, music and action preparation).

The left posterior STS has been implicated in a variety of linguistic processes such as lexical access (Kemeny et al., 2006), verb representation (Kemmerer et al., 2008) and, more recently, combinatory (Forgács et al. 2012, Shetreet et al., 2010) and inflectional (Marslen-Wilson and Tyler, 2007) operations. This activation is modality independent and was found also for signed languages (Malaia and Wilbur, 2010; Newman et al., 2010). At the same time the very same region (but bilaterally) has been implicated in the perception of biological motion (Pelphrey et al., 2005; Grosbras et al., 2012a; Gilaie-Dotan et al., 2013, Van Kemenade et al., 2012; Bidet-Caulet et al., 2005; Thompson, 2005).

We have suggested that observation of dance choreographies implicates hierarchically organized perception (syntax), however dance's matter (arguably more so than in language or music) is human 'biological' motion. The activation we observe in the pSTS could be then either a reflection of (abstract, amodal) structure sensitive processes (as with language or music), or the consequence of the presence of biological motion. A third option is that the overlap in activation between biological motion perception and language reflects a common mechanism. A natural candidate would be the semantic representation of action or movement (be it verbally or visually presented: Grèzes and Decety, 2001; Gennari, 2012; Knott, 2012; Bedny and Caramazza, 2011). However this explanation would not extend to the specific role for this region in hierarchical or combinatory process (that is, not semantic but syntactic dimension of language, Shetreet et al., 2010; Pallier et al., 2011), which are orthogonal to the movement or action properties of the linguistic stimuli.

An alternative, less explored, perspective (cf. Redcay, 2008) on a common role for the pSTS in language and biological motion perception

is that both domains require configurational integration of information over time and space (cf. Lange and Lappe, 2006 for biological motion and Roark, 2001; Levy, 2008; Roark et al, 2009; Traxler, 2014 among many others for language). We put forward a speculative hypothesis that neurons in the pSTS perform an update function of complex configurational (multimodal) representations, a function shared by (at least) language, music and biological motion detection. Lange and Lappe (2006) describe and test a computational model where biological motion is computed in two stages. At the first stage, global, static configurational frames of posture are calculated without temporal information. At the second stage, that they associate specifically with the pSTS, global movement is calculated via comparison of the current most active frame with the model's expectations (given previous frames). Predictive language processing models as the ones described by Roark (2001) or Levy (2008) also involve a comparison between a predicted syntactic structure or configuration and the observed input. Similar predictive mechanisms have been investigated in music as well (Pearce and Wiggins, 2012). Whether the stimulus is linguistic, musical or danced (our results), activity in this region increases with the length of the coherent sequence (or the size of the corresponding representation).

It is important to stress that while the observed sensitivity to structure in music and dance in ROIs defined by a study of structural sensitivity in language is intriguing, the data was collected in 3 different experiments with different subjects (with different expertises). In order to establish and further elucidate these possibly shared neural mechanisms a more direct within-participant comparison of brain response to configurational manipulations in these three domains will be required.

Conclusion

Dance spectating amounts to more than the observation of a sequence of isolated gestures, just as in language the comprehension of a sentence or a text goes beyond the accumulation of single words. By parametrically scrambling short contemporary dance choreographies we manipulated their temporal coherence and implicit structure. We found that watching increasing duration of coherent dance movements enhances brain activity in the dmPFC, which we associated with the mentalizing task of computing the protagonist's perspective (afforded by the coherent choreography), and in the superior parietal lobe which, we proposed, participates in the representation of the dance's syntax or the where and when of the (observed) moving body, through multi-modal integration of kinesthetic perception. An ROI analysis based on a similar manipulation using language stimuli revealed 3 regions, in the left IFG and pSTS, which are sensitive to coherence in dance (and also music). This overlap suggests that, despite multiple differences in content and function, common, structural mechanisms underlie these three fundamental human behaviors, opening the door to future experiments that will directly compare neural activity in these different domains within the same subjects.

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