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Dissociable substrates for body motion and physical experience in the human action observation network

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Abstract

Observation of human actions recruits a well-defined network of brain regions, yet the purpose of this action observation network (AON) remains under debate. Some authors contend that this network has developed to respond specifically to observation of human actions. Conversely, others suggest that this network responds in a similar manner to actions prompted by human and non-human cues, and that one's familiarity with the action is the critical factor that drives this network. Previous studies investigating human and non-human action cues often confound novelty and stimulus form. Here, we used a dance-learning paradigm to assess AON activity during observation of trained and untrained dance cues where a human model was present or absent. Results show that individual components of the AON respond differently to the human form and to dance training. The bilateral superior temporal cortex responds preferentially to videos with a human present, regardless of training experience. Conversely, the right ventral premotor cortex responds more strongly when observing sequences that had been trained, regardless of the presence of a human. Our findings suggest that the AON comprises separate and dissociable components for motor planning and observing other people's actions.

Introduction

An action observation network (AON) that responds to the observation of human actions has been identified in the premotor cortex, inferior parietal lobule (IPL), superior temporal sulcus (STS) and supplementary motor area of the human brain (Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996b; Buccino *et al.*, 2001; Grèzes & Decety, 2001; Jeannerod, 2001; Rizzolatti & Craighero, 2004; Zentgraf *et al.*, 2005; Cross *et al.*, 2006; Molnar-Szakacs *et al.*, 2006). This network is believed to contain mirror neurons (Rizzolatti & Craighero, 2004; Iacoboni & Mazziotta, 2007), and several different functions have been proposed for it, including action prediction (Prinz, 1997, 2006; Kilner *et al.*, 2007; Schütz-Bosbach & Prinz, 2007), action understanding (Rizzolatti *et al.*, 1996b, 2001; Rizzolatti & Fadiga, 1998), inferring the intention of others (Fogassi *et al.*, 2005; Hamilton & Grafton, 2006; Kilner *et al.*, 2006), and social cognition (Iacoboni & Dapretto, 2006). Some components of the AON also have a role in motor control (Brown *et al.*, 2006; Catmur *et al.*, 2007; Borroni *et al.*, 2008) and motor planning (Grafton & Hamilton, 2007; Williams *et al.*, 2007).

Previous imaging studies of this network with healthy individuals have not directly compared these functions in the same experiments to differentiate between them or to determine whether different components of the AON might serve specific functions. One unsettled issue is whether or not this network responds preferentially to observation of actions performed by other humans, or whether it responds in the same way to symbolic cues to action. Moreover, if the AON has a specific role in action prediction and action understanding, then manipulating the degree to which an action can be easily understood should also affect the level of activity in the AON. One way this can be evaluated is by varying the amount of direct experience one has in performing the observed action. In this study, we used a novel dance training paradigm to determine if activity within the AON is driven by action embodiment or by the form of the action stimuli.

If the AON is dedicated to biological action understanding, we might expect it to show a preference for stimuli that feature biological motion, as recent data suggest (e.g. Brass *et al.*, 2000; Tai *et al.*, 2004; Kessler *et al.*, 2006). Brass *et al.* (2000) were among the first to report that participants were measurably faster to imitate finger movements that were performed by another person compared with those that were cued by a spatial cue. Kessler *et al.* (2006) used whole-head magnetoencephalography to monitor participants' brain activity while they performed a finger-tapping movement. Movements were cued by a video of a finger tapping (biological movement condition) compared

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with a dot over the digit to move in a still photograph of a hand (non-biological movement condition). They report that left premotor and bilateral parietal and superior temporal cortices were more active during the biological movement condition. Tai and colleagues report converging findings when individuals watched grasping performed by a human compared with grasping performed by a robot model controlled by an experimenter (Tai *et al.*, 2004). They observed greater activity within the left premotor cortex when participants watched a human actor, which led them to conclude that the AON is specifically tuned to observation of biological movements.

However, the claim that the premotor component of the AON responds preferentially to human compared with non-biological action cues remains controversial. Several other studies have shown that this network, and the premotor cortex in particular, responds to non-biological stimuli in a similar way to biological stimuli (Press *et al.*, 2005; Gazzola *et al.*, 2007; Engel *et al.*, 2008). In one such study, Gazzola *et al.* (2007) monitored participants' neural activity with functional magnetic resonance imaging (fMRI) while they observed either a human hand or a robotic hand perform simple and complex actions. They observed robust activation across several regions of the AON, including dorsal and ventral components of the premotor cortex, superior parietal lobule and the middle temporal gyrus when participants observed a human or robotic hand perform an action, compared with static control images. Moreover, activation was greater when humans or robots were performing more complex, goal-oriented actions that were familiar to participants, such as grasping a cocktail glass, compared with simpler and possibly less relevant or familiar actions, like moving wooden blocks around. The authors interpret these findings as consistent with the notion that observation of familiar actions, or familiar action goals, will reliably and robustly activate the AON, regardless of the form of the acting agent (Gazzola *et al.*, 2007).

Overall, prior studies disagree on the response profile of the premotor cortex during observation of human actions compared with non-human actions. Moreover, any inferences that might be drawn from these prior studies (e.g. Brass *et al.*, 2000; Tai *et al.*, 2004; Press *et al.*, 2005; Kessler *et al.*, 2006; Engel *et al.*, 2008) are limited by the confounding of familiarity with human and non-human action cues. For example, participants in these previous studies were most likely very familiar with observing hands grasping objects, but were probably less likely to come across robots grasping objects, or abstract symbols cuing actions in their daily lives. Thus, human form is confounded with familiarity. In the present study, we have avoided this problem through the use of intensive training procedures, where participants were taught to perform novel dance sequences with both biological and symbolic action cues. Such a methodology enables a precise control of participants' familiarity and physical experience with the action stimuli they observe while being scanned. This permits a measure of brain responses during action observation where biological motion can be studied independently from experience.

The major objective of the present study was to clarify the contributions of several key components of the AON to the observation of action cues both with and without a human agent. Specifically, we tested whether the AON is driven by observation of other humans, independent of prior experience, or whether it is driven by observation of familiar or executable actions. During fMRI, participants watched movies of arrow sequences that served as cues for foot movements in a popular dance video game. We directly manipulated both the presence of a human dancer and participants' physical experience with the dance sequences through use of intensive dance training procedures and a two-by-two factorial design. If the AON responds uniformly as a function of observing humans or experiencing, then we would expect stronger responses across all components of the AON when observing biological motion compared with non-biological motion (e.g. Tai *et al.*, 2004; Kessler *et al.*, 2006), and when observing trained compared with untrained sequences (e.g. Calvo-Merino *et al.*, 2005; Cross *et al.*, 2006). However, if it is the case that the individual components of the AON are sensitive to different kinds of experience, then we expect that individual components of this system will respond differently based on experience and the presence of a biological agent.

Materials and methods

Participants

Seventeen physically and neurologically healthy adults were recruited from the Dartmouth College undergraduate and graduate student community to participate in 1 week of dance training and two scans (one pre-training scan and one post-training scan). All were monetarily compensated for their involvement. All participants gave their written informed consent to participate in the study. The Commmittee for the Protection of Human Subjects at Dartmouth College approved all experimental procedure according to the principals laid out by the Declartion of Helsinki. Participants had no significant prior experience dancing or playing dance video games. One participant was excluded from analyses due to an aberrant learning trajectory for behavioral training (> 2 SD below the group mean performance score). The remaining 16 participants (10 female) ranged in age from 20 to 32 years (mean age = 25 years). All participants were strongly right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971).

Stimuli and apparatus

Stimuli were 21 upbeat techno-dance songs with no lyrics (120–180 beats per minute; mean = 149.6 BPM). Unknown songs were chosen (and verified as 'unknown' by post-experiment interviews) so that participants would have no prior auditory or dance experience with any portion of the stimuli. Songs were edited into 30-s segments, and individualized files comprising dance steps synchronized to the music were created using the Dancing Monkeys MATLAB script (O'Keefe, 2003). This script analyses each song to determine where and when the steps should occur in order to be tightly synchronized with the music on whole, half and quarter beats. Each 30-s segment was then triplicated, resulting in 21 stimuli, each 1 min 30 s in length, and each containing three identical repeats of a song and step-sequence pairing.

Songs were then paired with visual cues instructing the participant how to dance to that track. A scrolling display of arrows moving upwards across the screen cued each move, and the participant had to make the indicated step when the arrows reached the top of the screen. The symbolic arrow sequences were generated for all 21 tracks. In addition, for 11 of these video stimuli, the instruction stimulus consisted of a video of an expert dancer accurately performing the steps with the arrows superimposed over it, providing a human model for how to accurately perform each sequence. The expert dancer performed the steps exactly in time with the arrows, such that when each arrow reached the top of the screen, the model dancer was striking the footpad in the correct position, thus modeling both the kinematics and timing of the specified dance sequence.

Each participant physically trained on three tracks with a human model and three without a human model (henceforth referred to as the 'danced' condition), for a total of six different dance sequences, every day for 5 days. Six of the remaining tracks were presented only during fMRI scanning and composed the ‘untrained’ condition. Participants also passively observed an additional six different tracks (three with a human model and three without) on the same schedule (the ‘watched’ condition). Participants danced or watched their assigned set of 12 stimuli in blocks of three (three danced, three watched, etc.). The individual stimuli that went into each block of three and the order of dancing and watching were randomized within participants across training days. The final three tracks were never seen at any point during scanning or training, and were used as entirely novel stimuli in a surprise retest portion of the study. Findings from the watched condition and the behavioral retest are reported elsewhere (Cross *et al.*, 2009).

Study design

The full set of experimental conditions fall into a three (training experience: danced, watched or untrained) by two (cue type: symbolic arrows plus human model, symbolic arrows without human model) factorial design. In the present study, because we were interested in only the danced and untrained conditions, the design became a two-by-two factorial design, as illustrated in Fig. 1. During scanning, participants viewed the six trained sequences that composed the ‘danced’ condition, the six trained sequences that composed the ‘watched’ condition, and the six untrained sequences that composed the ‘untrained’ condition. Note, however, that during the first week of imaging, all 18 sequences that were observed during scanning were novel to the participants.

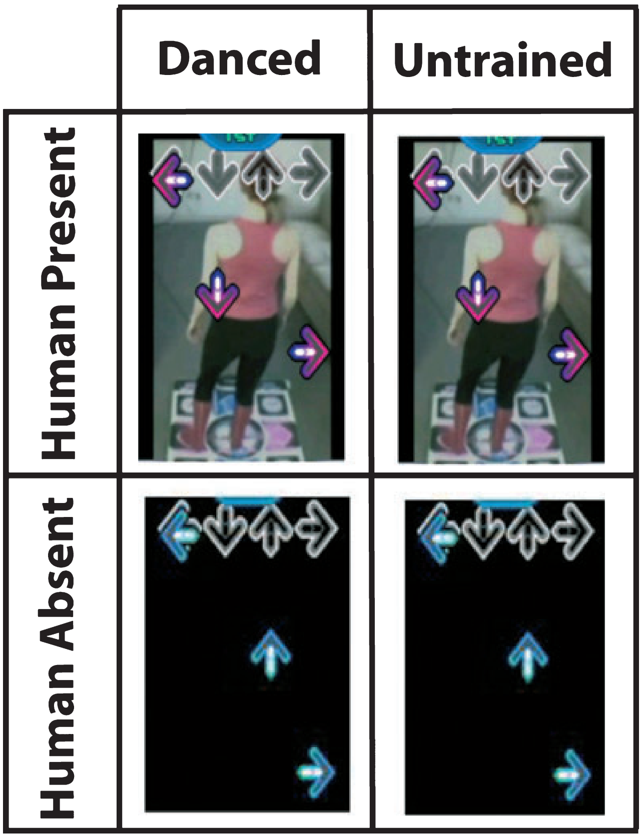

FIG. 1. Organization of study design. In this two-by-two factorial design, the variables were training experience (sequences were either danced across the training week, or untrained) and the presence of an expert human model (a model was either absent or present performing the dance sequences along with the scrolling arrows).

Neuroimaging

Neuroimaging procedure

A block design fMRI procedure was used to identify neural responses to training videos that either did or did not feature a human model performing dance sequences that were trained or untrained. During functional imaging, participants watched and listened to the same 18 StepMania dance sequence videos they were about to train on for a week (pre-training scan) or which they had viewed and practiced during the week of training (post-training scan). Although we do not specifically analyse auditory processing in the present study, we had participants listen to the music of each dance sequence in order to maintain a similar context between training sessions and scan sessions. As music was present in all scanning blocks and did not specify the action sequence, it cannot systematically impact on the results.

Instructions were to simply observe all the videos and to keep as still as possible. To ensure that participants were awake and attending to the videos throughout each scanning session, participants were required to make a simple keypress response on a fiber optic, scanner-compatible keypad at the end of each 30-s music video. Participants responded after > 95% of all videos across scanning sessions. In order to rule out the potential of action network activation as a consequence of participants tapping their feet or moving their bodies in the scanner along with the videos, participants were filmed during both scanning sessions and the films were evaluated offline for any foot or body movement. All participants were able to remain still throughout each scan, with no visible evidence of rhythmic movement to the auditory or visual stimuli. Each 30-s stimulus video was followed by 30 s of fixation. Video order was counterbalanced across training conditions, participants and scanning sessions. Participants saw the same 18 videos in both the week 1 pre-training session and the week 2 post-training scanning session. Following the second scanning session, all participants were asked whether they engaged in any kind of mental imagery during either scanning session. Each participant reported engaging in mental imagery during the second scanning session only.

The experiment was carried out in a 3T Philips Intera Achieva scanner using an eight-channel phased array coil and 30 slices per TR (3.5 mm thickness, 0.5 mm gap); TR: 1988 ms; TE: 35 ms; flip angle: 90°; field of view: 24 cm; matrix 80 × 80. For each of three functional runs, the first two brain volumes were discarded, and the following 181 volumes were collected and stored.

Neuroimaging analyses

In the present report, we focus on the imaging results from the post-training scan session, and report findings from the pre-training scan session where relevant. Further information on the pre-training scan session and additional contrasts are available elsewhere (Cross *et al.*, 2009). To remove sources of noise and artifact, functional data were realigned, unwarped and normalized to the Montreal Neurological Institute (MNI) template with a resolution of 3 × 3 × 3 mm in SPM2. Following this, 8-mm smoothing was applied to the images. A design matrix was fitted for each subject, with each type of video modeled as a boxcar function convolved with the standard hemodynamic response function. Covariates of non-interest (a session mean, a linear trend and six movement parameters derived from realignment corrections) were included in the design. SPM2 was used to compute parameter estimates (beta) and contrast images (containing weighted parameter estimates) for each comparison at each voxel.

The neuroimaging analyses pursued two objectives: to determine the independent effects of training and the presence of a human model. Rather than searching the whole brain for these effects, we focus on results within *a priori* regions of interest included in the AON. We generated an anatomical mask by placing overlapping spheres (20 mm diameter) at several key AON coordinates, such that STS, posterior middle temporal regions including extrastriate body area (EBA), inferior parietal cortex and premotor cortex (both ventral and dorsal portions) were all within the mask (Fig. A2). Only voxels within this mask were examined in the subsequent analysis.

For completeness, both main effects and the interactions were evaluated within the two-by-two factorial design. In order to evaluate the main effect of training, we compared neural activation between the danced and untrained conditions, collapsed across stimuli type. In a similar manner, to evaluate the main effect of the presence of a human model in the stimuli, we compared neural activation when watching dance sequences with a human model in them compared with those that featured just arrows, collapsed across training experience. Both directions of the interaction between training experience and stimuli were also calculated. Contrast images for all participants across all main effects were taken to the second level for random effects analysis. For completeness, we report all regions that survive a voxel-wise threshold of $P < 0.005$ uncorrected in Table 1. However, we focus further analysis and discussion only on the subset of these regions that also met the $P < 0.05$ cluster-corrected threshold.

For visualization purposes, beta estimates were extracted from a 5-mm sphere centered on the peak of each contrast, and were used to plot the blood oxygen level-dependent (BOLD) signal in each region and each condition. All imaging results are rendered on either a rendered cortical surface or slices from a high-resolution structural MRI scan of a standard brain from the MNI.

Behavioral training and evaluation

StepMania (http://www.stepmania.com), a freeware program similar to the popular video game Dance Dance Revolution (Konami Digital Entertainment, Redwood City, CA, USA), was used for step file modification, training and response recording outside of the scanner. Participants performed dance training and post-test evaluations on a 3′ × 3′ dance pad connected by USB to a desktop computer. Electronic sensors in the dance pad detected position and timing information that was then used to provide participants with real-time visual feedback. Full details of the StepMania set-up, scoring and stimulus construction are reported in Cross *et al.* (2009). Participants spent 5 days learning to perform the steps associated with six songs. Song assignments for each condition were randomized across participants, and the order in which participants watched or danced each song was counterbalanced across days.

Results

Participants' performance on the rehearsed dances improved significantly across training days, $F_{4,60} = 58.25$, $P < 0.001$, indicating that they learned the dances effectively through physical practice during the week of training. Additionally, a significant performance advantage emerged for sequences that featured a human model,

TABLE 1. Localization of averaged BOLD response during observation of dance music videos, relative to baseline, during the post-training scan session

		MNI coordinates					
Region	BA	*x*	*y*	*z*	Functional name	Cluster size	P_{uncor}-value
Danced > Untrained							
R Middle Frontal Gyrus	9	39	12	33		31	< 0.0001
R Inferior Frontal Gyrus	6/44	39	27	21	PMv	91	< 0.0001*
R Middle Temporal Gyrus	21	51	−24	−9		33	<0.0001
R Inferior Frontal Gyrus	45	36	24	−6		11	< 0.0001
L Inferior Parietal Lobule	40	−45	−51	42	IPL	7	0.001
L Middle Frontal Gyrus	9	−45	21	30		23	0.001
R Inferior Frontal Gyrus	6	45	0	3	PMv	6	0.002
R Inferior Frontal Gyrus	44	48	12	18		6	0.003
Human present > Human absent							
L Superior Temporal Sulcus	22	−51	−39	21	pSTS	577	< 0.0001*
R Inf. Temporal Gyrus	37	48	−75	−3	ITG/EBA	644	< 0.0001*
R Lingual Gyrus	39	21	−87	−12		27	< 0.0001
R Fusiform Gyrus	37	39	−45	−21		11	0.001
L Fusiform Gyrus	37	−42	−45	−27		25	0.001
Danced human + Untrained no human > Danced no human + Untrained human							
R primary/secondary somatosensory cortex	–	54	−24	24	SI/SII	11	0.001
R inf parietal lobule	–	63	−54	27	IPL	7	0.001
R middle temporal gyrus-ish	–	48	−45	−6	MTG	37	0.001
R postcentral gyrus/S1-ish	–	57	−18	45	S1	4	0.001
L superior temporal sulcus	–	−63	−54	12	STS	4	0.003
R superior temporal sulcus	–	57	−51	15	pSTS	4	0.004
Danced no human + Untrained human > Dancedhuman + Untrained nohuman							
L inferior frontal gyrus	6	−36	−9	27	IFG	11	< 0.0001
L inferior frontal gyrus	9	−45	12	30	IFG	20	< 0.0001

BA, Brodmann's area; EBA, extrastriate body area; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; L, left; MTG, middle temporal gyrus; PMv, ventral premotor cortex; pSTS, posterior superior temporal sulcus; R, right; SI/SII, primary/secondary somatosensory area. *Denotes the clusters that survived the $P < 0.05$ cluster correction and were examined in the region of interest analyses of each main effect (Figs 2 and 3). Significance at all sites for each contrast was tested by a one-sample *t*-test on beta values averaged over each voxel in the cluster, $P < 0.005$, uncorrected. Coordinates are from the Montreal Neurological Institute (MNI) template and use the same orientation and origin as found in the Talairach and Tournoux atlas (Talairach & Tournoux, 1988).

$F_{4,60} = 10.16$, $P = 0.003$ (Fig. A1). No interaction was present between training day and dance sequence type ($P = 0.47$).

After 1 week of dance training, fMRI revealed a main effect of training in several areas of the AON, including right premotor areas and a portion of the left IPL. These regions showed greater responses when participants observed dance sequences they had trained on, compared with untrained sequences (Fig. 2A; Table 1). From this contrast, the right ventral premotor cortex (PMv; Fig. 2B) cluster reached the cluster-corrected threshold of $P < 0.05$. When evaluating the main effect of the presence of a human model (human present > human absent), activation was observed in the bilateral posterior temporal cortex (Fig. 3A; Table 1). Two clusters in the right inferior temporal gyrus (ITG) and left STS met the cluster-corrected threshold (Fig. 3B and C). No regions from the interaction analyses survived the cluster-corrected threshold. Areas reaching significance without correction for multiple comparisons are presented in Fig. A3 as exploratory analyses.

To summarize, the main effects analysis revealed three regions that survived a cluster-corrected threshold: right PMv showing a main effect of training, and right ITG and left pSTS showing a main effect of the human model. We extracted parameter estimates from these three regions in order to examine them in more detail. Plots of the parameter estimates from the post-training scan are illustrated in Figs 2B, 3B and C alongside three-dimensional illustrations of each peak voxel in each region of interest.

Discussion

The objective of this study was to investigate specificity within the AON relative to experience and the presence of a human model. Specifically, we asked whether the AON requires observation of other humans, or whether it can be engaged by observation of cues linked to executable actions. If different components within this network are influenced by major differences in stimuli in a similar way, we would have expected stronger responses across the different components when observing biological motion compared with non-biological motion, as found by previous studies (Brass *et al.*, 2000; Tai *et al.*, 2004; Kessler *et al.*, 2006), and when observing danced compared with untrained sequences (Calvo-Merino *et al.*, 2005, 2006; Cross *et al.*, 2006). However, we instead found that some parts of this network respond preferentially and independently to physical experience (PMv), while others respond specifically to the presence of a human model (posterior temporal cortex).

Effect of motor experience

The finding that the PMv responds most strongly to cues for actions that have been physically experienced and not to the presence of a human model advances our understanding of what this region contributes to action cognition. Since the discovery of mirror neurons in an analogous region of monkey premotor cortex (area F5) (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996a), several hypotheses have been put forward for the role of the premotor cortex in motor and social cognition, including predicting the ongoing actions of others (Prinz, 1997, 2006; Wilson & Knoblich, 2005; Kilner *et al.*, 2007; Schütz-Bosbach & Prinz, 2007), inferring others' intentions (Fogassi *et al.*, 2005; Hamilton & Grafton, 2006; Kilner *et al.*, 2006) and social cognitive behaviors, including imitation and empathy (Iacoboni & Dapretto, 2006). A key question in distinguishing these hypotheses is the responsiveness of PMv to biological and non-biological stimuli. For example, if it were the case that PMv plays a specific role in social

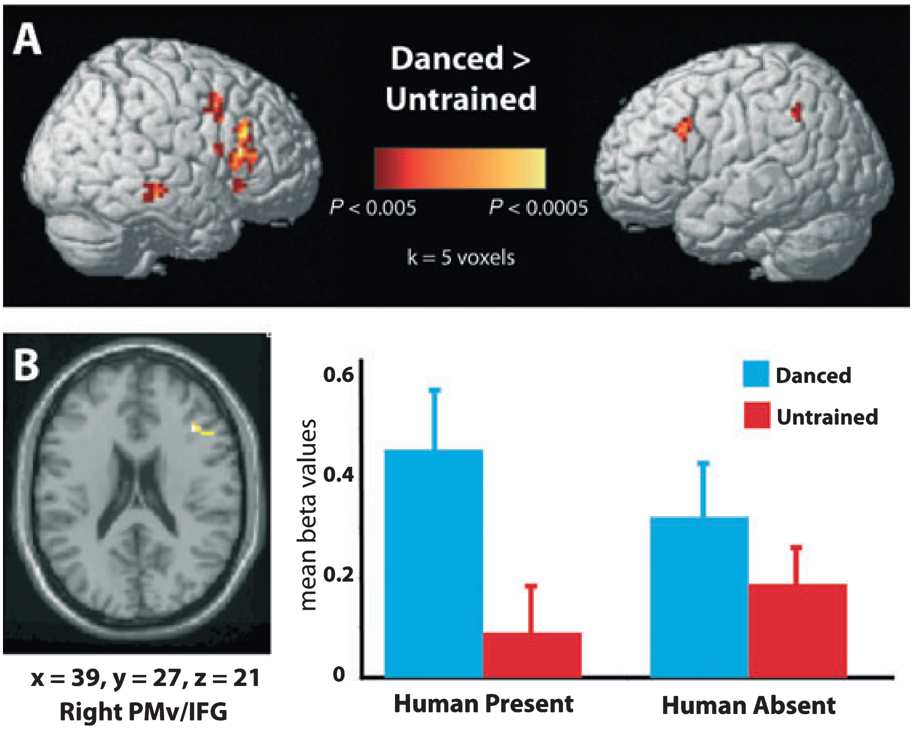

FIG. 2. Main effect of dance training. (A) Regions of neural activity in the contrast comparing observation of sequences participants learned to dance compared with observation of untrained sequences, collapsed across stimulus type (human present vs. human absent). This analysis was performed within the *a priori*-defined AON mask of brain regions (Fig. A2). (B) The mean beta values for the region of right ventral premotor cortex (PMv) that survived cluster correction at the $P < 0.05$ level are presented as a function of training experience and stimulus type. IFG, inferior frontal gyrus.

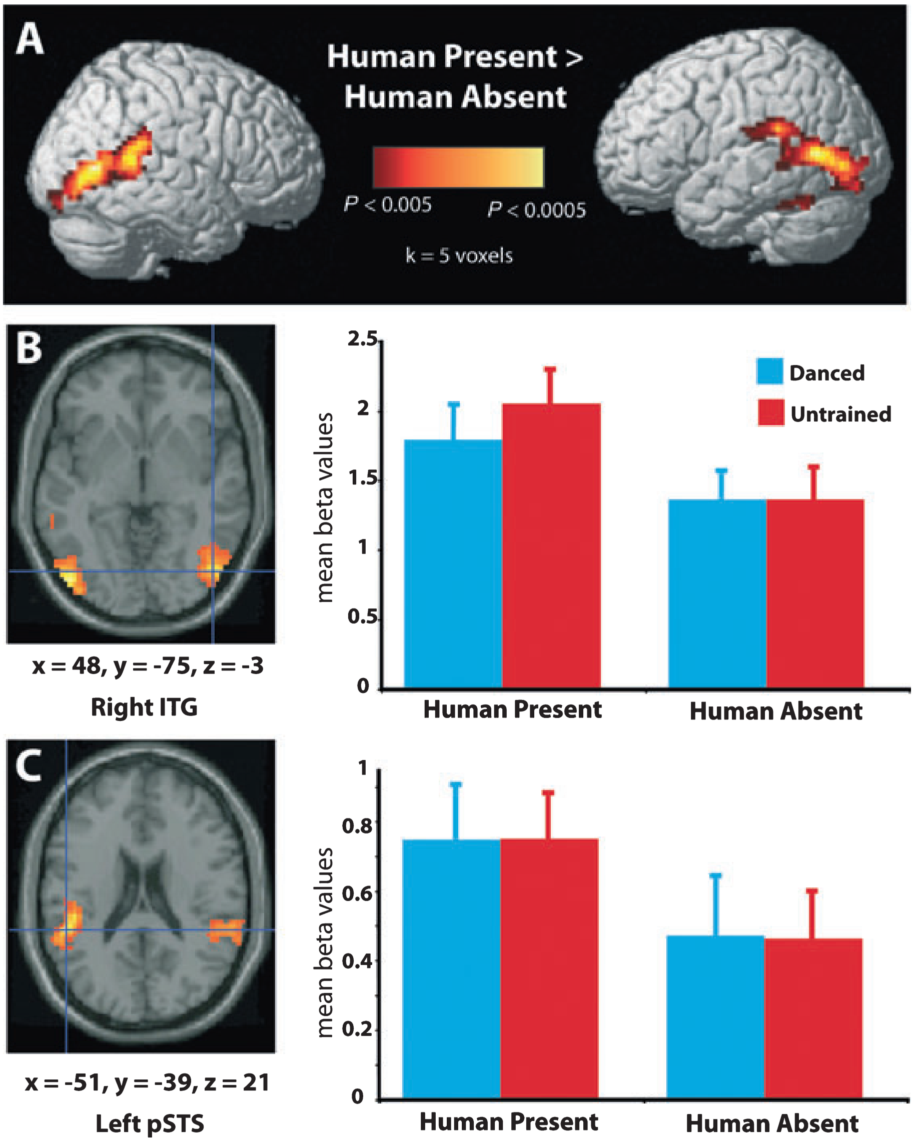

FIG. 3. Main effect of the presence of a human model. (A) Regions of neural activity in the contrast comparing observation of sequences that featured a human model and those without a human model, collapsed across training experience. This analysis was performed within the *a priori*-defined AON mask of brain regions (Fig. A2). The lower two panels depict the mean beta values for the right inferior temporal gyrus (ITG; B) and the left posterior superior temporal sulcus (pSTS; C) that survived cluster correction at the $P < 0.05$ level. These beta values are presented as a function of training experience and stimulus type.

cognition, then we would expect it to show stronger responses to observation of human actors. Results from previous studies of this issue have been mixed. Some researchers have reported PMv to show a strong preference for human stimuli (Brass *et al.*, 2000; Tai *et al.*, 2004; Kessler *et al.*, 2006), while others have shown this region to respond with equal robustness to actions performed by non-biological entities, such as robots (Press *et al.*, 2005; Gazzola *et al.*, 2007; Engel *et al.*, 2008). Symbolically represented actions are an ideal way to separate biological agency from action representation as the arrows do not resemble living agents but, following training, they are tied to specific motions. Thus, our data suggest that PMv does not respond specifically to human actions. Instead, PMv responses appear to be both flexible and dynamic, driven most by action cues that are familiar from previous experience. This finding is in line with a theory recently advanced by Schubotz, who suggests that activity within the premotor cortex during action observation serves to predict ongoing, familiar events (Schubotz, 2007). The present findings are also compatible with the notion that PMv is involved in motor preparation (both implicit and explicit) for familiar actions (Harrington *et al.*, 2000; Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004; Catmur *et al.*, 2008).

The role that the IPL might play in observation of physically practiced dance sequences also warrants brief discussion. The IPL is frequently paired with PMv as a core component of the AON (Grèzes & Decety, 2001). Moreover, it shares strong reciprocal connections with the premotor cortex, the integri that must remain intact for complex action performance (Heilman *et al.*, 1982; Ramayya *et al.*, 2009), and has also been shown to contain mirror neurons within the non-human primate brain (Fogassi *et al.*, 2005). In previous work from our laboratory, we have demonstrated that both PMv and IPL are modulated in a similar manner when observing actions that an observer is highly skilled at performing (Cross *et al.*, 2006). In the current study, we also report that IPL is modulated by physical experience (Table 1), and because it was close to the same significance level as that reported for PMv, we believe these findings are in line with past work reporting a similar sensitivity of these two regions to physical experience (Buccino *et al.*, 2001; Calvo-Merino *et al.*, 2005; Cross *et al.*, 2006).

We would like to draw attention to the fact that, while modest, the effect of dance training we report here is reinforced by our particular experimental paradigm. In prior studies that have investigated observation of trained and untrained complex actions, such as the study by Calvo-Merino *et al.* (2005) with professional ballet and capoeira dancers, researchers compared entirely different movement styles, in terms of kinematics, rhythm, music and other features. Moreover, the seminal studies by Calvo-Merino *et al.* (2005) investigating embodied expertise were not *de novo* training studies, i.e. none of the learning had taken place within the laboratory. In the present study, all features were identical between the trained and untrained dance sequences, and participants were randomly assigned which sequences they trained to dance and which remained untrained. This greater degree of similarity between the trained and untrained sequences likely explains the modest differences we observed between these conditions, but also suggests that the areas that did emerge from this contrast are critically involved in the coding of embodied actions, rather than encoding other extraneous features less related to physical embodiment. Our findings build upon the prior research on dance learning through strict control of training procedures and by demonstrating that both biological and non-biological learning cues influence behavioral performance and activation within the AON.

It is worth acknowledging that the increased PMv activation to physical experience was lateralized to the right hemisphere. Many experiments report left lateralization of PMv activation during complex action planning and execution tasks (Rizzolatti *et al.*, 1996b; Johnson-Frey *et al.*, 2005; Cross *et al.*, 2006), and work with split brain patients suggests left hemisphere dominance in linking perception and action when callosal influences are absent (Fecteau *et al.*, 2005). However, it is not the case that mirror neuron system-like activations are classically associated with the left hemisphere for ‘all’ kinds of action observation tasks. Accruing evidence supports the idea that right PMv encodes higher-order, more sophisticated elements of an action sequence being observed, such as recognizing the sequencing of individual action elements (Buccino *et al.*, 2004), the outcome (Hamilton & Grafton, 2008) or the intention (Liepelt *et al.*, 2008) of complex actions. Conversely, left PMv appears to be more involved in programming the actual kinematics required for action planning or execution (Grafton *et al.*, 1996; Iacoboni *et al.*, 1999; Johnson-Frey *et al.*, 2005). Such an account of the involvement of the right PMv in action observation is consistent with the present findings. Moreover, research comparing an individual with and without corpus callosa demonstrates that mirroring processes are bilaterally distributed among individuals with intact corpus callosa (Fecteau *et al.*, 2005). For completeness, we investigated the parameter estimates of the identical PMv region in the left hemisphere, and found the learning effect for this region to be non-significant (Fig. A4). In our task, it seems likely that participants were engaging higher-order cognitive processes related to the recognition of the overall sequence while watching videos they had trained to perform, instead of planning the specific motor program or kinematics required to execute the individual steps being cued.

Effect of cue type

A main effect of cue type was found in temporal regions, including posterior (p)STS and ITG, including the EBA. This contrasts with the main effect of training in PMv. The temporal regions responded most robustly to the presence of a human model, regardless of prior physical experience. A well-established literature has demonstrated robust activity within posterior temporal regions [including pSTS, the posterior superior temporal gyrus (pSTG) and ITG] during observation of biological motion (Allison *et al.*, 2000; Grossman & Blake, 2002; Beauchamp *et al.*, 2003; Puce & Perrett, 2003). One interpretation is that pSTS and pSTG are critically involved in the automatic identification of animate entities at a very early level of visual processing (Schultz *et al.*, 2005).

Reliable activation of STS during tasks designed to explore properties of action resonance has resulted in the inclusion of STS as a component of the human mirror neuron system (Iacoboni & Dapretto, 2006; Kilner *et al.*, 2006; Gazzola *et al.*, 2007; Keysers & Gazzola, 2007; Engel *et al.*, 2008). However, taking the present findings into account, it appears that the contribution of STS to action resonance results from the observation of another human or biological form, not action cues. This result is consistent with recent data that demonstrate that observing and imagining moving shapes activates premotor and parietal components of the AON, but only observation of moving entities that participants construe as animate leads to STS activation (Wheatley *et al.*, 2007). We suggest that STS might be involved in visual analysis of socially relevant conspecifics’ actions, and this processing subsequently feeds into premotor and parietal mirror neuron areas, but also to other brain regions for teleological processing (Csibra, 2007). Such an account of the involvement of pSTS in a person processing cognition is in accord with a recent meta-analysis performed on this regions’ functional profile (Hein & Knight, 2008). This means we should not just consider STS as an input to putative mirror system regions, but it instead appears to have distinct functions of its own, likely including contributions to social cognition.

Relation to previous data

It is important to consider how these new data relate to previous studies that have reported contradictory results regarding the AON’s response to human and non-human action cues (Tai *et al.*, 2004; Kessler *et al.*, 2006; Gazzola *et al.*, 2007; Engel *et al.*, 2008). A persistent problem with many previous studies examining questions of action resonance is the issue of familiarity or experience with the action being observed or cued. The actions in some conditions may be more familiar than the actions in other conditions (Tai *et al.*, 2004; Gazzola *et al.*, 2007; de Lange *et al.*, 2008). Prior work performed with dancers has demonstrated that the more physically familiar an action is, the more the PMv responds when observing that action (Calvo-Merino *et al.*, 2005, 2006; Cross *et al.*, 2006, 2009). It is thus plausible that the discrepant results concerning PMv activation in response to observation of actions featuring human and non-human cues are due to different degrees of experience with an action or action cue, and not the biological status of the agent, *per se*. Further research is needed to evaluate this hypothesis directly.

In the present study, we have sidestepped this issue by training participants to perform complex sequences of dance movements that were novel before the study began. Our findings that the premotor cortex responds more strongly to training than the presence of a human model, and that posterior temporal areas respond to the presence of a human model but not to training, suggest that the AON comprises dissociable components involved in different aspects of action cognition. In particular, we suggest that activation of PMv does not necessarily reflect selective processing of human-related action stimuli. Instead, the present data emphasize the impact of motor familiarity on PMv responses and the presence of a human model on posterior temporal responses. Put another way, our data suggest that we can use a physical agent to amplify learning (as our behavioral data demonstrate), but once new action sequences have been embodied, the presence of a visible human body does not enhance activity in the anterior components of the AON.

One issue raised by the current study that is ripe for future investigation is the possibility of an interaction between physical experience and the presence of a human agent. As we report here, this interaction approached significance (corrected for multiple comparisons) within two regions of the left inferior frontal gyrus (IFG; Table 1; Fig. 3A). While the current results demonstrate the plausibility of individual components within the AON showing differential responses to observing stimuli that have been physically trained, based on the presence or absence of a human model, the current interaction effects must be considered exploratory given their moderate statistical certainty. Further research is required to determine possible interactions between physical experience with an action and the biological nature of the action cue within the AON.

The present data are also consistent with recent findings concerning the role of the STS in higher-level cognitive operations, such as those that require theory-of-mind processing (e.g. Pelphrey *et al.*, 2004; Brass *et al.*, 2007; de Lange *et al.*, 2008). In one such study, Brass and colleagues measured participants' brain activity while watching videos featuring plausible and implausible simple actions (Brass *et al.*, 2007). These authors reported that STS and pSTS were engaged most by observation of actions that require a greater degree of inferential reasoning in order to make sense of them (such as why an individual would turn on a light switch with her knee when her hands were free), compared with performance of more contextually plausible actions. Brass and colleagues suggest that STS is not involved in action simulation as such, but is instead most strongly recruited when a greater degree of inferential reasoning or mentalizing is required to make sense of another individual's actions. Integrating these prior findings with the current data, it is plausible to conclude that physical experience changes activity in simulation areas, such as PMv, but not those linked to inferential reasoning. It remains to be determined if training-associated changes in inferential reasoning would alter responses in areas such as STS.

Limitations

Several limitations of the present findings warrant discussion. One important issue is the potentially confounding effects of attention on our findings. It could be the case that the differences we see between the danced and untrained conditions, and between the human present and human absent conditions, are not due to training and the presence of a human dancer, respectively, but are instead due to differential engagement of attention. We suggest that the data do not support this interpretation. A highly relevant functional imaging investigation of attention to visual motion has unequivocally demonstrated that cortical responsiveness can be enhanced by increased attention to the visual stimulus (Büchel *et al.*, 1998). In this study, Büchel *et al.* (1998) reported widespread activation within a broad network of cortical regions, including the frontal eye fields, posterior parietal, premotor, cingulate and prefrontal cortices, when participants actively attended to videos of moving dots, compared with passively observing the moving dots. At first glance, it might appear that our data are not inconsistent with this account, and that the greater activation we report in the right PMv when participants watch danced compared with untrained videos could simply be due to participants attending more to this condition. However, upon closer inspection of the right premotor focus where Büchel *et al.* (1998) report attentional modulation, our premotor region of interest is 23 mm away from their region, located more ventral and anterior to their premotor region. Careful comparison of each of their frontal and parietal activations that showed significant effects of attentional modulation with the regions we report in our danced > untrained contrast in Table 1 reveal that none of our regions overlap with their reported regions, with a distance of ≥ 10 mm between their reported activations and what we found in the present study.

The same attention argument could conceivably be applied to our findings concerning the presence of a biological agent. A relevant paper to consider here is a recent review of goal-directed attentional processing (Corbetta *et al.*, 2008). Corbetta and colleagues review an extensive literature that provides evidence for a ventral attentional network comprising pSTS, temporal parietal junction, IFG, and middle frontal gyrus that responds in concert with a more dorsal attentional network when an unexpected but behaviorally relevant event occurs. The bilateral STS activations we find to respond when participants observe videos with a human present compared with videos with no human certainly falls into the ventral attentional network discussed by Corbetta *et al.* (2008), but the presence of a human is hardly unexpected or surprising in the present experimental context. Moreover, an attentional explanation of our result would have to claim that some other (unidentified) brain network identifies the presence of a human in the stimulus and then drives an attentional process that increases the BOLD signal in STS. We suggest is it more parsimonious to interpret the temporal activations observed in the present context as being driven directly by the presence of the human figure. Such an interpretation is coherent with many other studies that have investigated the perception of biological motion (Grèzes & Decety, 2001; Keysers & Perrett, 2004; Pelphrey *et al.*, 2004; Calvo-Merino *et al.*, 2005; Brass *et al.*, 2007; Wheatley *et al.*, 2007; Hein & Knight, 2008).

A related limitation worthy of consideration is the fact that we did not include a third experimental factor that included a dancer only, with no arrows. With such a condition, we could ensure that participants only attended to the human form and could more precisely distinguish the impact of human and arrow cues. We speculate that the differences observed between the human present and human absent contrast (Fig. 3) would become even more robust, as there would be no chance of attention being diverted to the moving arrows. However, it was not feasible to train participants to perform the dances without the arrow cues. Further research will be needed to compare the impact of human and arrow forms on the AON in more detail.

Implications

A significant implication of this work concerns models of how action information is processed. Prior research provides abundant evidence that experience modulates action perception (Buccino *et al.*, 2004; Calvo-Merino *et al.*, 2006; Cross *et al.*, 2006, 2009). The present findings demonstrate that such perceptual changes occur within premotor and parietal areas, and are not due to changes within the visual association cortex. This is a valuable demonstration, as it refutes predictions that might be made by the dominant alternative information processing model, the so-called social network of perceptual processing (Allison *et al.*, 2000; Pelphrey & Carter, 2008). According to this model, salient action information is mediated by STS and EBA as it progresses from earlier visual areas to parietal and premotor components of the AON (Allison *et al.*, 2000; Iacoboni, 2005; Iacoboni & Dapretto, 2006). Our data underscore the notion that PMv is linked to understanding of salient action cues, while the posterior temporal cortex does not appear to play a direct role in processing action information on the basis of embodiment. This is compatible with the idea of multiple complimentary systems for action understanding, where different brain regions make different contributions, rather than a unitary or homogenous AON (Hamilton & Grafton, 2009).

Supporting Information

Additional supporting information may be found in the online version of this article:

Fig. S1. Behavioral training results across the week of dance training.

Fig. S2. Anatomical mask of the action observation network regions of interest.

Fig. S3. Interaction analyses: training experience and stimulus form.

Fig. S4. Main effect of dance training in left hemisphere ventral premotor cortex.

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Abbreviations

AON, action observation network; BOLD, blood oxygen level-dependent; EBA, extrastriate body area; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; MNI, Montreal Neurological Institute; PMv, ventral premotor cortex; pSTG, posterior superior temporal gyrus; STS, superior temporal sulcus.

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