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The role of the extended MNS in emotional and nonemotional judgments of human song

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Abstract In the present study, we examined the involvement of the extended mirror neuron system (MNS)—specifically, areas that have a strong functional connection to the core system itself—during emotional and nonemotional judgments about human song. We presented participants with audiovisual recordings of sung melodic intervals (two-tone sequences) and manipulated emotion and pitch judgments while keeping the stimuli identical. Mu event-related desynchronization (ERD) was measured as an index of MNS activity, and a source localization procedure was performed on the data to isolate the brain sources contributing to this ERD. We found that emotional judgments of human song led to greater amounts of ERD than did pitch distance judgments (nonemotional), as well as control judgments related to the singer’s hair, or pitch distance judgments about a synthetic tone sequence. Our findings support and expand recent research suggesting that the extended MNS is involved to a greater extent during emotional than during nonemotional perception of human action.

Keywords Mirror neuron system · Mu event-related desynchronization · Emotion perception · Action perception · Superior temporal gyrus

Emotion is rooted in motion (Casasanto & Dijkstra, 2010). When joyful, people may jump and exclaim, gesturing in a

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way that reveals their emotion. When sad, they may exhibit a stooped posture and lowering of the larynx, releasing pharyngeal constriction, leading to a sobbing vocal quality (Harris, Harris, Rubin, & Howard, 1998). When observing another person’s emotions, it is common to remark that individuals are “moved” with compassion or pity. Such remarks are viewed by more than one theorist as being more than just metaphor; rather, when we feel empathy, we do so through a process of simulating movement—neurally, via specialized mirroring mechanisms (McGarry & Russo, 2011; Molnar-Szakacs & Overy, 2006; Rizzolatti & Craighero, 2004), and peripherally, through facial mimicry (Chartrand & Bargh, 1999; Dimberg, Thunberg, & Elmehed, 2000; Riskind & Gotay, 1982)—in a kind of embodiment of another person. In the present study, we used a task-driven design in which participants were asked to make emotional or nonemotional judgments of identical stimuli (sung melodic intervals) in order to examine the neural underpinnings of top-down emotional attention during the perception of human movement.

A number of different neural mechanisms of embodiment are likely to be activated during the perception of human action, but a reasonable candidate network is the mirror neuron system (MNS). This is a system of neurons in the frontal and parietal regions of the human and nonhuman primate brains that appears to be responsible for the execution and perception of meaningful action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; for a review, see Rizzolatti & Craighero, 2004), and it is hypothesized to be linked to simulation of the emotional actions of others (Aragón, Sharer, Bargh, & Pineda, 2013; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Chartrand & Bargh, 1999; McGarry & Russo, 2011). Neurons in the MNS will fire during one’s own execution of an action, as well as during perception of the same action by other agents (di Pellegrino et al., 1992). Additionally, these

same neurons will fire during the execution and perception of different actions that convey similar intentions (Umiltà et al., 2001). Over the past two decades, numerous studies have further characterized the MNS in humans through functional magnetic resonance imaging (fMRI; Carr et al., 2003; Cross, Hamilton, & Grafton, 2006; Iacoboni et al., 2005), electroencephalography (EEG; McGarry, Russo, Schalles, & Pineda, 2012; Pineda, 2005, 2008), and magnetoencephalography (MEG; Hari et al., 1998), as well as through a single-cell recording in a clinical population (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Accumulating functional evidence has suggested that, although there are differences between primates, the MNS serves functions in humans that overlap with those that have been identified in monkeys (Keysers & Gazzola, 2009; Mukamel et al., 2010).

The MNS does not function in isolation and receives inputs from a variety of regions and sends outputs to an equal variety of regions, including the sensorimotor cortex. Hence, the notion of an extended MNS is defined to include a much wider range of areas that are functionally connected with the classical MNS to instantiate embodiment, imitation, and empathy during perception of meaningful movement (Pineda, 2008). These extra-mirroring regions likely include the insula (Carr et al., 2003; Mukamel et al., 2010), as well as the medial and superior temporal gyrus (MTG and STG) and the superior temporal sulcus (STS; Mukamel et al., 2010; Pineda, 2008). From an information-processing perspective, signals are assumed to enter the MNS at the superior temporal sulcus (STS) via visual and auditory sensory streams (Barracough, Xiao, Baker, Oram, & Perrett, 2005; Keysers et al., 2003). The STS has been implicated in the processing of biological motion, face processing, and social attention (Iidaka, 2012; Redcay, 2008). It is less certain whether the STS itself possesses mirror neurons (but see Iacoboni et al., 2001; Molenberghs, Brander, Mattingley, & Cunnington, 2010), but it does integrate auditory and visual information before the information is sent on to the ventral premotor cortex (Keysers et al., 2003). Some findings have implicated the STS as a mirroring region, because it shows enhanced activation during imitation of actions, in similar areas as those activated during the observation of actions (Iacoboni et al., 2001). Iacoboni et al. (2001) believed that the STS is involved in creating a visual sensory copy of an imitated action, through receipt of signals from parietal and frontal mirroring areas, rather than being a mirroring region in its own right. The STS has also been reported to show people selectivity, with enhanced responsiveness to faces and voices as opposed to other types of auditory and visual stimuli (Watson, Latinus, Charest, Crabbe, & Belin, 2014). That information is then relayed to mirror neuron areas, including the precentral gyrus (PCG), containing the ventral premotor cortex, the posterior part of the inferior frontal gyrus (IFG), specifically the operculum, and the inferior parietal lobule (IPL), particularly the

supramarginal gyrus (Buccino et al., 2001; Rizzolatti & Craighero, 2004).

In humans, EEG measurement of MNS activation involves indexing event-related desynchronization (ERD) to human action. This index is temporally sensitive and considered to be the result of fronto-parietal mirroring activity on the coordination of neurons in the sensorimotor cortex (Pineda, 2005, 2008). Mu ERD is enhanced (i.e., greater desynchronization) during the visual and auditory observation or performance of biological movement in healthy individuals (Pineda, 2005). Moreover, during observation, mu ERD is only enhanced by movements performed by other humans and not by object movements (Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998).

Several studies have supported the premise that emotional systems stimulate classical mirroring systems to be activated more strongly during emotional versus nonemotional perception of action (Enticott, Johnston, Herring, Hoy, & Fitzgerald, 2008; Pineda & Hecht, 2009; Wicker et al., 2003; Zaki, Weber, Bolger, & Ochsner, 2009). This could be because emotional actions reliably tend to be more salient than neutral actions (Talmi, Luk, McGarry, & Moscovitch, 2007), and therefore more interesting to simulate. It could also be because emotional actions are more evolutionarily important to simulate (McGarry & Russo, 2011). Other studies suggest that social mirroring is adaptive in order to meet the demands of a varied social environment (Aragón et al., 2013).

Previous studies have used primarily visual stimuli in their examination of the role of the MNS in emotion perception (Carr et al., 2003; Enticott et al., 2008; Perry, Troje, & Bentin, 2010; Pineda & Hecht, 2009; Wicker et al., 2003; Zaki et al., 2009). However, it has also been suggested that the MNS is involved in the perception and production of human speech and song (Overy & Molnar-Szakacs, 2009; Warren et al., 2006). For instance, Lévêque and Schön (2013) demonstrated that mu ERD was greater during perception of human vocal melodies as opposed to nonvocal melodies. Warren et al. (2006) have previously examined a similar question using human vocalizations, and they found MNS enhancement toward emotional versus neutral vocalizations in the left IFG and presupplementary motor area (pSMA). However, this type of stimulus possesses some potential confounds characteristic of stimulus-driven studies. In particular, emotional vocalizations could contain systematic differences in low-level auditory features, such as loudness or pitch quality, that contribute to any observed neural differences between emotional and neutral vocalizations. Although these low-level differences are considered necessary components of emotional sounds (Scherer & Oshinsky, 1977), it becomes difficult to determine which difference may have led to changes in reactions to the stimuli, or whether it is the essence of the emotion itself that contributes. In the present study, we addressed this potential confound by equating the stimuli across task conditions and manipulating task instead of stimulus conditions.

Similarly, previous studies using visual stimuli that consider the MNS in the context of emotional judgments have typically done so using distinct stimuli for emotional versus nonemotional judgments. Some issues are unavoidable with this type of design. First, there tend to be systematic differences between emotional and neutral stimuli, such as speed of movement, movement contour, and the saliency of movement that could contribute to any differences between conditions (Scherer & Oshinsky, 1977; Talmi et al., 2007), and this is arguably what makes certain stimuli emotional. It becomes very difficult in these cases to pinpoint the specific cause of differences between emotional stimuli, as these low-level differences may contribute to perceptual differences, but do not necessarily make up the complete essence of an emotion. One potential solution is to include a large number of emotional and neutral stimuli that vary on these low-level qualities. However, it is still likely that emotional stimuli will be louder, more variable in pitch, and so on. This has motivated our task-driven design, in which we used identical stimuli between conditions.

In the present study, we examined the role of the MNS in the top-down perception of emotion in human movement. Specifically, we looked at the role of the MNS in emotional versus structural judgments of human song. We sought to clarify the level of activation as well as the source of activation during emotion-related judgments as opposed to intention-related judgments that do not involve emotion (i.e., pitch distance). These judgment conditions were compared with each other, as well as with two control conditions, in order to control for the role of movement-related judgments (by asking participants to judge whether the singer's hair was up or down), or the presence of biological movement (by requesting pitch distance judgments of a moving oval accompanied by beeping sounds). In addition, we used a source localization procedure in order to determine which areas of the MNS contribute more activity to certain types of judgments than others. The stimuli chosen were melodic intervals (two-note sequences), namely the perfect fifth, tritone, major third, and minor third. These intervals vary both in emotionality (positive or negative; Schellenberg & Trehub, 1996; Thompson, Russo, & Quinto, 2008) and structure (small or large interval size; Russo, Sandstrom, & Maksimowski, 2011; Russo & Thompson, 2005), allowing for different judgment conditions to apply equally well to the same stimuli.

We indexed MNS activity using mu ERD (Pfurtscheller & Lopes da Silva, 1999; Pineda, 2005, 2008) during the perception of dynamic audiovisual presentations of human song. In order to enhance mu ERD power, all stimuli were presented audiovisually (McGarry et al., 2012). Across all judgment conditions, our audiovisual stimuli consisted of recordings of the aforementioned melodic intervals. Keeping the stimuli consistent across the judgment conditions allowed us to attribute differences in the neural response to the task alone. We

predicted greater mu ERD during emotion judgments as compared to pitch distance judgments, indicating that the MNS is involved to a greater extent during task-driven emotional versus nonemotional perception. We also predicted that the hair judgment would elicit less activation than the movement-oriented emotion and pitch distance judgments, due to a lack of movement-oriented attention, and that this would be followed by a lack of activation in the control task, due to lack of biological movement.

Method

Participants

Twenty healthy adults (17 females, three males) with no psychiatric or neurological disorders were tested. This sample size was chosen following the work of Moore, Gorodnitsky, and Pineda (2012), who used a similar data analysis method (independent components analysis) to successfully find mu ERD during an emotion-related task.

The average age (standard deviation) was 21.85 years (3.63), and the average number of years of education was 14.75 (4.34). All but two participants were right-handed. Participants were fully consented and debriefed. Our research protocol was approved by the Research Ethics Board at Ryerson University.

Design

The study was based on a within-subjects design. The within-subjects variable was the type of judgment made during test: emotional, pitch distance, hair, or control. The dependent variable was the mu ERD occurring during the observation of sung melodic intervals.

Stimuli

The stimuli consisted of audiovisual recordings of sung melodic intervals spanning one of four pitch distances (see Fig. 1). Each video was 3,000 ms long. Examples of the four pitch distances were produced by each of two female actors. The four intervals represent a perfect crossing of size and emotional valence. The minor third and the tritone are reliably rated as conveying negative emotion, whereas the major third and perfect fifth are reliably rated as conveying positive emotion (Schellenberg & Trehub, 1996; Thompson et al., 2008). The perfect fifth and the tritone also have a greater pitch distance between notes than the major and minor thirds. Prior research has demonstrated that the relative sizes of these intervals can be scaled accurately, regardless of musical training (Russo et al., 2011; Russo & Thompson, 2005). The stimuli were identical for the emotion, pitch distance, and hair

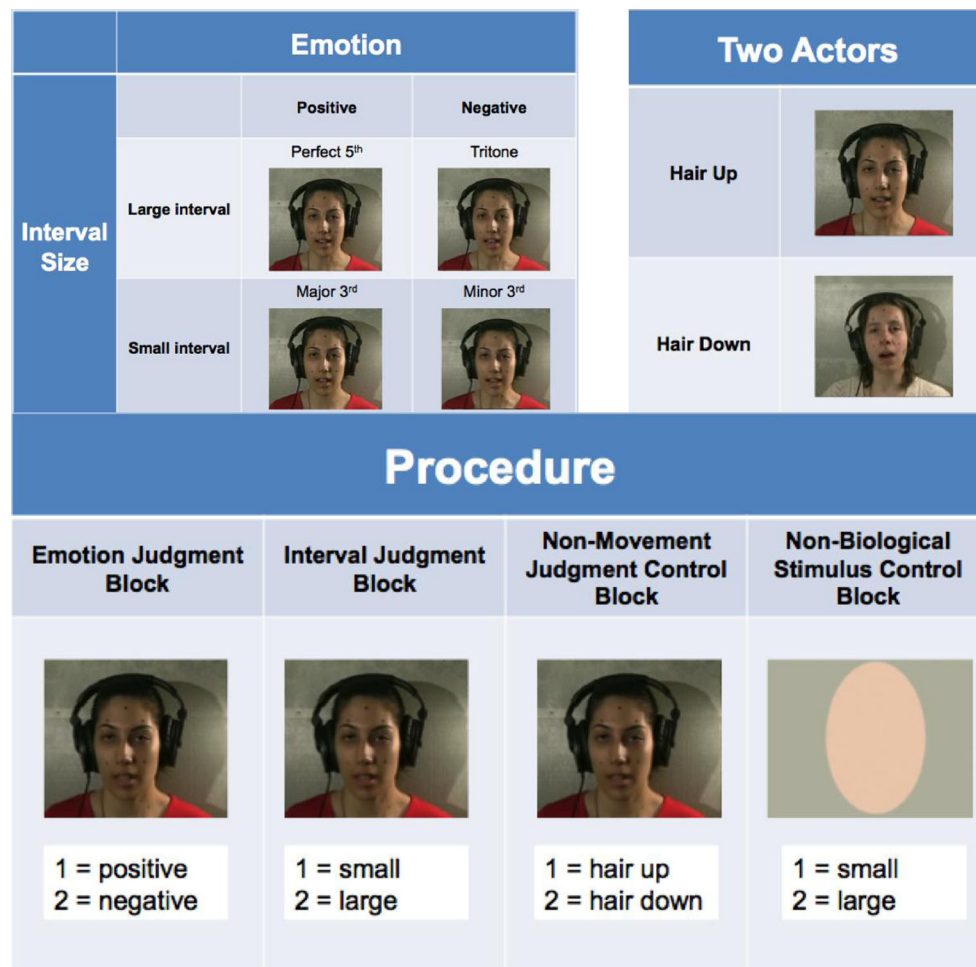


Fig. 1 Stimuli and procedure. The stimuli consisted of audiovisual recordings of sung melodic intervals spanning one of four pitch distances. The four intervals represent a perfect crossing of size and emotional valence: The perfect fifth and tritone have a greater pitch distance between notes than the major and minor third, and the tritone are reliably rated as conveying negative emotion, whereas the major third and perfect fifth are reliably rated as conveying positive emotion. Two actors were featured, one whose hair was tied up, and one whose hair was down at her shoulders. In the structural judgment

block, participants were asked to judge whether the sung interval was small or large (1 = *small*, 2 = *large*). In the emotion judgment block, participants were asked to judge whether the sung interval was positive or negative (1 = *positive*, 2 = *negative*). In the hair judgment block, participants were asked to indicate whether the singer's hair was up or down after each trial (1 = *hair up*, 2 = *hair down*). In the control block, participants were asked to judge the pitch distance of nonbiological stimuli consisting of a moving circle and auditory beeps

judgment control conditions. The nonbiological control stimuli consisted of beeping sounds accompanied by a moving oval. The beeps were matched to sung stimuli for average pitch and consisted of two simple (pure) tones at the same average pitch as the experimental stimuli. The moving circle was controlled in order to ensure that the magnitudes of movement were equivalent to those observed in the human song stimuli. This control was accomplished by making the circle equal in size to the head of the actor producing the intervals, starting movement at the same start point as the actor, and ending movement at the same endpoint as the actor.

The stimuli were piloted prior to testing. The chosen stimuli were equivalent with regard to the difficulty of the emotional or nonemotional judgment (i.e., pilot testing confirmed

that there was no difference in accuracy or reaction times between the task conditions).

Apparatus

Data were collected using a 64-channel Biosemi ActiveTwo EEG system at a sample rate of 512 Hz. Electrodes were placed using the International 10–20 System layout. All electrodes were of interest, as a source localization procedure was planned on the data.

Procedure

Upon arrival at the lab, participants provided informed consent to participate. The EEG cap was attached. Participants

were tested in a sound-attenuated chamber and situated 60 cm from the computer screen. Speakers were located within the computer monitor, and stimuli were presented at a consistent volume.

Participants viewed four blocks of 12 videos depicting the four types of sung intervals, each video 3,000 ms long, with each trial followed by the button-press judgment screen. Order was counterbalanced across participants and stimuli were blocked by judgment type. In the structural judgment block, participants were asked to judge whether the sung interval was small or large (1 = *small*, 2 = *large*). In the emotion judgment block, participants were asked to judge whether the sung interval was positive or negative (1 = *positive*, 2 = *negative*). In the hair judgment block, participants were asked to indicate whether the singer's hair was up or down after each trial (1 = *hair up*, 2 = *hair down*). This condition was added in order to determine whether simply attending to movement-related aspects in the other two conditions, versus non-movement-related aspects of the stimuli in this condition, would lead to greater MNS activation. In the control block, participants were asked to judge the pitch distance of nonbiological stimuli consisting of a moving circle and auditory beeps.

Data analysis

The EEG data were analyzed using EEGLab, an open-source MATLAB program (Delorme & Makeig, 2004). Electrode data were subjected to a source-localization procedure in order to isolate specific brain sources contributing to electrode activity at the scalp. Specifically, we wished to isolate mu sources. We found that multiple sources were contributing to activity at the central electrodes, where mu is typically measured. Therefore, the data were examined in source space. Fronto-parietal and parieto-central sources were isolated for further analysis, because these are the areas of the brain considered to generate mu activity. Sources were examined for the amplitude of activity taking place in the 10- and 20-Hz ranges, which are characteristic of the mu rhythm: alpha (8–13 Hz) and beta (15–25 Hz).

First, the data for each participant were imported into EEGLab and referenced to the average level of activity from all electrodes. Channels were identified according to a BESA head model, and eight facial muscle reference channels were deleted. Data were selected to only include trials and to exclude intertrial intervals. Activity that occurred during a 1,000-ms prestimulus baseline was subtracted from each 3,000-ms trial. Next, the data were filtered from 3 to 30 Hz. Following this step, trials with artifacts greater than 150 μ V on 33 % of the electrodes were excluded. An independent components analysis (ICA) was then run on the data to separate them into 64 brain sources. The Adjust plugin for EEGLab was used to automate the exclusion of ICA sources that represented eyeblink, muscle activity, or other types of general artifacts,

on the basis of defined criteria (Mognon, Jovicich, Bruzzone, & Buiatti, 2011). Following this, a coarse dipole-fitting procedure was applied (see the EEGLab Wiki for more information on the coarse dipole-fitting procedure and the other data analysis steps mentioned here; Delorme & Makeig, 2013), and data were saved separately according to condition. The data for each participant from each condition were then saved in an EEG “Study” file and component clustering was performed.

Component clustering took place using the K-means procedure and excluding outliers greater than three *SDs* from the mean. The components included in a cluster were those with less than 40 % residual variance. Ten clusters were formed.

Results

Of the ten clusters that were formed, three were located in brain areas that are theoretically consistent with the MNS, in the right precentral gyrus (considered part of the classical MNS; Buccino et al., 2001; Rizzolatti & Craighero, 2004) and left superior temporal gyrus and insula (each considered part of the extended MNS; Pineda, 2008). Next, we examined event-related spectral perturbations (ERSPs) for each cluster. ERSPs are three-dimensional displays of power across time on the *x*-axis and frequency on the *y*-axis. Power is indicated by the presence of warmer colors, whereas desynchronization is indicated by cooler colors. We were interested in the power in the alpha and beta bands of mu that was desynchronized during the perception of action. Two of these clusters showed ERSPs yielding the expected pattern (emotional judgment > nonemotional judgment, as signified by a greater amount of desynchronization, or cooler-colored activity, in the 8–13 Hz range across the time series of interest); however, this pattern only reached significance for the left-central cluster (detailed below). We found no significant differences between conditions for any other clusters.

Left-central cluster analysis

The left-central cluster that yielded the expected pattern of activity across conditions had Talairach coordinates at (–55, –15, 5), in the left superior temporal gyrus (STG; left cerebrum, temporal lobe; see Fig. 2). This is only 13.49 mm away from the ventral premotor cortex, an area of the MNS that we also found to exhibit greater activity toward audiovisual perception of emotion in a previous study (McGarry et al., 2012), suggesting that the source might be related. We analyzed the ERSPs for each condition within this cluster across the alpha and beta bands of mu. An analysis of variance (ANOVA) comparing all four conditions (emotion, pitch distance, hair judgment, and control pitch distance) was significant in many

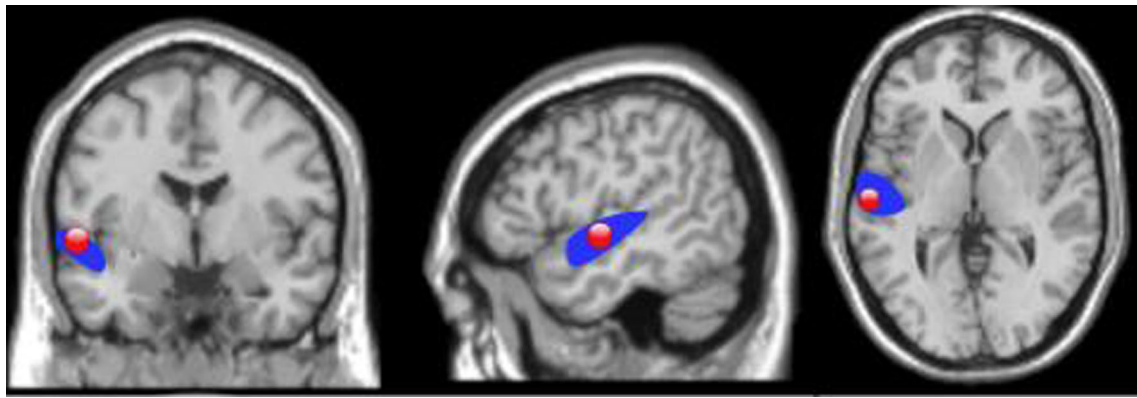


Fig. 2 In this figure, a manual tracing of the left STG (part of the extended MNS) is depicted, whereas the significant mean dipole location is depicted as a central dot. This cluster exhibited patterns of activation consistent with our predictions

places across the time/frequency window (see Fig. 3a), in the alpha band only. A follow-up pairwise comparison of the emotion and control conditions was significant, as well (see Fig. 3b). However, a pairwise comparison of the emotion judgment and the nonemotion judgment was not significant.

Due to the multiple comparisons that need to be made when comparing multiple time/frequency points across a window of interest, power is reduced by statistical corrections. As an alternative, we used the MATLAB Statistics Toolbox to complete a secondary analysis based on the averaged power across time and frequency windows. This secondary approach revealed that the pitch distance judgment activity was not different from hair control activity, but that both the pitch distance and hair control conditions had marginally greater mu ERD than the nonbiological control condition (see Fig. 4), $F(3, 236) = 2.47, p = .06$. Although this ANOVA was only marginally significant, follow-up *t* tests were conducted between the conditions of interest to see what differences might have been driving this trend. It was found that the emotion condition generated significantly more mu ERD than the control condition, $t(118) = 2.2759, p = .025$. No other differences reached significance when examined across the entire time/frequency window (see Table 1).

Right precentral gyrus cluster

A right-sided cluster with Talairach coordinates at (35, -16, 43) in the right PCG (right cerebrum, frontal lobe), although not significant, demonstrated trends in activity in the alpha band that resembled those in the left STG cluster (see Fig. 5 and Table 1). Mu desynchronization in the alpha range was greatest for the emotion condition, followed by the pitch distance condition, the hair control condition, and then the nonbiological control condition (Figs. 6a, b). These trends can be easily observed when the data are collapsed across time and frequency bands in the alpha range (see Fig. 6b). See Table 1 for all results.

Other clusters

Although we sought to make conditions as identical as possible by manipulating task instead of stimuli, high-level differences that varied systematically between judgment conditions still could have contributed to the differences in mu desynchronization. For instance, emotional judgments could be considered to be more engaging or arousing than nonemotional judgments, which would lead to desynchronization in other brain regions, in addition to MNS-related regions. For this reason, we were careful to examine any differences between occipital brain sources that could be reflective of enhanced visual attention (Sauseng et al., 2005). However, there were no differences across judgment conditions for occipital brain sources. We also observed no differences in any other brain sources, suggesting that our judgment manipulation did not cause unwanted systematic differences in attention/arousal between conditions.

Gender differences

The performers in videos were both female. Most of our participants were also female (17 female, three male). There is some evidence that females are more expressive than males (Cheng et al., 2009) and that they have a more developed MNS, corresponding with a greater level of empathy (Cheng et al., 2009). Thus, it is possible that the effects reported here might have been inflated in our mostly female sample. However, the patterns of activation between emotional and nonemotional conditions have not generally been found to change across sexes in prior research.

Discussion

In the present study, we found enhanced mu ERD during emotion judgments versus nonemotional judgments to sung

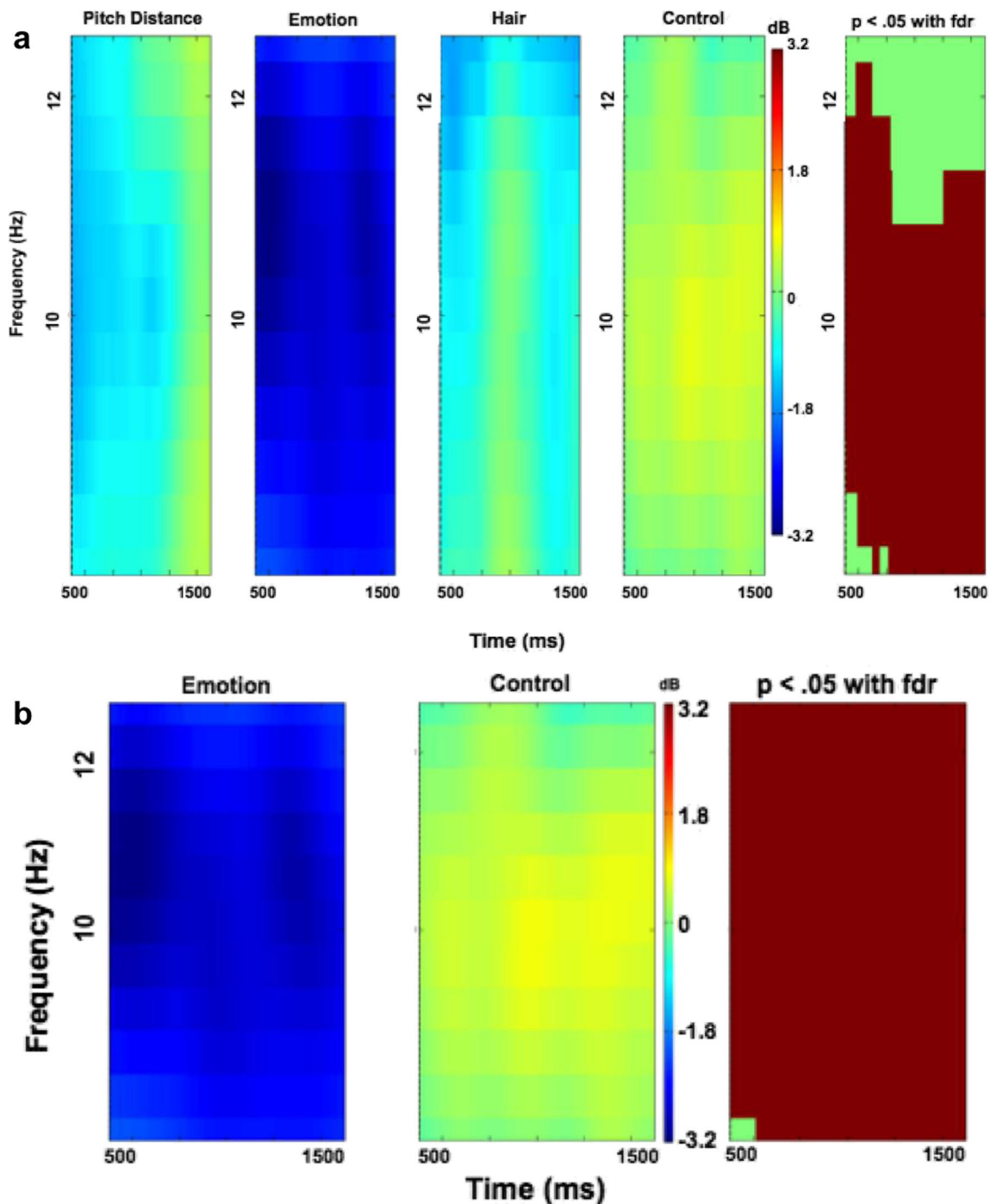


Fig. 3 (a) Event-related spectral perturbations for the cluster originating from the left superior temporal gyrus (STG). In the 8- to 13-Hz alpha frequency band, the emotion judgment condition led to greater mu event-related desynchronization (ERD, depicted in darker colors) than did the nonemotion judgment condition or the hair and nonbiological control conditions. This pattern was significant. A series of F tests were performed for several time and frequency combinations across the event-related spectral perturbation (ERSP) window, with a false-discovery rate (FDR) correction for multiple comparisons, and areas in the box on the

right that are dark in color are considered significant at the $p < .05$ level. (b) Event-related spectral perturbations for the emotion versus the nonbiological control condition, originating from the left STG cluster. A series of pairwise comparisons were performed for various time and frequency combinations across the ERSP window, and these are depicted in the box on the right with an FDR correction. Significant comparisons are dark in color. The emotion condition was found to lead to significantly greater mu ERD than the nonbiological control condition. This was the only significant pairwise comparison for this cluster

stimuli, localized to the left STG. Although the STG is considered to be part of the extended MNS, there is uncertainty

whether it possesses mirroring properties per se (but see Iacoboni et al., 2001; Molenberghs, Cunnington, &

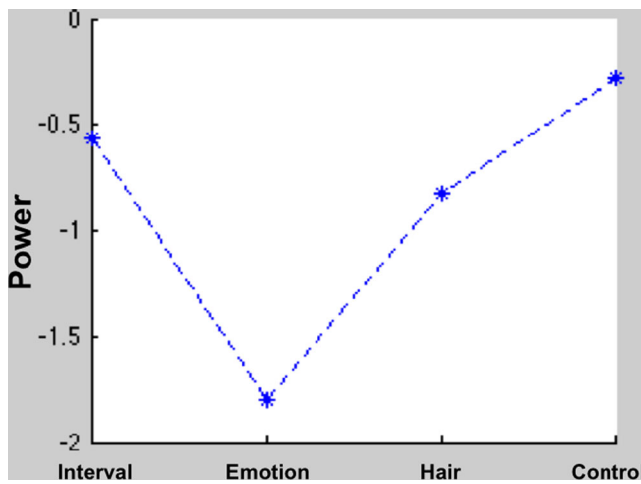


Fig. 4 Patterns of mu ERD originating from the left STG cluster, collapsed across the 8- to 13-Hz frequency window, and collapsed across the 500- to 1,500-ms time window of interest. This simpler graph illustrates the greater level of desynchronization to the emotion task condition than to the other conditions

Mattingley, 2012). There has been marginal support for a comparable pattern of activation found in the right PCG, an area believed to contain mirror neurons (Iacoboni et al., 2005). The present results support recent research suggesting that the extended MNS plays a distinctive role in the perception of emotional information, and further advances our understanding by demonstrating that this enhancement can occur under task-driven conditions. This finding supports the premise that it is the task-driven emotional attributes of the stimuli, rather than individual low-level systematic differences contributing to perception of emotional versus neutral stimuli, that lead to enhanced MNS responsivity during the perception of emotional action in this study.

As predicted, we found a trend toward a step function in terms of mu ERD during different judgment conditions. Pitch distance and hair judgments led to marginally greater mu ERD than the nonbiological control condition, and emotion judgments led to significantly greater mu ERD than control conditions. Pitch distance and emotion judgments were marginally different from each other. These data indicate that the

greatest amount of extended MNS activity in the left STG occurs during an emotion-related judgment, as opposed to a different type of movement-intention-related judgment, or a non-movement-related judgment.

Because we were asking participants to make emotional judgments, the lateralization of our STG finding is somewhat surprising. Many studies have demonstrated a right-sided bias for emotional processing in the brain (Davidson, 1998; Davidson & Irwin, 1999; Schwartz, Davidson, & Maer, 1975) although this evidence has been contested (Wager, Phan, Liberzon, & Taylor, 2003). Watson et al. (2014) and Kreifelts, Ethofer, Shiozawa, Grodd, and Wildgruber (2009) also found that social processing, such as people-selective and voice-selective processing, occur mainly on the right side in the STS and STG. One difference between the present study and these previous studies is that the emotionality of our task came from a top-down judgment, rather than from passive viewing of emotional versus neutral stimuli. Thus, participants were using inferential judgments to decide on the emotionality of the stimuli, which could preferentially recruit the left side (Gazzaniga, 1995). The left STG has also been implicated in auditory short-term memory (Leff et al., 2009), so this could also have played a role, as the participants may have engaged their short-term memory of the auditory stimuli during processing in order to make a correct judgment.

The marginally enhanced activity in the right PCG toward emotion judgments may indicate that areas of the extended MNS stimulate classical MNS activation during emotion perception. Since this cluster was situated in the frontal lobe, it could be indicative of MNS activity involved in intentional attributions (Iacoboni et al., 2005). As one might expect, there was marginally greater activity in the pitch distance condition than the control conditions in this cluster, indicating responsivity to nonemotional intention judgments as well. The right lateralization of this cluster could be driven by the emotion judgment, given that emotional vocalizations have been found to be processed preferentially in the right hemisphere (George et al., 1996; Schirmer & Kotz, 2006).

No differences emerged between conditions when the data were examined in channel space. This is likely because

Table 1 All statistical results, collapsed across time and frequency, for each cluster of interest

Region	Talairach Coordinates			ANOVA: Emotion, Pitch Distance, Hair, Control	Emotion–Pitch Distance	Emotion–Hair	Emotion–Control	Pitch Distance–Hair	Pitch Distance–Control	
	x	y	z							
Left superior temporal gyrus	-55	-15	5	F	2.47	t -1.74	-1.5	-2.28	0.51	-0.54
				p	.06	p .08	.14	.025*	.61	.59
Right precentral gyrus	35	-16	43	F	0.36	t -0.53	-0.87	-1.01	-0.24	-0.41
				p	.78	p .6	.38	.32	.81	.68

* $p < .05$

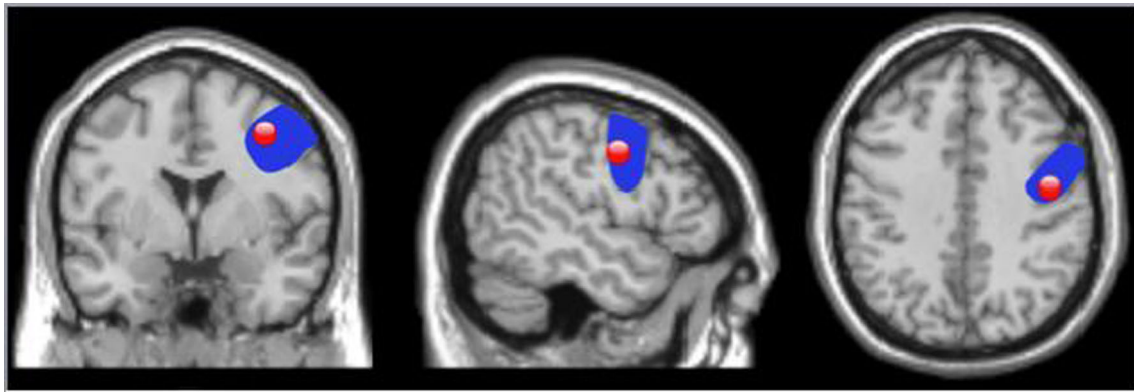


Fig. 5 Cluster originating in the right precentral gyrus (PCG), which is considered to be part of the classical mirror neuron system (MNS). This cluster exhibited nonsignificant trends consistent with our predictions.

The larger colored areas are manual tracings of the right PCG, and the mean dipole location of the cluster contributing the pattern of activation found in the present study is depicted as a central dot

multiple brain sources were found to contribute to activity at the central electrodes, making it difficult to find differences as clearly as in source space. For instance, several occipital sources were found to contribute to activity at the central electrodes in our study, where μ is typically measured. This is problematic, given that the alpha activity from occipital sources could easily mask μ activity originating from motor sources when observed in channel space (McGarry et al., 2012; Moore et al., 2012).

It is important to note that the differences we observed across experimental conditions cannot be attributed to difference in task difficulty. In a pilot study, we found that the emotion and pitch distance judgments were equal in difficulty. Although our nonbiological control was not included in the pilot, we assume that difficulty level was comparable to that of the experimental conditions given that participants were asked to make interval size judgments on these stimuli as well.

A good deal of debate has focused on the existence and function of the MNS in humans (Dinstein, Thomas, Behrmann, & Heeger, 2008). Some of this debate has stemmed from controversial claims regarding the possible evolutionary role of the MNS in language development and socio-emotional communication (Dinstein et al., 2008), whereas some is due to the lack of direct evidence for “mirror neurons.” The latter issue stems from the complications involved with single-cell recording in humans. Nonetheless, multiple lines of evidence do support the existence of some form of action observation, or “mirror,” network in humans (for a review, see Rizzolatti & Craighero, 2004). For parsimony, we choose to refer to that network as the MNS despite the minimal evidence for “mirror neurons” in humans.

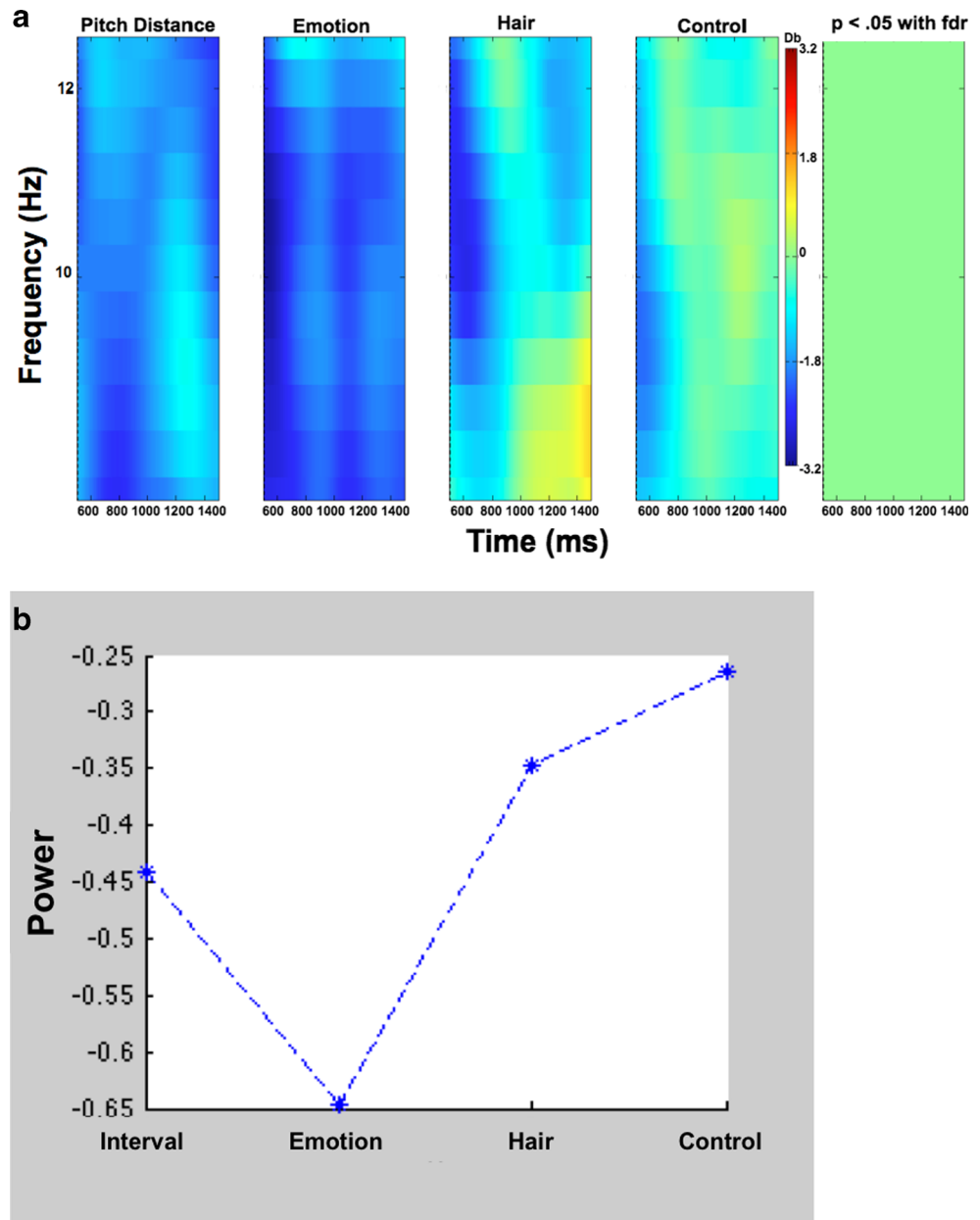
One controversial claim that has sparked wide interest is the possible role of the MNS in emotional understanding. Although some empirical evidence supports this role (Carr et al., 2003; Ferri et al., 2013; Grosbras & Paus, 2006; Oberman et al., 2005), questions remain about the extent to which findings may have been due to differences in stimulus

properties. This was one reason for our interest in comparing emotional versus nonemotional judgments of movements in the same set of actions. Our results are consistent with the view that there is an action-observation network, and our evidence suggests that it is context-dependent. Specifically, we found that the results were judgment-dependent rather than stimulus-dependent.

To elaborate, several lines of empirical research evidence point to a role of the MNS in the understanding of emotions. It has been shown, for example, that when we see someone smiling, we automatically mimic their smiling action (reliably measured via electromyography; Dimberg, Thunberg, & Elmehed, 2000). Indeed, “smiling” (zygomaticus major) muscles are activated more during perception of positive emotions, whereas “frowning” (corrugator supercilli) muscles are activated more during perception of negative emotions (Dimberg et al., 2000), and mimicry is greater toward emotional than toward nonemotional movements (Moody & McIntosh, 2011). Facial mimicry has been observed in response to dynamic signals including speech (Hess & Blairy, 2001) and song (Chan, Livingstone, & Russo, 2013), and thus does not depend upon prolonged exposure to the apex of an emotional expression. Some evidence suggests that facial mimicry is mediated by the MNS (Carr et al., 2003). Presumably, the MNS relays this information to the limbic system, thus helping us empathize with another person (Carr et al., 2003; LeDoux & Phelps, 1993).

Research on individual differences provides more evidence that the MNS is involved in empathy. For instance, it has been found that individuals scoring highly on empathy scales exhibit greater-than-average MNS activation in general during social perception (Gazzola, Aziz-Zadeh, & Keysers, 2006; Singer et al., 2004). In addition, individuals with autism, who have difficulty with empathy, have been noted to have lower-than-average MNS activity during perception of other people’s movements, but normal activity during execution of their own movements (Oberman et al., 2005; Williams et al.,

Fig. 6 (a) Event-related frequency perturbations originating from the right PCG cluster, for each condition, across the 8- to 13-Hz alpha frequency band, a component of mu. Visual examination of these ERSPs indicates greater desynchronization during the emotional task condition, followed by the nonemotional action intention task condition, followed by the two control conditions. Although these differences are not significant, they suggest a trend in the predicted direction that might originate in the classical MNS. (b) Mu ERD collapsed across the 8- to 13-Hz frequency band and the 500- to 1,500-ms time band of interest. This simpler graph illustrates marginally greatest mu ERD in the emotion judgment condition (indicated by a lower mean value), followed by the nonemotional intention judgment condition and the control conditions; this is a nonsignificant pattern that is consistent with our predictions



2006). This finding has led to the provocative hypothesis that problems with empathy in autism may be related in some manner to a dysfunctional MNS (Dapretto et al., 2006; Oberman et al., 2005).

In addition to individual differences studies, several studies have specifically examined the role of the MNS in emotion processing (Aragón et al., 2013; Carr et al., 2003; Enticott et al., 2008; Ferri et al., 2013; Grosbras & Paus, 2006; Perry et al., 2010; Pineda & Hecht, 2009; Wicker et al., 2003; Zaki et al., 2009). For instance, Carr and colleagues (2003) examined fMRI activation during the observation and imitation of emotional facial expressions. They found activation in equivalent areas for observation and imitation, including MNS regions such as the bilateral inferior frontal cortex, and

extended “emotional” mirroring areas such as the right insula, an area known to communicate with the limbic system. Carr et al. (2003) concluded that the MNS is involved in both the observation of and imitation of emotional action. Furthermore, they suggest that when we observe emotional action, we simulate this action neurally. This simulation presumably feeds into the limbic system, allowing us to feel how we would feel if we were making the perceived emotional expression ourselves. Wicker and colleagues (2003) conducted a similar study involving odor perception. They asked participants to smell pleasant or unpleasant odors, or to watch someone else smell a pleasant or unpleasant odor. They observed enhanced BOLD activation in the MNS and the limbic system, indicating again that the MNS is involved in both the

experience and observation of emotional states. The role of simulation in the perception of emotional action has been supported in various other fMRI (Ferri et al., 2013; Grosbras & Paus, 2006; Zaki et al., 2009), MEG (Enticott et al., 2008), and EEG (Perry et al., 2010; Pineda & Hecht, 2009) studies. In an fMRI study, Zaki and colleagues found that accuracy on an emotion perception task was correlated with activation in several areas of the MNS as well as other areas involved in mental attribution. Pineda and Hecht found enhanced EEG responses in the MNS toward static emotionally expressive images. Grosbras and colleagues found enhanced activation in the IFG, anterior STS, STG, precentral sulcus (PCS), insula, and amygdala toward human grasping movements that were performed in an angry manner as opposed to a neutral manner, demonstrating that the classical MNS as well as extensions of the MNS are involved to a greater extent during emotional than neutral movements. Ferri and colleagues found enhanced MNS activity, specifically in the IFG, PCG, and parietal lobe (PL) toward grasping movements that were accompanied by an emotional facial expression. They concluded that the surrounding emotional context influences the degree of MNS activity during movement perception.

There is also some precedent for the notion that the MNS is relevant for the perception of song (Lévêque & Schön, 2013). Our results suggest that in the domain of song, perception can occur through a structural (i.e., interval size) or emotional lens, and when perception occurs through an emotional lens, the left STG of the extended MNS is recruited more heavily. Speech, similarly, has been shown to involve the MNS (Warren et al., 2006), and can also be considered to have a structural (linguistic) and emotional aspect (Warren et al., 2006). Although our focus is often on the linguistic qualities of speech, we presumably require more MNS activation in speech when we're interested in its emotionality. A future direction of the present study would be to compare song and speech in terms of their reliance on the MNS during emotional versus structural processing.

The present study supports and advances recent findings that the extended MNS plays a special role in the perception of emotional action (Enticott et al., 2008; Pineda & Hecht, 2009; Singer et al., 2004; Wicker et al., 2003; Zaki et al., 2009). Enhanced activation was found in the left STG toward audio-visual perception of human song when participants were asked to make an emotional judgment. The manipulation of task conditions while holding stimuli constant supports the premise that emotion-oriented processing of stimuli contributes to enhanced activity in the extended MNS and that this enhancement does not depend on systematic differences between emotional and neutral stimuli.

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