Emotion

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Separating Neural Activity Associated With Emotion and Implied Motion: An fMRI Study

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Previous research provides evidence for an emo-motoric neural network allowing emotion to modulate activity in regions of the nervous system related to movement. However, recent research suggests that these results may be due to the movement depicted in the stimuli. The purpose of the current study was to differentiate the unique neural activity of emotion and implied motion using functional MRI. Thirteen healthy participants viewed 4 sets of images: (a) negative stimuli implying movement, (b) negative stimuli not implying movement, (c) neutral stimuli implying movement, and (d) neutral stimuli not implying movement. A main effect for implied motion was found, primarily in regions associated with multimodal integration (bilateral insula and cingulate), and visual areas that process motion (bilateral middle temporal gyrus). A main effect for emotion was found primarily in occipital and parietal regions, indicating that emotion enhances visual perception. Surprisingly, emotion also activated the left precentral gyrus, a motor region. These results demonstrate that emotion elicits activity above and beyond that evoked by the perception of implied movement, but that the neural representations of these characteristics overlap.

Keywords: emotion, implied motion, functional MRI, MRI

Although emotions are typically associated with subjective feelings, they are actually complex physiological experiences that involve biological, cognitive, and motoric components (Ekman & Cordaro, 2011; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Scherer, 2005; Wager et al., 2015). A myriad of research has characterized these different systems; however, relatively few studies have examined how these processes interact on a neural level. Delineating the precise neural structures involved in emotional perception has proved challenging, partly because brain structures are seldom limited to isolated functions, as noted in several meta-analyses (Kober et al., 2008; Lindquist et al., 2012; Vytal & Hamann, 2010; Wager et al., 2015). Structures typically associated with emotion are also often implicated in movement. For example, the amygdala is often active in response to physiologically arousing stimuli—whether the emotional valence is positive or negative—and processes this information to coordinate an appropriate response (Cunningham & Brosch, 2012; Zald, 2003); directly stimulating the amygdala produces changes in the sympathetic nervous system that likely prepare the organism for action (Iwata, Chida, & LeDoux, 1987). Additional research has found increased amygdala activity in response to dynamic versus static stimuli independent of emotion, indicating that the amygdala may be more generally concerned with biologically relevant information than strictly with emotional behaviors (Grezes, Pichon, & de Gelder, 2007). The insula has been implicated in a wide variety of emotions (for various meta-analyses and reviews see Chang, Yarkoni, Khaw, & Sanfey, 2013; Kober et al., 2008; Lindquist et al., 2012; Vytal & Hamann, 2010; Wager et al., 2015), but is also active in interoceptive awareness (Craig, 2009), as well as situations requiring intentional action (for review see Brass & Haggard, 2010). Similarly, a number of neuroimaging meta-analyses have reported emotion-dependent activity in brain regions traditionally associated with movement, particularly within the supplementary motor area (SMA), basal ganglia, and midcingulate cortex (e.g., Kober et al., 2008; Kohn et al., 2014; Lindquist et al., 2012; Phan, Wager, Taylor, & Liberzon, 2002). These results provide converging evidence for the fact that emotions influence the activity of motoric regions of the brain.

Studies using transcranial magnetic stimulation (TMS) demonstrate that the emotional modulation of motoric regions extends to white-matter tracts exiting the brain as well. In an early study of this phenomenon, Oliveri et al. (2003) stimulated the SMA by applying alternating subthreshold and suprathreshold pulses using the same TMS coil (Kobayashi & Pascual-Leone, 2003). Once the SMA was stimulated, participants were shown emotional or neutral images to which they performed a simple motor task. Motor evoked potentials (MEP) were recorded from their hand muscles. The amplitude of the MEP indicates the strength of the signal sent from the SMA as this region sends signals to the primary motor cortex which relays the signal to the hand, instructing it to move

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(Oliveri et al., 2003). Because the SMA is stimulated by emotional images (via limbic input) and by TMS pulses, an increase in MEP amplitude for negative over neutral images suggests a role in emotional processing, as was observed. This study indicates that emotion sensitizes the corticospinal tract, thus priming the motor system in case an overt response was required (Oliveri et al., 2003). Similar results have been observed in numerous subsequent experiments using different types of emotional stimuli (Baumgartner, Willi, & Jancke, 2007; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Coombes et al., 2009; Hajcak et al., 2007; Schutter, Hofman, & Van Honk, 2008; van Loon, van den Wildenberg, van Stegeren, Hajcak, & Ridderinkhof, 2010).

Researchers have also noted emotion-movement interactions in neural structures outside of the brain. Using functional MRI of the spinal cord, Smith and Kornelsen (2011) found that viewing negative emotional images increased activity in motor and sensory nuclei in the cervical spinal cord. Subsequent research found that this modulation was quite specific; stimuli depicting upper-limb responses had a greater influence on the cervical spinal cord (which innervates the upper limbs) than did stimuli depicting lower-limb responses (McIver, Kornelsen, & Smith, 2013). These results are nicely complemented by a recent electromyography experiment. Videos of actors opening a door and then expressing angry or fearful body language were presented while activity was recorded from participants' biceps, triceps, deltoid, and trapezius muscles (Huis In 't Veld, Van Boxtel, & de Gelder, 2014). Participants first passively viewed the videos and then actively mimicked them while viewing them a second time. Viewing the angry actor produced activation in all four muscles in both active and passive conditions (Huis In 't Veld et al., 2014). Viewing the fearful actor produced activation in the triceps, deltoid, and trapezius muscles, but showed inhibition of the biceps. These results indicate that the emo-motoric response is quite specific, as different emotions are associated with different patterns of neural and muscular activity.

Although the studies reviewed above provide powerful demonstrations of the emotional modulation of motoric regions, they do come with a caveat: the preparatory motor responses to threat may be due to the emotion *or* to the motion implied in the stimuli. Many studies unintentionally confound these two variables; emotional stimuli typically consist of an action-oriented scene (e.g., one person attacking another) whereas neutral images are often relatively static in nature (e.g., one person talking to another). As a result, it is often difficult to separate the effects of perceived emotion and motion. In order to separate such effects, Borgomaneri, Gazzola, and Avenanti (2012) used TMS to compare the amplitude of MEPs arising during the perception of implied motion and emotion. Participants viewed images of actors portraying positive, negative, neutral, or static body postures. Positive, negative, and neutral images elicited greater MEP amplitudes than the static condition, indicating a main effect of implied motion (Borgomaneri, Gazzola, & Avenanti, 2012). However, no significant difference in motor activity was found between negative, positive, and neutral images, contradicting the notion that emotion modulates motoric responses. The researchers posited that much of the motor activity previously described is due to the mirror neuron system responding to implied motion, rather than to emotion.

Despite its far-reaching implications, there is an important limitation to the Borgomaneri et al. (2012) study. TMS is limited to the small network of structures being stimulated; it does not provide information about brain activity outside of this network of interest. Other neuroimaging techniques (e.g., fMRI) can measure activity from the entire brain and can more precisely delineate the networks of activity related to emotion, implied movement, and their interaction.

The present study used fMRI to examine the complex relationships between the perception of emotion and motion. To do so, we developed a stimulus set consisting of the following four stimulus types: (a) negative stimuli implying movement, (b) negative stimuli that do not imply movement, (c) neutral stimuli implying movement, and (d) neutral stimuli that do not imply movement. We expected that neural activation would be greater for negative over neutral (e.g., amygdala), and for motion implied over no motion implied conditions (e.g., premotor cortex, primary motor cortex, basal ganglia). We also predicted an interaction such that the greatest overall activity would be found for negative images implying motion.

Method

Participants

Eighteen participants between the ages of 18 and 30 were scanned (five males, 16 right-handed). Five data sets were removed due to technical difficulties ($n = 2$), motion artifacts (movement exceeding 2 mm, $n = 1$), concussion history (reported after scanning, $n = 1$), and self-reported discomfort and distraction during participation ($n = 1$). Analysis was conducted with 13 data sets (five males, 12 right-handed). Although the small sample size is a limitation of our study, the block design contributes to the power required to produce statistically significant results with correction for multiple comparisons. Ethical approval was obtained from the University of Manitoba's Bannatyne Human Research Ethics Board and the University of Winnipeg's Human Research Ethics Board. Prior to scanning, participants gave written informed consent and completed MR safety screening. Participants received $25 for their time.

Stimulus Materials

Stimuli consisted of 240 images, divided into four conditions: (a) negative images implying movement, (b) negative images not implying movement, (c) neutral images implying movement, and (d) neutral images not implying movement (see Figure 1). Motion implied images included humans performing actions using their upper limbs. Images without implied motion were paired with similar objects at similar angles (see Figure 1). The images were obtained from the International Affective Picture System (IAPS), public image searches, and staged photographs. Images were pilot tested on a separate group of 30 students. These participants rated the images on a 7-point scale for arousal, valence, and implied motion; high scores indicated high arousal, strong negative emotion, and high implied motion. The 45 images that best matched each condition were used in the fMRI experiment (see Table 1). Images were fitted to 320 × 240 pixels and were presented centrally on a white background. During the study, all stimuli were projected into the magnet bore and were reflected onto a mirror attached to the head coil.

Figure 1. Examples of stimuli used in the fMRI procedure. Clockwise from upper left: (negative, no implied motion); (neutral, no implied motion); (neutral, implied motion); (negative, implied motion).

Experimental Design

Each scanning session began with the acquisition of a high-resolution anatomical brain scan on which to overlay the functional runs. Following this, participants completed four functional runs, each lasting 340 s. Only one type of image (e.g., negative images implying movement) was presented within a single run. Each run followed a boxcar design in which three 60-s blocks of images were interleaved by 40-s rest periods (containing a black fixation cross on a white screen; see Figure 2). Each 60-s block contained 15 images, each shown for 4 s. Stimuli were presented in counterbalanced runs, but negative stimuli always followed neutral stimuli (and vice versa) to reduce repetition suppression (i.e., decreased responding over time to similar stimuli). Thus, both ABAB and BABA schemes were used.

fMRI Scanning Parameters

Scanning was conducted using a 3-Tesla Siemens scanner at the Winnipeg Regional Health Authority MRI Clinic. T1-weighted

Table 1
Mean (±SD) Ratings (1–7) for Valence, Arousal, and Implied Motion Across Four Image Conditions: (a) Negative Stimuli Implying Movement, (b) Negative Stimuli not Implying Movement, (c) Neutral Stimuli Implying Movement, and (d) Neutral Stimuli not Implying Movement

Image type	Arousal	Emotion	Implied motion
Negative, implied motion	4.90 (.67)	5.89 (.62)	4.61 (.60)
Negative, no implied motion	4.20 (.72)	5.81 (.62)	2.95 (.54)
Neutral, implied motion	3.28 (.58)	3.15 (.71)	4.56 (.73)
Neutral, no implied motion	3.11 (.52)	3.20 (.80)	2.61 (.90)

Note. High arousal, strong negative emotion, and high implied motion are indicated by high values.

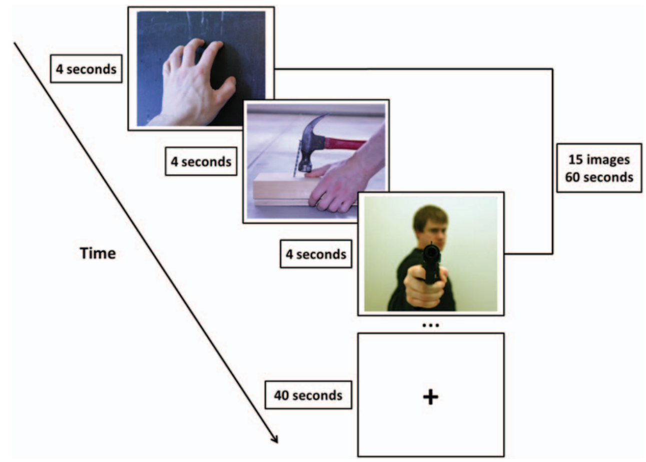

Figure 2. A sample 60-s block, consisting of 15 images, each presented for 4 s. Each run consisted of three 60-s blocks, each followed by a fixation cross for 40 s. Each run displayed one condition (e.g., negative, implied motion).

(MP-RAGE) images were collected, consisting of 176 slices. The following scanning parameters were used: TE = 16 ms, TR = 1,900 ms per volume, with 256 mm × 256 mm resolution and 0 mm between slices. The original voxel size was 1.000 mm × 0.977 mm × 0.977 mm.

The four fMRI runs each consisted of 111 volumes (340 s). The volumes consisted of 40 slices each and were sampled transversely using a conventional whole brain echo-planar imaging sequence with the following parameters: TE = 75 ms, TR = 3,000 ms per volume, 3.75 mm × 3.75 mm resolution, slice thickness = 3 mm, and field of view (FOV) = 240 mm × 240 mm.

fMRI Processing

Data were preprocessed and analyzed using BrainVoyager QX 2.8.4 (Brain Innovation, Inc., Maastricht, the Netherlands). Anatomical scans were automatically iso-voxelized to 1 mm^3 and transformed to Talairach space. Brains were normalized manually if the program failed to find the ACPC plane, or any of the other bounding parameters. Functional data were corrected for three-dimensional (3D) motion (trilinear/sync interpolation), slice scan time, and temporal filtering before being coregistered and linked to the corresponding Talairach brains. To ensure that participant movement did not significantly differ across stimulus conditions, the log files produced from the 3D motion correction were analyzed in six one-way ANOVAs (one per direction; SPSS 19.0; IBM Corp., Armonk, NY) after obtaining the root-mean-square of the movement parameters in each of the three translations and three rotations per subject. The four stimulus conditions did not significantly differ in terms of participant motion in any of the three translations or three rotations (translations x: $F(3, 48) = 0.013$, $p = .998$; y: $F(3, 48) = 0.043$, $p = .988$; z: $F(3, 48) = 0.743$, $p = .532$; rotations x: $F(3, 48) = 0.257$, $p = .856$; rotations y: $F(3, 48) = 0.535$, $p = .661$; rotations z: $F(3, 48) = 0.166$, $p = .918$).

After the preprocessing was complete, a single-study general linear model (GLM) was conducted on each fMRI run. Each subject was then grouped into a multiple-study GLM using % transformation and single subject predictors. The grouped data were then overlaid onto a Talairach brain and a 2 × 2 random-effects ANCOVA was performed. Main effects, interaction effects, and four contrasts of interest ([negative, implied motion > negative, no implied motion]; [negative, implied motion > neutral, implied motion]; [negative, no implied motion > neutral, no implied motion]; and [neutral, implied motion > neutral, no implied motion]) were performed using a cluster threshold of 20 voxels. The main effects and interaction used $p = .045$ while the contrasts used $p = .040$ (both p values false discovery rate (FDR) corrected for multiple comparisons). Clusters were converted to volumes-of-interest which yielded Talairach coordinates for the peak voxels, probability values, and number of voxels active. Talairach-daemon software (http://www.talairach.org/daemon.html) identified the anatomical structures associated with each set of Talairach coordinates.

Results

As expected based on Borgomaneri et al. (2012) study, the main effect of implied motion was significant (Figure 3a). Images implying motion produced greater neural activity than those not implying motion. Activity was seen bilaterally in the middle temporal gyrus, the insula, the cingulate gyrus, and visual areas (right lingual gyrus, left inferior occipital gyrus; Table 2). Additional activity was observed in the right hemisphere in the superior temporal, angular, and parahippocampal gyri, and in the left fusiform gyrus.

In contrast to Borgomaneri et al. (2012), a main effect was observed for emotion (Figure 3b). Greater activity for negative versus neutral images was observed in bilateral visual regions (peaking in right cuneus and left middle occipital gyrus; see Table 2). Activity was also detected in the right inferior and right subgyral parietal lobe, as well as left lateralized activation in the precentral, cingulate, and parahippocampal gyri.

The interaction between emotion and implied motion was also significant (Figure 3c). Considerably fewer clusters were observed than for either main effect. These clusters were observed in the right inferior parietal lobe, the right precentral gyrus, and the left culmen, an anterior region of the cerebellar vermis (see Table 2). Based on the percent signal change values (see Figure 4), precentral gyrus regions responded more to negative motion implied, and

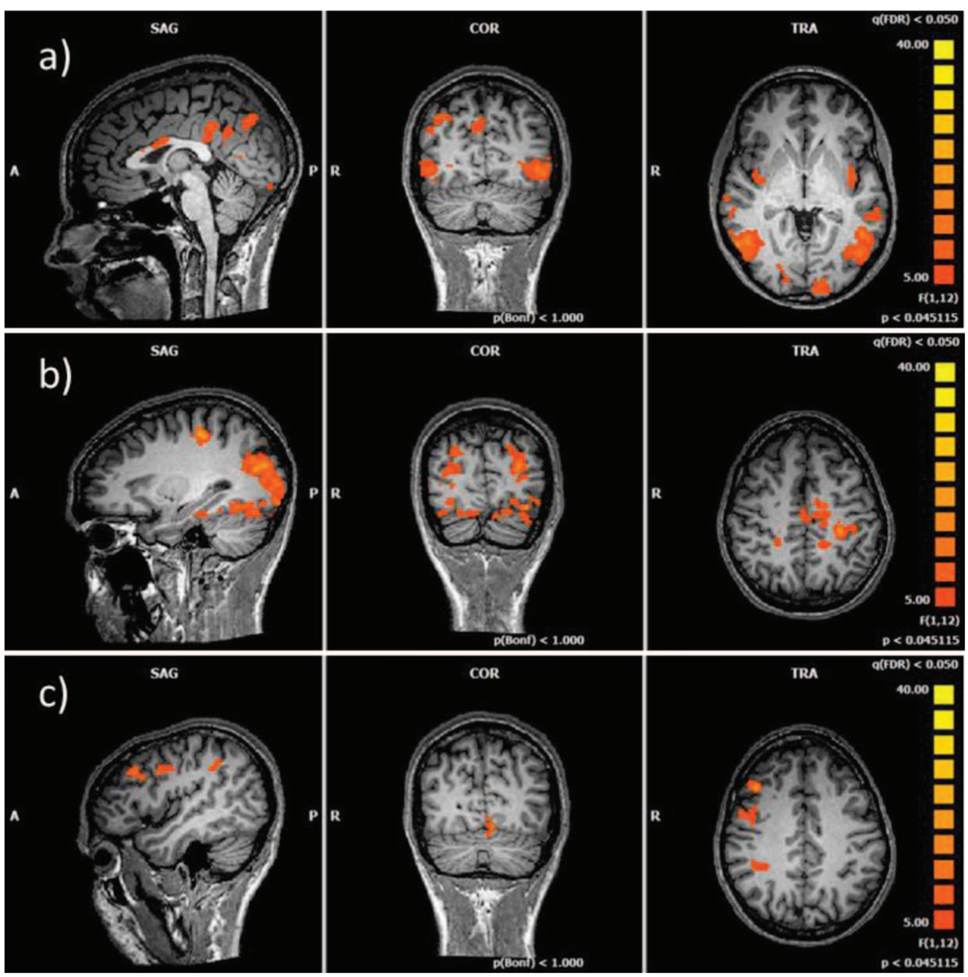

Figure 3. Random effects ANCOVA superimposed on a Talairach brain using a cluster threshold of 20 voxels ($N = 13$) displaying (a) main effect of implied motion, (b) main effect of emotion, and (c) interaction between emotion and implied motion.

Table 2
Talairach Coordinates for Peak Voxels for Main and Interaction Effects Using a Cluster Threshold of 20 Voxels and a p-Value of .045

Region	x	y	z	*p*-value	Voxels	BA
Main effect of implied motion						
Right middle temporal gyrus	54	−34	−5	.000405	1,018	21
Right superior temporal gyrus	60	−34	19	.001704	1,192	42
Right middle temporal gyrus	55	−58	4	.000001	6,727	37
Right angular gyrus	45	−61	34	.000075	2,556	39
Right insula	39	−1	−2	.001209	606	13
Right lingual gyrus	9	−88	−14	.000106	2,963	18
Right parahippocampal gyrus	24	−43	−8	.000146	1,406	36
Right posterior cingulate	6	−31	25	.000716	6,427	23
Left cingulate gyrus	−6	2	25	.000267	1,916	24
Left cingulate gyrus	−9	17	16	.005930	558	
Left inferior occipital gyrus	−9	−91	−5	.000414	2,571	17
Left fusiform gyrus	−27	−37	−14	.004929	623	37
Left middle temporal gyrus	−54	−59	4	.000093	5,073	37
Left insula	−39	−1	4	.000359	1,179	13
Left middle temporal gyrus	−54	−31	−5	.002260	715	21
Main effect of emotion						
Right inferior parietal lobule	48	−34	25	.001078	576	40
Right cuneus	18	−94	4	.000106	12,669	17
Right cuneus	18	−83	34	.002273	1,511	19
Right subgyral parietal lobe	24	−40	49	.000989	699	40
Left medial frontal gyrus	−15	−10	46	.000628	1,620	6
Left middle occipital gyrus	−30	−82	22	.000100	14,286	19
Left cingulate gyrus	−12	−40	37	.002238	828	31
Left parahippocampal gyrus	−33	−31	−11	.002805	570	36
Left precentral gyrus	−27	−28	46	.000156	1,341	4
Left middle occipital gyrus	−48	−64	−8	.000346	963	37
Interaction						
Right inferior parietal lobule	36	−46	46	.002222	740	40
Right precentral gyrus	42	5	34	.001191	619	9
Right precentral gyrus	39	23	37	.000159	667	9
Left culmen	−6	−67	−8	.000361	664	

Note. BA = Brodmann Area; $N = 13$.

negative no motion implied conditions. The small effects of the neutral no motion implied condition are likely the driving factor for the interaction.

Both contrasts for emotion (negative > neutral) were significant, indicating that emotion is significant above and beyond implied motion (Figure 5a–b). The contrast for negative, implied motion > neutral, implied motion produced activity in the right middle temporal gyrus, bilateral occipital gyrus, and left culmen and fusiform areas (see Table 3). Similarly, the contrast for negative, no implied motion > neutral, no implied motion yielded bilateral activity in the culmen and middle occipital gyrus (see Table 3). This contrast also produced activity in the right precentral gyrus and left fusiform gyrus (see Table 3).

The two contrasts for implied motion (implied motion > no implied motion) were also significant, indicating that implied motion elicits activity independent of emotion (Figure 5c–d). The contrast for neutral, implied motion > neutral, no implied motion produced activation in the bilateral temporal lobes and in the right precentral gyrus (see Table 3). The contrast for negative, implied motion > negative, no implied motion yielded activity only in bilateral temporal gyri (see Table 3). The implications of these patterns of activity, including how they inform the relationship between emotion and implied motion, are discussed below.

Discussion

The primary goal of the current research was to determine whether implied movement could account for the observed effects of emotion on brain activity, or whether emotion elicited unique neural responses beyond those generated by the perception of implied motion. A recent TMS experiment examining this issue found a main effect of implied motion, but not emotion (Borgomaneri et al., 2012). Although these researchers did *not* claim that their results negated neuroimaging research, their astute observation that implied motion was present in many emotional, but not neutral, stimulus sets is worth noting. This potential confound was accounted for in the current experiment, thus allowing us to use fMRI to examine the relationship between emotion and implied movement.

Main Effect of Implied Motion

The main effect of implied motion produced bilateral activity in the insula and in two bilateral pairs of clusters in the middle temporal gyrus. Each paired region had almost identical peak voxel coordinates (see Table 2). The middle temporal gyrus is commonly known to process visual motion (Tootell et al., 1995), which is an interesting finding as motion was only implied via static images. However, previous research has found activation in the middle temporal gyrus for implied motion in abstract paintings (Kim & Blake, 2007). The superior temporal gyrus was also active and has been implicated in biological motion perception (Saygin, 2007).

A few clusters within the cingulate gyrus were active, with more active voxels in the posterior region (see Table 2). Yamasaki, LaBar, and McCarthy (2002) found that the posterior cingulate responds primarily to attentional tasks. It is possible that different conditions (i.e., implied motion) garnered more attention, thus explaining the different cingulate activity between emotion and implied motion conditions; however, behavioral data are needed to substantiate this hypothesis.

Activity was also detected within some regions associated with more general visual processing, specifically the left inferior occipital gyrus and the right lingual gyrus. The results of an early positron emission tomography (PET) study suggest that this activity may be related to making judgments about human movements (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000). In this study, participants viewed images of comic strips and were asked to judge the characters' intentions, to make physical judgments about characters (which required knowledge of the character's movement, weight, size, etc.), or to make physical judgments of objects (which required knowledge of an object's movement, weight, size, etc.). The contrast of the physical judgments of characters and the physical judgments of objects showed activity in the lingual gyrus, with greater activity in the right hemisphere. Thus, activity in the lingual gyrus was elicited by images depicting human physical characteristics and movement. This result may explain the lingual gyrus activity observed in the current study. The parahippocampal area was also active and is involved in encoding new information about places (Epstein, Harris, Stanley, & Kanwisher, 1999); the observed activity in the current study therefore likely reflects the encoding of information about the scene in which the motion was taking place.

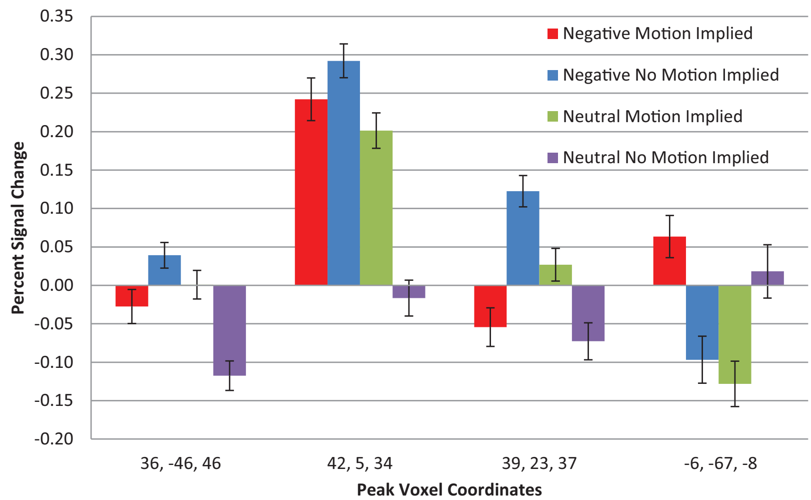

Figure 4. Average percent signal change for the inferior parietal lobule (x, y, z = 36, −46, 46), the precentral gyrus clusters (x, y, z = 42, 5, 34; x, y, z = 39, 23, 37), and the left culmen (x, y, z = −6, −67, −8) in the interaction for all four conditions (negative implied motion, neutral implied motion, negative no motion implied, and neutral no motion implied, ±*SE*).

The main effect of implied motion indicates that various regions were recruited for integrating different senses. Activity was observed in the posterior insula (Figure 3a); a recent meta-analysis indicates that the posterior insula is important for merging sensory information from different modalities, as well as extero- and interoceptive processing (Chang et al., 2013; Craig, 2009). The left fusiform gyrus has been implicated in integrating visual, auditory, and tactile information of objects (Kassuba et al., 2011). Additionally, the angular gyrus appears to have a role in multimodal integration (for review see Seghier, 2013).

In sum, the main effect of implied motion appears to be centered on processing visual motion, as well as integrating information from different modalities. However, it should be noted that some activation presently observed has previously been encountered in emotion research, such as the insula and the cingulate gyrus (Chang et al., 2013; Yamasaki et al., 2002).

Main Effect of Emotion

A subset of the activity associated with the main effect of emotion overlapped with that observed for the main effect of implied motion. For example, the left cingulate gyrus was active, as was the parahippocampal gyrus, albeit in the left, rather than the right, hemisphere (see Table 2). The left medial frontal gyrus was also activated, although the cluster appeared to be mostly contained within the cingulate gyrus (Figure 3b).

We observed a large volume of activity that is commonly elicited during the visual perception of emotion. Specifically, we noted a high level of bilateral visual activity, peaking in the right cuneus and left middle occipital gyrus (Brodmann Areas [BA] 17 and 19). These regions are basic visual processing areas (DeYoe et al., 1996). Another cluster of significant activity was observed in the left middle occipital gyrus, peaking in BA 37. The junction between BA 19 and BA 37, the middle temporal area, is typically responsible for processing visual motion (Zeki et al., 1991). The right inferior parietal lobe—which belongs to the dorsal visual stream—was also significantly active. The dorsal visual stream, often conceptualized as the "where pathway," is primarily concerned with where objects are in space and with directing actions toward them (Goodale & Milner, 1992). The increased activity in these visual regions suggests a greater level of visual processing for the negative images, a pattern noted in several previous studies (e.g., Bekhtereva, Craddock, & Muller, 2015; Morris et al., 1998; Phelps, Ling, & Carrasco, 2006; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Surguladze et al., 2003). The fact that the dorsal pathway also showed emotion-dependent activity suggests that negative images may modulate activity in regions related to visually guided movements, possibly including defensive responses.

Significant responses were also detected in the right precentral gyrus which, in monkeys, includes a zone for tactile stimulation (Cooke & Graziano, 2004). Electrical stimulation of this region results in defensive behavior of the hands and arms. An analogous region exists in the human premotor cortex (Bremmer et al., 2001). The middle frontal gyrus, including portions of the premotor cortex (BA 6) was also active. When taken together, the visuomotor activity observed in the negative valence fMRI runs suggests that negative stimuli elicit a preparatory defensive response (e.g., shielding the face).

Interaction

The interaction between emotion and implied movement was also significant, with little effect from the neutral, no motion implied condition (see Figure 4). The observed interaction makes sense from a survival perspective. Negative moving stimuli (e.g., a man pointing a gun) are more immediately hazardous than less emotional moving stimuli (e.g., a man throwing a Frisbee), or static negative stimuli (e.g., rotten food).

Activation was observed in the right inferior parietal lobe, as well as in two clusters in the right precentral gyrus (Figure 3c), as seen for the main effect of emotion. Interestingly, the peak coor-

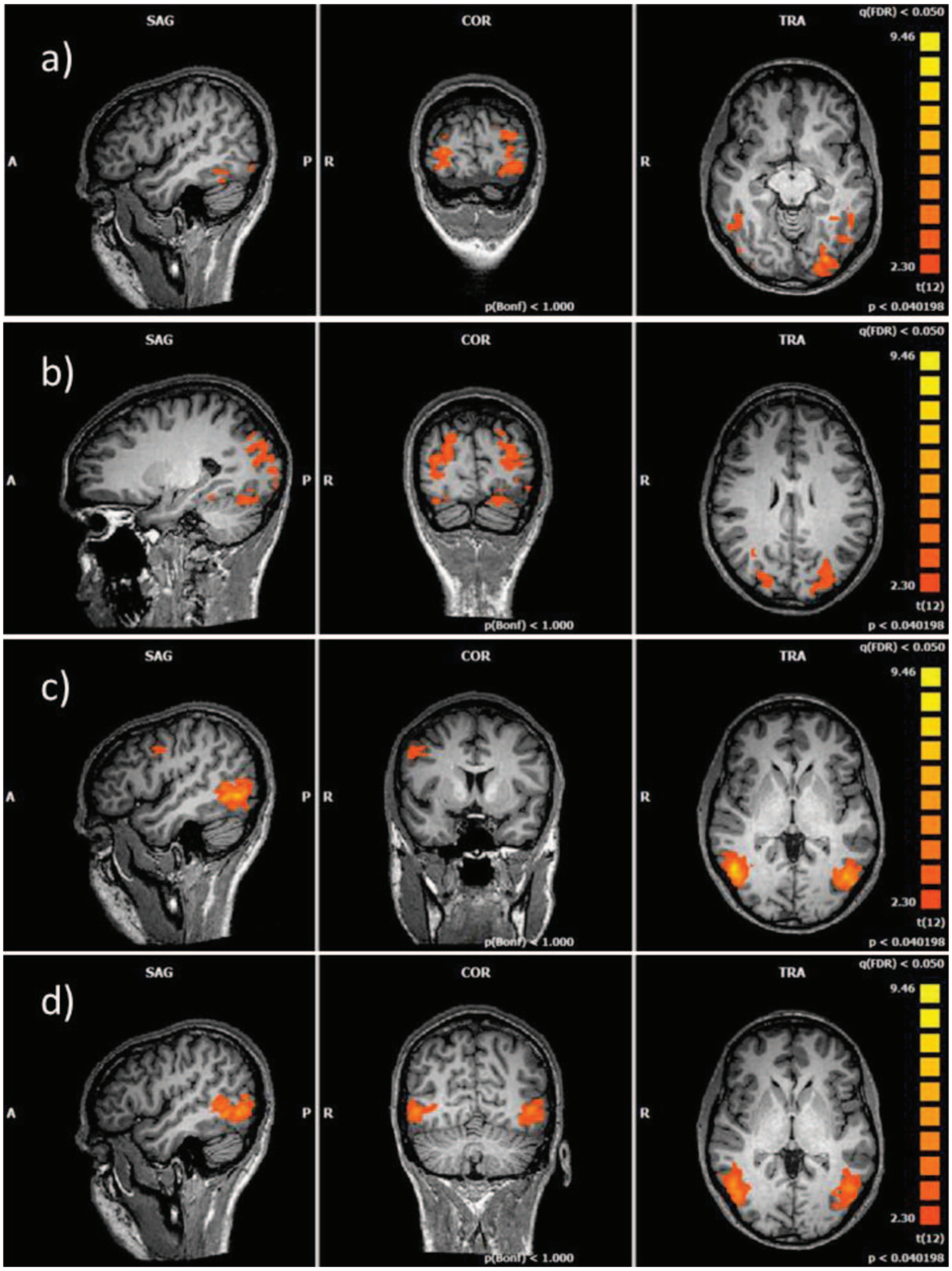

Figure 5. Random effects ANCOVA superimposed on a Talairach brain using a cluster threshold of 20 voxels ($N = 13$) displaying (a) negative implied motion > neutral implied motion, (b) negative no implied motion > neutral no implied motion, (c) neutral implied motion > neutral no implied motion, and (d) negative implied motion > negative no implied motion.

dinates in the present study (x, y, z = 42, 5, 34) are fairly similar to those observed for an interaction between dynamic and static fear condition in a study by Grèzes, Pichon, and de Gelder (2007) (x, y, z = 53, 5, 39, converted from Montreal Neurological Institute [MNI] coordinates).

The culmen, a region in the anterior vermis of the cerebellum, was also active. Culmen infarcts often produce ataxia in the patient's limbs and in 30% of cases studied caused ipsilateral lateropulsion (involuntary movement) without vertigo, an uncommon finding for infarcts in other cerebellar regions (Ye et al., 2010). Thus, the culmen likely has an important role in voluntary movement. However, damage to the vermis can be associated with the flat affect seen in cerebellar cognitive affective syndrome, and may play a role in emotional regulation as well (Schmahmann & Sherman, 1998). Given these diverse functions, it is plausible that this structure is involved in emotion-movement interactions.

However, one caveat associated with the current results is that the motion implied images contained human bodies while the no

Table 3
Talairach Coordinates for Peak Voxels for: (Negative Implied Motion > Neutral Implied Motion), (Negative No Implied Motion > Neutral No Implied Motion), (Neutral Implied Motion > Neutral No Implied Motion), and (Negative Implied Motion > Negative No Implied Motion) Contrasts

Region	x	y	z	*p*-value	Voxels	BA
Negative, Implied Motion > Neutral, Implied Motion						
Right middle temporal gyrus	55	−52	−11	.001599	604	37
Right middle occipital gyrus	27	−85	7	.000049	2,429	19
Left middle occipital gyrus	−27	−79	−8	.000001	7,247	18
Left culmen	−33	−52	−14	.000044	2,462	
Negative, No Implied Motion > Neutral, No Implied Motion						
Right culmen	21	−43	−11	.000042	4,789	
Right precentral gyrus	42	5	34	.000528	868	9
Right middle occipital gyrus	24	−85	13	.000011	11,088	18
Left middle occipital gyrus	−30	−70	13	.000014	10,832	19
Left culmen	−33	−46	−17	.000506	601	
Left fusiform gyrus	−48	−55	−14	.000074	743	37
Neutral Implied Motion > Neutral No Implied Motion						
Right inferior temporal gyrus	45	−64	1	.000000	7,202	37
Right precentral gyrus	51	2	37	.003151	697	6
Left middle temporal gyrus	−42	−64	1	.000001	7,672	37
Negative Implied Motion > Negative No Implied Motion						
Right inferior temporal gyrus	45	−61	1	.000006	6,326	37
Left middle temporal gyrus	−42	−67	7	.000012	6,621	37

Note. A cluster threshold of 20 voxels and a *p*-value of .040 (corrected for multiple comparisons) were used. Beta values and their standard error (*SE*) were included for each cluster (BA = Brodmann Area; $N = 13$).

motion implied images did not. Although this difference was present for both negative and neutral images, it is theoretically possible that it influenced one type of stimulus more than the other. Thus, a limitation to this study is that brain regions involved in, for example, motor responses may be more active for the perception of images that imply movement simply because they contain human hands compared to those that do not (i.e., contrasts for implied motion). Future research can further tease apart the unique contributions of emotion, implied motion, and the presence of human bodies using parametric analyses.

Emotion Contrasts

The majority of the activity for emotion, either when motion was or was not implied, was related to an increased visual response (Table 3; Figure 5a–b). Both contrasts also produced substantial culmen activation, which makes sense in light of its apparent role in cerebellar cognitive affective syndrome (Schmahmann & Sherman, 1998). Interestingly, activation was not observed in "emotional regions," such as the amygdala. A possible explanation for this absence is that the amygdalae respond rapidly, but habituate quickly (Breiter et al., 1996). It is possible that amygdalar activity occurring in response to the initial stimuli in each block habituated and was not detected as part of the block-level analyses.

Motion Contrasts

The contrast comparing implied motion to no motion implied for neutral stimuli produced significant activity in the bilateral temporal gyrus, as seen for the main effect of motion. The right precentral gyrus was also activated, with a pattern of activity similar to that already discussed with regard to the interaction analysis. The contrast comparing implied motion to no motion implied for negatively valenced stimuli produced bilateral activation in the temporal gyrus (Table 3; Figure 5d). These results seem to support the general findings already presented: Implied motion activates regions necessary for multimodal integration while emotion enhances visual processing.

Conclusion

The current results highlight the functional overlap between neural structures associated with emotional and motoric processing. Some regions historically considered emotional (e.g., insula, cingulate) were significantly active for the main effect of implied motion while some regions traditionally associated with motion (e.g., precentral gyrus) were active for the main effect of emotion. However, the main effects from the current study also suggest that implied motion and emotion elicit unique patterns of activity. The data indicate that generally, emotional stimuli lead to enhanced visual processing while stimuli implying motion produce more activation in regions related to multimodal integration. Together, these data suggest that although emotion and implied motion recruit overlapping networks, emotion does elicit activity above and beyond that generated by implied movement. The current results also demonstrate the importance of controlling for implied movement when conducting studies investigating the neural substrates of emotion.

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