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ARTICLE

Generating facial expressions of disgust activates neurons in the thoracic spinal cord: a spinal fMRI study

Stephen D. Smith[a], Jennifer Kornelsen[b] and Theresa A. McIver[c]

[a]Department of Psychology, University of Winnipeg, Winnipeg, Manitoba, Canada; [b]Department of Radiology, St Boniface Hospital MRI Centre, Winnipeg, Manitoba, Canada; [c]Department of Psychology, Queen's University, Kingston, Ontario, Canada

ABSTRACT
Facial expressions of disgust, which involve movement of the levator labii muscles on the nose, allow an organism to restrict the intake of potentially aversive stimuli by constricting the air cavities in the nostrils and reducing the speed of air intake. In the current research, we used fMRI of the thoracic spinal cord to measure neural activity related to (1) the contraction of the intercostal muscles that modulate the velocity of air intake and (2) the sensory feedback associated with this contraction. Thirteen participants completed two spinal fMRI runs in which the thoracic segments of the spinal cord were measured. Each five-minute 40-second run consisted of three 60-second blocks in which participants repeatedly generated a disgusted facial expression or a non-emotional expression consisting of repeated stretching of the lips (which did not involve the nasal cavity). Forty-second rest blocks were interleaved between each expression block. The results demonstrated that generating emotional expressions of disgust produces significantly more activity than producing non-emotional facial expressions. This activity occurred in both ventral (motoric) and dorsal (sensory) regions of the upper segments of the thoracic spinal cord and demonstrates a link between the generation of facial expressions and embodied emotional responses.

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Spinal cord; embodied emotion; facial expressions; disgust; spinal fMRI

Although facial expressions are used to communicate an individual's current affective state, recent research indicates that these expressions also serve to biomechanically regulate the intake of sensory information. For example, facial expressions of disgust involve a decrease in eye aperture and a wrinkling of the nose that restricts air intake (Susskind et al., 2008). These biomechanical changes decrease the quantity of sensory information being taken in, possibly limiting the intake of contaminants and leading to sensory rejection. This functional account of emotion puts facial expressions into an evolutionary context in which emotion-related changes in the geometry of facial musculature are not random, but instead serve a survival-related role. Susskind and colleagues (2008) also noted that disgusted expressions are linked to a decrease in the air velocity in the nasal passages. These changes in the speed of inhalation and exhalation are performed by the intercostal muscles surrounding the lungs; these muscles are innervated by the thoracic spinal cord (Ratnovsky, Elad, & Halpern, 2008). In the current research, we used fMRI of the thoracic spinal cord to measure neural activity related to this muscle constriction, thus providing a neural link between the previously observed facial-expression-dependent changes in the velocity of air intake and the musculature that modulates it.

Recent studies of emotion-dependent activity in the spinal cord suggest that an examination of this structure's role in embodied responses would provide novel insight into emotional behaviors. Although the spinal cord is often thought of as a relatively simple neural structure, its physiology and relevance to emotional experiences are actually quite nuanced. The spinal cord consists of four regions—cervical, thoracic, lumbar, and sacral. Each region consists of a number of different segments (e.g., the thoracic cord consists of 12 segments) that project to and receive sensory information from different areas of the body. Additionally, each segment consists of ventral and dorsal aspects, which are involved with motoric and sensory activity, respectively. Functional magnetic resonance imaging (fMRI) scanning sequences allow researchers to detect activity in spinal cord neurons in the same way that brain activity is measured (Stroman, 2005; Stroman et al., 2014). Indeed, spinal fMRI has been used to detect emotion-dependent activity in the cervical

CONTACT Stephen D. Smith s.smith@uwinnipeg.ca Department of Psychology, University of Winnipeg, 515 Portage Avenue, Winnipeg, Manitoba, R3B 2E9 Canada

(McIver, Kornelsen, & Smith, 2013; Smith & Kornelsen, 2011) and thoracic (Kornelsen, Smith, & McIver, 2015) regions of the spinal cord. This technique is ideal for addressing the question of embodiment, as it allows researchers to link activity in individual spinal cord segments to both motoric behaviors and somatosensory feedback in precise regions of the body.

In the current research, spinal fMRI was used to examine the relationship between the generation of facial expressions and embodiment. For this initial proof-of-principle study, we focused on the emotion disgust. The proposed evolutionary function of disgust —the rejection of aversive chemosensory stimuli that could affect the respiratory and gustatory systems— implies a strong link between the emotional expression and bodily responses such as the tightening of chest and stomach muscles. Contraction of muscles in these regions should lead to increased activity in both motoric and sensory nuclei in the upper segments of the thoracic spinal cord (segments T1-T5), which innervates musculature from the middle of the chest to the abdomen.

Methods

Participants

Thirteen healthy, right-handed undergraduate university students (eight female, age range = 18–26, mean age 21.2 years) participated in this study in exchange for a $25 honorarium. All participants underwent MR safety screening prior to scanning. This experiment received ethics approval from the National Research Council and the University of Winnipeg Human Research Ethics Boards. All participants provided informed, written consent prior to beginning the study.

Facial expression training

Participants received instructions on the generation of disgusted and non-emotional facial expressions prior to entering the scanner. When modeling their disgusted expression for the experimenters, participants were reminded to wrinkle their nose (i.e., levator labii muscles), move their eyebrows closer together, and raise their upper lip. The non-emotional facial expression involved participants stretching their lips horizontally and raising their eyebrows slightly. Such an expression produced a similar amount of facial movement as a disgusted expression, but did not involve the levator labii muscles. Importantly, none of the participants indicated that this expression produced any emotional response or physical discomfort.

Experimental design

Participants completed two separate neuroimaging runs, each lasting 340 s. Each run consisted of a blocked design in which one-minute blocks of facial expressions (i.e., disgust or neutral) were interleaved by 40-second rest blocks. A blocked design was used to maximize signal detection and is commonly used in spinal fMRI studies (e.g., Kornelsen et al., 2015). The same facial expression was performed during all three blocks of a given fMRI run. During each stimulus block, participants were asked to produce the facial expression by a written prompt—"Disgust" or "Stretch Your Lips"—that appeared every five seconds. Participants were allowed to relax their face following each response.

MR methodology

The experiments were conducted with a 3.0-Tesla Siemens Magnetom Trio MR system with a standard Siemens RF body coil used for excitation and a Siemens Spine Matrix used for reception. Spinal fMRI was performed using a single-shot fast spin-echo sequence with partial Fourier sampling (HASTE) to acquire seven 2-mm-thick contiguous sagittal slices with the following acquisition parameters: TR = 1000 msec per slice; TE = 38 msec; flip angle = 125°; 195 Hz/pixel bandwidth; 128 X 90 matrix size; echo spacing = 9.68 msec; field of view (FOV) = 200 X 100 mm; and FOV phase encode = 50%. Slices were centered rostrocaudally on the T5 vertebra and spanned all 12 thoracic spinal cord segments. Spatial saturation pulses were applied to reduce motion artifacts arising from regions anterior to the spine and to reduce aliasing caused by signals from areas outside of the FOV.

The functional imaging parameters of the current study were identical to those used in our previous examinations of the thoracic spinal cord (Kornelsen et al., 2013, 2015). The advantages of the imaging parameters employed in our previous, and current, examinations of the spinal cord include a single-shot fast spin-echo method that produce images free of the magnetic field inhomogeneity distortions that gradient-echo methods suffer, and sagittal slice acquisition that allows for a greater rostrocaudal span of the spinal cord to be imaged, with reduced aliasing, albeit at the cost of the higher in-plane resolution of images acquired axially. Although a previous study suggests that an echo time of 75 ms provides an optimal contrast-to-noise ratio, our research employs a more moderate echo time of 38 ms in an effort to facilitate comparison with our previously published research on the role of the spinal cord in emotion processing (Kornelsen et al., 2015). Our previous spinal fMRI studies of the thoracic spinal cord, which employ an echo time of 38 ms, demonstrated sufficient sensitivity and contrast. Echo times in the range of 30–40 ms are commonly employed and allow for a combination of BOLD and SEEP contrast to be detected (Figley, Leitch, & Stroman, 2010; Stroman et al., 2014).

Data analysis

Data were preprocessed and analyzed with custom-written scripts using MatLab software (Mathworks, Inc., Natick, MA). Data from two participants were removed because of movement of the spinal cord out of the FOV. Each spinal fMRI data series was realigned using a raw data image to define the location and curvature of the spine (Stroman, 2006). The C7/T1 and T8/T9 intervertebral disks were marked in the sagittal plane. Reference lines were then manually drawn along the anterior, posterior, left, and right edges of the cord. The data at each time point were combined into a three-dimensional volume and linearly interpolated to 0.5 mm cubic voxels. The volume was resliced transverse to the manually drawn reference line. The reference lines were used to realign the slice data to correct for motion between time points and to apply spatial smoothing in the rostro-caudal direction.

Each series was analyzed using the general linear model (see Stroman, 2006). The basis set was generated for the block paradigm described above, with 40 s rest periods presented before and after 60 s blocks of facial expression generation. The analyzed individual results were then spatially normalized by reslicing the spinal cord every 1 mm along the length of the reference lines between C7/T1 and T8/T9 discs and by scaling to a 140 mm length and fine-tuning the alignment in each transverse slice. Random effects analyses were conducted to produce activity maps of the significantly activated voxels for each condition (t-threshold = 3.5, df = 10, $p = 0.0029$). The number of active voxels was tabulated for both spinal fMRI runs for all participants, thus allowing us to compare activity detected in the two conditions. T-tests of the voxel counts for each condition for our particular spinal cord segments of interest (T1-T5) and for a more exploratory analysis of the remaining thoracic spinal cord segments were calculated. The average percent signal change from baseline was calculated for each data series with the baseline being the mean intensity during the 40-second rest blocks; this value was then averaged for both conditions.

Results

Consistent with our hypothesis, generating emotional expressions of disgust produced significantly more activity than generating non-emotional facial expressions in the upper five segments of the thoracic spinal cord (29 vs. 0 active voxels; $p = 0.031$, two-tailed). As shown in Figure 1, disgust-related activity was particularly prominent in segment T4 (11 active voxels). Generating disgusted expressions elicited activity in both motoric and sensory nuclei. Ventral (motoric) activity was detected in segments T1 (right) and T2 (bilateral). The majority of the dorsal (sensory) activity (24 active voxels) was detected in segments T2 (left), T3 (bilateral), T4 (bilateral), and T5 (bilateral). These data indicate that generating disgusted expressions produces motoric responses in spinal cord segments related to chest muscles and extensive sensory feedback from muscles throughout the chest and abdomen.

An exploratory analysis was also performed to examine activity occurring outside our region of interest (i.e., segments T6-T12). This analysis showed no differences between the disgust and non-emotional conditions (9 and 8 active voxels, respectively). This result supports our claim that producing disgusted expressions selectively activates *upper* thoracic spinal cord segments related to the constriction of muscles in the upper chest.

As in our previous studies of the thoracic spinal cord, the average percent signal change did not differ significantly between conditions ($p = 0.70$, two-tailed). The average signal change from baseline was 4.94% for the disgust condition and 5.16% for the neutral condition. Such values are consistent with previously reported spinal fMRI signal change values (Lawrence, Kornelsen, & Stroman, 2011; Stroman, 2005).

Discussion

The results of the current study complement earlier research by Susskind et al. (2008) demonstrating that disgusted faces reduce the intake of sensory information. In that study, producing a disgusted expression was associated with decreased eye aperture, nasal cavity volume, and inhalation velocity. Our results demonstrated that forming a disgusted expression elicited increased activity in segments of the thoracic spinal cord that innervate the chest muscles associated with inhalation and exhalation; this provides a neural mechanism for the previously observed change in the velocity of air intake (Ratnovsky et al., 2008). The contraction of these muscles could help to restrict air intake as well as the ingestion of potential toxins, suggesting that the embodied response serves an important survival function.

It is important to note that thoracic spinal cord activity was elicited by simply moving facial muscles

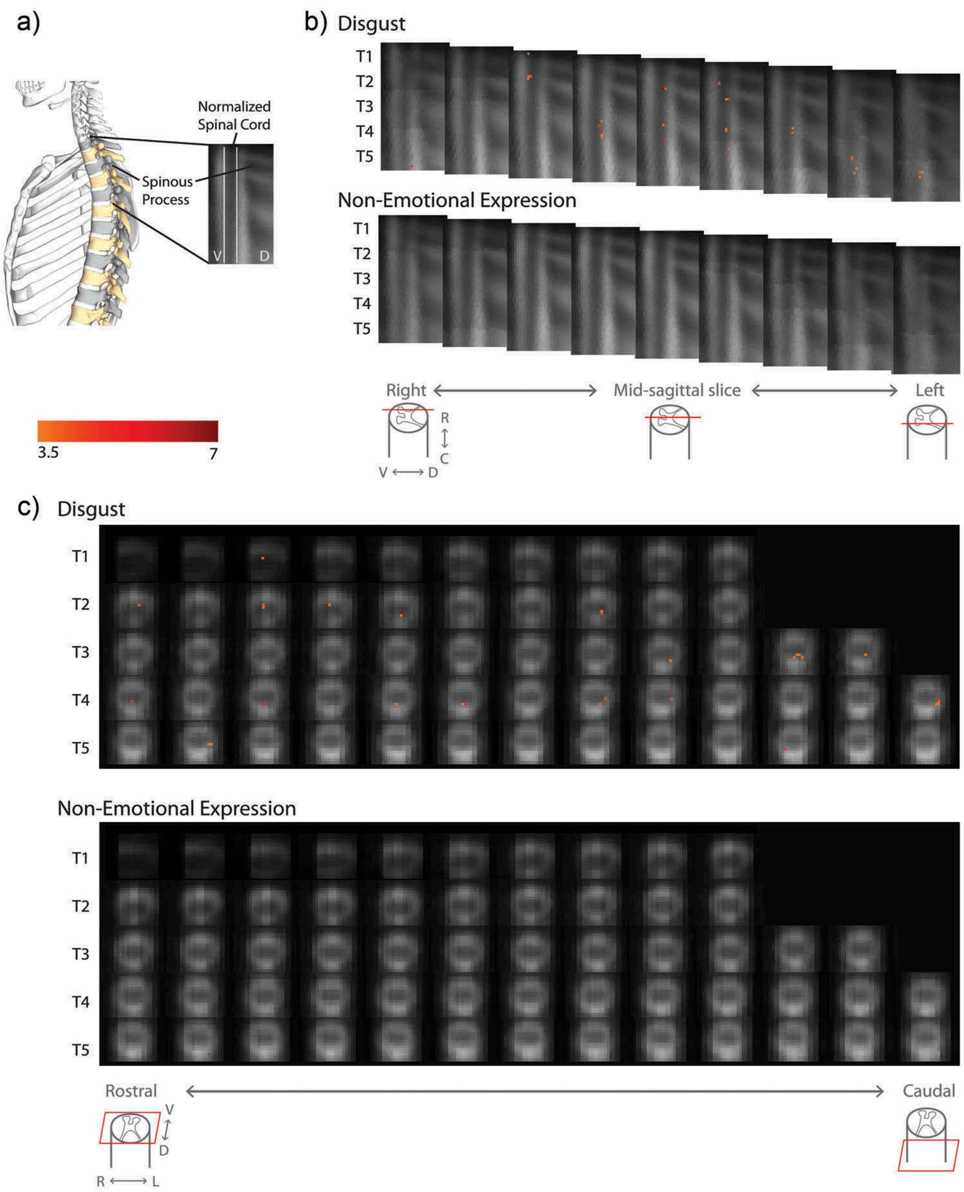

Figure 1. Results of the spatially normalized, group-level random effects analysis overlaid on a normalized background image revealing significant active voxels for each condition. a) The assessed region of thoracic spinal cord is shown, with the spinal cord outlined in white in the sagittal view on a spatially normalized background, with the ventral (V) and dorsal (D) aspects of the cord indicated. The color bar is shown indicating t-values, with a minimum t-threshold of 3.5, corresponding to p = 0.0029. b) Results of the random effects analysis are displayed over a spatially normalized background. The approximate T1 through T5 segments are noted, for each condition, Disgust (upper) and Non-emotional Expression (lower). As indicated in the diagrams, slices move from the right to left side of the cord, with the dorsal aspect toward the right of each frame. c) To facilitate viewing, results are also displayed in axial orientation, with the dorsal (D) aspect of the cord toward the bottom of each frame.

into a disgusted expression. Participants were not shown photographs of faces to mimic, nor were they asked to generate emotional feelings or to retrieve memories associated with disgust. Indeed, no participant reported feeling disgust while generating disgusted facial expressions. It is possible, however, that producing disgusted expressions triggered a subtle emotional response as seen in studies of the facial feedback hypothesis (Ekman, Levenson, & Friesen, 1983; Izard, 1971; see Davis, Senghas, & Ochsner, 2009; for a recent review). Therefore, our results may be due to both the biomechanical characteristics of the disgust response as well as to a subtle *feeling* of disgust. Future studies will be needed to tease apart these, likely complementary, effects.

The results of this study highlight the need for more research into the link between emotional facial expressions and embodied responses. An obvious limitation of the current study is that only one emotion—disgust—was assessed. This decision was logical for a proof-of-principle study; the chemosensory constriction associated with disgust appeared likely to produce a motoric response detectable with spinal fMRI. Additionally, at this level of the spinal cord, other emotions presented methodological challenges. For example, fear involves an expansion of the chest cavity due to a rapid intake of breath; this inhalation may cause a movement artifact, possibly even moving the cord out of the scanner's field of view. These methodological challenges notwithstanding, future studies, should examine whether other emotional expressions trigger activity in the thoracic spinal cord. It would also be informative to examine facial-expression-dependent activity in other regions of the cord. The cervical spinal cord innervates muscles in the neck, shoulders, and upper limbs. We predict that disgust will stimulate the rhomboid and paraspinal muscles; these muscle groups are innervated by C3-C4 and C1-C6, respectively. Spinal fMRI of this region of the central nervous system would therefore enhance existing depictions of the neural architecture of disgust (e.g., Harrison, Gray, Gianaros, & Critchley, 2010) and would prove useful in delineating the neural substrates of other emotions as well.

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Disclosure statement

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