

A Role for the Motor System in Binding Abstract Emotional Meaning

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Sensorimotor areas activate to action- and object-related words, but their role in abstract meaning processing is still debated. Abstract emotion words denoting body internal states are a critical test case because they lack referential links to objects. If actions expressing emotion are crucial for learning correspondences between word forms and emotions, emotion word-evoked activity should emerge in motor brain systems controlling the face and arms, which typically express emotions. To test this hypothesis, we recruited 18 native speakers and used event-related functional magnetic resonance imaging to compare brain activation evoked by abstract emotion words to that by face- and arm-related action words. In addition to limbic regions, emotion words indeed sparked precentral cortex, including body-part-specific areas activated somatotopically by face words or arm words. Control items, including hash mark strings and animal words, failed to activate precentral areas. We conclude that, similar to their role in action word processing, activation of frontocentral motor systems in the dorsal stream reflects the semantic binding of sign and meaning of abstract words denoting emotions and possibly other body internal states.

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Introduction

A fundamental property of the human language system is the possibility to learn, for a huge vocabulary, the arbitrary links between word forms and their meanings (de Saussure 1916; Pulvermüller and Fadiga 2010). The nature of the sign-meaning relationship has, however, been a matter of much debate. A dominant view puts that semantic learning emerges when words are related to objects in the world and the child stores the word-world relationship by correlating the word occurrence with that of objects (see, e.g., Locke 1909/1847). In recent years, this empiricist position led to the proposal that word meaning is embodied in perceptual symbol systems of the mind (Barsalou 1999; Lakoff and Johnson 1999) and organized in the brain by neuronal circuits connecting together word form circuits in the left-perisylvian language cortex and visual perceptual circuits in the inferior-temporal object-processing or “what” stream (Pulvermüller 1999; Martin 2007; Pulvermüller and Fadiga 2010). Object and word knowledge would therefore be joined together by circuits spread out over perisylvian language cortex and inferior-temporal areas in the ventral stream. Unfortunately, this explanation fails for words not related to concrete objects, especially for abstract words and for words whose meaning relates to internal states of the body, such as “fear.” How does the mapping of sign to meaning occur for these words? As activation evoked by abstract words has been found in multiple regions including left dorsolateral prefrontal (Binder et al. 2005), frontotemporal (Noppeney and Price 2004), and parietal cortex

(Manenti et al. 2010), as well as right frontal and temporal areas (Grossman et al. 2002), it is clear that further research requires focus on well defined and tightly controlled subsets of abstract words (Pulvermüller and Hauk 2006). As such, we here use the example of abstract emotion words to further elucidate the neuronal basis of word meaning in the mind and brain and, on a broader level, to draw inferences on the development of such organization that can be applied to broader semantic theory.

There is currently a paucity of strong empirical data concerning the neuronal grounding of emotion words. Indeed, when one surveys the literature, it is evident that most previous studies attempted to obtain brain correlates of emotional-affective meaning processing by contrasting words with extreme valence (being judged as either very positive or very negative and therefore receiving high arousal ratings, following Osgood et al. 1975; Lang and Bradley 2009) with average valence (and therefore low-arousal) words. High-arousal words (i.e., items with either very high or very low valence) were found to activate orbital, medial and dorsolateral prefrontal cortex, anterior and posterior portions of the cingulate cortex, the insula, basal ganglia, thalamus, and amygdala, along with different sections of temporal cortex, especially on the left (Beaugard et al. 1997; Maddock and Buonocore 1997; Whalen et al. 1998; Crosson et al. 1999; Maddock 1999; Hamann and Mao 2002; Fossati et al. 2003; Maddock et al. 2003; Cato et al. 2004; Kuchinke et al. 2005; Nakic et al. 2006; Hirata et al. 2007; Herbert, Ethofer, et al. 2008). These results are consistent with previous postulates that words with strong emotional-affective links spark brain regions of emotion processing, possibly due to connections of cortical word processing circuits that reach deep into the limbic system (“limbic tails” of word-related cortical cell assemblies, Pulvermüller and Schumann 1994). While such activations in limbic areas would hypothetically hold true for words denoting actual emotions, these studies did not directly address the brain correlates of emotion word processing as they employed high-arousal words referring to concrete objects or entities with an emotional connotation (such as “murder,” “explosion,” and “faeces”) rather than emotions per se.

How can the meaning of emotion words, which are used to speak about internal states of the body and therefore typically have abstract meaning (e.g., “fear,” “dread,” and “spite”), be learnt? The classic explanation of meaning, which links words to referent objects, does fail here because the objects the words relate to are, if existent at all, not directly accessible. Therefore, the teacher cannot point to an object and say: “This is fear.” A solution to this problem has been offered by language theorists. Accordingly, the meaning of an abstract emotion word is typically established by using the word in action contexts, when language learners naturally express relevant emotions in their

behavior (Wittgenstein 1953; Bennett and Hacker 2006). The relationship between action and emotion is the subject of a vast psychological literature. At the most general level, internal states are expressed externally in the most basic avoidance and approach behaviors (see Braitenberg 1984, e.g., as to how these behaviors in robots are attributed emotional significance). This is one way in which likes, dislikes, and other internal states are grounded in behavior. More specifically, the now classic work of Ekman and collaborators is strongly demonstrative of the way in which certain emotions are associated with facial expressions that are argued to be evolutionary and pan-cultural (Ekman et al. 1981; Ekman 1989). The “universal emotions,” anger, contempt, fear, surprise, sadness, disgust and happiness, have larger families within which expressive characteristics are shared: for example, a range of more than 60 concepts of anger all share muscular patterns such as lowered and drawn brows and tightened lips. Others have similarly emphasized the importance of the arms and hands in the expression of emotion (Tracy and Robins 2004; Aviezer et al. 2008), noting a substantial impact, facilitative when congruent with facial expressions, of hand and arm actions upon emotion recognition (Kline and Johannsen 1935; McClenney and Neiss 1989; Meeren et al. 2005; Hietanen and Leppänen 2008). The incorporation of gesticulatory hand and arm movements in emotion-recognition robots in the field of artificial intelligence is further evidence of this link (Itoh et al. 2006; Zecca et al. 2006). As such, it could be strongly held that neural circuits controlling facial expressions and bodily actions related to an emotion concept like “anger” are tightly linked to our neural representation of the word denoting it.

If emotional meaning of words is indeed grounded in emotion-expressing actions, such semantic linkage should be manifest in emotion word processing. This is indeed the case for words semantically related to actions typically performed by moving different parts of the body (such as “talk” and “walk”), which activate body-part-specific representations in sensorimotor cortex (Pulvermüller et al. 2000; Hauk et al. 2004; Kemmerer et al. 2008; Pulvermüller and Fadiga 2010). Therefore, if abstract emotion words are semantically bound to emotion-expressing action schemas as the literature suggests, one may expect that these words activate motor regions controlling the body movements that typically express emotions. This position predicts face and arm motor and premotor cortex activation in emotion word processing, even for abstract emotion words without sensorimotor semantic links.

To test whether this prediction is valid, we presented emotion words together with action words (arm- and face-related verbs) and with control stimuli in a passive reading paradigm and used event-related functional magnetic resonance imaging (fMRI) to map hemodynamic brain responses. With tighter control over stimuli, we attempted to avoid complications introduced by the aforementioned studies which investigated brain correlates of emotional-affective meaning processing using emotionally charged nouns, most of which failed to dissociate affective-emotional word properties from perceptually related semantic ones. While high-arousal words evoked activation in regions such as the orbitofrontal cortex, the insula, and the temporal cortex, certain sensorimotor aspects of word meaning are also reflected in these areas, such as that words with acoustic connotations—sound words such as “telephone,” “bell,” and indeed “explosion”—were seen to activate the temporal auditory system (Kiefer et al. 2008) and words related to olfaction—odor words such as “cinnamon,”

“rose,” or indeed “faeces”—activated olfactory brain areas in the orbitofrontal cortex and the insula (González et al. 2006). A confound consequently exists in previous studies where it is unclear to what degree the reported brain activity to high-arousal words might be due to sensorimotor semantic properties. The present study aimed to clarify this issue by controlling both types of semantic information about words, affective-emotional and sensorimotor referential information. To this end, word categories with low emotional ratings were introduced and the category of emotion words was split into subgroups with and without sensorimotor semantic links.

Activation of precentral cortex by emotion words, overlapping with somatotopic activation of body-part-specific areas by arm- and face-related words, was found for a wide selection of emotion words and confirmed for the subset of emotion words that were highly abstract in meaning and matched for psycholinguistic properties to the action words. Our results support intrinsic action grounding of abstract emotional meaning, and we thus postulate a critical role of emotional behaviors and therefore the motor system in the mapping of sign to meaning for these words.

Materials and Methods

Subjects

All 18 participants were right-handed, monolingual native English speakers. Their mean age was 29 (standard error [SE] = 2.8), and they had a mean laterality quotient of 90 (SE = 3.1) (Oldfield 1971). Participants had normal or corrected-to-normal vision and no history of neurological or psychiatric illness; they were not taking any psychotropic drugs at the time of the study. IQ scores, assessed in all but one of the participants using Form A of the Cattell Culture Fair test (Cattell and Cattell 1960), were above average (mean = 110, SE = 3.0). Ethical approval was obtained from the Cambridge Psychology Research Ethics Committee (CPREC 2008.64). Participants were informed of the nature of the experiment, gave full written consent, and were all paid for their time.

Stimuli

Prior to the fMRI experiment, a semantic rating study was performed on a large vocabulary to obtain a suitable list of stimulus words. Ten native speakers of English were recruited to provide ratings for each word for a number of semantic variables, covering 1) sensorimotor meaning features—including imageability, concreteness, and action-relatedness—and 2) affective-emotional features—including arousal and valence (Osgood et al. 1975; Bradley and Lang 1994). Previous work on emotional-affective meaning relied on valence and arousal ratings to classify words as emotional or non-emotional. As mentioned in the Introduction, these ratings do not allow for a separation of words used to speak about emotionally-charged objects and actions from “true” emotion words used to speak about emotions per se. To obtain a more direct index of whether words are used to speak about emotions, we administered explicit semantic ratings of emotion-relatedness (Question: “Is this word typically used to speak about an emotion?”), in addition to standard arousal and valence ratings. Details of the behavioral procedures are described elsewhere (Pulvermüller et al. 1999; see also Supplementary Table S1). Based on the semantic ratings and a range of psycholinguistic features assessed by consulting a standard psycholinguistic database (Baayen et al. 1993), matched sets of 40 arm-related action words, 40 face-related action words, and 40 emotion words were selected, which were presented together with 240 filler words and 120 hash mark strings that were matched in length with the 360 word stimuli. Hash mark strings were used as baseline condition and, to confirm motor activation against a baseline of meaningful words not related to action, a set of 40 animal names were chosen from the set of filler words. All experimental words had

a dominant use as verbs; the emotion word category contained words describing feelings (such as “rile,” “dread,” or “spite”), whereas all face-related (“gnaw,” “grunt,” or “chew”) and arm-related words (“carve,” “peel,” or “grasp”) are typically used to speak about actions. Word groups were matched for length, letter bigram and trigram frequency, number of orthographic neighbors (Coltheart’s N [Coltheart et al. 1977]), and number of meanings (see Supplementary Table S1) but differed substantially in the ratings of their semantic links to action and emotion and in imageability (Fig. 1). Whereas action words were rated as strongly face- or arm-related and, in addition, as highly imageable and concrete, emotion words were judged to have significantly weaker semantic links to the effectors of the body ($F_{2,119} = 5.394$, $P < 0.01$) and to be significantly lower in valence than the action items ($F_{2,119} = 46.739$, $P < 0.001$).

Containing words describing feelings that one can experience and evoke in others (such as “rile,” “peeve,” “dread,” “daunt,” and “spite”), the emotion word category was designed to differ from the more mechanically based face-related words (“munch,” “lick”), though the category did include some words which related to more concrete or sensorimotor emotional actions (such as “wail” and “scream”). To investigate further whether any activation caused by emotion words could possibly be due to those items with a degree of sensorimotor associations (such as, indeed, “wail” and “scream”), we removed all of these partly sensorimotor items from a second set of analyses, which therefore focused on a subset of highly abstract emotion items only (hereby referred to as “abstract emotion words” in the analysis in order to distinguish them from the larger emotion word category and containing exemplars such as “dread” and “spite”). Compared with the sensorimotor emotion words, the abstract emotion words were significantly lower in action-relatedness ($t_{58} = -2.285$, $P < 0.03$) and imageability ($t_{58} = -2.114$, $P < 0.04$) (see Supplementary Table S2 for psycholinguistic and semantic properties). They were selected on the basis of the ratings participants gave each word on the semantic variable concreteness/abstractness, whereby the 20 more concrete emotion words with sensorimotor links were partitioned from the 20 more abstract words. An additional benefit of the analysis of abstract emotion words was that it allowed for even closer matching between our experimental word categories. Though matching of logarithmic word frequencies between action word groups and the full set of emotion words was not possible, by removing 4 items from each action word category, both action word groups could be matched with the abstract emotion word group for this variable: as such, comparisons with abstract emotion words always employed these more closely matched action word subsets. Separate values and statistical results for the 2 selections of emotion and action words—all emotion, arm- and face-related words, and the subgroups of face-related, arm-related, and abstract emotion words—can be seen in supplementary data (Supplementary Tables S1 and S2, respectively). In statistical contrasts, we also employed a control category of animal names (such as “snail,” “hen,” and “whale”). Though it does not appear in the supplementary materials, the animal

name category was matched to the 3 experimental conditions and additionally to the abstract emotion category in length, bigram and trigram frequency, and number of orthographic neighbors. Please see Appendix 1 for the full list of experimental words.

Procedure and Experimental Design

In the fMRI experiment, words were presented tachistoscopically, for 150 ms, in a passive silent reading task, which was divided into 3 blocks of approximately 7 min each. Such short presentations were used to discourage eye movements and to make it necessary to continuously attend to the screen in order to perform well on the task. This event-related paradigm has been successfully employed in a number of previous investigations into semantic activation (Hauk et al. 2004; Kronbichler et al. 2004; Pulvermüller et al. 2009). Following word presentation, participants focused on a central fixation cross for an average of 2350 ms, with stimulus onset asynchrony varied randomly between 2250 and 2750 ms (average 2500 ms). Two pseudorandomized stimulus lists were presented, counterbalanced between subjects. Participants were instructed to read the words silently without moving their lips or tongue and to stay as still as possible. Participants were observed during scanning in order to rule out the effect of overt movements on results. Minor muscle activity, such as in the face muscles, could not be observed during scanning. However, previous analyses of electromyographic (EMG) data recorded during word presentation failed to reveal any reliable differences in language-elicited EMG activity between word categories (Pulvermüller et al. 2006).

Immediately after the scan and without previous warning, participants were given a short word recollection test containing a combination of experimental and novel distracter words. Results were used to confirm that subjects had been attentive continuously during the silent reading task.

Imaging Methods and Data Analysis

Subjects were scanned in a 3-T Siemens Tim Trio magnetic resonance device with a head coil attached. The echo-planar (EPI) session parameters were time repetition = 2000 ms, time echo = 30 ms, and a flip angle of 78°. The functional scans consisted of 32 slices in descending order covering the whole brain (slice thickness was 3 mm, in-plane resolution 3 × 3 mm, interslice distance 0.75 mm). SPM5 (Wellcome Department of Imaging Neuroscience, London, UK) was employed throughout the analysis. Images were corrected for slice timing and realigned to the first image using sinc interpolation. The EPI images were coregistered to the structural T_1 images, which were normalized to the 152 subject T_1 template of the Montreal Neurological Institute (MNI), and the resulting transformation parameters applied to the coregistered EPI images. During this preprocessing, images were resampled with a spatial resolution of 2 × 2 × 2 mm and spatially

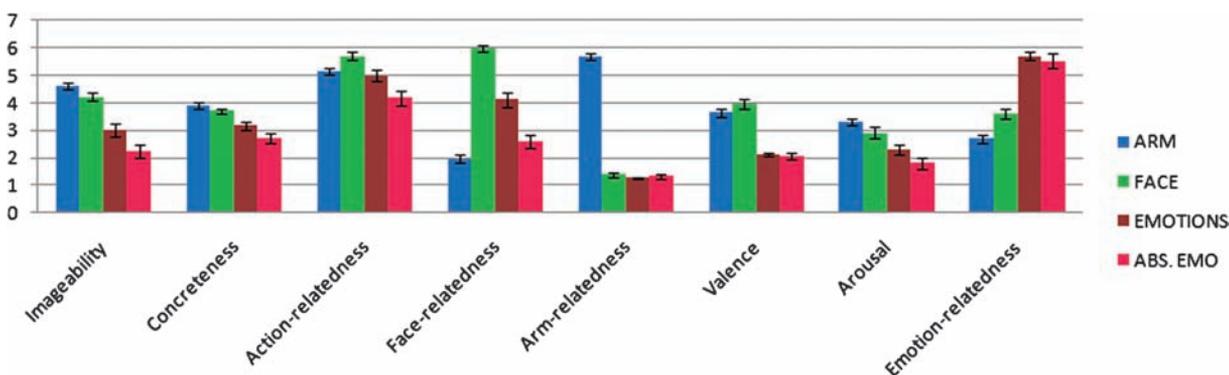


Figure 1. Graphs depicting the semantic differences between our word categories for the sensorimotor variables imageability, concreteness, action-relatedness, arm-relatedness, and face-relatedness and for the emotional-affective variables valence, arousal, and emotion-relatedness. Arm words are represented in blue, face words in green, emotion words in red, and abstract emotion words in light red. Error bars, as in all other figures, reflect standard error values. The values in the graphs are taken from an independent semantic rating study in which 10 native English speakers rated all of the stimuli. A 7-point rating scale (Hauk et al. 2004) has been applied, in which 7 = very strong, 1 = very weak/no relationship. Please also see Supplementary Tables S1 and S2 for figures and statistics of psycholinguistic matching and semantic relationships between all experimental words.

smoothed with an 8-mm full-width half-maximum Gaussian kernel. Single-subject and second-level statistical contrasts were computed using the canonical hemodynamic response function of the general linear model. Low-frequency noise was removed by applying a high-pass filter of 128 s. Onset times for each stimulus were extracted from Eprime output files and integrated into a model for each block in which each stimulus category was modeled as a separate event. Group data was then analyzed with a random-effects analysis. Activation to words was compared statistically against baseline (the hash mark condition) as was that to each of the individual word categories. Stereotaxic coordinates for voxels are reported in the MNI standard space.

Regions of interest (ROIs) were defined using the Marsbar function of SPM5 (Brett et al. 2002). In a data-driven approach, activation elicited by arm, face, and emotion words contrasted against baseline was used to extract parameter estimates for 5 loci where activation was found with the smallest error probabilities. Average activation in spheres of 2-mm radius was calculated for each word type for these loci and an analysis of variance (ANOVA) (5 ROIs \times 3 word categories) was calculated. Because preexisting research (and equally the present results) demonstrated reliable activation to action-related words in motor, premotor, and adjacent inferior precentral cortex (Kemmerer and Gonzalez-Castillo 2010; Kemmerer et al. forthcoming), these areas were systematically analyzed using a ROI approach. To this end, the entire lateral-to-inferior part of the frontocentral cortex was covered by columns of ROIs, each including 8 dorsal-to-ventral ROIs. The 3×8 ROIs (radius 2 mm) were approximately equally spaced between coordinates $-38, -9, 62$ and $-62, -8, 0$ (central strip), coordinates $-53, 4, 50$ and $-62, 6, 0$ (precentral strip), and coordinates $-38, 24, 56$ and $-44, 33, -8$ (prefrontal strip). Note that these ROIs included the sites where previous studies had shown activation specific to face- and arm-related action verbs. An ANOVA included the factors Posterior-Anterior (with the 3 levels motor, premotor, prefrontal), Superior-Inferior (with 8 levels), and Word Category (3). When appropriate, Huynh-Feldt correction was applied to correct for sphericity violations. In this case, epsilon values and corrected P values are reported throughout.

The baseline condition, hash marks, has been employed in all graphics and analyses. However, as a secondary measure, all analyses were rerun employing our filler word category, animal names, as a contrast against experimental word categories (replacing the hash mark condition). As ANOVA reflects differences in mean activation and variance in the data and differences between conditions are not affected by changing baselines, the use of a different baseline common to all critical conditions did not change the results. Therefore, unless explicitly stated, the analyses and figures following employ hash marks as the baseline comparison and were replicated (and also significant) with the animal baseline.

Results

Behavioral Results

Ratings of semantic features of our word stimuli revealed a significant double dissociation of arm- and face-relatedness between action word categories, thus confirming that the arm words and face words selected were, indeed, respectively, related to actions preferentially performed by either the arms and hands or by the face and articulators (significant interaction: Word Category \times Rating Dimension [arm vs. leg relatedness], $F_{1,78} = 1283.08$, $P < 0.001$). Emotion words were significantly lower in action-relatedness than action words (while a small discrepancy arose in slightly higher scores for face words than emotion words in arm-relatedness, this difference was non-significant). As a further result of importance, the explicit ratings of emotion-relatedness led to higher scores for our emotion words compared with the action word categories, thus once again confirming the grouping of stimuli in their semantic categories. Interestingly, the classic variable used in most previous studies to scrutinize “emotion-relatedness,” namely

arousal, led to lower ratings for the emotion words than for the action items, and a similar dissociation was seen for valence, too. The dissociations between explicit semantic ratings and valence/arousal judgments were manifest in significant interactions of the Word Category and the Rating Type variables (Rating Type [arousal vs. emotion] \times Word Category: $F_{2,117} = 73.951$, $P < 0.001$; valence vs. emotion \times Word Category: $F_{2,117} = 138.30$, $P < 0.001$); see Figure 1 for depiction of these semantic relationships (and Supplementary Tables S1 and S2 in supplementary materials for figures and statistics of semantic and psycholinguistic properties).

In the word recognition test administered after the fMRI experiment, performance was above chance (average hit rate: 76.2% [SE = 4.2%], false positive rate: 56.8% [SE = 5.2%]). Together with the language-related brain activations obtained, these results are evidence that subjects had been attentive during the passive reading experiment.

fMRI Results

Figure 2 presents the distribution of brain activation evoked by all words contrasted with the baseline condition of hash mark perception at a false discovery rate (FDR)-corrected significance level of $P < 0.05$. A large cluster of activation emerged in left motor and premotor cortex and in the supplementary motor cortex, mirrored by a smaller cluster in right motor cortex. Activation foci in the left hemisphere also included the inferior frontal gyrus (a large cluster with the greatest peak in the insula), the supramarginal gyrus, middle temporal cortex, and the fusiform gyrus, while bilateral activation was found in the middle cingulate cortex (see Supplementary Table S3).

An ANOVA compared activation patterns elicited by the 3 word categories related to action and emotion and a control comparison, animal names, all contrasted against baseline. Values were extracted at the 5 loci where clearest evidence for activation was found in the contrast all-words-versus-baseline (Fig. 2). A significant interaction between the Word Category and Region factors was found ($F_{12,204} = 1.972$, $\epsilon = 0.814$, $P < 0.041$). This significant interaction demonstrates that the 4 word categories elicited topographically different patterns of activation. Additionally, the same interaction remained significant when animal names were taken out of the ANOVA as a word category and instead used as a contrast for each of the experimental word categories (arm, face, and emotion words) rather than the baseline condition ($F_{8,136} = 2.503$, $\epsilon = 0.992$, $P < 0.02$).

Interestingly, the interaction was driven by the most strongly activated part of the brain, the motor system (coordinates $-54, -8, 42$), where a significant main effect of word category was found ($F_{3,51} = 2.801$, $P < 0.05$). T -tests within this region revealed stronger activation to arm- and emotion-related words compared with face-related and animal words ($t_{17} = 2.975$, $P < 0.01$). While a main effect of word category did not reach significance in the other ROIs individually, it is notable that category-specificity, reflected by differential topographies for the word categories (see Figs 4 and 5 below), emerged in this most strongly activated region about which our predictions relate.

Figure 3 shows lateral left-hemispheric views of the activation patterns elicited by different word categories and groups as compared against baseline. Figure 3's part A, displaying an activation overlay for face and arm words, shows that in central and precentral cortex (BA 4 and 6) arm words evoked more dorsal activation than face words. Such premotor and motor activation is consistent with the semantic somatotopy revealed

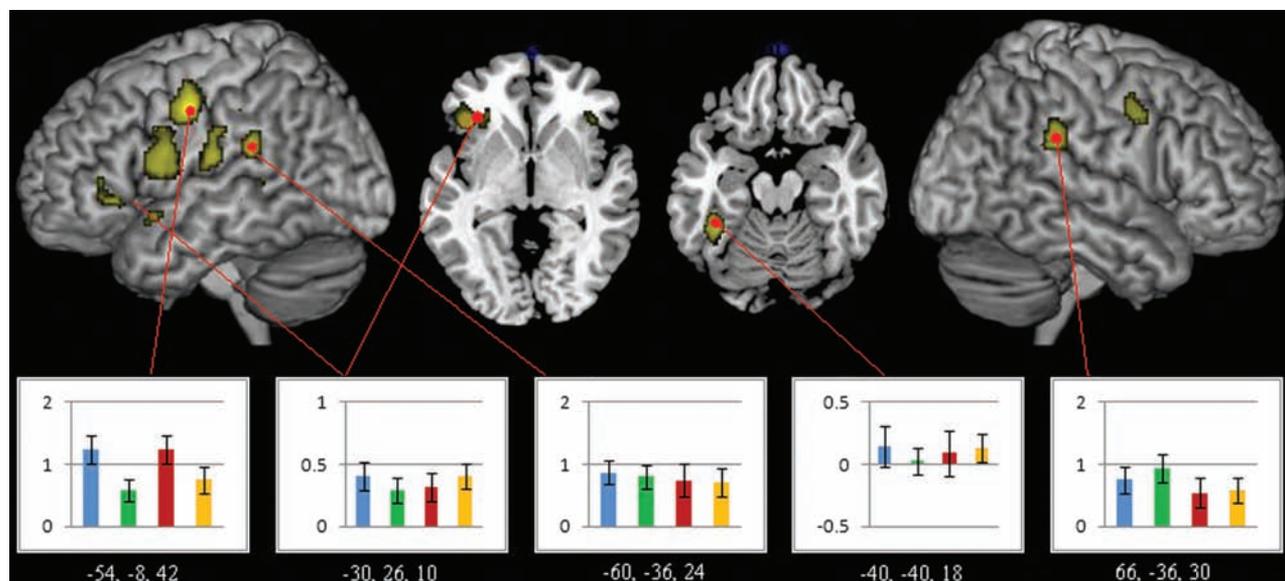


Figure 2. Significant activation elicited by all experimental words (arm, face, and emotion words) compared with the hash mark baseline condition, plotted at an FDR-corrected significance level of $P < 0.05$. The graphs displayed at the bottom of the image show activations for each word category (blue = arm words, green = face words, red = emotion words, and yellow = animal names) in 2 mm-radius ROIs centered at the 5 coordinates where maximal effect sizes were found for this contrast. From left to right, these MNI coordinates and their locations are 1) left precentral cortex ($-54, -8, 42$), 2) left insula, operculum, and inferior frontal cortex ($-30, 26, 10$), 3) left supramarginal gyrus ($-60, -36, 24$), 4) left fusiform gyrus ($-40, -40, 18$), and 5) right supramarginal gyrus ($66, -36, 30$). Please also see Supplementary Table S3 for MNI coordinates generated by this contrast.

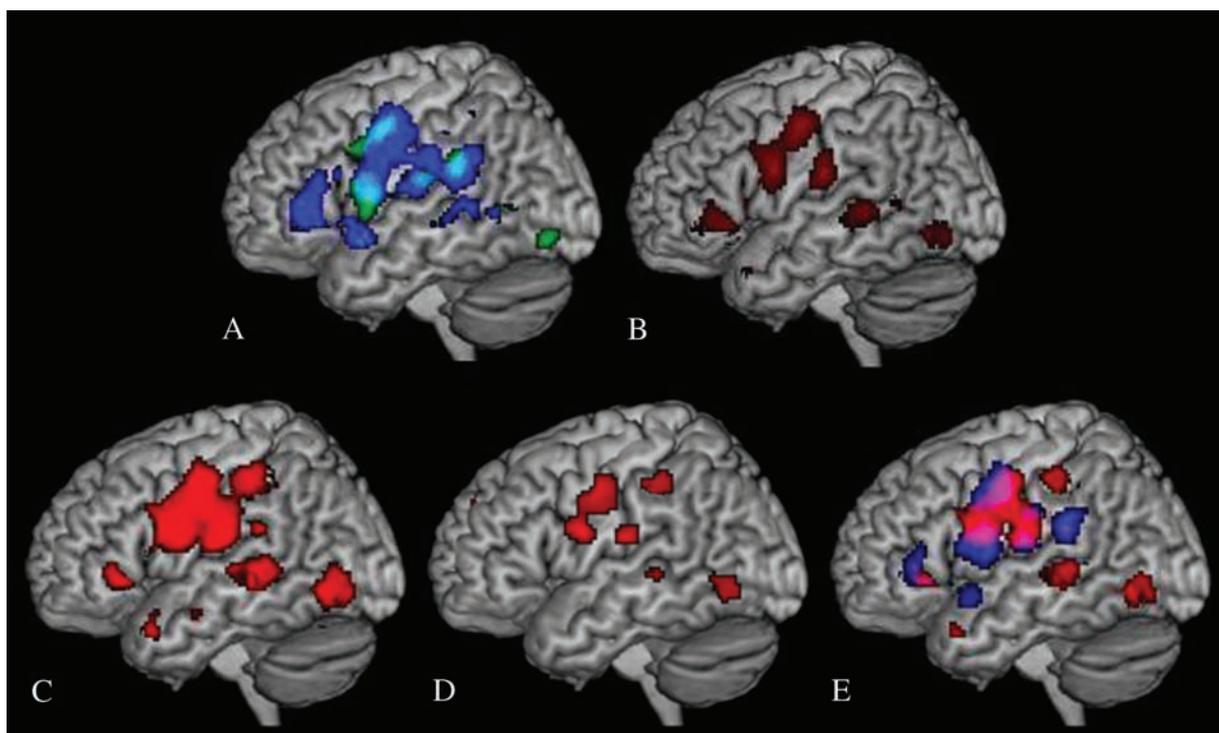


Figure 3. Activation evoked by individual word categories: all are plotted at a significance level of $P < 0.005$ (uncorrected) except for part E, which uses an FDR-corrected threshold of $P < 0.05$. Activation evoked by (A) arm words (in blue) and face words (green) against baseline (please see also Supplementary Table S4 in supplementary data for activation loci for these contrasts); (B) all emotion words against baseline (hash mark strings, dark red); (C) abstract emotion words (bright red) against baseline. Figure part D presents a direct comparison between activation to abstract emotion words (red) and that to a word category without semantic links to actions (animal names). Figure part E depicts activation evoked by concrete action words (blue) contrasted with that to abstract emotion words (red).

in previous literature, in which action words have been shown to activate their corresponding motor circuits in dorsal (arm) and ventral (face) motor system (Pulvermüller et al. 2000; Hauk et al. 2004; Kemmerer et al. 2008; Pulvermüller and Fadiga 2010). Activation for both categories also appeared in the inferior

frontal cortex, in pars opercularis, pars triangularis, and pars orbitalis (BA 44, 45, and 47, respectively), regions frequently implicated in semantic processing (Bookheimer 2002). Arm words produced more pronounced activation in the left supramarginal gyrus, superior temporal sulcus, and middle temporal

gyrus, while the fusiform gyrus showed general activation to all word types, consistent with its nonspecific role in visual word-form processing (Cohen et al. 2002; Kronbichler et al. 2004), though face words showed specific activation of posterior fusiform and temporo-occipital areas, consistent with a category-specific semantic role of these regions (Price 2000). Supplementary Table S4 lists activation loci for arm and face words.

Figure 3, parts *B* and *C* show comparisons of left-hemispheric activation patterns elicited by different selections of emotion words against a hash mark baseline: for all emotion words (*B*) and the group of abstract emotion words only (*C*). Part *D*, presenting a direct contrast between abstract emotion words and a subgroup of the filler words (animal names), confirms that frontocentral activation to abstract emotion words persists in the comparison with meaningful words unrelated to actions. Part *E* contrasts action word- with abstract emotion word-elicited activation, thresholded at an FDR-corrected significance level of $P < 0.05$. It can be seen that motor activation to emotion words remained consistent through all 4 of the latter plots, with a tendency for abstract emotion words to activate the motor system in a more widespread fashion compared with the other word kinds examined here.

A direct comparison between activation patterns to arm, face, and all emotion words (all contrasted against the hash mark baseline condition) is shown in Figure 4. Emotion word-evoked left precentral activation extended from dorsal BA 4 to ventral BA 6, where it overlapped with face and arm word-elicited activation, reaching down deep into the insula and into the inferior frontal gyrus across pars opercularis (BA 44) and pars triangularis (BA 45) and descending more ventrally into pars orbitalis (BA 47) and ending just within the orbitofrontal cortex (BA 11); a small left-hemispheric cluster was also seen in the frontopolar region (BA 10), mirrored by a smaller cluster in the right hemisphere. Motor systems and inferior frontal activation

tended to be bilateral, though with clear left dominance (cf. Fig. 2). A large cluster of activation was found in the middle and anterior cingulate (including part of BA 32 and BA 24). Emotion words also evoked parietal activity in the left inferior somatosensory cortex (BA 1–3), broaching BA 43, and in the supra-marginal gyrus (BA 40). Another large cluster extended from left superior to inferior temporal and fusiform regions (BA 21–22, 37). Table 1 lists activation loci for emotion words and for abstract emotion words. Generally, similar results were obtained for both selections of emotion words, as referenced by Figure 3, but motor activation for abstract emotion words appeared more pronounced in its spread and overlap with action words, including an extensive cluster covering much of the lower left precentral gyrus. Incorporated in this cluster, activation in the inferior frontal gyrus (BA 44, 45, and adjacent BA 47) descended more deeply than that to action words and reached the left insula and basal ganglia (caudate and putamen). Abstract emotion word activation in corticolimbic structures such as the cingulate also tended to be more pronounced compared with the other emotion word selection. The previously observed bilateral clusters in frontopolar cortex also increased in size and additional clusters emerged in the right basal ganglia. MNI coordinates, cluster sizes, and locations of activation for the emotion word groups can be seen in Table 1 (please see supplementary materials for activation tables for other word groups).

Our results demonstrate substantial left-hemispheric motor system activation by hand, arm, and emotion words (though not by animal words); they also suggest that there are local differences in the word-specific activation patterns in this region. To determine significance of word category related activation differences in these critical left frontocentral areas, we carried out a systematic analysis of ROIs covering left frontocentral cortex (design: Word Category \times Anterior-Posterior [prefrontal, premotor, and motor cortex] \times Superior-Inferior [9 equally spaced regions, see Materials and Methods, Fig. 5]). These regions

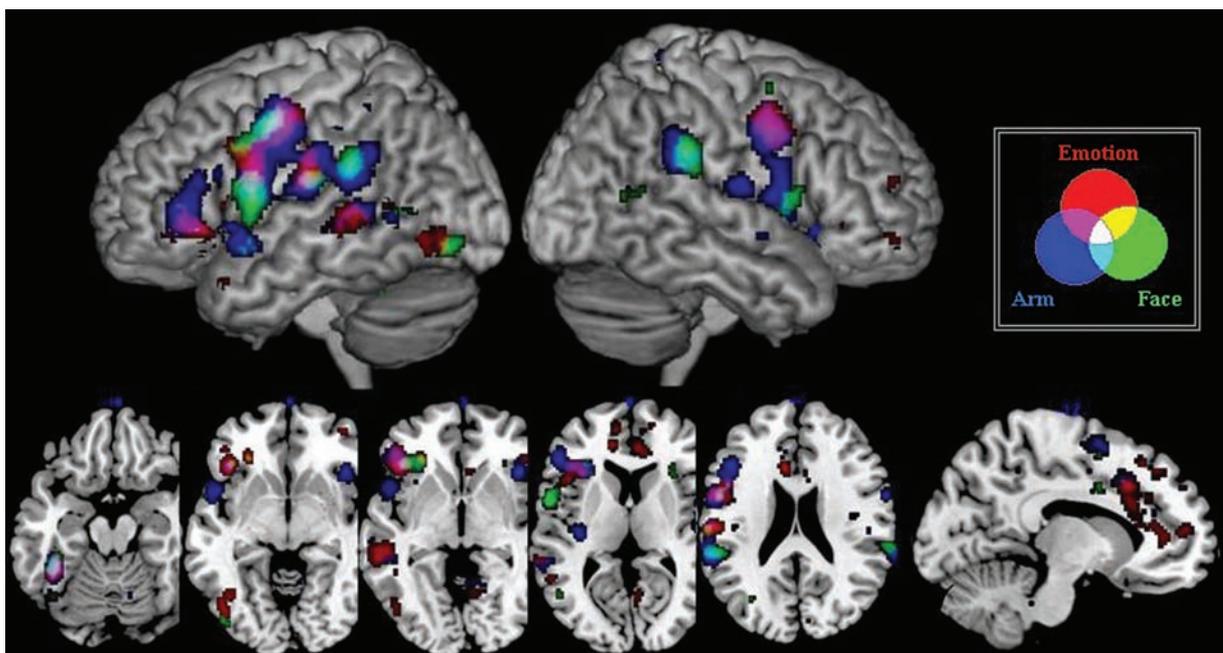


Figure 4. Activation overlays for arm words (blue), face words (green), and emotion words (red). Activation is plotted at a threshold of $P < 0.005$ (uncorrected).

Table 1

MNI coordinates for the contrasts emotion words (all) against baseline and abstract emotion words against baseline

	x	y	z	Cluster size	t	P
All emotion words						
L. precentral gyrus (BA 4)	-56	4	24	1354	5.69	<0.001
L. precentral gyrus (BA 4)	-50	-10	44		5.51	<0.001
L. pars orbitalis (BA 47)	-44	26	-2		5.07	<0.001
R. precentral gyrus (BA 4)	60	2	38	178	4.98	<0.001
R. SMA (BA 6)	8	22	52	1288	6.38	<0.001
L. middle cingulate (BA 32)	-8	22	38		5.72	<0.001
R. anterior cingulate (BA 32)	6	40	10	104	4.51	<0.001
L. frontopolar cortex (BA 10)	-10	54	12	32	3.41	<0.002
L. pars orbitalis (BA 47)	-28	34	-5	50	4.14	<0.001
L. middle temporal gyrus (BA 21)	-56	-34	2	298	5.60	<0.001
L. inferior temporal gyrus (BA 37)	-38	-44	-14	474	4.95	<0.001
L. fusiform gyrus (BA 37)	-40	-62	-12		4.66	<0.001
L. inferior parietal cortex (BA 2)	-48	-34	38	117	3.55	<0.001
L. supramarginal gyrus (BA 40)	-52	-38	30		3.28	<0.001
R. lingual cortex (BA 18)	8	-62	2	190	3.93	<0.001
L. lingual cortex (BA 17)	-2	-70	2		3.46	<0.001
Abstract emotion words						
L. precentral gyrus (BA 6)	-56	4	24	7339	7.45	<0.001*
L. precentral gyrus (BA 4)	-48	-12	40		7.66	<0.001*
L. precentral gyrus (BA 4)	-56	-8	44		4.66	<0.001*
R. precentral gyrus (BA 4)	56	0	40	1140	5.77	<0.001*
R. postcentral gyrus (BA 43)	60	2	24		4.79	<0.001*
L. frontopolar cortex (BA 10)	-10	56	12	143	4.03	<0.001*
R. frontopolar cortex (BA 10)	8	52	8	44	3.98	<0.001*
L. middle temporal gyrus (BA 21)	-60	-34	2	467	5.80	<0.001*
L. fusiform gyrus (BA 37)	-40	-40	-14	968	6.40	<0.001*
L. inferior occipital cortex (BA 19)	-44	-74	-8		4.40	<0.001*
L. superior temporal pole (BA 38)	-48	16	-26	32	4.36	<0.001*
R. superior temporal gyrus (BA 22)	50	-32	24	47	3.81	<0.001*
R. fusiform gyrus (BA 37)	36	-64	2	40	4.60	<0.001
R. superior parietal cortex (BA 5)	16	-50	64	74	3.57	<0.001
R. basal ganglia	28	24	6	190	4.69	<0.001*
R. insula	34	-16	22	44	3.36	0.001

Note: The asterisk sign (*) indicates coordinates that survived FDR-correction at the significance level indicated at $P < 0.05$, while indented coordinates reflect coordinates that arose as part of a larger cluster. SMA, supplementary motor area.

covered all the areas where previous research had found activity specific to action word categories semantically related to the arm and face, respectively (Pulvermüller et al. 2000; Hauk et al. 2004; Kemmerer et al. 2008). The ANOVA revealed a significant main effect of the factors Posterior–Anterior ($F_{2,34} = 4.914$, $\epsilon = 0.894$, $P < 0.017$) and Superior–Inferior ($F_{7,119} = 5.960$, $\epsilon = 0.660$, $P < 0.001$), and a significant interaction between both topographical variables ($F_{14,238} = 5.046$, $\epsilon = 0.720$, $P < 0.001$). There was also a marginally significant interaction between the Word Category factor and the topographical variable Superior–Inferior ($F_{14,238} = 1.998$, $\epsilon = 0.570$, $P < 0.051$). Importantly, a significant 3-way interaction emerged between the Word Category factor and both topographical variables (Posterior–Anterior [3 levels] and Superior–Inferior [8 levels]) demonstrating different activation patterns for the 3 word groups, arm, face, and emotion words, which were matched for a range of psycholinguistic variables, in the frontocentral cortex ($F_{28,476} = 1.571$, $\epsilon = 0.808$, $P < 0.05$). While this initial interaction employed the hash mark baseline as a contrast for experimental word categories, it remained consistent when animal names were used as the contrast instead ($F_{28,476} = 0.808$, $P < 0.05$). This interaction was due, in part, to the well-known semantic somatotopy of arm and face words in premotor cortex revealed by a range of previous studies (Hauk et al. 2004; Kemmerer et al. 2008). Consistent with this preexisting evidence, face word activation tended to dominate over arm word activation at inferior premotor areas (e.g., -62, 6, 0), whereas arm words

activated dorsolateral precentral gyrus more strongly than face words (e.g., -54, 4, 50). Importantly, in most sections of the motor system, emotion words elicited activity comparable with the strongest of both action word categories. In prefrontal cortex, including both orbitofrontal and dorsolateral prefrontal regions (e.g., -62, 23, 15; -44, 33, -3), emotion word activation tended to be stronger than that to action words. Figure 5 illustrates this interaction by showing representative ROI activations. Importantly, the significant 3-way interaction was confirmed for the comparison between the optimally matched subsets of action words and abstract emotion words (Word Category \times Anterior–Posterior \times Superior–Inferior interaction: $F_{28,476} = 1.612$, $\epsilon = 0.862$, $P < 0.04$). As previously mentioned, the results of both analyses were fully replicated when the animal names were used as a contrast with experimental words instead of the hash mark condition.

Discussion

Passive reading of emotion words, even if their meaning is abstract, elicits substantial and widespread activation in the motor system. While somatotopic activation elicited by arm- and face-related action words resembled that of previous studies (Pulvermüller 2005; Kemmerer and Gonzalez-Castillo 2010), strong hemodynamic responses to emotion words were found both in inferior motor areas where face-related words elicited pronounced activation and equally in dorsolateral areas where arm-related action words gave rise to body-part-specific motor activation. Results were obtained for a large group of emotion words that included emotion words with overt sensorimotor semantic links but, importantly, results were confirmed for emotion words rated as highly abstract. In addition to motor systems, emotion words activated limbic areas previously found to relate to emotional-affective processing, including orbital prefrontal, cingulate, and insular cortex. All word categories tested led to activity in standard language regions, including inferior frontal (Broca's region), inferior parietal, superior temporal (Wernicke's region), and fusiform cortex.

As emotion word-elicited motor activation suggests the retrieval of action knowledge in abstract emotion word processing, these results contribute to the long-standing debate about the nature of the meaning of words typically used to speak about inner states of the body. For establishing the link between the form and meaning of internal state words such as abstract emotion words, motor knowledge may be crucial (Wittgenstein 1953).

Action and Emotion Words Activate the Motor System

Motor system activation to emotion words was mainly comprised within the regions also activated by action words typically used to speak about overt actions. In premotor cortex, different activation patterns were seen for words referring to actions preferably performed by moving the face and articulators (face words) or the arm and hand (arm words). In line with earlier work (Pulvermüller et al. 2000, 2009; Hauk et al. 2004; Shtyrov et al. 2004; Pulvermüller, Shtyrov, et al. 2005; Tettamanti et al. 2005; Aziz-Zadeh et al. 2006; Ruschemeyer et al. 2007; Kemmerer and Tranel 2008; Boulenger et al. 2009; Willems et al. 2010), action words were found to activate the precentral gyrus in a somatotopic fashion so that aspects of the meaning of these words—their face- or arm-relatedness—was

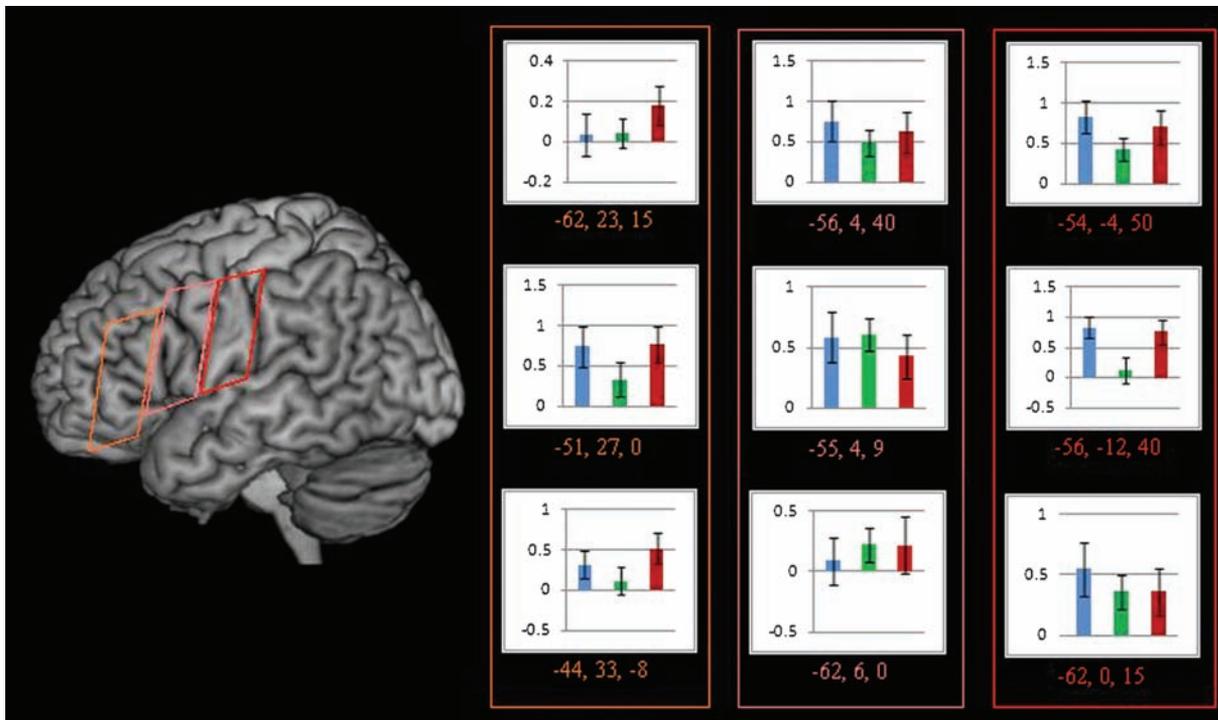


Figure 5. Patterns of activation in motor, premotor, and prefrontal cortex elicited by words typically used to speak about hand/arm actions (blue bars), mouth/face actions (green bars), and emotions (red bars). The cortex was subdivided into three strips over left inferior and lateral motor, premotor and prefrontal regions, each including 8 ROIs. Displayed are activation patterns illustrating the significant interaction of the Word Category factor with the topographical variables Posterior–Anterior (3) and Superior–Inferior (8). MNI coordinates are given for each displayed ROI.

reflected in motor activation (so-called “semantic somatotopy”). Face words led to specific activation in the inferior part of the precentral gyrus and that to arm words emerged in dorsolateral precentral areas, with additional precentral areas showing comparable increases in blood flow to both action word types (see Figs 3A and 4). fMRI, unfortunately, does not provide the precise temporal resolution necessary to rule out the possibility that such activations reflect a post-comprehension and merely epiphenomenal process, as some researchers have suggested (Mahon and Caramazza 2008). However, strong evidence points to the early emergence of these effects, as methods with high temporal resolution (electroencephalography and magnetoencephalography) have confirmed that semantic somatotopic activation occurs alongside other lexico-semantic processes within 200 ms of word presentation, thus ruling out post-comprehension interpretations (Pulvermüller and Shtyrov 2006; Hauk et al. 2008). Furthermore, the appearance of automatic interaction and interference (or “motor/semantic resonance” Rueschemeyer et al. 2009) between concurrent semantic-linguistic and motor tasks provides direct evidence that motor and language systems of the brain exert causal effects on each other (Pulvermüller, Hauk, et al. 2005; Boulenger et al. 2006, 2008; Zwaan and Taylor 2006; Scorolli and Borghi 2007). Lesion evidence further underpins the crucial role frontocentral areas play in the processing of words with action-related meaning (Bak et al. 2001; Pulvermüller et al. 2010; Kemmerer et al. forthcoming). These results argue in favor of an early automatic and functionally relevant role of motor activation in lexicosemantic processing and thus against the post-understanding and epiphenomenology position. Though this type of patient information is not presently available for our

subset of emotion words, similar evidence concerning patients with lesions to auditory cortex has indicated the functional relevance of this area for the processing of sound-related words (Kiefer et al. 2008; Trumpp N, Kliese D, Hoening K, Haarmeier T, Kiefer M. unpublished data). Furthermore, there is evidence for very early affective-emotional effects in semantic processing within the 100–200 ms time window (Skrandies 1998; Skrandies and Chiu 2003; Skrandies et al. 2004; Kissler et al. 2006, 2007; Kanske and Kotz 2007; Herbert, Junghofer, et al. 2008; Scott et al. 2009; Palazova et al. 2011; Rellecke et al. 2011). In order to make further claims about the functional relevance of the motor system for processing of emotion word stimuli, it is necessary both to further investigate the temporal dynamics of this activation via a method with fine-grained temporal resolution and to study processing of these words in patients with functional impairments to the motor systems.

As a further point of reference, it is notable that some authors (though notably not all, see Tokimura et al. 1996) have found unspecific activity in hand motor cortex caused by reading and other linguistic tasks (Floel et al. 2003; Meister et al. 2003), possibly due to general links between language and motor systems. Similarly, phonologically-related activation has been observed in the inferior part of the precentral cortex (Fadiga et al. 2002). Over and above such unspecific or phonologically-related language-action linkage, semantic somatotopy shows that motor system activations are modulated by the semantic word type under investigation, as demonstrated by our comparison with the filler word group (animals) and by the differential activations revealed by our ROI analysis. Part D of Figure 3 shows significant activation for abstract emotion words in the precentral gyrus which remains consistent when

directly compared with animal words, a filler word group without (or with very little) action association. Furthermore, in a similar way as in earlier studies, arm word activation was stronger than that for face words in the dorsal precentral cortex (hand area) and the opposite pattern emerged at inferior precentral sites, as seen previously for face-related action words. Our arm- and face-related action words were precisely matched for a range of psycholinguistic variables and differed only in their semantic links to the effectors of the body; therefore, the differences in activation observed can be confidently attributed to their semantic difference. Since, in almost all premotor regions of interest, emotion words activated the motor system as strongly as the stronger of the 2 body-part-specific action word types we used here as control items, our data speak against an interpretation in terms of generic motor activity related to language (note significant ROI \times Word Category interactions). They rather provide evidence that the emotional meaning of these terms leads to motor activation. The same argument can be cited against the possible lexical confound in our study between our 3 experimental word categories (largely verb-based) and animal names (nouns). However, as local differences in motor systems activation related to the words' semantic relationships with bodily effectors (consistent with preexisting predictions) appeared withstanding strict psycholinguistic matching between categories (for factors including logarithmic word frequency, bi/trigram frequency, number of neighbors, and length), the different action and emotion word categories probed in our study act as controls for each other. As our emotion word category consisted largely (though not exclusively) of verbs, it remains to be investigated whether the activation of motor systems would generalize over other lexical/syntactic classes of emotion words, for example, adjectives (such as "lonely") or nouns ("pride"). Contemporary views suggest that the distinctions that commonly arise between nouns and verbs are a by-product of their different semantic properties (see Shallice 1988; Pulvermüller et al. 1999), so that "grammatical class per se is not an organizational principle of knowledge in the brain" (Vigliocco et al. 2010, p. 407). Further research is, however, required in this area to conclusively generalize our findings.

Emotion words activated a large part of the premotor cortex, with most of this activation contained in foci also activated by face words, arm words, or both. This activation was robust, persisting across both selections of emotion words consistently despite precise control of psycholinguistic properties (Fig. 3). Most crucially, it was clearly manifest and even most pronounced to emotion words with highly abstract meaning and without overt action relationship revealed directly by semantic ratings. The motor activations seen to emotion words are consistent with the theoretical position that abstract concepts are, in part, embodied in modal systems storing information about situations and the internal and external states related to these concepts (Barsalou 1999; Lakoff and Núñez 2000; Gallese and Lakoff 2005). Empirical support for such action-perception grounding of abstract concepts and metaphors comes from behavioral studies that find abstract or metaphorical linguistic statements to be associated with physical space: expressions like "down in the dumps" are suggested to link valence concepts with a spatial continuum (positive as "up," negative as "down," Lakoff and Johnson 1980), as do morality statements with a reference to one's right-hand side (such as the use of "right" to imply moral

decency in idioms like "do the right thing," Casasanto 2009), and numbers are proposed to be positioned on a mental number line associated with the individual's finger-counting habits, typically with smaller numbers on the left-hand side and larger numbers on the right (Pinhas and Fischer 2008) and corresponding lateralized activation of motor cortex (Tschentscher N, Hauk O, Fischer MH, Pulvermüller F, unpublished data). For emotion words, we suggest that semantic representations consist of limbic circuits relating to the internal states the words are used to speak about plus, crucially, the motor circuits programming action schemes for expressing these same emotions, through which the link between emotion word and feeling can be made.

Indeed, apart from supporting a general model of action-grounded abstract conceptual processing, the present activation of premotor cortex to abstract emotion words—which are usually not used to speak about overt actions—contributes to a long-standing debate about the nature of the meaning of these terms and about the nature of meaning more generally. The classic semantic theory (e.g., Locke 1909/1847), which equates the meaning of a word with the object it stands for, fails to account for emotion word meaning (Wittgenstein 1953; Bennett and Hacker 2003). As the entities emotion words refer to are private objects hidden within individuals, it is impossible for different persons to refer to the same object when applying the word, thus resulting in the logical impossibility to teach the meaning of abstract emotion words, including "fear" and "loathing." A bridge between word and meaning is created by way of the expression of internal states in action. A child can be taught an emotion word when experiencing the corresponding emotion and expressing the emotion in its behavior. In this condition, the teacher can use the word that matches the emotion expressed in motor actions. (Note that only after an initial stock of emotion expressions has been acquired in this manner can emotion terms be used to define each other.) In this learning situation, the cortical circuits carrying the word and that programming the action are being coactivated, leading, by way of Hebbian learning, to the semantic linkage of word form circuits with action and emotion circuits. There is empirical support for the important role of language-action contingencies in language acquisition in infants (James 2010; James and Swain 2011) and language learning in adults (Liuzzi et al. 2010; Pulvermüller et al. 2011), although it is beyond doubt that the learning of correlations between words and actual actions is only one of many factors contributing to the semantic learning; correlations between perceptual patterns and language also play a role along with contextual learning based on combinatorial information (for review, see Pulvermüller 2011). Though we do not currently possess data recording the in situ acquisition of meaning for emotion words in children or adults, the present results do provide support for a Wittgensteinian account of semantic acquisition for emotion words because 1) motor areas are being activated by emotion words even though these words are not usually used to speak about actions (as confirmed by our semantic rating study) and 2) the motor foci sparked by emotion words were almost entirely contained in the regions seen active to words usually used to speak about face actions and arm actions. This meets precisely the prediction that emotion words should elicit activation in motor-semantic regions that represent those parts of the body with which emotions are typically expressed, that is, the arms and the face. On the other hand, structures frequently found to be linked to general semantic processing,

especially the temporal poles and anterior–inferior temporal cortex (Patterson et al. 2007), did not show prominent activation to the emotion or action words tested here. This is consistent with a degree of category-specificity of these ventral stream regions (Pulvermüller et al. 2011). A ROI analysis of activity for each word category in the 5 loci of most pronounced activation equally confirmed a pattern of category-specificity, as did the analysis of regions scrutinizing the prefrontal, premotor, and motor cortices.

In summary, these results are consistent with the view that, for linking an emotion word to its abstract emotional meaning, the action markers of the respective emotions are critical. Our work ties in with complementary approaches viewing cognition and emotion circuits of the brain as intrinsically connected with each other (Damasio 1994).

Emotion Circuits

A range of brain regions previously found to be active in emotion word processing were confirmed in our present study when subjects read abstract emotion words. These areas included orbitofrontal cortex, the anterior and middle cingulate gyrus, and the anterior insula. Similar to motor systems activations, these hemodynamic changes in limbic structures were largely constant over different stimulus selections; especially, they were clearly present for abstract emotion words. These results are partly consistent with the neuro-metabolic correlates of the emotional-affective semantic features arousal and valence studied in a range of previous studies using object-related nouns. Arousal- and valence-related activation was seen in orbitofrontal cortex (Beauregard et al. 1997; Maddock et al. 2003; Kuchinke et al. 2005) and in the insula (Crosson et al. 2002; Fossati et al. 2003; Maddock et al. 2003). Higher arousal values were typically linked to stronger hemodynamic responses, although insula deactivation was reported with performance on emotional Stroop tasks (Whalen et al. 1998). The anterior and posterior cingulate have also been frequently implicated in processing of nouns with high arousal and extreme valence (Maddock and Buonocore 1997; Whalen et al. 1998; Fossati et al. 2003; Maddock et al. 2003; Cato et al. 2004; Nakic et al. 2006). All 3 regions, orbitofrontal cortex, cingulate, and insula, are well known to be involved in emotion processing, with some sub-areas showing specificity to particular emotions (Sprengelmeyer et al. 1998; Calder et al. 2001). Our emotion words also evoked activity in the frontopolar cortex (cf. Cato et al. 2004) and around the subcortical caudate, putamen, and globus pallidus (Beauregard et al. 1997; Hamann and Mao 2002). However, other well-known emotion sites were not confirmed active in the present study. In particular, no significant activation was seen in our study in the amygdalae or the thalamus, though previous studies had reported activation in these areas for high arousal and low valence items (Hamann and Mao 2002; Maddock et al. 2003; Nakic et al. 2006). This lack of activation may be in part attributable to the relatively small size of the structures and the well-known spatial blurring caused by the spatial normalization procedure applied (Crivello et al. 2002). In addition, it must be noted that the involvement of the amygdala during processing of words with extreme valence is by no means consistent among the studies mentioned, several of which failed to find it (Beauregard et al. 1997; Crosson et al. 1999; Cato et al. 2004; Kuchinke et al. 2005): it is known to be mediated by many

variables, such as task demands and the emotional reactivity of the stimuli (for discussion, see Herbert, Ethofer, et al. 2008). Despite the fact that these studies do not employ emotion words per se and are thus not directly comparable, the areas implicated in emotion circuit activations for our abstract emotion words (orbitofrontal cortex, frontopolar cortex, insula, anterior and posterior cingulate, caudate, and putamen) are consistent with previously found foci sparked by high-arousal or extreme-valence words and with the prefrontal, limbic, and subcortical regions implicated in general emotion processing (LeDoux 1995; Lane et al. 1997; Sprengelmeyer et al. 1998; Maddock et al. 2003). This indicates that the emotional-affective aspects of our present selection of emotion words are reflected in the brain response.

To our knowledge, no previous study of emotional words has investigated verbs describing emotional states of the body like “ail” which are primarily accessible by the individual experiencing them. As mentioned, most language studies have instead focused on words of high or low valence, generally nouns that refer to objects, events, or actions in the world (such as “mutilation,” Maddock et al. 2003). While exhibiting a relationship to emotions, such items also denote visual, auditory, somatosensory, olfactory, gustatory, and other perceptions all of which may have corresponding category- and modality-specific effects on brain activation, as in the aforementioned example in which olfactory words (“cinnamon” and “lilac”) activated a range of cortical and subcortical regions classically associated with emotion processing (amygdala, anterior cingulate, orbitofrontal cortex, and anterior insula, González et al. 2006). To separate effects related to processing of sensory features of referent objects from brain correlates of emotion per se, it is imperative to investigate words that relate to emotions at an abstract level. The status of our emotion words as emotion related was established by semantic ratings and showed a clear dissociation from action words—and, interestingly, arousal ratings showed the opposite dissociation with higher ratings of action words compared with emotion words (Fig. 1). It seems that arousal and valence ratings are not only influenced by emotional-affective meaning of an item but equally by the degree of overt action-relatedness. While very few studies have investigated arousal and valence features of verbs, the fact that the classic conceptualization of arousal conveyed to our participants correlates and is interrelated with activation, both physiological as well as emotional (relaxed/stimulated; sleepy/wide-awake; sluggish/frenzied; Osgood et al. 1975; Bradley and Lang 1994), predicts at least moderate arousal ratings for action words. Arousal and action/motor properties are therefore intrinsically linked and, consequently, the moderate ratings of 3.04 and 2.92 (where 7 indicates high arousal) respectively for our arm- and face-related words were unsurprising. Considering the relationship between action and arousal, it is also important to note that many emotion words relating to low-activity emotions such as depression or disappointment (like, indeed, “mope,” “dread,” or “daunt”) might rate lowly on arousal while still being strongly associated with emotions. Indeed, as mentioned previously, the majority of studies investigating high arousal “emotion words” in fact describe object-, action-, or event-related nouns with extreme positive or negative associations (e.g., “murder,” “earthquake,” and “accident”) and failed to control for action properties that might influence arousal. The latter point and findings cast further doubt on the idea that the factors arousal and

valence provide a safe pathway to emotion circuits in the brain—particularly when one takes into account unarousing, depressive emotions like hopelessness—and suggest the use of more direct ratings of semantic emotion-relatedness in future studies. Note that the high-arousal words of this present study, namely the action words (see Fig. 1), indeed failed to activate some of the limbic structures found active previously to high-arousal items. It seems important to separate out the effects of emotional-affective meaning and antecedent actions and objects to which words relate. In the present study, this was possible by investigating abstract emotion words, which are typically not used to speak about objects or actions but about internal states of a person instead.

Activation of Left-Hemispheric Language Circuits

Increased blood flow was seen for all words in all classic left-hemispheric language regions. In the inferior frontal gyrus, this activation was largely comprised in Broca's region—BA 45 (pars triangularis) and BA 44 (pars opercularis)—and adjacent areas—BA47 (pars orbitalis), precentral cortex and underlying frontal operculum, and insula. In the parietal lobe, such general activation emerged in inferior postcentral gyrus and in the supramarginal gyrus, where activation tended to be strongest for arm words and negligible for emotion words. Posterior temporal activation was strongest for emotion words and fusiform activation equally prominent for all word groups (Fig. 4), consistent with a general role of this area in visual word form processing (Cohen et al. 2002; Kronbichler et al. 2004). The supramarginal and the premotor foci were the only regions that were also found active in the right hemisphere, though minimal activity for arm and emotion words appeared in right pars triangularis. These results are largely consistent with the broadly accepted idea of a left-lateralized network in perisylvian language cortex supporting the processing of word forms. Through Hebbian mechanisms, these word-form circuits come to extend into the parts of the brain that are generally used for perceiving and interacting with the world around us, such as that action words, as in this paper, come to activate the cortical motor system while words describing visible objects come to activate the ventral object-processing stream in inferior temporal lobe (Pulvermüller 2001).

Conclusions

We here aimed to elucidate the neural representation of meaningful words lacking any relationship to concrete objects. For the first time, we observed that words for abstract emotional states evoke activation that overlaps with the somatotopic, effector-specific activation in the motor system sparked by face- and arm-related words. This finding is consistent with the critical role of the face and body in communicating internal emotional states (Ekman et al. 1969; Aviezer et al. 2008) and offers novel conclusions on the nature of one specific type of abstract semantics. In the case of emotion concepts, common emotional behaviors made by the arms, hands, or face (gesticulating, clenching fists, and frowning), as the external criteria for internal states, would seem to act as a concrete bridge between these words and their abstract meanings. Activation in the motor system is the embodied manifestation of this link between visible and abstract concepts and is as such suggested to reflect a process of associative semantic learning through which emotion words

come to activate the regions critical for signaling emotions to others.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>

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Appendix 1 Experimental Word Categories: Arm-Related, Face-Related, and Emotion-Related Words and the Filler Category, Animal Names. Within the Table, the Abstract Subset of Emotion Words Are Marked by Asterisks (*) to Distinguish Them From Sensorimotor Emotion-Related Words

Arm words	Face words	Emotion words	Animal names
Braid	Drone	Ail*	Sloth
Carve	Grunt	Chafe*	Snail
Grasp	Stare	Chide*	Snake
Peel	Peck	Dread*	Pike
Frisk	Drool	Gibe*	Skunk
Hack	Slur	Gloat*	Gull
Slash	Munch	Gripe*	Clam
Poke	Lick	Grouse*	Hawk
Grip	Sip	Hate*	Hare
Pinch	Cough	Daunt*	Mouse
Bind	Puff	Irk*	Crab
Shake	Shout	Miff*	Trout
Throw	Taste	Mock*	Sheep
Pull	Guess	Mope*	Bear
Stir	Bite	Peeve*	Bull
Steer	Sniff	Rile*	Whale
Grope	Slurp	Scare*	Moose
Fold	Sigh	Spite*	Goat
Scoop	Blink	Spurn*	Goose
Grab	Suck	Sulk*	Duck
Pat	Hum	Bawl	Hen
Scrape	Choke	Huff	Shrimp
Knit	Yawn	Frown	Wasp
Click	Wink	Glare	Frog
Switch	Blow	Gnash	Shark
Clap	Gawk	Groan	Dove
Bash	Gnaw	Hiss	Vole
Wash	Kiss	Jeer	Cow
Skim	Chew	Leer	Mole
Wave	Laugh	Moan	Fox
Stab	Lisp	Rant	Crow
Tug	Swig	Retch	Moth
Dunk	Croak	Roar	Slug
Tie	Sing	Scream	Pig
Tear	Chat	Shriek	Seal
Delve	Croon	Smirk	Squid
Knead	Chomp	Sneer	Quail
Stroke	Breathe	Sob	Deer
Seize	Snort	Wail	Toad
Chop	Gasps	Weep	Worm

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