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Somatotopic Representation of Action Words in Human Motor and Premotor Cortex

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Summary

Since the early days of research into language and the brain, word meaning was assumed to be processed in specific brain regions, which most modern neuroscientists localize to the left temporal lobe. Here we use event-related fMRI to show that action words referring to face, arm, or leg actions (e.g., to *lick, pick, or kick*), when presented in a passive reading task, differentially activated areas along the motor strip that either were directly adjacent to or overlapped with areas activated by actual movement of the tongue, fingers, or feet. These results demonstrate that the referential meaning of action words has a correlate in the somatotopic activation of motor and premotor cortex. This rules out a unified "meaning center" in the human brain and supports a dynamic view according to which words are processed by distributed neuronal assemblies with cortical topographies that reflect word semantics.

Introduction

Among the most intensely debated issues in the cognitive neuroscience of language is the question of the cortical "seat" of word meaning (Martin and Chao, 2001; Pulvermüller, 1999). Although there is little doubt that areas in left inferior frontal and superior temporal cortex—sometimes referred to as Broca's and Wernicke's regions—play a major role in language processing, the location of additional areas possibly contributing to semantic processing remains controversial. Most theories localize meaning-related mechanisms in areas anterior, inferior, and posterior to Wernicke's area in the left temporal lobe (Hickok and Poeppel, 2000; Mummery et al., 1998; Price et al., 2001; Scott and Johnsrude, 2003). However, since most studies investigating the issue have focused on the cortical processing of highly imageable concrete nouns and concepts related to their meaning, it is possible that other word types engage semantic representations in other cortical regions. When hemodynamic and neurophysiological imaging studies compared words referring to objects with words that have a clear semantic relationship to actions, typically action verbs (Dehaene, 1995; Kellenbach et al., 2002; Preissl et al., 1995; Pulvermüller et al., 1996) or nouns referring to tools (Chao et al., 1999; Ishai et al., 1999; Martin et al., 1996), the latter elicited strong frontal activation including premotor cortex, suggesting that the frontal activation might reflect aspects of the action-related meaning of action words (Martin and Chao, 2001; Pulvermüller, 1996). If so, the cortical locus of meaning processing could be, in part, determined by the general neuroscientific principle of Hebbian learning according to which neuronal correlation is mapped onto connection strength (Hebb, 1949; Tsumoto, 1992). If word forms frequently cooccur with visual perceptions (object words), their meaning-related activity may be found in temporal visual areas, whereas action words frequently encountered in the context of body movements may produce meaning-related activation in the frontocentral motor areas (Braitenberg and Pulvermüller, 1992; Martin and Chao, 2001; Pulvermüller, 1996, 2003). To our knowledge, we provide here the first compelling evidence that word-meaning processing elicits specific activity patterns in frontocentral action-related areas, including motor and premotor cortex.

The motor system is a convenient place to examine this theory, given that the cortical representations of the face, arm, and leg are discrete and somatotopically organized in the motor and premotor cortex (Leyton and Sherrington, 1917; Penfield and Rasmussen, 1950; Rizzolatti and Luppino, 2001) (Figure 1A). In the case of words referring to actions performed with the face, arm, or leg, neurons processing the word form and those processing the referent action should frequently fire together and thus become more strongly linked, resulting in word-related networks overlapping with motor and premotor cortex in a somatotopic fashion (Pulvermüller, 1999). Following up on earlier neurophysiological work (Pulvermüller et al., 2001), we tested this proposal in an fMRI study and here provide evidence that action words from different semantic subcategories (referring to movement of parts of the face, arm, or leg) activate the motor cortex in a somatotopic fashion that overlaps in premotor and motor cortex with the activation pattern observed for actual movements of the relevant body parts.

In order to find appropriate stimulus words, a rating study was first performed to evaluate semantic properties of a large number of English words. Subjects were asked to rate words according to their action and visual associations and to make explicit whether the words referred to and reminded them of leg, arm, and face movements that they could perform themselves (Figure 1B). From the rated material, 50 words from each of the three semantic subcategories were selected and presented in a passive reading task to 14 right-handed volunteers, while hemodynamic activity was monitored using event-related fMRI. The word groups were matched for important variables, including word length, imageability, and standardized lexical frequency, in order to minimize physical or psycholinguistic differences that could influence the hemodynamic response. To identify the motor cortex in each volunteer individually, localizer scans were also performed, during which subjects had to move their left or right foot, left or right index finger, or tongue.

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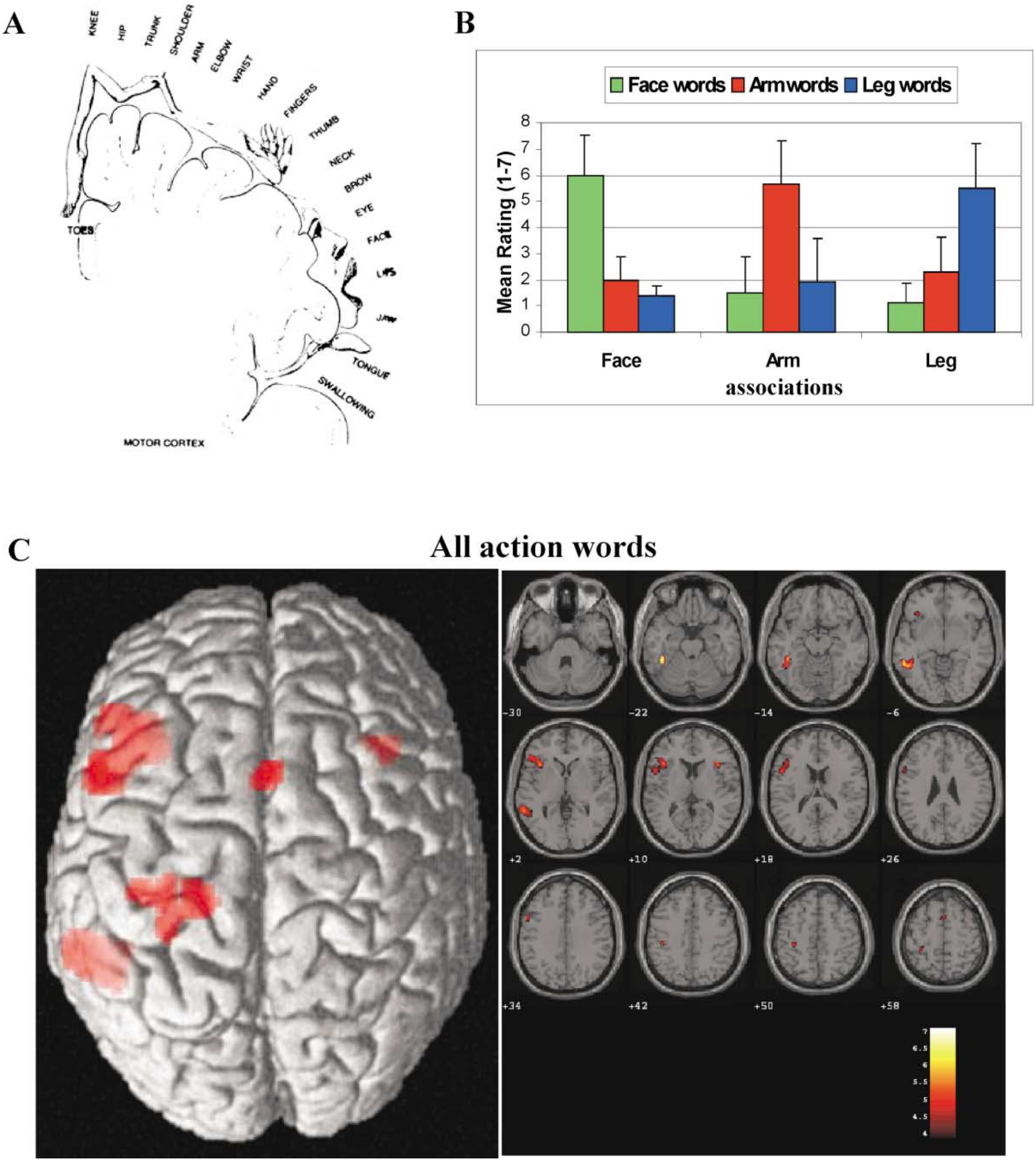

Figure 1. Action Words Activate Classical Language Areas as well as Frontocentral Motor Regions

(A) Illustration of the somatotopic organization of the motor cortex (after Penfield and Rasmussen, 1950).

(B) Mean ratings for the word stimuli obtained from study participants. Subjects were asked to give ratings on a 7 point scale whether the words reminded them of face, arm, and leg actions. The word groups are clearly dissociated semantically (face-, arm-, and leg-related words).

(C) Activation produced by all action words pooled together ($p < 0.001$, $k > 33$). Results are rendered on a standard brain surface (left) and on axial slices of the same brain (right). Numbers below separate slices indicate z coordinates in MNI space.

Results and Discussion

Comparison of all action words to the baseline (Table 1, Figure 1C) revealed activation in the left fusiform gyrus (focus at standardized stereotaxic coordinate −42 −40 −20), a region that is close to an area that has been called the visual word form area (center at −42 −57 −15; Dehaene et al., 2002). However, left inferior temporal cortex is also well-known to contribute to semantic processing (area around −44 −62 −16; see Price and Friston, 1997), and so activation seen in the present study may reflect processes of meaning access common to all words under study (Devlin et al., 2002; Tyler and Moss, 2001). Importantly, passive word reading activated left inferior frontal cortex, and there was also activation along the precentral gyrus (motor cortex) and posterior middle frontal gyrus (premotor cortex). This confirms earlier reports that processing of action-

Table 1. Coordinates and Statistics for Activation Peaks Produced by All Action Words and by Separate Subcategories of Action Words

Brain Region	MNI x/y/z	T(13)
All action words		
Fusiform gyrus	LH: −42/−40/−20	7.06
Inferior frontal gyrus	LH: −36/20/4	6.22
	LH: −50/12/14	5.53
	RH: 38/20/10	5.41
Precentral gyrus	LH: −32/−38/60	4.82
	RH: 38/20/10	5.41
Superior prefrontal gyrus	RH: 2/12/56	4.69
Face words		
Inferior frontal gyrus	LH: −50/10/20	7.43
	RH: 54/18/20	6.26
Arm words		
Middle frontal gyrus	LH: −22/2/64	4.65
	RH: 32/−12/48	5.51
Precentral gyrus	LH: −38/−20/48	4.61
Leg words		
Pre- and postcentral gyrus	LH: −22/−3/64	6.13
Superior frontal gyrus	RH: 2/8/54	4.56
Dorsomedial frontal region	LH: −8/−26/64	4.52

related words activates premotor cortex (Martin et al., 1996) in addition to the activation of areas known to contribute unspecifically to the processing of all types of words and concepts. Our present results indicate that such action-related activation can involve primary motor cortex and does not require a linguistic task (e.g., naming) but is elicited by stimulus words per se, even in a passive reading task.

The prediction under investigation in the present study concerns possible differences between the cortical activation patterns elicited by action words of different semantic subcategories and, more specifically, their relation to motor areas. The body movements studied in the localizer task were accompanied by regionally specific increases in hemodynamic activity covering the motor and somatosensory areas in the pre- and postcentral gyri (Figure 2A). As expected, tongue movements (shown in green) activated inferior-frontal areas, finger movements (red) produced activation in a dorsolateral area, and foot movements (blue) produced dorsal activation on the midline.

Figure 2B shows the activity pattern elicited by face-, arm-, and leg-related words compared to the baseline condition (viewing hash marks). The left-hemispheric inferior-temporal and inferior-frontal gyrus foci were seen for all three word types alike. Face words (areas highlighted in green) specifically activated inferior-frontal premotor areas bilaterally. Specific activation for arm words (in red) was found dorsal to these in the premotor cortex in the middle frontal gyrus bilaterally and in the motor cortex in the precentral gyrus of the left hemisphere. Leg words (in blue) produced specific foci in dorsal areas in left and midline pre- and postcentral gyri and in dorsal premotor cortex on the midline. This pattern is consistent with a somatotopic organization of cortical activity induced by action words along the motor strip and in premotor cortex. A relationship between action and action word processing is further suggested by the resemblance of the action- and word-evoked hemodynamic changes documented in Figures 2A and 2B.

The mean parameter estimates for the action word-specific activation clusters in the left hemisphere (shown in Figure 2B) are presented in Figure 2C. The diagram confirms the triple dissociation among the word categories. In each cluster, the target word category (for example, arm words for the cluster activated by arm words) shows distinctively higher parameter estimates than the other two word categories. Importantly, the remaining two categories produce parameter estimates which are both lower than for the target category and of roughly equal magnitude to each other, indicating that the triple dissociation suggested by the significance maps in Figure 2B is not just due to an appropriate choice of the significance threshold. A two way (cluster × word category) ANOVA on the parameter estimates averaged over the voxels in each cluster revealed a significant interaction of the factors cluster and word category [$F_{(4,52)} = 2.97$, $p < 0.05$].

To more precisely determine the relationship between the cortical localization of actions and action words, overlap regions were computed between corresponding conditions. Whereas tongue movements elicited activation in premotor areas just posterior to the inferior frontal patch activated by face words, the other word types and their related body movements produced significant overlapping activity in the motor cortex (Figure 2D; Table 2, bottom). Activation for finger movements overlapped with arm word-related blood flow increases in left precentral gyrus and in right middle frontal gyrus. Activation for foot movements overlapped with activation produced by leg words in dorsal premotor areas on the midline and in left dorsal pre- and postcentral gyri. These results demonstrate that the reading of words referring to actions performed with different body parts activates the motor and premotor cortex in a somatotopic fashion. Areas involved in making movements of parts of the body are also active during reading of words semantically related to movements of those same body parts. This pattern was clearly evident in the left hemisphere and was detectable in the right, nondominant, hemisphere as well.

Earlier studies in man and monkey have indicated that processing of action-related information (such as perceiving the action itself or recognizing sequential patterns) activates a system of mirror neurons in premotor cortex (Buccino et al., 2001; Rizzolatti et al., 2002; Schubotz and von Cramon, 2002). EEG results have indicated differential activation in frontocentral recording at around 200 ms, when action words from different semantic subcategories are processed (Pulvermüller et al., 2001). Here, we could precisely localize this specific activation to action word subcategories in motor and premotor cortex and demonstrate their overlap with areas contributing to action programming. It may be that multimodal mirror neurons contributing to both language and action are the basis of the observed overlap in cortical activation.

We tested the hypothesis that action words should elicit a somatotopic activation pattern within premotor and primary motor areas. This hypothesis was confirmed by our data: body part-specific primary motor activation was found for arm- and leg-related words, while premotor cortex was activated by arm- and face-related stimuli. Furthermore, we found overlap between

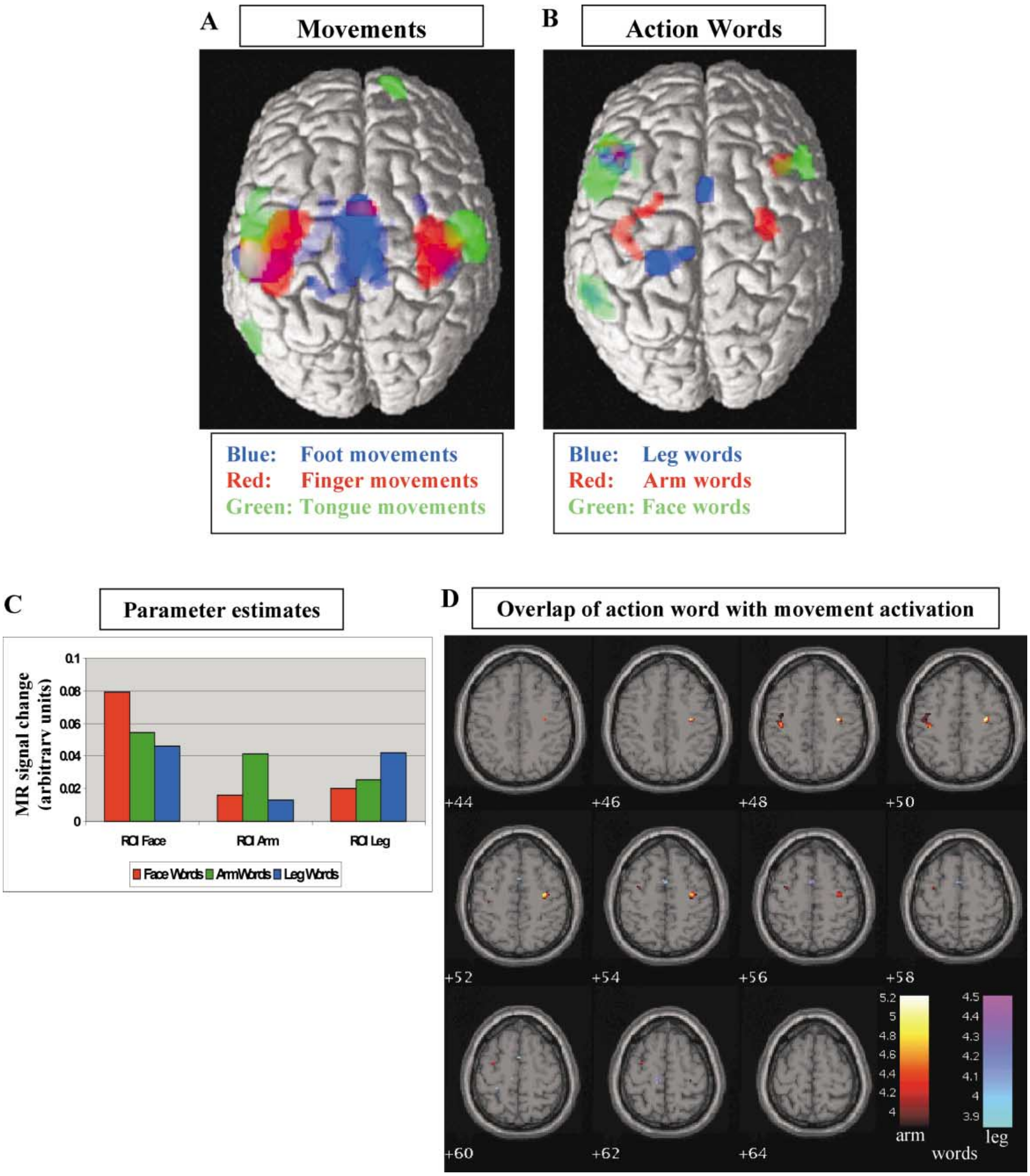

Figure 2. Brain Areas Activated by Subcategories of Action Words Are Adjacent to and Partly Overlap with Activations Produced by the Corresponding Movement Types

(A) Hemodynamic activation during tongue, finger, and foot movements (localizer scans).

(B) Hemodynamic activation during reading action words related to face (green), arm (red), and leg (blue) movements ($p < 0.001$, $k > 33$). Results are rendered on a standard brain surface.

(C) Mean parameter estimates (in arbitrary units) for clusters differentially activated by subgroups of action words in the left hemisphere.

(D) Overlap of activation produced by “arm” and “leg” words with that produced by finger and foot movements, respectively. Numbers below separate slices label z coordinates in MNI space, and the color scales indicate t values for arm and leg word related activation separately.

activation produced by arm and leg words and the corresponding finger and foot movements but not for face word and tongue movement activation. This may be explained by the fact that the tongue is mostly involved in articulatory movements. The face words employed in our study referred to a wider range of movements involving the jaw or the whole head (such as “bite,” “chew,” etc.). The corresponding movements would not have been suitable for our localizer experiment, since they could cause severe movement artifacts. In contrast, small finger and foot movements are relatively unproblematic in the scanner, and these body parts are usually involved in movements performed with the whole arm or leg, such as in grasping or walking movements, re-

Table 2. Coordinates and Statistics for Activation Peaks Produced by Tongue, Finger, and Foot Movements along the Cortical Motor Strip, as well as for the Brain Areas in which Overlap between Those and the Action Word Activation Occurred

Brain region	MNI x/y/z	T(12)
Tongue		
Inferior frontal region	LH: −54/−20/22	8.60
	RH: 46/−16/32	6.62
Fingers		
Dorsolateral central region	LH: −36/−8/60	8.02
	RH: 38/−20/48	9.95
Feet		
Centrodorsal region	LH: −2/−10/66	7.54
	RH: 10/−18/64	7.84
Overlap of action word and movement activation		
Arm		
Middle frontal gyrus	RH: 32/12/48	5.51
Precentral gyrus	LH: −38/20/48	4.61
Leg		
Pre- and postcentral gyrus	LH: −22/−34/62	5.42
Dorsal frontal gyrus	Ct: 0/8/52	4.27

All activations listed for the overlap regions were significant after small volume correction using ROIs defined on the basis of the localizer scans ($p < 0.05$, SV corrected). LH, left hemisphere; RH, right hemisphere; Ct, central.

spectively. We investigated this issue experimentally in a separate rating study. Eight volunteers rated our stimuli on a 7 point scale according to whether the corresponding movements indeed involved the tongue, hands, or feet. We found that face-related words were rated significantly lower on "tongue involvement" (mean 3.0) than arm words on "hand involvement" (5.2) or leg words on "foot involvement" (5.1). We subjected these data to a one-way ANOVA with the factor word category and obtained a highly significant main effect [$F_{(2,14)} = 17.96$, $p < 0.001$]. The actual overlap of activity evoked by arm and leg words and that produced by finger and foot movements, and the proximity of activity related to tongue movements and that related to face words, should therefore be interpreted as strong evidence that the processing of action words involves brain areas within primary motor or premotor cortex.

It is important to note that our subjects were kept naive about the objective of the experiment until the very end of the experimental session. Nothing in the instructions or the procedure biased their attention toward action-related aspects of the stimuli. To the contrary, they were explicitly discouraged to perform any movement in the scanner during the word reading experiment. Therefore, we consider it unlikely that the activation pattern we observed was caused by an intentional or conscious preparation or even execution of the corresponding movements.

Our results are best explained by an associative model of word processing in the brain according to which words and the actions and perceptions they regularly relate to and frequently cooccur with are cortically represented and processed by distributed neuronal assemblies with distinct cortical topographies (Pulvermüller, 1999, 2003). For action words, these assemblies appear to include neurons in specific motor and premotor areas in both hemispheres, and this motor component may be critical for the processing of these words (Neininger and Pulvermuller, 2001, 2003).

These data support a dynamic view of word meaning in the human brain. In contrast to other authors who suggest that semantics is represented in meaning-specific brain regions that process all words alike (Hickok and Poeppel, 2000; Mummery et al., 1998; Lichtheim, 1885; Price et al., 2001; Scott and Johnsrude, 2003; Wernicke, 1874), we propose that semantic representations are distributed in a systematic way throughout the entire brain. More specifically, in this study we have shown that the pattern of cortical activation elicited by an action word reflects the cortical representation of the action to which the word refers. This may indicate that one aspect of the meaning of a word, its reference, is laid down by specific corticocortical links. The pattern of hemodynamic changes induced by action words may be uniquely determined by the principle of somatotopic organization of the motor and premotor cortex and by the correlation learning principle. These two principles are sufficient for explaining the observed dependence of cortical activation on word meaning.

Experimental Procedures

Imaging Methods

Fourteen monolingual, right-handed, healthy native English speakers participated in the study. Their mean age was 25 years (SD 5). Subjects were scanned in a 3T Bruker MR system using a head coil. Echo planar imaging (EPI) sequence parameters were TR = 3.02 s, TE = 115 ms, flip angle = 90 degrees. The functional images consisted of 21 slices covering the whole brain (slice thickness 4 mm, interslice distance 1 mm, in-plane resolution 1.6 × 1.6 mm). Imaging data were processed using SPM99 software (Wellcome Department of Cognitive Neurology, London, UK).

Images were corrected for slice timing and then realigned to the first image using sinc interpolation. Phase maps were used to correct for inaccuracies resulting from inhomogeneities in the magnetic field (Cusack et al., 2003; Jezzard and Balaban, 1995). Any nonbrain parts were removed from the T1-weighted structural images using a surface model approach ("skull-stripping") (Smith, 2002). The EPI images were coregistered to these skull-stripped structural T1 images using a mutual information coregistration procedure (Maes et al., 1997). The structural MRI was normalized to the 152 subject T1 template of the Montreal Neurological Institute (MNI). The resulting transformation parameters were applied to the coregistered EPI images. During the spatial normalization process, images were resampled with a spatial resolution of $2 \times 2 \times 2$ mm^3. Finally, all normalized images were spatially smoothed with a 12 mm full-width half-maximum Gaussian kernel, globally normalized, and single-subject statistical contrasts were computed using the general linear model (Friston et al., 1998). Low-frequency noise was removed with a high-pass filter (action word experiment: time constant 60 s; localizer scans: 300 s). Group data were analyzed with a random-effects analysis. A brain locus was considered to be activated in a particular condition if 33 or more adjacent voxels all passed the threshold of $p = 0.001$ (uncorrected). Stereotaxic coordinates for voxels with maximal z values within activation clusters are reported in the MNI standard space (which resembles very closely the standardized space of Talairach and Tournoux, 1988; see Brett et al., 2002b).

For those clusters that were identified by the random-effects analysis in the language-dominant left hemisphere as differentially activated by specific action word categories (Table 1), we computed the average parameter estimates over voxels for each individual subject. This was done using the Marsbar software utility (Brett et al., 2002a). These values were subjected to an ANOVA including the factors cluster (arm-, face-, and leg-related activity foci) and word category (arm, face, and leg words). The mean values (in arbitrary units) over subjects are shown in Figure 2C.

Small Volume Correction

We hypothesized that activation produced by action words should overlap with that produced by movements as revealed by the localizer scans. A region-of-interest (ROI) analysis with small volume (SV) correction was therefore carried out; this used specific movement activations (e.g., for finger movements) as the ROI of the respective word categories (e.g., arm-related words). Small-volume analysis was carried out for both hemispheres separately. To exclude cerebellar activity and inferior brain areas that were either not consistently sampled in all subjects or suffered from geometric distortion owing to field inhomogeneities, loci with stereotaxic z coordinates lower than -10 mm were excluded. We used a threshold of $p < 0.005$ for defining the boundaries of the ROIs. Table 2 (bottom) reports the coordinates and t values for significantly activated foci ($p < 0.05$, SV corrected).

Stimuli and Experimental Design

One hundred and fifty action words, 50 from each of the categories of face-, arm-, and leg-related words, were selected using established procedures (Pulvermüller et al., 1999). They were matched for word length, standardized lexical frequency, and imageability but differed with regard to their semantic associations, as assessed in a rating study (Figure 1B). One hundred and fifty filler words with arbitrary semantic content were added in order to avoid focusing the subjects' minds on action-related aspects of the stimuli. Stimuli employed during 150 baseline trials consisted of strings of meaningless hash marks varying in length. The average length of action words and hash marks was matched. In addition, 50 null events were included in which a fixation cross remained on the screen. The SOA was 2.5 s, so that TR and SOA differed by $\sim$500 ms. Two pseudorandomized stimulus sequences were alternated between subjects. For statistical analysis, the SPM99 canonical hemodynamic response function (HRF) was used to model the activation time course.

The localizer scan always followed the action word experiment, in order not to bias the subjects' attention toward action-related aspects of the stimuli. Instructions on which extremity to move were presented visually on a computer screen. Instructions appeared on the screen for 21 s each and were repeated four times in pseudorandomized order. The predicted activation time course was modeled as a box-car function.

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