Category-specific Conceptual Processing of Color and Form in Left Fronto-temporal Cortex

To investigate the cortical basis of color and form concepts, we examined event-related functional magnetic resonance imaging (fMRI) responses to matched words related to abstract color and form information. Silent word reading elicited activity in left temporal and frontal cortex, where category-specific activity differences were also observed. Whereas color words preferentially activated anterior parahippocampal gyrus, form words evoked category-specific activity in fusiform and middle temporal gyrus as well as premotor and dorsolateral prefrontal areas in inferior and middle frontal gyri. These results demonstrate that word meanings and concepts are not processed by a unique cortical area, but by different sets of areas, each of which may contribute differentially to conceptual semantic processing. We hypothesize that the anterior parahippocampal activation to color words indexes computation of the visual feature conjunctions and disjunctions necessary for classifying visual stimuli under a color concept. The predominant premotor and prefrontal activation to form words suggests action-related information processing and may reflect the involvement of neuronal elements responding in an either-or fashion to mirror neurons related to adumbrating shapes.

Keywords: abstract concepts, fMRI, language, prefrontal cortex, reading

Introduction

A great challenge in cognitive neuroscience is to describe the cortical areas engaged in processing semantic meaning of words and concepts. Many researchers agree that temporal cortex provides a unique substrate for semantic binding. Definitions of and concepts. Many researchers agree that temporal cortex involves neuronal elements responding in an either-or fashion to mirror neurons related to adumbrating shapes.

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words (Preissl et al., 1995; Martin et al., 1996; Pulvermüller et al., 1999). Among the action words, those related to movements of the face, arm or leg activated fronto-central cortex in a somatotopic fashion (Hauk et al., 2004; Shtyrov et al., 2004), consistent with the claim that sensorimotor cortex processes action-related aspects of word meaning (Pulvermüller, 2001, 2005). These results can be explained by the so-called sensorimotor theory of conceptual and semantic processing: sensory and action-related semantic features are attached to a symbol by correlation, typically when a child perceives words in the context of specific objects and actions (Wernicke, 1874; Freud, 1891; Warrington and Shallice, 1984; Shallice, 1988; Humphreys and Forde, 2001; Kiefer and Spitzer, 2001). Because perceptions through different senses and actions are processed by different areas of cortex, this explains a dissociation into categories of knowledge; for example visually related and motor categories (Warrington and Shallice, 1984), and even fine-grained semantic categories, such as face-, arm- and leg-action words (Pulvermüller, 2001, 2005). Although the sensorimotor theory explains a range of neuropsychological dissociations in patients with disease of the brain (Humphreys and Forde, 2001) and a multitude of facts revealed by neuroimaging experiments (Pulvermüller, 1999; Martin and Chao, 2001), it has systematic difficulty explaining abstract knowledge (Grossman et al., 2002; Jackendoff, 2002). Words such as ‘rhomb’, ‘hope’ and ‘nevertheless’ do not refer to objects in the world but have abstract meaning, and the brain areas where such abstract knowledge is stored are still largely unknown.

Neuroimaging work comparing symbols with abstract and concrete meaning has shed light on the issue, but could not determine an area, or set of areas, consistently activated by abstract meaning processing. Some results suggested differential laterality: highly abstract grammatical function words such as ‘it’ and ‘the’ led to pronounced left-lateralized neurophysiological activity, which contrasted with the more bilateral responses to concrete nouns and verbs (Neville et al., 1992; Pulvermüller et al., 1995). Also, more strongly left-lateralized brain responses to abstract nouns compared with concrete nouns were revealed by event-related potential (ERP) experiments (Kounios and Holcomb, 1994). However, a general difference in laterality related to abstractness could not be confirmed (Friederici et al., 2000). Recent imaging work using functional magnetic resonance imaging (fMRI) indicated left-hemispheric correlates of abstract semantics in Broca’s area (Fiebach and Friederici, 2004), angular gyrus (Skosnik et al., 2002), superior (Wise et al., 2000) and posterior temporal cortex (Grossman et al., 2002), or a widespread set of areas including temporal pole along with inferior temporal and inferior frontal cortex (Noppeney and Price, 2004). In contrast
with previous findings of a predominantly left-hemispheric locus of abstract semantics, a few studies also reported stronger activation for abstract words relative to concrete words in different areas of the right non-dominant hemisphere (Kiehl et al., 1999; Perani et al., 1999; Grossman et al., 2002). However, consistent with the differential laterality hypothesis, a recent study by Binder and colleagues reported that concrete word identification led to activation of distributed sources in both hemispheres, whereas abstract words activated a left frontal region including areas in the inferior and middle frontal gyri and lateral premotor cortex (Binder et al., 2005).

This variability of results may be due, in part, to the fact that in all earlier studies, widely defined categories of abstract and concrete words were compared with each other. Since the brain basis of concrete action and object meaning can vary substantially, it is reasonable to assume similar local specificity for abstract concepts as well. Crucially, the cognitive abstraction processes necessary for understanding grammatical function words, such as ‘it’ or ‘nevertheless’, are fundamentally different from those related to emotionally related words, such as ‘hope’, which are, in turn, different from those triggered by words referring to visual shapes, such as ‘rhomb’. Thus, the cognitive processes of abstraction differ between subtypes of abstract words, and so may the loci of their cortical processing. To elucidate processes of abstraction, it may therefore be useful to focus on subtypes of words with specific abstract semantic features.

Here, we investigated items that still have links to action and object features, but abstract away from concrete entities by referring to form or color features many objects have in common. We looked at words semantically related to color and form, whose meaning is at an intermediate level on the continuum between highly concrete, imageable, object-related words and highly abstract words. According to the MRC Psycholinguistic Database (Coltheart, 1981; Wilson, 1988), concreteness ratings for highly concrete words are >600 (e.g. ‘mouse’, 624; ‘eye’, 634), whereas highly abstract words are rated as <400 (‘love’, 311; ‘plan’, 357). Our stimuli were in the intermediate range (between 400 and 600: ‘blonde’, 502, ‘curve’, 447). As our stimuli were carefully matched for important properties, including physical features, visual imageability, familiarity, abstractness and a range of psycholinguistic variables, a unitary semantic system approach would predict congruent activation of this system for both word categories. A version of the sensorimotor theory, however, may predict differential activation of frontal and temporal circuits as a function of the action- and object-relatedness of the semantics of the stimulus words.

Whereas a concrete word, e.g. ‘door’ directly relates to its reference object, a form or color word, e.g. ‘rectangle’, refers to a feature of most of its reference objects that needs to be separated and extracted from other object features. This visual feature extraction process can be computed by neurons in the vicinity of the areas engaged in object processing. Elementary color features of visual stimuli are processed already in primary visual cortex (Hubel, 1995) and tempo-ral-occipital areas have been found to preferentially respond to color processing (McKeefry and Zeki, 1997). To compute a color concept — which covers a range of possible colors, with different levels of brightness and saturation — several alternative feature conjunctions must be classified together, possibly by neural units at higher levels located at gradually more anterior cortical sites. Neural correlates of color concept processing may therefore be present in the temporal lobe, anterior to the temporoo-occipital and fusiform areas preferentially activated during color perception (Martin et al., 1995). In animal research, neurons in anterior peri- and entorhinal areas have been proposed to compute increasingly complex conjunctions and disjunctions of features represented by neurons in inferior temporal lobe and closer to the visual input (Bussey and Sakida, 2002; Bussey et al., 2002; Tyler et al., 2004). In the same way, concrete objects can be classified as exhibiting the same shape (e.g. rhomb shape). Establishing a form/shape concept necessitates computation of disjunctions over large sets of concrete objects and elementary visual feature. Again, the neural substrate of progressively abstract computations may be in primary visual (elementary visual features: Hubel, 1995), lateral occipital (object shapes: Kourtzi and Kanwisher, 2001) and inferior and medial temporal cortex. However, in contrast to color concepts, shape concepts always have a motor correspondence, since shapes, but not colors, can be outlined or adumbrated by specific sequences of body movements. Also, when looking at a shape, eye movements follow the shape contour. Because the form of objects can be outlined with different body parts, the brain basis of abstract form concepts may comprise sensorimotor, especially premotor cortex, where action representations are still somatotopic (Rizzolatti et al., 2001), but also neurons in prefrontal cortex related to motor planning (Fuster et al., 2000). Prefrontal cortex just anterior to premotor cortex would be ideally placed for computing conjunctions and disjunctions over sets of specific action programs and could therefore provide a neural substrate for action aspects of abstract form.

Here, we set out to investigate the brain basis of words related to abstract color and form concepts (e.g. ‘brown’, ‘blonde’ and ‘bronze’ versus ‘rhomb’, ‘square’, ‘arc’). Word groups matched for physical features, visual imageability, familiarity, abstractness and a range of psycholinguistic variables were presented in a passive reading task while event-related blood-flow changes were measured. We hypothesized that the color- and form-related meaning of these words is reflected by category-specific activation in temporal lobe, and that form-related words specifically activate premotor and prefrontal cortex.

Materials and Methods

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 3 T Bruker MR system using a head coil. Echo planar imaging (EPI) sequence parameters were $T_E = 3.02$ s, $T_R = 115$ ms, flip angle $= 90^\circ$. The functional images consisted of 21 slices covering the whole brain (slice thickness $= 4$ mm, inter-slice distance $1$ mm, in-plane resolution $1.6 \times 1.6$ mm, FOV $20$ cm, matrix size $21 \times 128 \times 128$). Imaging data were processed using SPM99 software (Wellcome Department of Cognitive Neurology, London).

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 (Jezzard and Balaban, 1999; Cusack et al., 2003). Any non-brain parts were removed from the $T_1$-weighted structural images using a surface model approach (‘skull-stripping’) (Smith, 2002). The EPI images were co-registered to these skull-stripped structural $T_1$-images using a mutual information co-registration procedure (Maes et al., 1997). The structural MRI was normalized to the 152 subject $T_1$ template of the Montreal Neurological Institute (MNI). The resulting transformation parameters were applied to the co-registered EPI images. During the spatial normalization process, images were resampled with a spatial resolution
of 2 × 2 × 2 mm³. 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 with time constant 60 s. Group data were analyzed with a random-effects analysis. A brain locus was considered to be activated in a particular condition if 20 or more adjacent voxels all passed the threshold of $P = 0.001$ (uncorrected). In some cases, correction for multiple comparisons in the left hemisphere was administered using the False Discovery Rate correction approach ($P < 0.05$) (Genovese et al., 2002). Stereotaxic coordinates for voxels with maximal $z$-values within activation clusters are reported in Talairach space (Talairach and Tournoux, 1988).

Clusters in the left language-dominant hemisphere, which were found to be active in the random-effects analysis of the contrast words versus matched hash mark stings (Fig. 1), were used to define three ‘canonical’ regions of interest (ROIs), in inferior frontal (IF), fusiform (FUS) and parahippocampal gyrus (PH) respectively (see Table 1). Additional ‘supplementary’ ROIs were defined on the basis of earlier findings. Since previous research found an area in the middle temporal gyrus whose activation related to semantic and lexical processing (Chao et al., 1999; Devlin et al., 2004), a middle temporal gyrus (MT) ROI was selected ($3 \times 3 \times 3$ voxels centered at $-60/-40/0$). Because a large proportion of precentral gyrus was activated by action words in an earlier study (Hauk et al., 2004) and recent work indicated involvement of premotor cortex in abstract word processing (Binder et al., 2005), possible involvement of premotor cortex dorsal to the inferior frontal language area was probed ($-45/0/35$). As abstract action concept processing was predicted in dorsolateral prefrontal cortex and earlier work confirmed involvement of the middle frontal gyrus in abstract concept processing (Binder et al., 2005), an additional ROI was placed in a dorsolateral prefrontal area and anterior to premotor cortex ($-50/25$). Previous research has documented activation of this region in a range of tasks tapping into typical prefrontal functions, as for example, abstract mappings between stimuli and responses (Duncan and Owen, 2000). For each subject and each of the six ROIs, average parameter estimates over voxels were calculated. These values were subjected to ANOVAs including the factors Region of Interest and Word Category (color and form). An additional ANOVA was carried out separately on data from canonical ROIs only. Paired two-tailed $t$-tests were used as planned comparison tests for between condition differences in individual ROIs. The mean values scaled to HRF-peak percentage signal change relative to the mean over all voxels and scans within the corresponding ROI and standard errors over subjects are shown in Figure 2.

**Stimuli and Experimental Design**
Words semantically related to visual information, 50 color- and 50 form-related items, were selected using established procedures (Pulvermüller et al., 1999). Stimulus groups were matched for word length counted in letters and syllables (4.3 versus 4.1 letters, all monosyllabic), standardized lexical frequency (27.9 versus 50.9 occurrences/million words: Francis and Kucera, 1982) (also matched according to Baayen et al., 1993), imageability and concreteness/abstractness [mean concreteness ratings (SE): 533 (9.2) versus 522 (8.6); Coltheart, 1981; Wilson, 1988].

![Figure 1. Cortical activation during passive reading of concrete words semantically related to visual information ($P = 0.001$, uncorrected). A lateral view is shown on the upper left and frontal slices of an average brain are displayed from top left to bottom right. The diagram at the bottom left gives semantic ratings (and their standard errors) for color and form words; ratings of semantic relatedness to general visual information, form information and color information are given (see Materials and Methods).](https://academic.oup.com/cercor/article-abstract/16/8/1193/455594/16951284)
Stimulus word groups were also matched for their semantic relationship to objects that can be visually perceived, but from which they differed in terms of their semantic relatedness to shape and color, as assessed in a rating study (Fig. 1, bottom). Subjects were asked whether they considered the word as being semantically related to (i) an object that can be perceived visually, (ii) a visual shape or form and (iii) a color. Ratings were given on a scale from 1 to 7, following procedures described in an earlier publication (Hauk and Pulvermüller, 2004). One hundred and fifty filler words and 50 pseudo-words were added in order to avoid focussing the subjects’ attention on specific aspects of the stimuli. The filler words included the face- and arm-related words used in the study by Hauk and colleagues (Hauk, 2004). Stimuli employed during 150 baseline trials consisted of strings of meaningless hash marks varying in length and matched to the word stimuli in length. In addition, 50 null events were included during which a fixation cross remained displayed. Stimuli were presented for 100 ms, and the stimulus onset asynchrony (SOA) between two stimuli was 2.5 s, so that stimulus presentation and scanner trigger were out of phase by ~500 ms. Two pseudo-randomized stimulus sequences were alternated between subjects. For statistical analysis, the SPM99 canonical haemodynamic response function (HRF) was used to model the activation time course.

Results

Words activated an area in the left fusiform gyrus in the inferior temporal lobe (activation peaks at ~36/-38/-24 and ~42/-47/-13) close to and overlapping with the site labeled the visual word form area (VWFA, ~42/-57/-15; McCandliss et al., 2003). In addition, an area of inferior frontal cortex comprising the posterior part of Broca’s area, Brodmann’s area 44, and its anterior section, Brodmann area 45, became active (activation peaks at ~52/10/20 and ~46/28/12). The activation of the VWFA together with inferior frontal areas during passive reading of single words is consistent with earlier findings (e.g. Dehaene et al., 2002; Hauk et al., 2004). There was an additional activation focus in anterior parahippocampal gyrus (~28/-12/-18; see Fig. 1, Table 1). No significant activation was seen in the right hemisphere.

Comparison of color and form words showed that both word categories activated the inferior temporal VWFA. This activation...
General Word-related Activation

Passive reading of all word stimuli grouped together led to enhanced blood flow in the left temporal lobe, in fusiform cortex, anterior to an area previously related to the processing of prelexical word-related or letter string information (Cohen et al., 2000; Dehaene et al., 2002). Because the stimulus words under study were highly imageable and semantically related to objects known through the visual channel, the present data are also open to the interpretation that word-evoked fusiform activation indicates semantic processing (Price, 2000; Price and Devlin, 2003). In this context, it is noteworthy that the fusiform activation maximum elicited by color words was posterior to that elicited by form words, and that fusiform activation was generally stronger for form words than for color words. This argues in favor of a semantic origin of the present fusiform activation, i.e. a specialization of subareas of fusiform gyrus in the conceptual processing of color and/or form information. Apart from temporal cortex, left-inferior frontal cortex, including Broca’s area, was also generally activated by all word forms. This confirms earlier reports on a general role of this brain region in word processing (Price et al., 1996; Binder et al., 1997; Pulvermüller et al., 2003; Wilson et al., 2004). The inferior-frontal neurons included in word-related neuronal ensembles would thus be activated not only during speech but during language comprehension as well (Pulvermüller and Preisig, 1991). The role of these inferior frontal neurons may be analogous to that of mirror neurons with a role in action control but also responding to perceptual aspects of actions (Gallese et al., 1996; Iacoboni et al., 1999; Rizzolatti et al., 2001; Kohler et al., 2002). The present study confirms earlier reports on a general role of this brain region in word processing (Price et al., 1996; Binder et al., 1997; Pulvermüller et al., 2003; Wilson et al., 2004). The inferior-frontal neurons included in word-related neuronal ensembles would thus be activated not only during speech but during language comprehension as well (Pulvermüller and Preisig, 1991). The role of these inferior frontal neurons may be analogous to that of mirror neurons with a role in action control but also responding to perceptual aspects of actions (Gallese et al., 1996; Iacoboni et al., 1999; Rizzolatti et al., 2001; Kohler et al., 2002). In this case acoustic signals uniquely identifying lexical elements (Fadiga et al., 2002). However, we cannot decide on the basis of the present neuroimaging data whether the inferior frontal activation is due to mirror neurons or to canonical multimodal neurons that do not respond specifically to actions, but rather to objects involved in actions (Rizzolatti and Craighero, 2004). The left-hemispheric parahippocampal activation not generally seen for words could tentatively be attributed to the abstract meaning aspects of the stimulus words (but see Discussion below).

Category-specific Semantic Activation

Category-specific activation was reported in a variety of earlier studies (e.g. Dehaene, 1995; Martin et al., 1995, 1996). However, as argued previously (for review, see Pulvermüller, 1999), much earlier work did not control for important physical, psychological and psycholinguistic stimulus features, therefore making it difficult to draw inferences on a semantic origin of the observed effects. Although category-specific brain activation was not always observed when these factors were empirically assessed and controlled for (Devlin et al., 2002), a number of studies confirmed differences between the brain activation patterns elicited by words from different semantic categories. Differences were found between widely defined and increasingly specific categories, ranging from content and function words, nouns and verbs, animal and tool names, to action word subtypes with different meaning (e.g. Brown and Lehmann, 1979; Preisig et al., 1995; Pulvermüller et al., 1995, 2005; Cappa et al., 1998, 1997; Chao et al., 1999; Kiefer, 2001; Hauk et al., 2004; Devlin et al., 2005). The present study provided particularly extensive stimulus control and matching of word categories for variables including word length,
standardized lexical frequency, familiarity, abstractness, imageability and the degree to which the words were semantically related to visually perceivable objects. On the other hand, empirical evidence was gathered that stimulus groups differed significantly on semantic scales of color- and form-relatedness (Fig. 1), a difference at the cognitive level that was reflected by differential activations of a range of cortical areas. The differential activation to color and form words in different sets of regions of interest argues in favor of an interpretation in terms of semantic and conceptual information linked to the word stimuli at an abstract level.

Specific Activation in Temporal Lobe
Our results provide evidence that cortical areas differentially contribute to the semantics of color and form words and therefore support established theories of category-specific semantic processes in human cortex (Warrington and McCarthy, 1983; Shallice, 1988). Information about color and form is mainly extracted from the visual input and therefore cortical processing differences were expected in the inferior-temporal ventral stream of visual processing. The observed category differences in fusiform gyrus and middle temporal gyrus are consistent with previous imaging work and neuropsychological studies revealing distinct inferior temporal systems preferentially engaging in color and form processing (e.g. Martin et al., 1995; Martin and Chao, 2001; McClelland and Rogers, 2003). An explanation in terms of different inferior temporal neural systems specialized for color and form information can account for the differential activation of fusiform gyrus, in particular the 12 mm distance between form and color word maxima. The specific activation of parahippocampal cortex to color words is consistent with results of recent studies of fine-grained neuro-psychological deficits in processing color-knowledge related to objects, suggesting that the mesial temporal structures are specifically involved in representing or accessing object color knowledge (Miceli et al., 2001).

As color and form words differentially activated areas in parahippocampal, fusiform and middle temporal gyrus, it might be possible to relate these differences to aspects of the meaning of these stimuli. Parahippocampal activation specific to color words can tentatively be explained by the visual feature conjunction model (Bussey and Saksida, 2002; Bussey et al., 2002): to classify visual information under a concept, such as a color, logical operations including ‘and’ and ‘either-or’ computations need to be performed by neural elements over a range of input patterns. It is well known that this requires additional sets of neural elements operating on the input (Kleene, 1956; Minsky and Papert, 1969; McClelland and Rumelhart, 1985), which in the inferior visual stream must be located progressively anterior to visual cortex. It is possible that feature conjunctions and disjunctions for color concepts, e.g. binding the different tones and luminances covered by a given color concept, are computed by parahippocampal neurons receiving input from posterior color-related inferior temporal areas. This is consistent with the idea that aspects of color concepts linked to words are processed by anterior temporal sites, thereby supporting the posterior-anterior model of visual feature abstraction (Bussey and Saksida, 2002; Bussey et al., 2002; Tyler et al., 2004). However, as form words did not activate parahippocampal cortex although their meaning, similarly to color words, is abstract and independent of any specific object (feature conjunctions and disjunctions), it appears that other areas in temporal cortex can contribute to conjunctive processing too. For form words, the fusiform and middle temporal cortices are relevant here and the suggestion may therefore be that there are different streams in temporal lobe that can play a category-specific role in feature conjunction or disjunction processing.

Specific Activation in Frontal Lobe
All words under study were strongly related to visually defined perceptual information, but lacked any obvious action meaning, as, for example, tool names and action verbs usually do. Established theories of category-specificity would therefore predict activity differences between color and form words related to visual information processing in temporal lobe, but not in frontal cortex. The specific inferior frontal and middle frontal activation to form words can be tentatively accounted for as follows. An action relationship of form words is evident from the fact that a shape or form can always be outlined or adumbrated by a specific set of body movements. Premotor activation seen for form words may therefore be related to implicit action aspects of the meaning of form words. However, there is a clear difference between the action relatedness of a concrete action word, e.g. ‘kick’, and an abstract form word, e.g. ‘rhomb’. The former relates to a defined body part whereas

Figure 3. Lateral view of the brain with activation maps for abstract form/shape words (in red) contrasted with the areas activated by concrete action words related to specific body parts (face in blue, arm in green; diagram on the left) and actions performed with these body parts (diagram on the right) (cutoffs: $P < 0.001$, uncorrected, for words, $P < 0.05$, FDR-corrected, for actions). Note that form words elicited prefrontal activation in the first and second frontal gyrus not evoked by concrete action words or actions (yellow circle). All word activations overlapped in the left inferior frontal cortex (white area, diagram on the left) but actions and abstract word processing did not elicit overlapping activation patterns (right diagram).
the latter refers to a shape that can be adumbrated using the hand or finger, but equally well by a head movement or a series of saccades. The form-related action concept should therefore include information that abstracts away the body part information but leaves open the alternatives of using different body parts for perceptually related actions, which we could expect in prefrontal cortex adjacent to premotor areas.

To directly test this prediction, an experiment on action words related to different body parts (face-, arm- and leg-related action words, such as ‘lick’, ‘pick’ and ‘kick’, see Hauk et al., 2004) was done with the participants in the color-/form-word study (see Materials and Methods). Consistent with the earlier findings, face- and arm-words produced somatotopic activation in motor and premotor cortex, which partly overlapped with activation during movements of corresponding body parts. The left inferior-frontal activation to form words overlapped with action word activation (Fig. 3, diagram on the left), but no clear overlap was seen between word activation and the precentral activation observed during simple body movements (diagram on the right). Crucially, frontal activation elicited by form words was not restricted to premotor areas (as for concrete action words), but extended into prefrontal cortex in both inferior and middle frontal gyri including Brodmann areas 9 and 46. These areas are anterior to premotor cortex and therefore ideally located for controlling premotor activity. We suggest that the dorso-lateral prefrontal activation specific to form words relates to the activation of neural networks computing conjunctions and disjunctions on concrete action patterns therefore specifying action concepts at an abstract level. The activation of a left inferior frontal area, including middle frontal gyrus and premotor cortex, is consistent with earlier findings about abstract words in general (Binder et al., 2005). As the premotor activation, which reached significance for form words, did not reliably differentiate this word category from color words, the dorso-lateral prefrontal focus seen more active for form than color words might be of particular functional relevance for computing abstract form-related action concepts (yellow circles in Fig. 3).

Conclusion

On the basis of these data, the sensorimotor theory of conceptual and semantic processing (Warrington and Shallice, 1984; Humphreys and Forde, 2001) can be extended to incorporate a model of concepts that may be considered as partially abstract. Neuron populations storing abstract concepts would accordingly be housed in areas adjacent to, and connected with, areas where more elementary and concrete concepts are laid down. Modality-specific systems may be located in inferior temporal, middle temporal and parahippocampal gyri that compute feature conjunctions and dysjunctions on visual form and color features. The mirror and/or canonical neuron system in premotor cortex as a site where actions and perceptions are linked together offers a unique basis for action-related abstraction, which could be carried out by neurons in the adjacent prefrontal cortex performing either-or operations on motor patterns stored in premotor cortex. This view, which covers partially abstract concepts still grounded in action or visual concepts, suggests similar mechanisms of abstraction in different cortical lobes for specific abstract categories. Although future research is necessary to decide whether this view can be generalized to the various types of abstract words and concepts, corroborating evidence from studies of highly abstract lexical items suggests that the prefrontal circuits play a general role in the computation of abstract semantic information.

In conclusion, we report evidence that two subtypes of partially abstract concepts have their respective brain basis in specific temporal and frontal areas. Color/form word-evoked category-specific activation in fusiform, middle temporal and inferior frontal gyri may be shared in part with other semantic categories. Specific activation in dorsolateral prefrontal and parahippocampal gyri may be most characteristic for abstraction processes necessary for classifying sensory and motor patterns into color and form concepts.

Notes

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