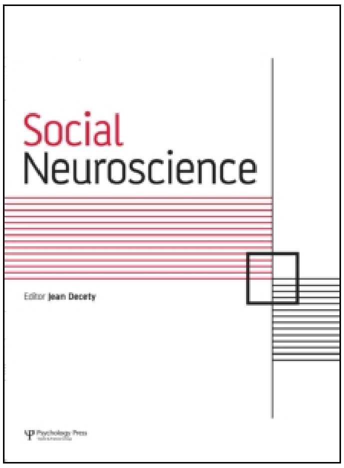

Social Neuroscience
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t741771143

Modulation of the FFA and PPA by language related to faces and places

Lisa Aziz-Zadeh[ab]; Christian J. Fiebach[cd]; Srini Naranayan[ce]; Jerome Feldman[ce]; Ellen Dodge[ce]; Richard B. Ivry[c]
[a] University of California and International Computer Science Institute, Berkeley, California, USA [b] University of Southern California, Los Angeles, California, USA [c] University of California, Berkeley, California, USA [d] University of Heidelberg, Heidelberg, Germany [e] USA International Computer Science Institute, Berkeley, California, USA

First published on: 31 May 2007

To cite this Article Aziz-Zadeh, Lisa , Fiebach, Christian J. , Naranayan, Srini , Feldman, Jerome , Dodge, Ellen and Ivry, Richard B.(2008) 'Modulation of the FFA and PPA by language related to faces and places', Social Neuroscience, 3: 3, 229 — 238, First published on: 31 May 2007 (iFirst)

To link to this Article: DOI: 10.1080/17470910701414604

URL: http://dx.doi.org/10.1080/17470910701414604

SOCIAL NEUROSCIENCE, 2008, 3 (3–4), 229–238
Psychology Press
Taylor & Francis Group

Modulation of the FFA and PPA by language related to faces and places

Lisa Aziz-Zadeh
University of California and International Computer Science Institute, Berkeley, and University of Southern California, Los Angeles, California, USA

Christian J. Fiebach
University of California, Berkeley, California, USA, and University of Heidelberg, Heidelberg, Germany

Srini Naranayan, Jerome Feldman, and Ellen Dodge
University of California, and USA International Computer Science Institute, Berkeley, California, USA

Richard B. Ivry
University of California, Berkeley, California, USA

Does sentence comprehension related to faces modulate activity in the fusiform face area (FFA) and does sentence comprehension related to places modulate activity in the parahippocampal place area (PPA)? We investigated this question in an fMRI experiment. Participants listened to sentences describing faces, places, or objects, with the latter serving as a control condition. In a separate run, we localized the FFA and PPA in each participant using a perceptual task. We observed a significant interaction between the region of interest (FFA vs. PPA) and sentence type (face vs. place). Activity in the left FFA was modulated by face sentences and in the left PPA was modulated by place sentences. Surprisingly, activation in each region of interest was *reduced* when listening to sentences requiring semantic analysis related to that region's domain specificity. No modulation was found in the corresponding right hemisphere ROIs. We conclude that processing sentences may involve inhibition of some visual processing areas in a content-specific manner. Furthermore, our data indicate that this semantic-based modulation is restricted to the left hemisphere. We discuss how these results may constrain neural models of embodied semantics.

INTRODUCTION

The theory of embodied semantics states that conceptual representations accessed during linguistic processing include sensory and/or motor representations related to the concept in question (Barsalou, 1999; Feldman & Narayanan, 2004; Gallese & Lakoff, 2005; Glenberg, 1997; Glenberg

---

Correspondence should be addressed to: Lisa Aziz-Zadeh, University of Southern California, 3641 Watt Way, Ste. B20, Los Angeles, CA 90089–2520, USA. E-mail: lisa.azizzadeh@usc.edu

This study was supported by a NIH grant (P01 NS40813) and the Klaus Tschira Foundation. CJF was supported by an Emmy-Noether grant from the German Research Foundation (DFG).

We thank Stephen M. Wilson and Miriam R. L. Petruck for their assistance with this study and members of Mark D'Esposito's laboratory at UC Berkeley for providing stimuli for the localizer task.

www.psypress.com/socialneuroscience DOI:10.1080/17470910701414604

& Kaschak, 2002; Lakoff & Johnson, 1999). This idea has been supported by studies showing activation in motor areas during the comprehension of action phrases (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermuller, 2004; Hauk & Pulvermuller, 2004; Tettamanti et al., 2005). Moreover, the activation in premotor cortex is, to some degree, somatotopic. For example, phrases such as "grasping" activate premotor areas responsive to hand actions while phrases such as "kicking" activate premotor areas responsive to foot actions. Thus, premotor areas engaged during action production also respond during action observation (Buccino et al., 2001; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004) and during language-based action comprehension (Aziz-Zadeh et al., 2006; Hauk et al., 2004; Tettamanti et al., 2005) in an effector-specific manner. The effects of action-related modulation during language comprehension appear to be limited to the left hemisphere.

While premotor areas show increased activity during action observation, listening to action sounds (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Gazzola, Aziz-Zadeh, & Keysers, 2006), or semantic comprehension, primary motor areas appear to be inhibited during semantic comprehension (Buccino et al., 2005).[1] This is in contrast to action observation, which activates both premotor and primary motor areas in a somatotopic fashion (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Buccino et al., 2001). Thus, the direction of modulation appears to depend on the level or role of a particular area within a distributed network.

Various hypotheses, overlapping to some degree, have been suggested to account for the dissociation between the engagement of primary and secondary motor areas during language comprehension. First, it has been proposed that conceptual knowledge requires multimodal representations (Geschwind, 1964). Premotor areas are activated by execution, observation, and sounds of actions, suggesting relatively abstract, multimodal representations of actions. Activation in primary motor areas is more closely linked to planned or executed actions. Thus the primary motor cortex might be unfit for providing a "convergence zone" for abstract semantic representation, though it might participate in a network for conceptual representation at a different level (Damasio, 1989; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004).

Second, inhibition of primary motor cortex during linguistic comprehension of action phrases may relate to the fact that language requires more general, abstract representations than those engaged during motor execution. Consider the concept "grasp". In the primary motor cortex, the motor repertoire for grasping may engage a specific configuration of the hand, with associated recruitment of a specific set of muscles, forces, and other parameters related to a particular instance of grasping. The general concept "grasp," however, may not code these specific representations. Thus it is possible that gesture-specific representations in primary motor cortex might need to be inhibited for a more generalized conceptual representation (Buccino et al., 2005).

Third, inhibition of primary motor cortex may be needed to prevent the movement of the limb during language comprehension given the recruitment of conceptual representations that include premotor areas. In a theoretical review on the link between language and motor representations, Gallese and Lakoff (2005) argued that primary sensorimotor areas, in contrast with secondary areas, should be inhibited to minimize cross-talk between the general representation of a given concept and its actualization.

While embodied semantics potentially applies to many kinds of concepts, less attention has been given to the engagement of areas outside of the motor system. Considering concepts beyond

---

[1] In addition to the study by Buccino et al. (2005), which shows inhibition, a study by Pulvermuller's group may also indicate inhibition. Pulvermuller et al. had participants perform a vocal lexical decision task while TMS was applied to different regions of motor cortex (Pulvermuller, Hauk, Nikulin, & Ilmoniemi, 2005). RTs were facilitated in an effector-specific manner; e.g., judgments of hand-related words were faster when TMS was applied over the hand area compared to the foot area. They interpreted these results as consistent with the notion that activation of motor cortex supports effector-specific lexical retrieval. However, if the TMS pulses are considered to add noise, then one could argue that the effector-specific improvements in RT might be due to the transient disruption of potentially competing signals from motor cortex. For example, judging that the letters "POKE" spell a hand-action word might be faster if a representation of the current posture of the hand is disrupted. Three points suggest that this alternative interpretation is more parsimonious. First, the effects of single-pulse TMS are usually viewed as disruptive to normal processing, rather than facilitatory. Second, a main effect on RT was associated with hand area TMS, a result attributed to the spread of interference effects to the mouth area. Third, this interpretation is consistent with the more direct assay provided by Buccino et al. (2005).

action representation, embodied semantics might predict that concepts regarding visual movement (i.e., a phrase like ‘‘flew past me’’) would modulate activity in MT, concepts regarding ‘‘hearing’’ would modulate temporal auditory cortex, and so forth. However, to our knowledge, only one neuroimaging study has directly evaluated how functionally localized perceptual areas are modulated by linguistic tasks related to that perceptual domain; Chao and Martin (1999) reported that overlapping voxels in the lingual gyrus and the inferior temporal cortex were active for both color perception and color naming.

Here we consider conceptual representation of faces and places. There is now considerable evidence that the visual processing of faces and places activates differential brain areas: the fusiform face area (FFA) and the parahippocampal place area (PPA), respectively (Epstein, Harris, Stanley, & Kanwisher, 1999; Kanwisher, 2001; O’Craven & Kanwisher, 2000). We examined whether language related to faces would modulate activity in the FFA and language related to places would modulate activity in the PPA. In order to circumvent the notorious issues of intersubject variability (Mazziotta et al., 2001), we looked for a congruence between observation of faces/places and language related to faces/places at a subject by subject level. We predicted that sentence comprehension would lead to domain-specific modulation of activation in these regions of interest, and that this modulation would be especially pronounced in the left hemisphere. We did not have strong a priori predictions concerning the direction of this modulation. If activity in FFA and PPA is related to multimodal abstract representations of faces and places, respectively, then we might expect to see a domain-specific increase in activation during sentence comprehension, akin to what has been observed in premotor cortex during action comprehension. Alternatively, if FFA and PPA are more analogous to motor cortex, serving as ‘‘primary’’ processors for face and place perception, then we might expect the modulation to be one of inhibition.

METHODS

Participants

Fourteen healthy right-handed volunteers participated in the study. Three subjects were not included in the analyses due to excessive noise and/or movement in their functional data. Thus 11 subjects contributed to the analyses (7 men, 4 women; mean age = 22.5; range = 18–39). All participants gave informed consent and the study was approved by University of California, Berkeley, Committee for the Protection of Human Subjects. All participants had normal or corrected-to-normal vision. Prior to scanning, participants completed a screening questionnaire to exclude participants who were on prohibited medications or had a history of neurological or psychiatric disorders, substance abuse and other proscribed medical conditions.

Stimuli

The stimulus set consisted of a total of 240 auditory digitized sentences. All sentences were recorded using the voice of a native Californian female speaker and were grouped into five semantic categories. For two of the categories, the sentences focused on facial features, either related to a famous face (e.g., ‘‘George Bush has wrinkles around his eyes’’) or a generic face (e.g., ‘‘The farmer has freckles on his cheeks’’). Similarly, two of the categories involved sentences pertaining to places, either related to a famous place (e.g., ‘‘The Taj Majal faces a long thin reflecting pool’’) or a generic place (e.g., ‘‘The house has a couch near the fireplace’’). The fifth category was of control sentences. These referred to generic objects (e.g., ‘‘The television has a long antenna’’). Our aim was to describe a person’s face or a specific scene without directly mentioning the word ‘‘face’’ or ‘‘place.’’ For each face and place category, 36 sentences were constructed in which the semantics constituted an accurate or reasonable statement. In addition, there were 4 other sentences in which the semantics constituted an inaccurate or unreasonable statement (e.g., ‘‘Marilyn Monroe has a large square jaw’’). We constructed 80 control sentences describing objects, 72 of which entailed reasonable declarative statements and 8 of which entailed unreasonable statements (e.g., ‘‘The cell phone has signal from other planets’’). Half of these were used in the face run and the other half were used in the place run (see below). The five categories were matched in terms of word length and number of syllables (average syllable length per condition = 11). We also did extensive pretesting in an attempt to match the sentences for understandability and difficulty. During pretesting, subjects were accurate on over 95% of the trials and reaction times were similar across the different conditions (average 3 seconds from trial onset).

Procedures

Each participant completed three functional runs in the scanner. In the first run, subjects listened to sentences pertaining to generic faces, generic places, and control objects. In the second run, subjects listened to sentences pertaining to famous faces, famous places, and a different set of control objects. Forty sentences of each type were presented in each run for a total of 120 sentences. Each sentence was presented on average for 2.88 s. Sentences were presented over headphones using an MR confon (Magdeburg, Germany) audio system. The total duration of these 2 language runs was 18 minutes and 20 s. Each run began with 20 s (10 TRs) of dummy scans, which were excluded from the analyses. We used a jittered intertrial interval (6, 8, or 10 s) and BOLD responses during these intertrial intervals constituted the resting baseline. A cross-hair was visually present at the center of the screen during all trials and participants were asked to maintain fixation at this location.

Participants were instructed to listen to each sentence and press a button whenever the sentence described an inaccurate or improbable fact. By including only a few of these ‘‘catch’’ trials, we sought to ensure that participants would pay close attention to the meaning of the sentences while introducing minimal response-related activation in the primary data set of interest. The catch trials were modeled separately in the analysis. Catch trials were detected by all participants without problems, independent of sentence condition. All participants completed 10 practice trials prior to scanning to familiarize them to the task.

In the third run, subjects performed a functional localizer task that allowed us to functionally define ROIs on an individual basis. The functional localizer consisted of seven 16 s blocks of grayscale faces, grayscale scenes, or a fixation cross. In order to insure that subjects were attentive during the localizer task they were instructed to make simultaneous right and left button presses with the thumbs whenever an image repeated. This localizer task has previously been shown to reliably activate parahippocampal (PPA) and fusiform (FFA) regions of inferior temporal cortex for places and faces, respectively (Gazzaley, Rissman, & Desposito, 2004).

The order of the three runs was maintained across subjects in order to minimize motor imagery. We assumed that reading the generic phrases would evoke less imagery than the famous phrases and thus placed the generic task first. Note that each run (i.e., generic and famous) contained a control condition, so that no direct comparisons were made between runs. The localizer task was placed at the end of the session since we expected it might promote imagery given that it included actual faces and places.

fMRI acquisition

Functional MRI scanning was performed on a 4T Varian INOVA scanner using a T2*-weighted BOLD sensitive gradient echo echo-planar imaging sequence (TE = 28 ms, FOV = 22.4 × 22.4 cm, 64 × 64 matrix, resulting in-plane resolution 3.5 × 3.5 mm). Using a two-shot interleaved sequence, half of K-space was acquired in 1 s (i.e., total TR 2 s). A phase map correction was applied to remove Nyquist ghosts. 18 oblique axial slices of 5 mm thickness (1 mm gap) were acquired, providing coverage of the full extent of the frontal and temporal lobes. The dorsal-most aspect of the parietal lobe was not within the field of view in some participants. Each run was preceded by 10 s of dummy gradient RF pulses to achieve steady-state tissue magnetization. A T1-weighted, three-dimensional high resolution MP (magnetization-prepared)-Flash scan was obtained after the functional scans.

Data processing and statistical analysis

The fMRI data were preprocessed using tools from FSL (FMRIB’s Software Library, www.fmrib.ox.ac.uk/fsl). Skull stripping was performed with BET (Smith, 2002). Motion correction was carried out with MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002; Jenkinson & Smith, 2001). The data were smoothed with a Gaussian kernel (8 mm FWHM) and mean signal intensity was normalized across subjects using the program IP.

Registration was performed with the FSL tool FLIRT (Jenkinson & Smith, 2001; Jenkinson et al., 2002). For each subject, functional images were aligned to high-resolution coplanar images using an affine transformation with 3 degrees of freedom. High-resolution coplanar images were in turn aligned to MPFlash images, with an affine transformation with 6 degrees of freedom. Finally, MPFlash images were aligned to the standard MNI average of 152 brains using an affine transformation with 12 degrees of freedom.

Statistical analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.4, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). There was a separate explanatory variable for each of the 4 (runs 1 and 2; face sentences, place sentences, control sentences, false sentences) or 2 (run 3; face photos, scene photos) conditions. A slice-timing correction using Fourier-space time-series phase-shifting was applied as well as high pass temporal filtering (Gaussian-weighted LSF straight line fitting, with sigma = 37.5 s). Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Z (Gaussianized T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = .05$ (Worsley, Evans, Marrett, & Neelin, 1992).

Group analysis. Group analysis was performed with FMRISTAT with a mixed effects (i.e., random effects) linear model. Standard deviations from individual subject analyses were passed up to the group level. The resulting t-statistic images were thresholded at $t > 3.106$ ($df = 11$, $p < .005$, uncorrected) at the voxel level, with a minimum cluster size applied so that only clusters significant at $p < .05$ (corrected based on Gaussian random field theory) are reported.

Individual subject analysis. Regions of interest (ROIs) were chosen to test for differences in modulation of visual areas in each subject individually. A scene-selective ROI was defined with the localizer task GLM using a scene minus face contrast to obtain regions responsive to scene perception. The inferior temporal voxel with the highest t-value plus a 16 mm radius Gaussian centered upon the voxel constituted the PPA ROI in each hemisphere. Using the Gaussian radius, voxels further from the peak were weighted less strongly than voxels in the center of the sphere. The FFA ROI was chosen similarly, using the face minus place contrast. Even at minimal thresholds, 3 subjects did not exhibit a left hemisphere FFA (similar to that reported in previous studies, e.g., Wojciulik, Kanwisher, & Driver, 1998). Hence, for the left FFA ROI analysis, all analyses included 8 subjects. Two-way repeated-measures ANOVAs, Sentence Type (face, place) × ROI (FFA, PPA), were used to compare responses to linguistic phrases in these voxels to the control condition to determine whether signal change was dependent on sentence type. Four ANOVAs were run (famous sentences–left hemisphere; famous sentences–right hemisphere; generic sentences–left hemisphere; generic sentences–right hemisphere).

RESULTS

Group analyses

We first compared areas activated during language comprehension relative to rest in order to make sure that the expected language areas were activated. For this analysis, we averaged across the sentence types within a run, but performed the contrast separately for the generic and famous sentence runs. The results are summarized in Figure 1. As expected, compared to rest, language tasks significantly activated areas in the superior temporal gyrus bilaterally (MNI coordinate peak for generic sentences: Left hemisphere $x = -44$, $y = -20$, $z = -8$; Right Hemisphere $x = 58$, $y = -18$, $z = -8$; peak for famous sentences: Left hemisphere $x = -50$, $y = -18$, $z = -8$; Right hemisphere $x = 58$, $y = -20$, $z = -4$), and in the vicinity of Broca's area in the left hemisphere (generic sentences: $x = -46$, $y = 18$, $z = -2$). The generic sentences tended to produce greater activation than the famous sentences. While this may indicate processing differences between the sentence types, this difference may also reflect the fact that the generic sentences were always tested prior to the famous sentences. From our experience, initial runs generally show greater activity than subsequent runs.

Individual subject analysis

The main goal of this study was to assess modulation within FFA and PPA when people performed a comprehension task involving sentences describing faces or places. To account for inter-subject variability (Mazziotta et al.,

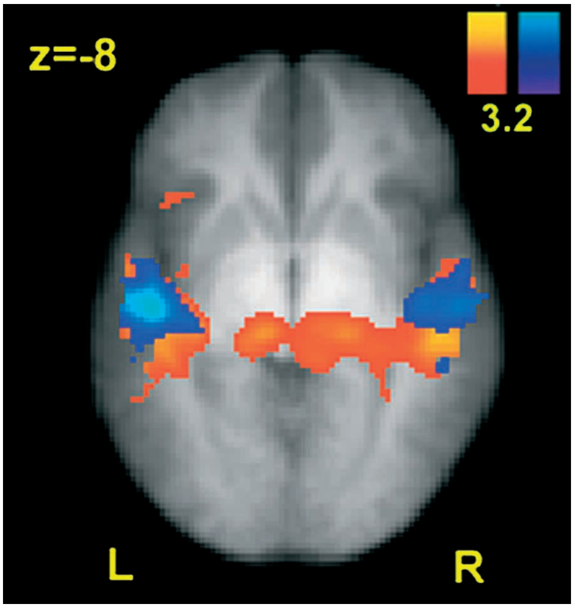

Figure 1. All language trials compared to rest. In red, listening to generic sentences (Run 1); and in blue, listening to famous sentences (Run 2). The temporal auditory areas are significantly active as are the posterior language areas. Broca's area is significantly active for Run 1. All statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = .05$ (Worsley, 1996).

2001), the primary analyses were conducted on individually defined functional ROIs (Friston, Rotshtein, Geng, Sterzer, & Henson, 2006; Saxe, Brett, & Kanwisher, 2006). For each subject, we identified the inferior temporal voxels that were most active during the localizer run in which participants performed a perceptual task involving faces or scenes. This procedure was applied in both the left and right hemispheres (Figure 2). Given that the localizer runs were used to identify the ROIs for the main experiment, we do not make any direct comparisons between the language runs and observation runs.

The top row of Figure 3 shows the percent signal change in the left and right hemisphere ROIs during the localizer run. Not surprisingly, given our method of identification, activation in the ROIs was most responsive when viewing stimuli of the ROI's related domain (e.g., viewing of faces for FFA ROI). The ROI × Picture Type interaction was significant in the left, $F(1, 7) = 80.39$, $p = .0021$, and right, $F(1, 12) = 15.14$, $p < .0001$, hemispheres. Activation in the PPA ROIs showed minimal response during the face perception task. In contrast, activation in the FFA ROIs was also observed during scene perception task. The average MNI coordinates were: left FFA (66, 36, 25), right FFA (23, 36, 25), left PPA (59, 41, 28), right PPA (31, 39, 28) with the corresponding standard errors: (0.7, 1.8, 1.1), (0.5, 2.1, 0.9), (0.3, 0.8, 0.6), and (0.4, 1.3, 1.2). These are within the vicinity of those reported by Kanwisher's group (O'Craven & Kanwisher, 2000): left FFA (63, 43, 28) right FFA (26, 45, 28), left PPA (59, 43, 34) and right PPA (29, 43, 33).

We then examined the response in these voxels during the sentence comprehension task. The percent signal change in these ROIs is shown for the comprehension run with famous sentences (middle row of Figure 3) and generic sentences (bottom row). For the left hemisphere, there was a significant Sentence Type × ROI interaction during the run with sentences involving famous faces or places, $F(1, 7) = 14.35$, $p = .0068$. The left PPA was significantly less active to place sentences compared to face sentences, $F(1, 12) = 5.36$, $p = .039$. A similar trend was observed in left FFA, although this reduction was not significant, $F(1, 7) = 1.78$, $p = .22$. The interaction

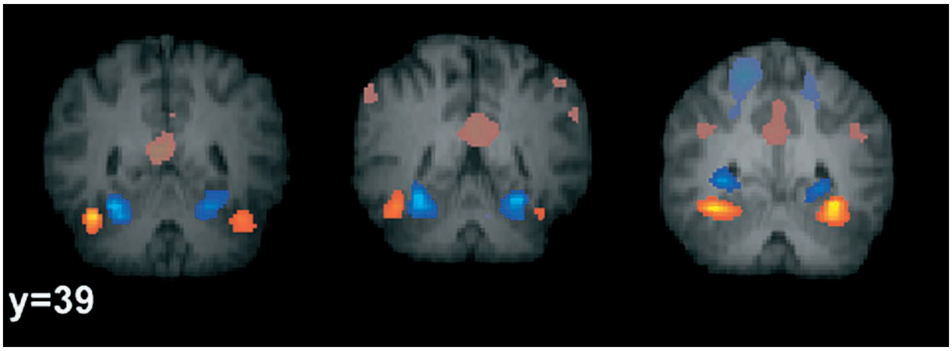

Figure 2. ROIs in three sample subjects: Observation of faces as compared to scenes activates the fusiform face area (FFA; red to yellow) and observation of scenes as compared to faces activates the parahippocampal place area (PPA; blue to light blue). In most participants, activations were bilateral. However in three participants a left hemisphere FFA was not observed. For each subject, the ROIs in each area consisted of the peak voxel with a surrounding 16 mm Gaussian.

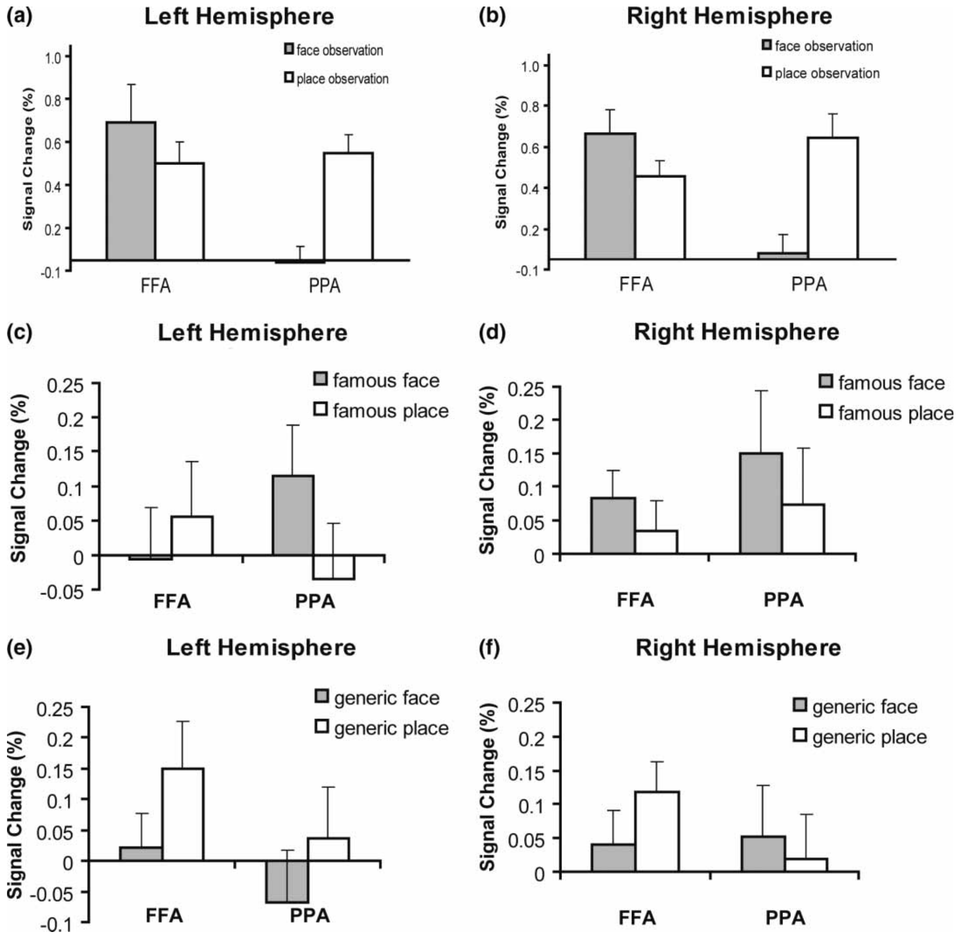

Figure 3. (a) Signal change in the FFA and PPA for observation of faces (gray) and places (white), in peak voxels for the FFA and PPA defined individually for each subject, compared to resting baseline. (b) Right hemisphere response in functionally defined FFA and PPA. Note that it is common to see that the FFA is also activated by observing scenes, and thus activations above 0 are expected for this condition (Ewbank et al., 2005). (c–f) Signal change in the FFA and PPA ROIs during language comprehension for sentences describing faces or places as compared to control sentences (objects). The middle panels are for the run with famous sentences (c–d) and bottom panels are for the run with generic sentences (e–f). The interaction is significant for the famous sentences in the left hemisphere, with activation lower for domain-related sentences.

was not significant during the run with sentences involving generic faces or places, $F(1, 7) = 0.08$, $p = .78$. For these sentences, the mean response in both left FFA and left PPA was lower when listening to face sentences as compared to place sentences.

Interestingly, the signal change in FFA and PPA of the right hemisphere during the sentence comprehension runs was similar in magnitude to that observed in the left hemisphere. However, for both the famous and generic runs, we did not observe a ROI × Sentence Type interaction in the right hemisphere, famous: $F(1, 12) = 0.52$, $p = .49$; generic: $F(1, 12) = 3.6$, $p = .82$. Thus, the modulation of activation in FFA and PPA during a sentence comprehension task was limited to the left hemisphere. Indeed, we found a significant three-way interaction for hemisphere, ROI, and stimulus type, indicating that the deactivation was limited to the left hemisphere for the famous set of stimuli, $F(1, 7) = 21.47$, $p = .0024$.

DISCUSSION

Our results reveal that activity in perceptually identified neural regions is modulated during a sentence comprehension task. Moreover, at least for FFA and PPA, the modulation is manifest as a reduction in activity for sentences that are content related. This effect was limited to the left hemisphere and only obtained in the run with famous faces and places. The modulation of PPA was stronger than the modulation of the FFA.

This may be due to the fact that the FFA is less reliably localized in the left hemisphere (Ishai, Schmidt, & Boesiger, 2005), thus lowering our statistical power for the left FFA. In addition, activity in FFA is observed to non-face stimuli (Grill-Spector, Sayres, & Ress, 2006), including the places used in our localizer task (Figure 3a). In an fMRI-habituation study, habituation to visually presented objects was observed in the FFA and the PPA (Ewbank, Schluppeck, & Andrews, 2005), which may explain why our control object sentences (the baseline in Figure 3) did not significantly differ from our experimental stimuli. We also conducted analyses comparing signal change in the ROIs to a resting baseline and also found the same patterns of results with the interaction reported here to be significant. This indicates that the differences between the two experimental conditions are significant, regardless of the baseline used.

In designing this study, we realized that finding content-specific increases in activation might reflect the use of mental imagery during sentence comprehension. For this reason, we opted to include both generic and famous face/place sentences, and complete the generic run prior to the famous run, based on the assumption that the sentences describing well-known faces or places would entail more imagery. The fact that the modulation was a content-specific reduction in activation rather than increase in activation argues against an imagery hypothesis as mental imagery of faces or places would predict increased rather than decreased activity in the FFA or PPA (O'Craven & Kanwisher, 2000).

Previous studies have shown that the FFA and/or PPA are modulated by expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; O'Craven & Kanwisher, 2000), attention (O'Craven, Downing, & Kanwisher, 1999; Wojciulik et al., 1998), visual imagery (Ishai, Haxby, & Ungerleider, 2002; Ishai, Ungerleider, & Haxby, 2000; O'Craven & Kanwisher, 2000), and emotion (Vuilleumier, Armony, Driver, & Dolan, 2001). Our findings indicate that language also modulates these perceptual processing areas. However, unlike in previous studies, the language effects on FFA and PPA activity observed here are inhibitory.

Modulation in a sensory processing area can show as either an increase in activity (as with premotor areas) or a decrease (as with primary motor cortex or here with the FFA and PPA). Decreases in activity can be explained with three partially overlapping hypotheses. First, during language processing, visual processing areas for the concept in question may need to be inhibited in order to prevent interference between current sensory inputs and the conceptual representations needed for linguistic comprehension (Gallese & Lakoff, 2005). For example, if a dark-haired speaker asks if Marilyn Monroe had blond hair, perception related to the speakers face and hair color could interfere with the retrieval of information required to respond to the linguistic query.

Second, language requires more abstract representation than visual observation. Hearing a phrase like ''Marilyn Monroe has blond hair'' or ''The farmer's chin has a mole'' prompts a more generalized representation than perceiving Marilyn Monroe's face with blond hair, her specific expression, tan, make-up, and hairstyle, etc., of the moment. Thus, in order to represent an abstract representation of Marilyn Monroe, it may be that specific visual representations of Marilyn Monroe need to be inhibited.

Third, multimodal processing might be an essential prerequisite for conceptual abstract representation. Areas such as the FFA, PPA, and primary motor cortex—that are not of multimodal nature—may therefore be unfit for providing a ''convergence zone'' for abstract processing. These results are in line with findings that the primary motor cortex, which codes specific motor representations, is inhibited during processing of language related to actions (Buccino et al., 2005) while premotor multimodal areas are facilitated (Aziz-Zadeh et al., 2006). Similarly, it is possible that multimodal areas functionally connected to the PPA or FFA (i.e., the temporal poles), are facilitated by face and place sentence processing and that these multimodal areas selectively inhibit the FFA and PPA during language processing. In a post hoc group analysis, however, we did not find any brain areas that were more active for face versus place sentences or vice versa. Further research is needed to yield a more complete model of the network of areas that process face and place sentence processing in the brain and their pattern of activations.

The content-specific decreases in activation were only found for famous sentences. This effect was not reliable for generic face and place sentences, although a similar pattern was found bilaterally for the FFA and in the right hemisphere for the PPA. It may be that the mechanisms leading to the decrease in activation may be related to the degree to which the sentences engage more concrete representations. The face of a generic farmer is a more abstract generalization than the face of Marilyn Monroe. Content-specific inhibition of perceptual areas such as FFA or PPA may be greatest for sentences that produce the greatest degree of imagery. This hypothesis is, of course, speculative and a question for future investigation.

Manuscript received 26 September 2006
Manuscript accepted 7 February 2007
First published online 31 May 2007

REFERENCES

Aziz-Zadeh, L., Iacoboni, M., Zaidel, E., Wilson, S., & Mazziotta, J. (2004). Left hemisphere motor facilitation in response to manual action sounds. *European Journal of Neuroscience*, *19*, 2609–2612.

Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2002). Lateralization in motor facilitation during action observation: a TMS study. *Experimental Brain Research*, *144*, 127–131.

Aziz-Zadeh, L., Wilson, S., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, *16*(18), 1818–1823.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*, 577–609 [discussion 610–560].

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, *13*, 400–404.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Research Cognitive Brain Research*, *24*, 355–363.

Chao, L. L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience*, *11*, 25–35.

Damasio, A. R. (1989). Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition*, *33*, 25–62.

Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, *92*, 179–229.

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: recognition, navigation, or encoding? *Neuron*, *23*, 115–125.

Ewbank, M. P., Schluppeck, D., & Andrews, T. J. (2005). fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. *NeuroImage*, *28*, 268–279.

Feldman, J., & Narayanan, S. (2004). Embodied meaning in a neural theory of language. *Brain and Language*, *89*, 385–392.

Friston, K. J., Rotshtein, P., Geng, J. J., Sterzer, P., & Henson, R. N. (2006). A critique of functional localisers. *NeuroImage*, *30*, 1077–1087.

Gallese, V., & Lakoff, G. (2005). The brains concepts: The role of the sensorimotor system in reason and language. *Cognitive Neuropsychology*, *22*, 455–479.

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform ''face area'' increases with expertise in recognizing novel objects. *Nature Neuroscience*, *2*, 568–573.

Gazzaley, A., Rissman, J., & Desposito, M. (2004). Functional connectivity during working memory maintenance. *Cognitive and Affective Behavioral Neuroscience*, *4*, 580–599.

Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). I hear what you are doing—An fMRI study of the auditory mirror system in humans. *Current Biology*, *16*(18), 1824–1829.

Geschwind, N. (1964). The development of the brain and the evolution of language. *Monograph Series in Language and Linguistics*, *1*, 186–187.

Glenberg, A. M. (1997). What memory is for. *Behavioral and Brain Sciences*, *20*, 1–19 [discussion 19–55].

Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin Review*, *9*, 558–565.

Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*, 301–307.

Hauk, O., & Pulvermuller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, *21*, 191–201.

Ishai, A., Haxby, J. V., & Ungerleider, L. G. (2002). Visual imagery of famous faces: effects of memory and attention revealed by fMRI. *NeuroImage*, *17*, 1729–1741.

Ishai, A., Schmidt, C. F., & Boesiger, P. (2005). Face perception is mediated by a distributed cortical network. *Brain Research Bulletin*, *67*, 87–93.

Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*, 979–990.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimisation for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, *17*, 825–841.

Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, *5*, 143–156.

Kanwisher, N. (2001). Faces and places: of central (and peripheral) interest. *Nature Neuroscience*, *4*, 455–456.

Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh: The embodied mind and its challenge to western thought*. New York: Basic Books.

Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., et al. (2001). A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). Philosophical Transactions of the Royal Society of London. *Series B: Biological Sciences*, *356*, 1293–1322.

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*, 584–587.

O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, *12*, 1013–1023.

Pulvermuller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, *21*, 793–797.

Saxe, R., Brett, M., & Kanwisher, N. (2006). Divide and conquer: a defense of functional localizers. *NeuroImage*, *30*, 1088–1096 [discussion 1097–1089].

Smith, S. (2002). Fast robust automated brain extraction. *Human Brain Mapping*, *17*, 143–155.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*, 273–281.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*, *30*, 829–841.

Wheaton, K. J., Thompson, J. C., Syngeniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage*, *22*, 277–288.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology*, *79*, 1574–1578.

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of fMRI data. *NeuroImage*, *14*, 1370–1386.

Worsley, K. J. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, *4*, 58–73.

Worsley, K. J., Evans, A. C., Marrett, S., & Neelin, P. (1992). A three-dimensional statistical analysis for CBF activation studies in human brain. *Journal of Cerebral Blood Flow Metabolism*, *12*, 900–918.