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Modality-specific encoding of conceptual person identity in the Fusiform Face Area

Original Paper

I employed multi-voxel pattern analysis to fMRI data from two functionally defined clusters in the Fusiform Face Area (FFA); mFus and pFus. Stimulus information was decoded from hemodynamic response patterns evoked by three fictional identities. These were comprised of sets of semantic person information and corresponding faces. By presenting identities with overlapping visual and semantic features we could attribute successful decoding to the differentiating feature. Our data suggest a functional differentiation between pFus and mFus. Analysis of response patterns in pFus indicated that this cluster is engaged in perceptual analysis during face presentation and in retrieval of the corresponding face representation during presentation of semantic stimuli. In mFus semantic items appear to evoke a single corresponding face representation whereas during face perception this cluster is likely to be engaged in retrieval of semantic features by activation of a collection of corresponding visual representations. I propose that mFus supports conceptual knowledge of people by activating visual features that correspond to semantic categories.

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INTRODUCTION

The human face perception system provides us with the extraordinary ability to recognize a seemingly unrestricted number of faces and quickly match them to available biographic information. A major node in the underlying neural network is The Fusiform Face Area (FFA), a patch of ventral temporal cortex on the posterior Fusiform Gyrus (FG) and mid-Fusiform Sulcus (Haxby, Hoffman and Gobbini,

2002). Besides its manifest role in visual face processing (e.g. Tong, Weinrib & Kanwisher, 2000; Yovel and Kanwisher 2005; Bruce and Young, 2011), there are also various reports that implicate the FFA in processing of non-visual semantic information related to people.

A fairly direct approach to measure whether a brain area encodes certain information employs multivariate analysis of fMRI data, known as multi-voxel pattern analysis (MVPA). It aims to find information present in the distributed pattern of activation across multiple voxels. Using MVPA Van den Hurk (2011) found that evoked activity patterns in the FFA could be consistently mapped to word stimuli in either a person context or a non-person context, suggesting that the FFA has access to non-visual semantic information. This is in line with Turk, Rosenblum, Gazzaniga, & Macrae (2005) who found that making a semantic judgment about a face on an individual level (i.e. the name of the person) is accompanied by an increase in hemodynamic response compared to judgments of a face on a category level (occupation) in the posterior Fusiform cortex among other regions.

Previously other researchers had pointed out a possible extensive role of the FFA in social cognition even when no face stimuli are presented. Schultz et al. (2003) found increased BOLD-responses in the FFA when movements of animated geometric shapes were interpreted as social interaction in a social attribution task (SAT). The region activated by the SAT closely overlapped with the FFA although its center of mass was slightly more medial and anterior. The authors propose that the functions of the region include encoding semantic attributes of people, which might aid in defining faces as distinct objects.

These findings of involvement of the FFA in processing of non-visual person information are remarkable because previous research has fairly unanimously implicated its location on the bilateral FG (BA 37) in relatively elementary, pre-semantic visual processing (e.g. Ungerleider & Haxby, 1994; Thompson-Schill, Aguirre, D'Esposito & Farah, 1999; Bright, Moss & Tyler, 2004). Furthermore the absence of increased FFA-response to famous faces (assumedly associated with richer semantic information) compared to unknown faces, has been a strong reason to rule out the availability of non-visual semantic information in the region (Kanwisher & Yovel, 2006).

Is FFA functionally subdivided?

Rare intracranial experiments in humans add to the dissonance in the debate on the role of the FFA in semantic person processing. When Parvizi (2012) electrically stimulated cells in the right FFA the subject reported highly selective changes in visual face perception. However other electronic brain stimulation (EBS) experiments demonstrated no distorted face perception but instead only deficits in naming faces (Allison et al., 1994; Puce, Allison, & McCarthy, 1999). Since from these earlier studies the exact location of the stimulated area cannot be distilled, discrepant findings may stem from stimulation of slightly different regions across studies (Parvizi, 2012).

This suggestion of fine-grained local differences in functionality within face-selective Fusiform cortex is supported by refined mapping of the region with improved functional magnetic resonance imaging methods. The face selective

region on the FG is now accepted to consist of at least two anatomically separate clusters (e.g.: Weiner and Grill-Spector, 2012). These clusters, located on the middle Fusiform Sulcus and on the posterior Fusiform Gyrus are named mid-Fusiform face cluster or mFus and posterior Fusiform face cluster or pFus respectively (also referred to as FFA-1 and FFA-2, respectively; Pinsk et al., 2009). Researchers have just begun to investigate whether these clusters differ functionally and in what respect.

Given the current parcellation of the FFA Van den Hurk (2013) could replicate his earlier finding of semantic representation in FFA and relate it to a functional subdivision of its two clusters, again by using MVPA. Subjects viewed semantic person information while actively associating this to a previously seen face. Semantic stimuli could be reliably decoded from the hemodynamic response patterns in pFus. However this was not the case in the more anterior mFus cluster. Neural activity in this cluster nevertheless proved to contain stimulus information when it was evoked by visual face stimuli, which was not apparent in pFus.

Van den Hurk's work seems to suggest that non-visual semantic information is present in pFus but not in mFus. However a functional allocation of semantic processing exclusively to the posterior cluster is not in line with the general increasing complexity of neural response properties along the ventral visual pathway (e.g. DiCarlo et al., 2012, but see Kravitz, Saleem, Baker, Ungerleider & Mishkin, 2013). This organizational principle has also been demonstrated specifically in the domain of face perception (Ungerleider and Haxby, 1994). If non-visual semantic processing is conducted in the FFA it would thus be expected to appear in its anterior part.

A visual account of semantic representations in FFA

The mentioned findings of responses in FFA elicited by non-face stimuli might be parsimoniously explained without assuming conceptual information being stored or processed in this area. Possibly the semantically induced activity in FFA reflects retrieval of visual representations. In Van den Hurk's (2013) study this is a particularly plausible scenario since subjects were explicitly asked to associate visual and non-visual information in the task. Indeed imagining faces has been demonstrated to activate the FFA similarly to face perception in neuroimaging experiments (O'Craven & Kanwisher, 2000).

The distinct response patterns in mFus during face presentation in Van den Hurk's study (2013) might result from retrieval as well. Plausibly visual representations of a person get activated when associated non-visual semantic information is retrieved upon the presentation of the face. This is implicitly predicted by the interactive modality-specificity hypothesis (Thompson-Schill, Aguirre, D'Esposito & Farah, 1999). It states that for objects that are predominantly defined by their visual form such as living things, retrieval of non-visual features is strongly associated with activity in areas involved in visual processing. This claim is supported by findings of increased activation in the FG when subjects retrieved semantic information about living things as opposed to non-living things (Thompson-Schill, et al., 1999; Chao, Haxby and Martin 1999).

When viewed in this light finding distinct activity patterns during retrieval of semantic information particularly in mFus fits the anterior shift in cortical activity

as observed by Martin, Haxby, Lalonde, Wiggs and Ungerleider (1995). When their subjects were asked to retrieve knowledge about color and motion of known objects an increased BOLD-response was detected slightly anterior to sites that showed maximum activation during perception of the same object features. According to the modality-specificity hypothesis this is also expected when retrieved information about persons is non-visual.

The present study

The information reflected in distinct neural activity patterns in FFA clusters might be visual, semantic or a combination (visuosemantic). In Van den Hurk's (2013) experiment the informational content remains unclear because local processing could reflect perception of the currently presented stimulus or retrieval of the associated information. Therefore we implemented a similar but slightly adapted design to investigate fMRI response patterns elicited by written words (conveying biographical information e.g. residence, hobby and occupation) and visual face stimuli. Fixed combinations of word and face stimuli defined three different fictional person identities. Subjects were asked to actively associate semantic and visual information belonging to the same identity and think of them as describing a person.

Key is that in the current experiment not every identity consisted of a unique face and unique semantic information. Instead two identities shared an identical face ('twins') and one of these shared (almost) identical biographical descriptions with the third identity. This enabled us to assign decodable activation patterns to the unique component and thus allowed disentangling neural activity representing visual face information from non-visual semantic identity information.

Contrary to the order of stimulus presentation in Van den Hurk's design, in the present study each identity started with presentation of the semantic stimuli followed by the corresponding face. Each block of semantic stimuli commenced with an item that was uniquely assigned to one identity, serving as a cue to notify the subject of the current identity (for two identities the remaining semantic stimuli were identical). The use of identical stimuli for different identities would otherwise provide insufficient information for the subject to associate face and semantic information. We assessed task feasibility outside the scanner with the same stimuli and similar procedure but different subjects (because of possible learning effects; Robinson-Long, Eslinger, Wang, Meadowcroft & Yang, 2009).

To the fMRI-data we applied multi-voxel pattern analysis (MVPA). In this procedure we decoded stimuli (written words or pictures) belonging to combinations of two different identities from their evoked responses in the two bilateral face selective clusters on the FG. Since each identity was construed of at most only one unique identity-component, correctly classified patterns must reflect activity that is related to this differentiating component or is otherwise visuosemantic.

We hypothesized that pFus response patterns evoked by semantic stimuli can only be accurately classified when the associated faces are different. Similarly we expected that mFus response patterns evoked by face stimuli are also only accurately classified when the face stimuli are different. This would support the idea that the intelligible patterns in FFA reflect visual representations.

METHODS

Participants

Two native Dutch speaking volunteers (1 female, age 32 and 27) were recruited to participate in the neuroimaging experiment. Both were right handed and had normal or corrected to normal eye sight. They were screened for fMRI compatibility and signed informed consent.

Stimuli

Semantic stimuli were created from a 5 * 2 word matrix, consisting of five categories (capital cities, professions, marital status, music styles and hobby's). We used only Dutch words, the native language of all participants.

The two different face stimuli were obtained from a stimulus set provided by Mark Steyvers (http://psiexp.ss.uci.edu/research/software.htm). The pictures were all taken under similar lighting with neutral facial expressions. We selected two faces that are easily recognizable but at the same time do not have obvious distinctive features (see figure 1).

Procedure

Sessions consisted of four runs, each of approximately ten minutes duration. Three identities, each comprised of a face and a set of semantic items, were presented in random order. A sequence of the three identities was repeated six times per run, resulting in 24 presentations per identity. Subjects were asked to actively associate semantic and face information belonging to the same identity.

Presentation of each identity (comprising an identity block) commenced with five semantic items, presented one at a time with a duration of 1800 ms and interstimulus interval of 200 ms. After the presentation of the semantic items a fixation cross was presented for twelve seconds to allow the BOLD-response to return to baseline level. Next a face stimulus was presented for two s. An interval of 12 - 16 s separated identity blocks to allow the BOLD-signal to return to baseline. Each participant was presented with fixed combinations of semantic items and faces. The three identities thus remained consistent in their visual and semantic attributes throughout each session. Across participants however the semantic items were scrambled within each category before assigning them to the different identities. Also the order in which the semantic items were presented was randomized form trial to trial.
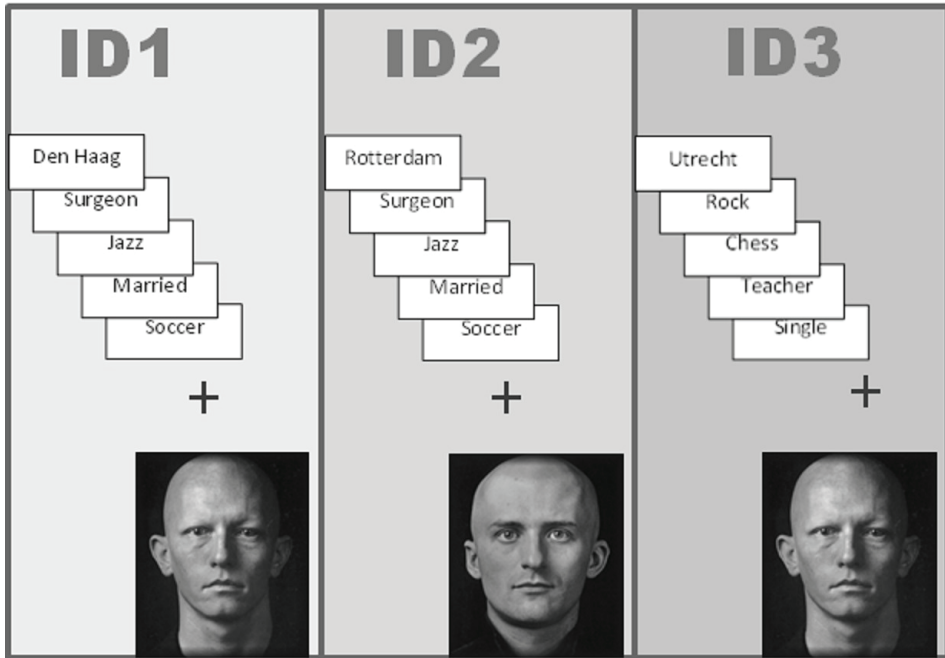
Figure 1. Example of three identities each composed of five semantic items and a face. For every subject the same set of stimuli was used, but across participants the semantic items within each category were scrambled before assigning them to the different identities. The order in which the semantic items were presented was randomized form trial to trial.

Based on the prior behavioral assessment we decided to let subjects view one block from the actual experiment (6 X 3 identities) with the actual stimulus combinations previous to scanning. We verbally verified whether the task was clear and if the subject was confident about his/her ability to associate the faces and semantics to their correct counterparts.

In separate runs face sensitive regions were localized as well as the nearby Visual Word Form Area (to be able to exclude responses to the mere shape of words in the semantic items). The participants passively watched blocks of faces, scrambled faces, houses, words and random letter strings. Each block consisted of ten gray scale images or white letters on a dark-gray background. Stimuli were presented for 1500 ms followed by 300 ms fixation. Blocks were repeated eight times and presented in random order, divided over two separate runs.

Materials

For the neuroimaging experiment we used a 3-T Siemens Magnetom Allegra head scanner (Siemens Medical Systems, Erlangen, Germany) using a standard head coil. Twenty-eight axial slices (2 X 2 mm, interslice distance 0 mm) covering the temporal lobe were collected using an echo-planar imaging sequence (repetition time [TR] = 2000 ms, matrix size 128 X 128, echo time [TE] = 30 ms). For each run the first two functional volumes were excluded due to T1 saturation.

Anatomical images covering the whole brain were obtained between experimental runs using a 1 X 1 X 1 mm resolution T1-weighted ADNI-sequence (TR=2250 ms; TE = 2.6 ms; flip angle = 9°). The participants were placed comfortably in the scanner with their head fixed with foam pads. The stimuli were projected on a screen, which was visible from inside the scanner via a mirror mounted on the head coil. Stimulus presentation was synchronized with MR data acquisition by triggering the Presentation® software (Version 16.3, www.neurobs.com) with the first MR pulse.

Analysis

Functional and anatomical data were preprocessed and analyzed using BrainVoyager QX 2.6 (Brain Innovation, Maastricht, the Netherlands). Functional volumes were first corrected for slice scan time differences and 3D head motion. Linear trends and low-frequency temporal drifts were removed from the data using a high pass filter, removing temporal frequencies below four cycles per run. No spatial smoothing was performed. After the preprocessing, functional data were co-registered to the high resolution anatomical volume and normalized to Talairach space.

Data from the localizer runs were analyzed by contrasting responses to faces with responses to scrambled faces and houses. The resulting functionally defined FFA-clusters served as regions of interest in the subsequent MVPA. Responses to words were contrasted with responses to random letter strings to localize the nearby visual word form area in order to prevent possible confounding from overlapping voxels.

For the experimental runs the pre-processed time series were split into responses to face stimuli (face trials) and responses to the blocks of five written words (semantic trials). This resulted in sets of 24 responses to face trials and 24 responses to semantic trials for each of the three identities, for each subject and for each of the four FFA-clusters. A general linear model was fitted to every voxel's response. The resulting regression coefficients were then used as a measure for each voxel's response amplitude from which trial-based response patterns were constructed, reflecting spatial differences in activation across voxels in the same ROI.

Subsequently each set of response patterns was randomly split into a train set consisting of 21 response patterns labeled with the corresponding identity and a test set with the remaining three unlabeled response patterns. A Support Vector Machine (SVM) algorithm was trained with two sets of train patterns belonging to the same stimulus category (semantic or visual), subject and ROI but to two different identities. SVM training entailed expressing the responses from the two train sets in a multidimensional space and determining an optimal decision boundary between the data from the two classes.

We tested the resulting model by assessing its accuracy in predicting the identities associated to the corresponding test patterns, based on the classification rule extracted from the train sets. Training and testing was done for each pair of identities (one pair with identical faces, one with overlapping semantics and one with different faces + different semantics), separately for face and semantic trials, for each subject and each of the FFA clusters. The whole procedure was repeated

40 times with different training/testing subsets. The number of times the response patterns in the test set were assigned to the correct identities yielded an average prediction accuracy (p.a.). This p.a. was ultimately tested against the empirically estimated chance level. Since Van den Hurk (2013) found no significant differences in p.a. between left and right hemispheres in a very similar identity-decoding paradigm we averaged the p.a.'s over subjects and hemispheres to increase statistical power.

For each identity pair the null hypothesis was empirically estimated by performing a permutation test. This yields the probability of making an accurate classification of response patterns if no systematic correspondence between patterns from the same class (identity) would exist. Similar to the MVPA described above, an algorithm was trained to learn the relation between response patterns and their identity-labels for each subject, FFA-cluster, identity-pair and stimulus category (face or semantics) separately. However in the permutation test the labels were randomly assigned to the training sample. Again training and testing was repeated 40 times, resulting in an average prediction accuracy. To test whether training the model with correctly labeled patterns yields significantly higher prediction accuracy than the permuted sample we used the nonparametric Wilcoxon signed-rank test.

RESULTS

Localizer results

We used two independent localizer runs per subject in order to bilaterally localize the mFus and pFus clusters as well as the nearby Visual Word Form Area (VWFA). Localization of the latter area would allow us to exclude responses to the mere shape of words in the semantic items. However we were not able to localize the VWFA in any of our subjects. Therefore mFus and pFus were bilaterally defined by the set of contiguous voxels in the mid-Fusiform Sulcus and posterior Fusiform Gyrus respectively that were significantly more active during presentation of faces than during presentation of scrambled faces and houses (p < .001). Four FFA-clusters were successfully localized in one subject, in the other subject mFus and pFus could only be localized in the left hemisphere.
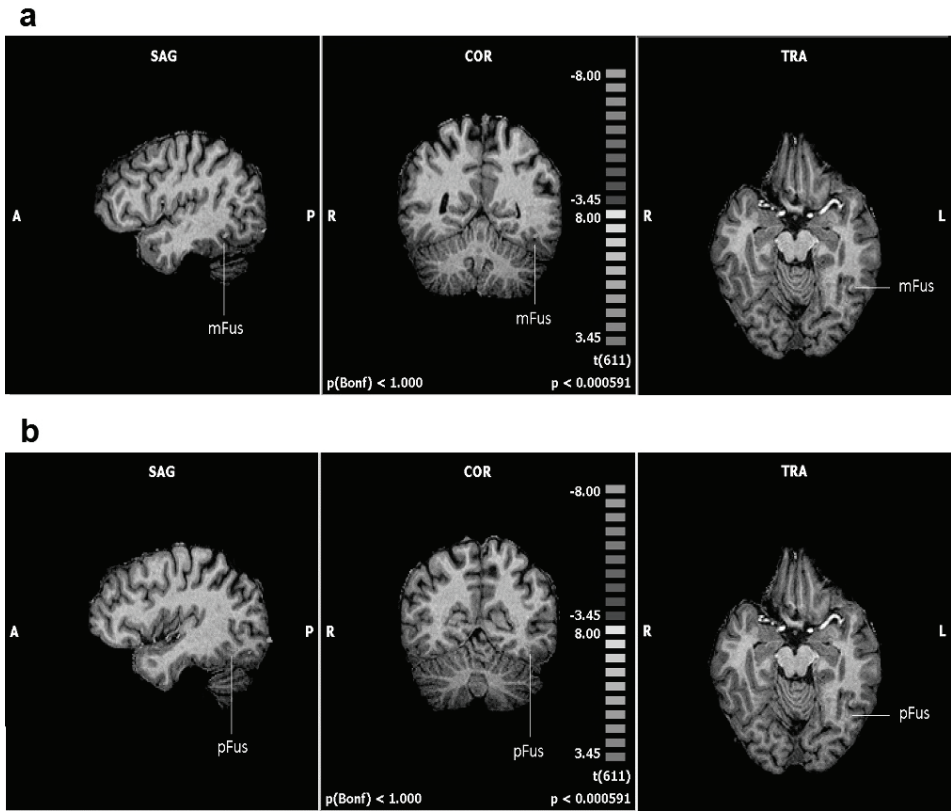
Figure 2. Univariate fMRI data from the localizer runs from one subject. Voxels in the mid-Fusiform Sulcus and posterior Fusiform Gyrus that were significantly more activated by faces than by scrambled faces and houses (p < .001) were defined as mFus (a) and pFus(b) respectively. This subject showed only face sensitive clusters in the left hemisphere.

MVPA results

Face trials in mFus

A Wilcoxon signed-rank test revealed that the p.a. for face trials in mFus (M = 59.582) was significantly higher than chance level (M = 49.742) for identity-pairs with identical faces but different semantics, Z = 4.667 p < .001. For identity-pairs with identical semantics but different faces the p.a. (M = 49.167) was not significantly different than chance level (M = 50.516), Z = -.646, p = .518, whereas p.a. for identities with different faces and different semantics (M = 60.003) was significantly above chance level (M = 48.810), Z = -4.382, p < 0,001 (see figure 3).

Semantic trials in mFus

For semantic trials in mFus p.a.'s (M = 43.464) were significantly lower than in the

permuted sample (M = 47.619) for identity-pairs with identical faces but different semantics, Z = -3.035, p = .002. For identity-pairs with identical semantics but different faces p.a.'s (M = 55.426) were significantly higher than in the permuted sample (M = 52.381), Z = -2.466, p = .014, whereas identity-pairs with different faces and different semantics (M = 50.973) could not be predicted better than chance (M = 50), Z = -.477, p = .633 (see figure 3).
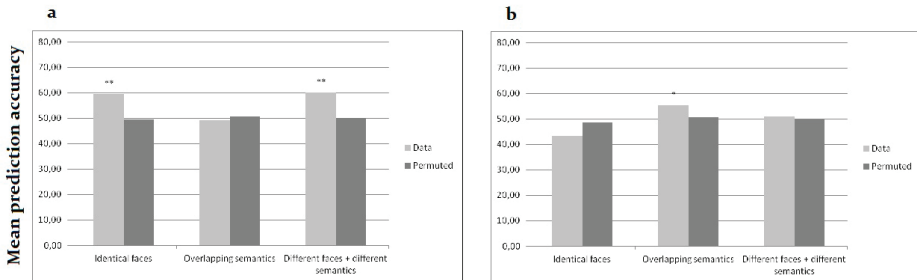

Figure 3. Mean prediction accuracies (p.a.'s, light gray) for response patterns evoked in mFus by face trials (a) and semantic trials (b) compared to their permuted counterparts (dark gray). P.a.'s were averaged over subjects and hemispheres.

Face trials in pFus

In pFus face trials yielded a p.a. (M = 48.478) that not significantly differed from chance (M = 51.191), Z = -1.187, p = .235 for identity-pairs with identical faces but different semantics. P.a. (M = 48.47) was also not significantly different than chance (M = 52.381) for identity-pairs with identical semantics but different faces, Z = -1.666, p = 0.096, while p.a. (M = 55.754) was significantly higher than chance level (M = 47.619) for identity-pairs with different faces and different semantics, Z = -3.922, p < 0,001 (see figure 4).

Semantic trials in pFus

Statistical analysis of p.a.'s for semantic trials in pFus indicated that performance (M = 49.585) was not different from chance level (M = 50) for identity-pairs with identical faces but different semantics, Z = -.459, p = .646. Identity-pairs with identical semantics but different faces were predicted significantly better (M = 56.943) than chance level (M = 51.191), Z = -3.210, p < .001, whereas p.a. for identity-pairs with different faces and different semantics (M = 54.308) did not differ significantly from chance level (M = 52.381), Z = -1.208, p = 0.227 (see figure 4).
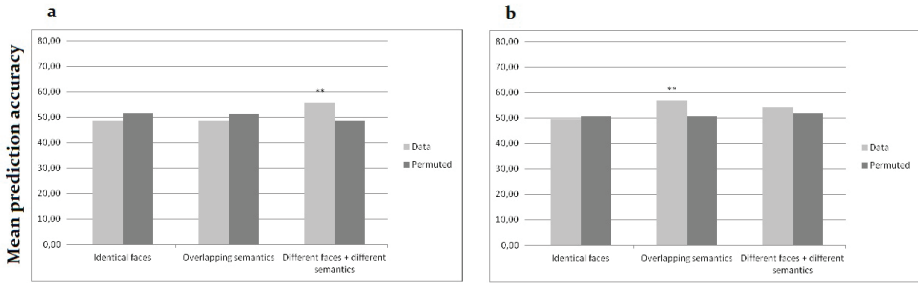
Figure 4. Mean prediction accuracies (p.a.'s, light gray) for response patterns evoked in pFus by face trials (a) and semantic trials (b) compared to their permuted counterparts (dark gray). P.a.'s were averaged over subjects and hemispheres.

DISCUSSION

pFus contributes to visual retrieval and perception

In pFus the successful decoding of responses evoked by overlapping semantics indicates activation of the associated unique face representations. It can thus be inferred that pFus response patterns in semantic trials predominantly reflected retrieved visual (face) information. Note that retrieval of associated information was explicitly instructed in the task. pFus responses to face trials did not yield above chance level p.a. for identities with identical faces, suggesting that this cluster is not involved in retrieval of semantic information. Neither did pFus responses to face trials allow for accurate decoding of identities with overlapping semantics. This suggests the absence of face information as well. However, the p.a. was above chance level for identity pairs with both different faces and different semantics. Plausibly pFus is engaged in perceptual analysis of face stimuli, but this only leads to decodable responses when unique semantic information is available, possibly enhancing the perceptual process (Turk et al., 2005). We can only speculate why distinct responses in this cluster and trial type were not found by Van den Hurk (2013) who exclusively used unique faces and semantics. The reason for this contradiction might conceivably be related to the reversed order of face and semantic information in the current experiment.

mFus contributes to retrieval of visual and semantic information

In mFus the p.a. was significantly lower than the empirically estimated chance level for identity-pairs with identical faces in semantic trials. This phenomenon of anti-learning is known to occur in some machine learning tasks when classification is done on small sample sizes in high dimensional feature spaces. Analysis of a synthetic dataset has demonstrated that anti-learning is a property of the data and is distinct from overfitting the model (Kowalczyk & Chapelle, 2005). However it is not clear how below chance-level prediction can be interpreted; therefore results from the concerned condition are not discussed further.

The remaining p.a.'s for face and semantic trials in this cluster showed a seemingly contradicting pattern. In semantic trials responses evoked by overlapping semantics (associated to different faces) could be reliably classified, suggesting retrieval of visual content. In face trials on the other hand, responses evoked by identical faces (associated to different semantics) allowed for accurate classification as well while responses to different faces (associated to overlapping semantics) did not, suggesting retrieval of semantic content. This seems to imply that the informational content of mFus changes modality between semantic and face trials. It is conceivable that this results from the activity of two different neuronal populations. This can be tested in an fMRI adaptation design (Chadwick, Bonnice and Maquire, 2012). However we propose that the seemingly opposing results can be parsimoniously reconciled under the assumption of only visual information being stored in the region.

Semantic person information encoded by face representations

According to the task instructions subjects retrieve semantic information during face trials. Response patterns in mFus during face trials appear to contain information about the semantic features of the identity. However this does not necessarily imply semantic or abstract representations in mFus. Instead retrieval of semantic features might activate the corresponding face representations in mFus. Thus mFus activity during face trials might not necessarily reflect a single individual face but instead encodes all visual information corresponding to semantic categories (e.g. surgeons, jazz fans and married men). For two identities with overlapping semantics, semantic retrieval would lead to a similar activation of two face representations simultaneously. For the identity with different semantics, semantic retrieval would lead to activation of only one face representation. Such a scheme predicts that in the current experiment face trials (cueing semantic retrieval) generate distinct response patterns for identities with identical faces (because these are associated to different semantics) but not for identities with overlapping semantics, which matches our results. On the other hand, during semantic trials the task instructions would instigate the person perception system to find a matching unique face representation. This would plausibly drive the system to activate a unique exemplar as is reflected in the above chance level p.a. for identity-pairs with overlapping semantics but different faces.

In this framework semantic content is encoded in mFus without requiring local processing of non-visual information. In the two clusters processes of perception and retrieval plausibly lead to different activations of essentially the same kind of visual representations. This account would also predict an above chance level p.a. for identity-pairs with both different faces and different semantics in the two clusters during semantic trials. However this was not found. It is possible that these identities were not accurately classified due to noise in the response patterns, although one of these identities was reliably decoded during classification of identity-pairs with overlapping semantics.

A modality-specific account of semantic retrieval

The successful decoding of identities that differ only in their semantic features suggests that the FFA is not merely involved in recognizing faces by their visual form. At least its anterior/medial part (mFus) seems to support the retrieval of semantic attributes by activating corresponding visual representations. This does not contradict the commonly found implication of the FFA in recognition of faces (Kanwisher & Yovel, 2006). Functional evidence indicates that the neural system for recognition of objects at least closely matches the system that enables semantic retrieval (Chao, Haxby and Martin, 1999). Interestingly it has been demonstrated that semantic retrieval evokes neural activation slightly anterior to some occipital sites that were maximally activated during perception of those visual features (Martin, et al., 1995). The current study indicates that a similar organizational principle might apply to the domain of face perception.

Our modality-specific account of conceptual person information in the FFA is in support of theories that describe semantic memory as a distributed network of sensory-motor features (e.g. Carbonnel, Charnallet, David & Pellat, 1997). We propose that conceptual person information is encoded by activating multiple corresponding visual feature representations simultaneously. Neuropsychology, modeling and neuroimaging evidence indeed indicates that concepts are represented by patterns of activation over multiple properties (Tyler & Moss, 2001). Certainly a distributed semantic memory might coexist with a more abstract level of representations where modality-specific representations are bound (Vinson, Vigliocco, Cappa & Siri, 2003). Adaptations of the paradigm presented in this paper might prove suitable to target these and other specific hypotheses about the representation and topological organization of conceptual information in the brain. It would for instance be interesting to learn if our findings generalize to other highly specialized object selective regions such as the Parahippocampal Place Area.

Unsuccessful localization of the VWFA

A possible confounding issue is presented by our inability to successfully localize the VWFA in any of our subjects. Therefore we cannot entirely exclude the possibility that some responses in voxels attributed to the FFA might have originated from the nearby VWFA responding to the shape of written words. Apparently the sensitivity of the contrast of words with random letter strings was too low to detect the VWFA in our subjects. Possibly contrasting pseudowords with phase scrambled words might have accomplished better localization results (Yeatman, 2013). However contamination of our data with VWFA responses is unlikely because it would systematically favor decodability of identities with different semantics (that have different word forms), which is not apparent from our data.

Conclusion

Our results demonstrate that the anterior/medial FFA-cluster (mFus) contains information about semantic features of people during retrieval of these features. They further suggest that this semantic information is expressed modality-specific

by activation of corresponding visual attributes (face representations). On the other hand when a unique person's face is retrieved mFus aids its posterior/lateral neighboring cluster (pFus) by homing in on a single face representation. During face perception the latter cluster appears to be involved in perceptual analysis with face representations being enhanced when unique semantic information is available.

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