Distributed subordinate specificity for bodies, faces, and buildings in human ventral visual cortex

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A B S T R A C T

Previous studies have revealed regions in human visual cortex with a strong preference for faces, headless bodies, and buildings. We investigated whether the pattern of activity in these category-selective regions is related to more subordinate distinctions among objects. Our experiments included two types of faces (elderly faces and baby faces), body parts (hands and torsos), and buildings (rural buildings and skyscrapers). Multi-voxel pattern analyses revealed very clear differences in the activation pattern between hands and torsos, and smaller but significant differences in the activation pattern between the two face conditions and between the two building conditions. The subordinate specificity was very distributed, as all category-selective regions were most selective for the distinction between hands and torsos, independently from their preferred category. The selectivity for hands versus torsos was preserved across exemplars and image orientations in all category-selective regions, indicating that the distributed subordinate selectivity is related to relatively invariant and higher-order properties of the images.

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Introduction

Many functional imaging studies over the last decade have revealed category-specific regions in the object vision pathway. Notable examples are regions specific for faces (Kanwisher et al., 1997; Kanwisher and Yovel, 2006), headless bodies (or “body parts other than faces”, Downing et al., 2001), and scenes/buildings (Epstein and Kanwisher, 1998; Ishai et al., 1999). Here we studied whether specificity can be detected in these category-specific regions for more subordinate distinctions within each of these categories.

Prominent questions in the investigation of category specificity have been the relative strength of specificity for different object categories, the extent to which this specificity is distributed across a wide cortical area, and the factors that might explain the category specificity. None of these questions has been answered fully, but some partial answers have been proposed. First, the aforementioned categories, faces, headless bodies, and buildings, are associated with stronger category specificity than a wide range of other categories (Downing et al., 2006; O’Toole et al., 2005). Second, category information is distributed across a wide cortical area for many object categories (Cox and Savoy, 2003; Haxby et al., 2001), with different voxels having a slightly different preference for a range of object categories. Nevertheless, for faces, headless bodies, and buildings, the category specificity might be more localized (Spiridon and Kanwisher, 2002). Third, several factors are associated with a pattern of specificity in the object vision pathway, including a shape/form map (Haxby et al., 2000; Op de Beeck et al., 2008c), a process map (Gauthier, 2000), and a functionality map (Mahon et al., 2007), but none of these proposed factors seems strong enough to explain the strong category specificity seen for faces, headless bodies, and buildings (Op de Beeck et al., 2008b).

Up to now, no study has investigated these questions for more subordinate distinctions between visual objects. In the context of this study, ‘subordinate’ is defined operationally as “a more specific level than the level investigated in previous studies”. As a consequence, ‘subordinate’ as defined here inherits the arbitrariness of the notion of ‘category’ in the literature. For example, apart from the many studies focusing on category selectivity for e.g. faces, headless bodies, and buildings, some other studies have focused on category selectivity for the more general distinction between living and non-living things or between animals and tools (e.g., Martin et al., 1996; Panis et al., 2008).

Can we expect to detect selectivity with fMRI for distinctions subordinate to the categories of faces, headless bodies, and buildings? Possibly not. For example, studies in monkeys revealing the existence of feature columns in monkey inferior temporal cortex have led to the proposal that only objects from different categories would activate different columns, and within-category distinctions might be a matter of within-column processing (Logothetis and Sheinberg, 1996). Along this line of reasoning, we would not expect any functional organization for subordinate distinctions since only between-column differences would be detectable given the coarse spatial resolution of...
fMRI. Consistent with this view, a recent study looked for signals that distinguished between two face images that differed in many important properties (including gender), and failed to find any effect in the lateral occipital and fusiform gyri where category-selective regions are typically located (Kriegeskorte et al., 2007). Nevertheless, other lines of research suggest that functional organization in terms of subordinate distinctions between objects might exist. First, if the shape or form of objects matters, as has been proposed before (Op de Beeck et al., 2008c), we would at least expect some specificity for finer distinctions between objects as long as their shape is clearly different. Second, another recent study, using common objects like teapots, was able to decode object-exemplar information slightly better than chance (Eger et al., 2008). Overall, the mere existence of any functional organization in the object vision pathway for subordinate distinctions is not clear, and evidence is especially lacking for the subset of categories that are associated with strong specificity at the category level (faces, headless bodies, and buildings).

We designed an experiment to study the existence of subordinate specificity for the categories of faces, headless bodies, and buildings, and to target each of the aforementioned questions that have been unexplored in the context of subordinate specificity. First, how strong is the subordinate specificity relative to the strong category specificity for these object categories? Second, how distributed is the subordinate specificity? Is it restricted to regions with corresponding category selectivity (e.g., only subordinate face information in face-specific regions), or it distributed across all object-selective regions? Finally, which factors explain or do not explain the subordinate specificity?

To study these questions, we divided each of the categories of faces, headless bodies, and buildings into two subordinate groups (Fig. 1): elderly African/Afro-American faces versus other-race baby faces (subordinate distinction by age and race), hands versus torsos (two nonface body parts included in headless bodies), and rural buildings versus skyscrapers. Multi-voxel pattern analyses revealed an organization in ventral visual cortex that extended to the subordinate level, with very clear differences in the activation pattern between hands and torsos, and smaller but significant differences in the activation pattern between the two face conditions and between the two building conditions. This selectivity was widely distributed, as it was found both in regions with strong selectivity for a particular object class (e.g., subordinate body part specificity in the extrastriate body area) and in other ventral visual regions. Finally, an additional experiment showed that the strong selectivity for hands versus torsos was preserved across exemplars and image orientations, indicating that this selectivity reflects exemplar- and orientation-invariant properties of the images. In conclusion, we have found distributed subordinate selectivity for several familiar object classes that is particularly strong for body parts.

Materials and methods

Subjects

Ten normal and naïve subjects participated in the first fMRI experiment. Analyses include the data of only nine subjects because of technical problems with the scanner during data acquisition of one
subject. Three of these subjects also participated in a second experiment ("generalization" experiment). Twenty other subjects participated in the behavioral shape rating experiment. The experiments were approved by the relevant ethical boards, that is, the ethical committee of the Faculty of Psychology and Educational Sciences (K.U.Leuven) and the committee for medical ethics of the K.U.Leuven.

**Stimuli**

In the first experiment, the stimulus set included 120 images, 20 exemplars from three times two conditions: elderly African/Afro-American faces versus other-race baby faces (subordinate distinction by race and age), hands versus torsos (two nonface body parts included in headless bodies), and rural buildings versus skyscrapers. Fig. 1A shows a few exemplars from each condition, all images are shown in Supplemental Fig. 1. For four subjects, images were presented in a colored format as shown in the left two columns. For the five other subjects, images were converted to gray-scale and normalized to have the same average luminance per condition. We included this manipulation to leave open the possibility that results would depend on color or overall luminance, but this did not seem to be the case. For example, the linear SVM classification performance for subordinate distinctions including all category-selective voxels revealed similar results in the two sub-groups of subjects. In each sub-group, the deviation from chance performance was significant (p<0.05) for buildings and for nonface body parts, and close to significant for buildings (original images: p = 0.06; normalized images: p = 0.07; so significant according to a one-tailed test). In addition, the subordinate specificity for nonface body parts was significantly stronger (p<0.05) than for each other category in each subject group. We did not include enough subjects to perform powerful analyses of the differences between the two subject groups in these and other analyses, but these tests indicate that subordinate specificity and the relative strength of it across object categories (our two main findings) were present in each subject group.

The pixel-by-pixel overlap between images from the six different conditions was quantified in a similar way as in previous studies (e.g., Grill-Spector et al., 1999; Op de Beeck et al., 2008c). For each pair of images, we computed the difference in each pixel (maximal difference 255), squared it, summed it across all pixels, took the square root of this sum, and normalized the resulting number by 255 times the square root of the number of pixels. As the resulting number is a difference measure (diff) instead of a similarity index (sim), we inverted it to get an index of pixel-based overlap: sim = 1-diff. The overlap measures for individual pairs of images were averaged across pairs containing images from the same two conditions, resulting in the 6 x 6 similarity matrix shown in Table 2.

In a second experiment, referred to as the generalization experiment, the stimulus set included only nonface body part images (Fig. 1B). This experiment was meant to test generalization across image transformations, and it only included body part conditions because the first experiment revealed the strongest subordinate specificity for body parts (see Results section). There were 40 images, which were the same images as in the first experiment or transformed versions of them. The images were divided in four separate conditions with 10 images each: (1) horizontally oriented compact hands, (2) vertically oriented more stretched hands, (3) horizontally oriented torsos, and (4) vertically oriented torsos. The conditions with the same body parts included different exemplars (so not just the same exemplars in a different orientation). There were 10 images in each condition.

**Behavioral ratings of shape similarity**

We performed a behavioral experiment in 20 subjects to assess perceived shape similarity for the stimuli used in the first experiment, using exactly the same procedure as Op de Beeck et al. (2008c). For each subject we randomly selected two images from each of the six conditions. After 10 subjects, all 20 images per condition were used once, and this image by subject grouping was then repeated for the other 10 subjects. For each subject the experiment started with a very short familiarization phase in which the 12 images were shown in a random order (1 s per image). This short preview was included in order to familiarize subjects with the range of objects in the experiment. Next, subjects were requested to rate the similarity in shape between two successively presented images (stimulus duration, 150 ms; inter-stimulus interval, 500 ms) by pressing a key from 1 (shape is not similar at all) to 7 (very similar in shape). Subjects were instructed to use the whole scale for their responses in the rating task, and the preview phase allows them to calibrate the scale (as such avoiding a short period of instability at the start of the rating task). This procedure allows us to compare the relative similarity of different object pairs with maximal sensitivity. For each subject, each permutation of the 12 object images was presented four times (528 trials per subject). No trials were included in which the two images were exactly the same, but the two images from the same condition were paired (e.g., hand1 versus hand2). The data were averaged to form a 6 x 6 similarity matrix in which cell(i,j) represents the average similarity between images from condition i and images from condition j (Table 3).

**Scanning**

Functional images were acquired in a 3 T Philips Intera magnet (Department of Radiology of K.U.Leuven) with a 8-channel SENSE head coil with an echo-planar imaging sequence (75 time points per time series or "run"; repetition time, 3 s; echo time, 30 ms; acquisition matrix 104 x 104, resulting in a 2.1 x 2.1 in-plane voxel size; 49 slices oriented roughly halfway between a coronal and horizontal orientation and including most of cortex except the most superior parts of frontal and parietal cortex, with slice thickness 2 mm and interslice gap 0.2 mm). We also acquired a T1-weighted anatomical image (resolution 1 x 1 x 1.2 mm).

Functional runs (first experiment: N = 8–12; generalization experiment: N = 10) consisted of 15 blocks of 15 s, including three fixation blocks (at the start, middle, and end of the run) and two blocks of each condition. The order of the conditions was counterbalanced across runs and across subjects. Twenty images (maximum size 8 visual degrees) were presented for 150 ms (inter-stimulus interval: 600 ms) in each stimulus block. The spatial position of each stimulus was determined randomly in a square region of 12 x 12 visual degrees centered at the fixation point.

Subjects performed a one-back task in the scanner. Two of the 20 images in a 15-s block were immediate repetitions. Subjects had to press a button if they noticed an immediate repetition. In the first experiment, subjects detected 79% of the one-back repetitions with performance ranging from 71% (SEM = 6%) for skyscrapers to 85% (SEM = 3%) for elderly faces. We checked whether the absolute difference in performance between conditions was related to the correlation (similarity) in selectivity pattern between conditions in the large ROI containing all category-selective voxels. The correlation between this absolute difference in performance and neural similarity was only 0.13, indicating that the relative difficulty of two conditions does not contribute to how similar two conditions are in how they activate category-selective regions.

The two experiments were performed in different scan sessions separated by an interval of several months.

**Analysis of imaging data**

Data were analyzed using the Statistical Parametric Map software package (SPM5, Wellcome Department of Cognitive Neurology, London), as well as custom Matlab code.
Preprocessing

Preprocessing involved realignment to correct for motion, co-registration of functional and anatomical images, segmentation (Ashburner and Friston, 2005) and spatial normalization to an MNI (Montreal Neurological Institute) template. During spatial normalization, functional images were re-sampled to a voxel size of 2×2×2 mm. Finally, functional images were spatially smoothed (4 mm full-width-half-maximum kernel). We have shown before that smoothing of twice the voxel size increases the signal-to-noise ratio for correlational multi-voxel analyses (Op de Beeck et al., 2008c).

Statistical analyses

Statistical modeling of the signal in each voxel in each subject included a general linear model applied to pre-processed images, with six independent variables (one variable for each stimulus condition) and six covariates (the translation and rotation parameters needed for re-alignment). Multi-voxel analyses were performed using the parameter estimates obtained after fitting the general linear model (termed ‘beta values’ in SPM). For ROI analyses we converted these parameter estimates into approximate values of percent signal change (PSC) compared to the implicitly modeled fixation condition by dividing the beta values by the constant term in the general linear model and multiplying the result by 100.

Regions of interest

We defined several ROIs. The purpose of these ROIs, except for the third type, was the application of multi-voxel analyses. First, in each subject a ROI was selected based on an F-contrast in which each condition was compared with each other condition—with the exception of subordinate distinctions (e.g. baby faces–hands, baby faces–torsos, but not hands–torsos). This exception turned out to be irrelevant, as we never observed voxels that were selective at a subordinate level and not at the category level (see Results section). We used F-contrasts because each direction of the contrast is meaningful (t-contrasts would have required twice as many contrasts). The ROI was defined as all voxels in lateral occipital and ventral occipitotemporal regions that were significantly activated at the threshold of P<0.0001 (uncorrected for the number of voxels).

Second, we defined ROIs selective for specific category contrasts: the fusiform face area or FFA (contrast of faces minus all four nonface conditions), the extrastriate body area or EBA (contrast of hands plus bodies minus all four other conditions), and the parahippocampal place area or PPA (contrast of buildings minus all four nonbuilding conditions).

Third, because the data showed strong selective responses for hands versus torsos (but not for the other subordinate contrasts, see Results section), we defined hand- and torso-selective regions in the extrastriate cortex (EBA_hand and EBA_torso) and in ventral occipitotemporal and fusiform cortex (FUS_hand and FUS_torso). These regions were defined by a contrast of only one body-part condition versus the average of the four other conditions (faces and buildings). A direct contrast of hands versus torsos did not consistently reveal significant activations in individual subjects, nor did a more stringent requirement that hands or torsos should give significantly more response than each of the four other conditions (especially in the fusiform gyrus).

Finally, area V1 was defined by a mask based on a probabilistic map of area 17/V1 in MNI space, derived from the Anatomy toolbox for SPM (www.fz-juelich.de/ime/spm_anatomy_toolbox).

Statistically unbiased ROI definition for multivariate analyses

We included multiple definitions of each functionally defined ROI that was used in multivariate analyses of Experiment 1 (correlation-based and pattern classification), so all aforementioned ROIs except the hand- and torso-selective regions. In these analyses, two subdivisions of the data are compared (e.g., runs(1–6) versus runs (7–12); odd runs versus even runs). It has been shown previously that the results of multivariate analyses and statistical analyses in general can be biased easily by the way in which the ROIs are selected (Baker et al., 2007). This would happen if voxel selection is partly based on consistence of responses across the two subsets of the data that are compared in the multivariate analyses. In our case, we would make this error if we would define our statistical contrasts using data from all runs. To avoid this bias, we selected as many variants of each ROI in each subject as we had subdivisions in the multivariate analyses (N=12). For example, if spatial correlations were computed between runs(1–6) and runs(7–12), then voxels were included if they were significantly selective in a contrast defined across runs(1–6) or across runs(7–12).

A similar bias might arise during the decision of which voxels are in the correct neuroanatomical position (e.g., fusiform gyrus for area FFA). Whether or not a significantly activated voxel will be included in the ROI depends on its anatomical position. The decision as to whether a particular set of voxels is still within the neuroanatomical region of interest might be influenced by whether voxels in this location were also significantly active in the other subset of runs, introducing a similar bias as described above but now based on subjective rather than statistical grounds. To avoid this problem, we have constraint the anatomical position of our ROIs in two steps. First, we selected all significantly active voxels in a particular contrast that were in the correct neuroanatomical region for each subject (e.g., fusiform gyrus for the FFA). Next, we composed a mask image for each subject that included all voxels that were selected in at least one of the other eight subjects and all voxels around them in a 4 mm radius. The voxels in the ROIs used in the multivariate analyses were then constrained to be in this other-subject mask.

The ROI definitions were based on the data from the first experiment. The data of the generalization experiment were acquired in a different scan session. This guarantees that the ROI definition is statistically independent from the data that are analyzed, so for the analysis of the generalization experiment we used only one of the aforementioned ROI definitions (based on the subdivision in odd and even runs).

The average number of voxels (with its standard error) in each of the ROIs used for multivariate analyses is as follows: general category-selective region, 1883±308; FFA, 309±57; EBA, 208±43; PPA, 455±150; V1, 5078±10.

Multi-voxel correlational analyses

We computed correlations following previously introduced methods for multi-voxel pattern analysis (Haxby et al., 2001). The data were divided in two random equally sized subsets of runs. We constructed lists as long as the number of voxels in a ROI, and each list contained the response (parameter estimate) for all voxels for a particular condition in one subset. These responses were converted into a measure of selectivity per voxel by subtracting the mean response across all conditions. Then the values in each list of the first subset were correlated with the values in each list of the second subset, resulting in an asymmetric 6×6 correlation matrix. This matrix was made symmetrical by averaging corresponding cells (e.g., cell(ij) with cell(ji); see Table 1). The procedure of dividing the data in two random subsets was applied 12 times, and the obtained similarity matrices were averaged across these 12 comparisons. For each subdivision of runs we used the same subdivision to define the ROI (see above).

Multi-voxel pattern classification

We used linear support vector machines (SVM) and a cross-validation procedure (e.g., Kamitani and Tong, 2005; Li et al., 2007) to further investigate the effects found in the correlational analyses. Linear SVM was implemented using the OSU SVM Matlab toolbox (www.sourceforge.net/projects/svm/). The input data were the same as used for the correlational analyses. The classification analyses were
slightly different for the two experiments. For each pair of conditions in the first experiment, a linear SVM was trained using the data from six individual runs to find the hyperplane that separates the data from the two conditions, and the performance of the classifier on this pairwise classification was calculated for the average data from the remaining six runs; this procedure was applied 12 times per pair of conditions with a random assignment of runs to the training and test set. For the generalization experiment, linear SVMs were trained in pairwise classification using the data from nine individual runs and tested using the data from the remaining run from either the same pair of conditions or a different pair of conditions (generalization).

The cross-validation involved data from one run, but is actually a leave-two-out procedure because this run provides two selectivity patterns, one from each condition. This is important, because a leave-one-out procedure is susceptible to overfitting and bias (Klement et al., 2008). We performed simulations in which we applied SVMs to random data and that replicated the overfitting and bias effects of Klement et al. (2008) in leave-one-out and no such problems in leave-two-out cross-validation. In addition, we performed permutation tests, with a random assignment of data values to the different conditions, for all instances in which we applied SVMs (each ROI, and each experiment), and in all cases we found chance performance to be around the expected 50% (average across all permutation tests was 49%). Classification performance was higher in the generalization experiment due to the smaller number of conditions (thus a larger number of blocks per condition per run). An additional control analysis of the generalization experiment, mentioned in the Results section, involved less training runs (three instead of nine) and a smaller number of voxels (only three voxels). The relatively mild drop in performance with such a small number of voxels is related to the fact that the data from neighboring voxels are not statistically independent—so the actual number of sources of variability in tests with more voxels is much smaller than the number of voxels. To make the results robust to the exact choice of training runs/voxels, we repeated this selection 50 times and we averaged the results across these repetitions.

Multidimensional scaling (MDS)

We performed MDS (using the ALSCAL algorithm of F. W. Young, UNC Psychometric Laboratory) to visualize the representation space of the six conditions according to the neural similarity data and the perceived shape ratings. MDS places the six conditions in a low-dimensional space in a way that optimizes the correspondence between the relative proximity among the stimuli and the similarity in the similarity matrix (Op de Beeck et al., 2001).

Results

Subordinate specificity in category-selective visual cortex

First we defined direct contrasts of conditions from the same category: elderly faces versus baby faces, hands versus torsos, and rural buildings versus skyscrapers. The subordinate contrasts for faces and buildings did not reveal significantly activated voxels in individual subjects at a family-wise corrected threshold of 0.05 or a more liberal uncorrected threshold of 0.0001. In contrast, the subordinate contrast of hands versus torsos revealed significantly activated clusters of voxels in multiple brain regions in all subjects using the same statistical thresholds (see top row of Fig. 2 for an example).

Given the unexpected strength of the subordinate specificity for nonface body parts, we wondered whether we would be able to pick up this specificity with split-half region of interest analyses, maybe even by comparing voxels in the same anatomical region (e.g., fusiform gyrus). We used the odd scan runs to identify regions that responded significantly stronger to hands or torsos in comparison to the other four conditions (faces and buildings). We used the even runs to measure the response to each condition independently from the data used to select the regions. We identified two regions of interest for each body part condition: one in the extrastriate cortex (EBA_hand and EBA_torso) and one in ventral occipitotemporal and fusiform cortex (FBA_hand and FBA_torso). Note that the contrasts used to identify these regions are less stringent than a direct contrast of hands versus torsos, and indeed the latter contrast does not result in significantly activated voxels in each anatomical region (extrastriate and fusiform) in each subject.

As shown in Fig. 3, there was an effect of the body part used for selecting the regions of interest in extrastriate as well as fusiform cortex. In EBA_hand, the difference in response to hands and torsos (hands more response than torsos) was significantly different compared to EBA_torso (almost equal response to hands and torsos), $(t(8)=3.24, p=0.012$. Likewise, in FBA_hand, the difference in response to hands and torsos (hands more response than torsos) was significantly different compared to FBA_torso (slightly stronger response to torsos than to hands), $(t(8)=5.13, p=0.0009$. In nearby FFA, there was a significantly stronger response to torsos compared to hands: $(t(8)=5.58, p=0.0005$; see Supplemental Fig. 2). Note that especially the fusiform body-selective regions were very small (see numbers in Fig. 3), which is consistent with the earlier report that fusiform body-selective and face-selective regions are difficult to distinguish with the spatial resolution of fMRI (Peelen and Downing, 2005; Schwarzlose et al., 2005). Also in accordance with this earlier work, we noticed that the two fusiform body-selective regions were located slightly more medial and anterior than the FFA (p-values across subjects in the range 0.013–0.079), but these differences were small (<4 mm) averaged across subjects. We did not observe systematic differences in the anatomical location of FBA_hand and FBA_torso. Nevertheless, despite the small size of some of these regions of interest, we were able to pick up the subordinate specificity for different nonface body parts with univariate region of interest analyses.

The location of the regions with subordinate specificity for nonface body parts suggests that we have not discovered new regions that were not identified yet in the literature on category selectivity. Indeed, these regions turned out to be a subset of the network of regions activated in contrasts at the category level (see bottom row of Fig. 2), such as (nonface body parts)–(faces and buildings) and (faces)–(nonface body parts and buildings). In none of the subjects did we ever find a single voxel that was activated by a subordinate contrast that was not activated by at least one of the possible pairwise contrasts of conditions from a different category. Thus, subordinate specificity, as far as it exists, involves the same network of regions that have been identified in previous studies to be category-selective.

In a next step, we identified these category-selective regions, defined by all voxels in lateral occipital, temporal, and occipitotemporal cortex that showed a significant difference in activation between conditions from a different category (e.g., baby faces versus hands). The activated regions encompass all the category-selective regions that have been identified before, or at least as far as they are found in an individual subject (see Fig. 4 for an example), including the occipital and fusiform face areas (FFA and OFA), the extrastriate and fusiform body areas (EBA and FBA), and the parahippocampal place area (PPA).
The contrasts used for this voxel selection did not include subordinate contrasts (e.g., rural buildings versus skyscrapers) so that the regions were selected as category-selective regions typically are (by their category selectivity) and were not biased to include potentially existing regions with subordinate specificity but no category specificity. However, as noted above, such regions with subordinate specificity but no category specificity do not exist. Thus, it did not matter whether or not we included the subordinate contrasts.

We applied correlational analyses (e.g., Downing et al., 2007; Haxby et al., 2001; Op de Beeck et al., 2008a) to investigate how the pattern of selectivity in this large category-selective region of interest differed between the six conditions. The data were divided in two subsets, and we correlated the across-voxel pattern of selectivity for each condition in the first subset with the pattern of selectivity for each condition in the second subset. The results from all pairwise comparisons are listed in Table 1, and the most important comparisons to assess subordinate specificity are shown in Fig. 5A. Confirming previous reports, we found strong positive correlations when we correlated the same condition in the two subsets, e.g. hands with hands, and this was found for all three object categories (faces, headless bodies, and buildings). Most importantly, we observed significantly lower correlations when we correlated the different subordinate groups within an object category (e.g., hands versus torsos): faces ($t(8)=4.93$, $p=0.0012$; two-tailed paired $t$-test across subjects), headless bodies ($t(8)=8.65$, $p=0.0002$), and buildings ($t(8)=2.37$, $p=0.046$). Albeit significant, the effect size was relatively small for faces and for buildings, significantly smaller than the subordinate specificity found for hands versus torsos (comparison with faces: $t(8)=8.1$, $p=0.0004$; comparison with houses: $t(8)=9.26$, $p=0.0002$). In fact, the selectivity pattern for torsos was as distinct from the selectivity pattern for hands (correlation between torsos and hands: $r=0.09$) as it was to the selectivity pattern for the two face conditions (old faces: $r=0.11$; baby faces: $r=0.05$).

We supplemented these correlational analyses with multivariate classification analyses (Fig. 5B). We trained classifiers, more specifically linear support vector machines, to classify selectivity patterns from one subset of the data as belonging to one out of two subordinate groups (e.g., binary classification of rural buildings versus skyscrapers). After training, we tested the classifier’s performance on another, independent dataset. Consistent with the findings in the correlational analyses, these classifiers performed significantly ($p<0.005$) better than chance (50%) on the subordinate distinction in each of the three categories (mean±SEM: faces: $0.61±0.026$; nonface body parts: $0.94±0.022$; buildings: $0.72±0.045$), again with the best performance for nonface body parts.

**Subordinate specificity is distributed**

Above we applied multivariate analyses to the pattern of selectivity across all category-selective regions. Would subordinate specificity be...
the same in all these sub-regions? Intuitively, one might expect subordinate specificity within a particular category to be stronger in a cortical region that is selective for that category. For example, the PPA is defined by a stronger response to buildings than to nonbuilding conditions. Thus, it makes sense to predict that the pattern of selectivity in the PPA will not be able to distinguish between specific groups of faces or between nonface body parts. Much to our surprise, subordinate specificity was not modulated by the category preference of a category-selective region. Fig. 6 shows the classification performance of linear support vector machines applied on the pattern of selectivity in a region of interest restricted to be specific for one object category, so either face-selective (FFA), nonface body-selective (EBA), or building-selective (PPA). The pattern of selectivity in each of these category-selective regions showed clear above-chance classification performance for the distinction between hands and torsos ($p<0.005$ in each region). The classification performance for each of the other subordinate distinctions was significantly lower than the performance for body parts in each ROI (two-tailed paired $t$-tests, $p<0.05$), even though it still tended to be above 50% in some cases (two-tailed paired $t$-tests), FFA for faces, $t(8)=2.16$, $p=0.063$; FFA for buildings, $t(8)=2.14$, $p=0.065$; PPA for faces, $t(8)=0.14$, $p=0.89$; PPA for buildings, $t(8)=2.27$, $p=0.053$; EBA for faces, $t(8)=1.76$, $p=0.12$; EBA for buildings, $t(8)=2.37$, $p=0.046$. Classifiers trained on the combined information from all three regions together obtained above-chance performance ($p<0.05$) for each subordinate distinction, as was shown above for the large region of interest containing all category-selective voxels. Thus, together these three regions contain information about each subordinate distinction.

To perform an explicit statistical test of whether the classification performance depended on the region of interest, we implemented a repeated-measures model with the two within-subject factors region-of-interest and category. This analysis showed a main effect of category (best performance for nonface body parts), $F(2,16)=30.53$, $p<0.0001$, and a main effect of ROI (weakest performance in the PPA), $F(2,16)=6.62$, $p=0.008$. Most importantly, we did not observe an interaction between these two factors $F(4,32)=1.29$, $p=0.29$. Thus, in contrast to our intuitive expectation, our results reveal that the pattern of subordinate specificity across the three object categories is not modulated by the category preference of a region.

The role of objective and subjective shape similarity among the images

Which factors might explain the magnitude of subordinate selectivity and its variability across object classes? From a conceptual point of view, many differences can be noted. A variation in the age
and race of faces is of course a very different manipulation compared to a variation in the exact body part. As explained in the Introduction, our aim was to maximize the odds of finding subordinate selectivity in each object class, given the current state of the literature.

However, it is definitely possible that the subordinate selectivity is related to an obvious physical or more subjective property of the images. In the next paragraph we will manipulate the image characteristics as one way to understand the functional properties of the underlying neural code. Here we will focus on a different approach, which is the quantification of the images according to various metrics and see how far they bring us in explaining the neural similarity found in category-selective cortex. Tables 1, 2, and 3 reveal the full similarity matrices among all six conditions for three metrics: the aforementioned neural similarity (correlations in activity pattern), pixel-by-pixel overlap, and subjective ratings of perceived shape similarity.

A first metric that we will compare with neural similarity is a measure of pixel-by-pixel overlap between images (Table 2), which has been used before as a benchmark metric (e.g., Op de Beeck et al., 2008c). This metric captures a few aspects of the neural similarity. First, according to this metric there is somewhat less overlap between images from a different subordinate group (average overlap 0.70) than between images from the same subordinate group (average overlap 0.73). Thus, this metric can explain the smaller neural similarity for images from a different subordinate group. Second, the pixel-based overlap between subordinate groups is much larger for the faces (average overlap 0.72) than for the body parts (0.68) and the buildings (0.69). Thus, this metric can explain the relatively minor subordinate selectivity for faces found in the neural data.

However, pixel-by-pixel overlap fails at several important points, which is to be expected given the obvious simplicity of the metric. First, the overlap between images from a different subordinate group of the same class (average overlap 0.70) is as small as between images from a different object class (average overlap 0.70). This is not the case for neural similarity, where the different-subordinate correlations (0.50 on average) are much higher than the different-class correlations (-0.30 on average). Second, the difference between body parts and buildings in the different-subordinate pixel overlap is very small, while the difference in neural subordinate selectivity is much more pronounced in the neural data. Thus, the pixel-by-pixel overlap metric cannot explain the large difference between body parts and buildings in terms of subordinate selectivity (much more pronounced for body parts than for buildings). Nor can it explain the fact that subordinate selectivity is the same for faces and for buildings, as it would predict selectivity to be much larger for buildings. Finally, according to pixel-by-pixel overlap torsos and skyscrapers are a bit more similar (overlap 0.69 vs. 0.68) than torsos and hands (which might be due to the similar aspect ratio of the torsos and the skyscraper images), while in each subject the neural similarity was less for torsos and skyscrapers (r = -0.37) than for torsos and hands (r = 0.09).

A second metric comes from subjective ratings of perceived shape similarity (Table 3). This metric captures several aspects of neural similarity. First, according to this metric there is less shape similarity between images from a different subordinate group (2.8) than between images from the same subordinate group (4.9). Thus, perceived shape similarity can explain the smaller neural similarity for images from a different subordinate group. Second, the perceived shape similarity

<table>
<thead>
<tr>
<th></th>
<th>Elderly</th>
<th>Baby</th>
<th>Hand</th>
<th>Torso</th>
<th>Rural</th>
<th>Skyscraper</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.72</td>
<td>0.71</td>
<td>0.72</td>
<td>0.71</td>
<td>0.72</td>
</tr>
<tr>
<td>Baby</td>
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<td>0.67</td>
<td>0.69</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
</tr>
<tr>
<td>Hand</td>
<td>0.73</td>
<td>0.68</td>
<td>0.73</td>
<td>0.69</td>
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<td>0.69</td>
</tr>
<tr>
<td>Torso</td>
<td>0.69</td>
<td>0.68</td>
<td>0.70</td>
<td>0.69</td>
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<td>0.69</td>
</tr>
<tr>
<td>Rural</td>
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<td>0.69</td>
<td>0.70</td>
<td>0.69</td>
<td>0.69</td>
<td>0.69</td>
</tr>
<tr>
<td>Skyscraper</td>
<td>0.74</td>
<td>0.69</td>
<td>0.70</td>
<td>0.69</td>
<td>0.69</td>
<td>0.69</td>
</tr>
</tbody>
</table>
between subordinate groups is much larger for the faces than for the body parts and the buildings. Thus, also this metric can explain the relatively minor subordinate selectivity for faces. However, it cannot explain the fact that subordinate selectivity is the same for faces and for buildings, as it would predict selectivity to be much larger for buildings. Finally, according to the shape ratings torsos and skyscrapers are significantly more similar in terms of perceived shape (probably due to the similar aspect ratio) than torsos and hands \((p < 0.001\) according to a \(t\)-test across subjects). In contrast, as mentioned before, the neural similarity is less for torsos and skyscrapers than for torsos and hands.

The clearest illustration of this last point comes from the similarity space that can be constructed based on the similarity matrices with a data visualization technique such as multidimensional scaling (MDS). Fig. 7 displays the similarity spaces related to the perceived shape similarity and the neural similarity. These spaces are most different in the position of the skyscraper and torso conditions. In the perceived shape space, the torso condition is close to the skyscraper condition and further from the hand and face conditions. In contrast, in the neural space the torso condition is nicely in the middle between the hands and the faces, resulting in a clear separation between two clusters: One cluster containing all four human body + head conditions, and the other cluster containing the two building conditions. The latter clustering was quantified by comparing all within-cluster distances with all between-cluster distances. The within-cluster distances were significantly smaller than the between-cluster distances for the neural space according to a two-sample \(t\)-test, \(t(13) = 3.85, p = 0.002\). In contrast, the same two sets of distances were not significantly different for the perceived shape space, \(t(13) = 1.56, p = 0.14\). The same discrepancy was found when the \(t\)-tests were performed on the similarity matrices.

In sum, these metrics can explain the fact that subordinate selectivity is more pronounced for body parts than for faces. However, the results for the building and torso conditions do not fit with either of these metrics. Thus, subordinate selectivity is not a simple function of these metrics.

**Table 3**

Subjective rating of perceived shape similarity between different conditions.

<table>
<thead>
<tr>
<th></th>
<th>Elderly</th>
<th>Baby</th>
<th>Hand</th>
<th>Torso</th>
<th>Rural</th>
<th>Skyscraper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elderly</td>
<td>5.3</td>
<td>4.0</td>
<td>1.9</td>
<td>2.1</td>
<td>1.7</td>
<td>1.8</td>
</tr>
<tr>
<td>Baby</td>
<td>5.5</td>
<td>1.6</td>
<td>1.9</td>
<td>1.6</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>Hand</td>
<td>3.5</td>
<td>1.9</td>
<td>1.7</td>
<td>1.7</td>
<td>1.9</td>
<td></td>
</tr>
<tr>
<td>Torso</td>
<td>5.0</td>
<td>5.0</td>
<td>1.8</td>
<td>3.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rural</td>
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<td>4.7</td>
<td>2.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skyscraper</td>
<td>5.4</td>
<td></td>
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</tbody>
</table>

Subordinate specificity for body parts generalizes across exemplars and orientations

Here we describe the generalization of the neural patterns of selectivity in ventral visual cortex across manipulations of the exact images in the two body part conditions. The strength and the distributed nature of the selectivity for hands versus torsos were unexpected. We wondered whether the selectivity for body parts in typical body-selective regions might be related to other stimulus properties than in e.g. building-selective regions. Many candidate properties can be identified, as we always used the same set of 20 images. In the original experiment we translated the images across the screen to avoid condition-specific biases in the stimulation of specific visual field positions, but many other properties might underlie the selectivity, e.g. the power spectrum of the images.

To resolve these ambiguities, we performed a generalization experiment in which we included two hand and two torso conditions with different exemplars in a different orientation (horizontal or vertical) and for hands even in a different pose (compact or fingers stretched). Only body parts were used in this experiment because the subordinate contrast of hands versus torsos revealed the strongest specificity. SVM classifiers were trained using one hand and one torso condition, and then we tested whether these classifiers could correctly differentiate between the other hand and the other torso condition. If they could, then this would mean that the across-voxel activity patterns contained information that was tolerant for the differences between the conditions and that allowed a generalization across exemplars, orientation, and pose.

Classifiers were trained using patterns from the aforementioned category-selective regions: FFA, PPA, and EBA (Fig. 8). Classifiers obtained very good performance when cross-validated with the same conditions as used during training, with close to perfect performance in each of three subjects tested (10 training/test combinations in each subject, performance significantly above chance in each subject \(x\) ROI combination, \(p < 0.01\)). Most importantly, they generalized very well to the untrained conditions (performance significantly above chance in each subject \(x\) ROI combination, \(p < 0.01\)). Across subjects, the performance for the untrained conditions was significantly different from chance performance in each of the ROIs \((p < 0.01, t\)-test across subjects, \(df = 2\)).

Selectivity patterns in primary visual cortex also allowed above-chance performance (75%) when classifiers were validated with the same conditions.
conditions as used during training \((p = 0.013, t\text{-test across subjects,}\ \ df = 2)\). This result suggests that simpler image features of the type represented in area V1 might contribute to above-chance classification performance with the same training and test conditions. However, in this ROI the classifiers did NOT generalize to the untrained conditions, with only 47% performance (chance is 50%), which is significantly smaller than the 75% performance with the same training and test conditions \((p = 0.03, t\text{-test across subjects})\). Thus, our generalization test was powerful enough to abolish any invariance in area V1.

In contrast to the findings in V1, the classification performance in category-selective regions in this generalization experiment was very good, at ceiling both when training and test involved the same stimuli or different stimuli. We performed additional analyses in which we strongly reduced the number of training patterns during training (from three instead of nine runs) and the number of voxels (to only three voxels per pattern). Under these circumstances the performance was more similar to the classification performance in V1 with the same training and test conditions: EBA: 85%, FFA: 82%, PPA: 75%. Nevertheless, each of these regions showed a significant above-chance performance (both within each subject and across subjects; \(p < 0.05\) for each ROI) when we tested generalization to other, untrained conditions: EBA: 75%, FFA: 78%, PPA: 70%. Although we observed a small overall reduction of the classification accuracy in the generalization test, from 81% to 74%, the distributed selectivity for hands versus torsos in category-selective cortex clearly sustains classification across changes in exemplars, orientation, and pose.

**Discussion**

Our results reveal significant subordinate specificity for finer distinctions than the traditionally studied category selectivity of faces versus other body parts versus buildings/scenes. The subordinate specificity was especially strong for hands versus torsos. The subordinate specificity turned out to be very distributed across different category-selective regions, all of them showing the strongest specificity for hands versus torsos. Finally, the strong selectivity for hands versus torsos was preserved across exemplars and orientations, indicating that this selectivity reflects exemplar- and orientation-invariant properties of the images.

The strength of subordinate selectivity for faces, nonface body parts, and buildings

We decided to focus on the three most-studied object categories for which previous studies have described focal category-selective regions. One reason for this decision is that a previous study failed to find specific patterns of activity in occipitotemporal cortex for face exemplars (Kriegeskorte et al., 2007), while some exemplar-specific activity was detected in another study using object categories that are not associated with focal category-selective regions (Eger et al., 2008). Combined, these two previous studies suggest that maybe subordinate specificity in the spatial profile of activity is present to a lesser extent for those categories that are associated with the strongest category specificity. Stated otherwise, the stronger clustering of selectivity at the category level might decrease the clustering for more subordinate distinctions. Nevertheless, our findings indicate that subordinate specificity is present also for the categories of faces, nonface body parts, and buildings.

In the context of this study, 'subordinate' is defined operationally as “a more specific level than the level investigated in previous studies”. We opted for this operational definition since concepts such as ‘subordinate’ and ‘category’ are relative concepts. However, it is obvious that the distinction between different sets of faces is of a different level than the distinction between hands and torsos. All faces share a common structure, while hands and torsos are very different stimuli. We also presented the similarity among the images in terms of pixel-by-pixel overlap and subjective shape similarity, and each of these metrics can explain why the subordinate specificity is small for faces. From this perspective it is not surprising that we find more subordinate specificity for hands versus torsos than for faces. Nevertheless, both the distinction between different face sets and the distinction between hands and torsos are subordinate relative to the conditions that are typically compared in fMRI studies (all faces versus all body parts versus all buildings). In that respect, our results are most relevant to qualify the tendency in the literature to focus on category specificity. Strong specificity for more subordinate distinctions calls into question the notion of category-selective regions. As we found strongest specificity for different body parts, our results qualify the notion of a body-selective region.

We also have to take into account that we scanned with relatively standard equipment (e.g., 3 T scanner, 8-channel coil). The ability to find subordinate specificity would most likely increase strongly at higher spatial resolution, possibly by the use of smaller and more sensitive coils (Grill-Spector et al., 2006), or scanning at stronger magnetic fields (7 T). Thus, this study is most likely not more than a beginning of the exploration of the extent of information about subcategory object distinctions that can be extracted from the spatial distribution of activity in the visual brain. Up to now studies have mostly investigated selectivity for small stimulus differences by the technique of fMRI adaptation in which the degree of adaptation is interpreted as reflecting the degree to which stimuli elicit similar responses (e.g., Gillebert et al., 2009; Grill-Spector and Malach, 2001; Jiang et al., 2006; Kourtzi and Kanwisher, 2000; Panis et al., 2008). Using fMRI adaptation, selectivity has been shown for fine differences between faces and between other objects (Gilad-Dotan and Malach, 2007; Jiang et al., 2006; Panis et al., 2008). It remains to be seen where the limit is for multi-voxel analyses.

Distributed subordinate selectivity for faces, nonface body parts, and buildings

One benefit of these three object categories is the ability to define functional regions of interest with a clear preference for one category over the other. These ROI analyses allowed a strong test of the extent to which subordinate specificity is distributed across the various category-selective regions of the brain. Surprisingly, subordinate specificity turned out to be very distributed. The distributed nature of subordinate specificity across a wide cortical region might explain why a previous study that focused on local patterns of selectivity failed to find specific patterns of selectivity for exemplars of faces (Kriegeskorte et al., 2007). In our study, subordinate specificity for faces failed to reach significance in the FFA, nor was it significant in the
The distributed nature of the subordinate specificity across ventral visual cortex immediately raises concerns about how to interpret specificity that is seen within smaller sub-regions. For example, studies investigating the representation of faces or buildings would naturally focus on FFA and PPA, respectively. Based on our findings, such studies might indeed find weak but reliable patterns of selectivity to differentiate different faces or buildings. The interpretation of such findings would seem very straightforward, e.g., PPA represents specific information about buildings. However, the story becomes more complicated when it is found that the same region contains as much or even more information about other, nonbuilding stimuli. This is what we found for different body parts in the PPA, and this finding has serious implications for any study focusing on within-category specificity.

One possible explanation for the distributed subordinate specificity is that the pattern of selectivity in category-selective regions is related to visual features that are not necessarily specific to the category preferred by each region. For example, PPA might process aspects of visual images which have proven useful to differentiate among buildings and scenes, but which also differentiate among other objects—sometimes even more than among buildings (as found for hands versus torsos). How category selectivity relates to selectivity for multiple features is an important question for future research (Op de Beeck et al., 2008b). The present findings illustrate how the theoretical distinction between distributed versus focal selectivity, which has attracted much interest in the context of basic-category selectivity (e.g., Haxby et al., 2001; Spiridon and Kanwisher, 2002), is also very relevant for the interpretation of selectivity for finer distinctions between objects.

The pool of possible candidate features for explaining the selectivity for hands versus torsos is greatly reduced by the results of the generalization experiment. This experiment revealed that the selectivity patterns for hands versus torsos are relatively invariant across changes in exemplars and overall image orientations in FFA, PPA, and EBA. It is still possible that the represented features are different in these three ROIs, but in each region these features are useful for differentiating between hands and torsos across various stimulus manipulations. This stands in contrast to the features represented in primary visual cortex.

Subordinate selectivity for body parts

Our results reveal that faces are not the only body part that is set apart from the rest of the body in terms of the pattern of selectivity in visual cortex. It might be more worthwhile to speak about a set of body-related patches of activity, all close together, of which the face-selective regions are a special case. Future studies with more conditions will be needed to investigate which body parts go together and which do not. For example, are the hand-selective regions hand-selective or extremity-selective (in the latter case they would also respond to feet)?

One study has looked at the role of the number of body parts for activating body-selective regions in the extrastriate and fusiform regions (Taylor et al., 2007). The results suggested that the fusiform gyrri respond most strongly when multiple body parts are shown together in their normal configuration, while the representation in the extrastriate cortex is more part-based (responses as strong to one as to multiple body parts). However, it is important to note that this study did not fully contrabalance the body parts across conditions. Torsos were never shown separately in the one-part condition, and they were always present in the multiple-part condition. Given that we found more evidence for torso-specific responses in the fusiform gyrus than in the extrastriate cortex (in the latter region all ROIs tended to prefer hands), it is possible that the multiple-part preference in the fusiform gyrus was in fact due to a torso preference.

The selectivity patterns associated with torsos turned out to be correlated as much with hand-related patterns as with face-related patterns, while the two latter conditions were very different. Intriguingly, torsos appear to have a similar position in neural space as they do in an actual body: they are the link between hands and faces. What is the cause for this particular pattern of pairwise similarities in neural space? As a first step, we might consider simple visual properties of the images. It is impossible to rule out all possible visual features or image statistics that might vary between the subordinate groups, but several obvious candidates can be excluded, even in the data of the original experiment. The color and average luminance of the images is not a determinant of the overall neural space, as we found very similar results with images that were equalized in these factors. The retinotopic envelope of the images is not a likely candidate either given the large position scatter of the images. Furthermore, this factor predicts a completely different pattern of results, including a low similarity between rural buildings and skyscrapers. We analyzed two additional metrics related to physical and subjective shape similarity, and none of them can explain the position of the torsos in the neural space. Finally, the generalization experiment, which revealed invariance across changes in exemplars and image orientation, is a strong indication that the underlying features are more high-level aspects of the stimuli.

One way to interpret the position of the torsos in the neural space is that the response patterns to torsos are influenced by their associations with other stimuli. One might even argue that these results are related to visual imagery: when subjects see a torso, they automatically imagine a face on top of it. However, previous data speak against an account in terms of visual imagery: the activation of the FFA by torsos is modulated by whether or not a roundish object is shown on top of it, with far less activation by torsos shown in isolation (Cox et al., 2004). This finding suggests that torsos presented in isolation (as we did) do not evoke the imagination of a face.

In sum, we have shown that the functional properties driving the organization of category-selective regions in ventral visual cortex do not stop at the level of abstraction typically studied, faces vs. nonface body parts vs. buildings. Finer distinctions can be made, some of which are even detectable with standard univariate analyses (hands vs. torsos), while other distinctions are only detectable with multi-voxel analyses. These findings are a nice illustration of the fact that these multi-voxel analyses increase the ‘conceptual’ resolution of fMRI: More similar conditions, images, or processes can be distinguished. This is something different than the spatial resolution of fMRI, which is related to the spatial scale that functional maps need to have before they are detectable with fMRI techniques, and which can go from very fine-scale maps at a resolution below the typical fMRI voxel size (e.g., orientation columns) up to large-scale maps spanning many mms (e.g., retinotopic maps). Given how difficult it is to prove that the information picked up by multi-voxel analyses is related to a fine-scale map (see e.g. Op de Beeck, 2010), it is very much possible that the subordinate specificity found in the present work is related to a relatively weak large-scale map. Thus, we have illustrated the fine conceptual resolution of multi-voxel fMRI without making any inference about its spatial resolution.

Acknowledgments

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Appendix A. Supplementary data

Supplemental Fig. 1 All images in Experiment 1 in the colored version.

Supplemental Fig. 2 Response in the fusiform face area for each condition. Error bars represent the standard error of the mean response across subjects.

Note: The supplementary material accompanying this article is available at (doi:10.1016/j.neuroimage.2009.11.022).

References


