Research Report

SEMANTIC CATEGORIZATION IN THE HUMAN BRAIN: Spatiotemporal Dynamics Revealed by Magnetoencephalography

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Abstract—We examined the cortical representation of semantic categorization using magnetic source imaging in a task that revealed both dissociations among superordinate categories and associations among different base-level concepts within these categories. Around 200 ms after stimulus onset, the spatiotemporal correlation of brain activity elicited by base-level concepts was greater within than across superordinate categories in the right temporal lobe. Unsupervised clustering of data showed similar categorization between 210 and 450 ms mainly in the left hemisphere. This pattern suggests that well-defined semantic categories are represented in spatially distinct, macroscopically separable neural networks, independent of physical stimulus properties. In contrast, a broader, task-required categorization (natural/man-made) was not evident in our data. The perceptual dynamics of the categorization process is initially evident in the extrastriate areas of the right hemisphere; this activation is followed by higher-level activity along the ventral processing stream, implicating primarily the left temporal lobe.

Categorization is prerequisite for a meaningful organization of semantic knowledge. Indeed, psycholinguists and cognitive psychologists have conducted many experiments in an effort to unveil and understand the principles of semantic categorization in humans, and many models of semantic organization have been proposed (for a review, see Smith, 1995). Animal research (e.g., Freedman, Riesenhuber, Poggio, & Miller, 2001; Thorpe & Fabre-Thorpe, 2001; for a review, see K. Tanaka, 1996) and neuropsychological studies (e.g., Newcombe, Metha, & deHaan, 1994; for reviews, see Farah, 1990; Forde & Humphreys, 1999) suggest that semantic categorization is also reflected on a neurophysiological level. However, knowledge about brain activity underlying semantic categorization in humans is still incomplete. Relevant studies published during the past decade explored perceptual categorization of visual stimuli with the goal of revealing the neural correlates of object recognition, specifically, selective activation by exemplars of particular object categories (e.g., Gerlach, Law, Gade, & Paulson, 1999; Martin, Wiggs, Ungerleider, & Haxby, 1996).

By and large, neuroimaging and electrophysiological studies in humans have provided evidence for a discrete categorical organization in the ventral pathway of the visual system. In particular, there is converging evidence that areas in the occipito-temporal cortex are specialized in processing ecologically important stimuli, such as faces and words (Allison, Puce, Spencer, & McCarthy, 1999; Kanwisher, 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Schendan, Ganis, &

Kutas, 1998), as well as other semantic categories, such as animals, fruits, buildings, chairs, and man-made tools (Aguirre, Zarahn, & D'Esposito, 1998; Chao, Haxby, & Martin, 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Moore & Price, 1999). These studies have successfully delineated the cortical topography of the visual perceptual system, but have not provided the evidence necessary to make a claim for semantic (in addition to perceptual) organization in the brain. The understanding of the dynamic principles of this putative organization would benefit from exploring the time course of categorization processes, as well as from demonstrating associations (in addition to dissociations) between patterns of activity elicited by concepts at different levels of categorization (cf. Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997). Although there is some evidence that, at least for experienced observers, perceptual categorization starts immediately with well-defined concepts (J.W. Tanaka, 2001), it is conceivable that the time course of processing semantic information is different from that of processing perceptual information.

In a recent study, Pulvermüller, Assadollahi, and Elbert (2001) found that neuromagnetic brain responses may reflect the meaning of words and their semantic association, and that this effect is observed prior to manifestations of grammatical categorization.

The present study used magnetic source imaging, an index of brain activity that combines high temporal resolution with useful spatial resolution, to uncover spatiotemporal properties of the semantic categorization process.

METHOD

Participants

The participants were 10 right-handed native German speakers (5 women) with normal vision. Their ages ranged from 23 to 35 years old.

Stimuli

The stimuli were pictures (8-bit gray scale) of 960 objects with a uniform background, and an identical resolution of 300 × 360 or 360 × 300 pixels. The objects were selected from four superordinate categories (forest animals, flowers, clothes, and furniture). Each superordinate category was represented by four different base-level concepts (animals: bear, wolf, deer, fox; flowers: rose, sunflower, orchid, tulip; clothes: jacket, pants, shoe, shirt; furniture: table, chair, sofa, wardrobe). Each base-level concept was represented by 60 pictures of different exemplars.

Task and Procedures

The participants were requested to indicate whether each stimulus was a man-made or a natural object by pressing one of two alternative

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response buttons. Responses were made with the index and middle fingers of the right hand; which finger was used for natural objects and which was used for man-made objects was counterbalanced. The series of 960 stimuli was divided into three blocks of 320 pictures each; 16 additional practice trials preceded the experimental run to familiarize subjects with the experimental task and stimuli. The stimuli were presented in a random sequence (randomized across and within blocks) via a mirror system. Exposure time for each picture was 750 ms, and the stimulus onset asynchrony was 1,500 ms. A fixation cross was presented at the center of the screen during the interstimulus interval.

Neuromagnetic Recording

A Magnes 2500 Neuromagnetometer system (4D Neuroimaging, San Diego, CA), installed within a magnetically shielded room, was used for magnetoencephalographic (MEG) recordings. The measuring surface of the sensor was helmet shaped and covered the entire cranium, with the 148 signal detectors (magnetometer type) being arranged in a uniformly distributed array.

Data were sampled at 678 Hz using a bandwidth of 0.1 to 200 Hz. After artifact correction by noise reduction, correction of ocular and cardiac artifacts, and off-line digital filtering at 0.1 to 30 Hz, the data were segmented in epochs of 1,000 ms, starting 100 ms before stimulus onset, and baseline corrected.

Data Analysis

For every subject, the event-related response was averaged separately for each of the 16 base-level concepts, and the individual grand mean across all concepts was subtracted from the grand mean for each single concept to remove activity not related specifically to it. Activity in the source space was determined by the minimum norm estimate including 197 dipoles located on a sphere (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). This distributed source model provides the best estimate of the sources underlying the extracranially recorded magnetic field when minimal a priori information about these sources is available.

Associations and dissociations among the patterns of neuromagnetic activity elicited by each base-level concept were determined using (a priori planned) within- and between-category correlational analyses and post hoc unsupervised clustering. Spatial activation in the source space was compared separately for 17 cortical areas (Fig. 1). On the basis of theoretical considerations as well as an empirically observed peak of neuromagnetic activity (see Results), we focused our analysis over two time epochs, one from 170 to 210 ms and the other from 210 to 450 ms. The first interval is one during which the initial stages of visual processing in humans are completed (Thorpe & Fabre-Thorpe, 2001), and the second is most likely associated with semantic activity.

Correlational analysis

The Pearson correlation coefficients for all possible pairs of the 16 base-level concepts were determined for the 17 areas across eight dipole locations in each area. These coefficients were Fischer Z transformed and averaged to yield two data points per subject for each area: one representing the mean level of correlation for pairs of base-level concepts within the same superordinate category, and the other repre-

Fig. 1. Schematic representation of the distribution of the 17 areas clustered for analysis (top view, nose up).

senting the mean level of correlation for pairs of base-level concepts across different categories. The difference between the Z scores (between categories subtracted from within categories) was calculated as a contrast score for each of the 17 cortical areas and mapped for the two time intervals, 170 to 210 ms and 210 to 450 ms.

Unsupervised clustering

This analysis was based on two unsupervised clustering algorithms operating on high-dimensional vectors comprising the averaged spatiotemporal neural activity elicited by stimuli denoting the base-level concepts in each category. The first algorithm was a hierarchical pattern classification, and the second was a self-organizing topographic feature map (SOM). The algorithms were independently applied to each of the 17 cortical areas, and to combinations of these areas.

The hierarchical pattern classification was based on a deterministic algorithm that, in sequential passes, clusters the two (euclidean) closest high-dimensional vectors, so that at each pass the number of clusters is decreased by one. After a cluster is formed, it is represented by the mean of the vectors composing it. At the end of the process, by necessity, all vectors form a single cluster. This procedure enables one to follow the dynamic formation of clusters and to identify which original vectors (i.e., base-level concepts) are included in each cluster (Duda, Hart, & Stork, 2000).

The SOM resulted from an unsupervised stochastic iterative learning algorithm that clusters high-dimensional vectorial data. At each iteration, a data vector (representing, in our case, 1 of the 16 base concepts) is randomly chosen (without replacement) and compared

with a set of vectors of the same dimension organized on a (usually) two-dimensional grid. At each comparison, the vector on the grid that is the most similar to the data vector (based on a high-dimensional metric function) is algorithmically modified, becoming even more similar to it, and so are its neighboring vectors. The size of this neighborhood decreases as the number of iterations increases. Upon convergence of the algorithm, the original data vectors are mapped on the grid such that vectors that are similar in their properties are placed at topographically nearby nodes (Kohonen, 2001).

In the present study, the map was two-dimensional (10×10 nodes), and the 16 original vectors were mapped onto it to form geometrically meaningful clusters. For illustration purposes, the U-MAT algorithm was implemented on the organized map (Utsch, 1993). This algorithm colors the organized map using a gray scale, such that the actual similarity between the high-dimensional vectors (concepts) that are represented by the nodes in the two-dimensional map is reflected by color density: Darker demarcation space reflects larger high-dimensional distance between the adjacent nodes.

RESULTS

Task performance was very good. Participants correctly categorized between 91% and 95.7% of the objects, with an average latency of 542 to 575 ms per category. There were no significant differences in accuracy or response time across the 16 categories, indicating that categories did not differ in perceptual complexity.

The processing of the visual stimuli was manifested by a peak of the evoked magnetic response with latency varying across subjects between 150 and 200 ms (Fig. 2a); the scalp distribution of this activity suggested occipito-temporal maxima with a tendency over the right hemisphere (Fig. 2b).

The results of the correlational analysis based on the minimum norm estimates calculated between 170 and 210 ms after stimulus onset showed that the spatial patterns of neuromagnetic activity were more similar for concepts within a superordinate category than for concepts between categories (Fig. 3a). An analysis of variance comparing the mean Z-transformed correlation coefficients, indexing the similarity of activity patterns within areas, showed that the correlations were significantly higher within superordinate categories than across categories, $F(1, 9) = 19.57$, $p < .001$. A post hoc contrast, comparing within- versus across-category coefficients, showed that this effect was most pronounced in right temporal cortex, $F(1, 9) = 20.14$, $p < .001$. During the subsequent time interval from 210 to 450 ms, a second maximum of contrasts, in addition to the right-temporal focus, appeared in the left temporal cortex (Fig. 3b).

The unsupervised hierarchical clustering process indicated a similar pattern during the second time interval, from 210 to 450 ms. As shown in Figure 4, this process revealed only within-category clustering during the first 12 passes. In fact, after 12 passes, the base-level concepts were clustered in the four superordinate categories to which they were a priori assumed to belong. As was the case for the correlational analysis in this time interval, this pattern was observed in the

Fig. 2. Typical evoked magnetic fields of 148 superimposed sensors averaged across stimuli for 2 subjects (a) and spatial patterns of neuromagnetic activity in the source space (b). The topographical maps (top view, nose up) show the minimum norm estimate (averaged for the time interval 170 to 210 ms after stimulus onset) for two base-level concepts from each of the four superordinate categories (from top to bottom: furniture, clothes, animals, flowers).

A) 170-210 ms **B) 210-450 ms**

Fig. 3. Z-transformed correlation coefficients for objects within and between categories (a) and self-organizing (Kohonen) map of base-level concept-related activity in the left temporal cortex (b). The bar chart in (a) presents the Z-transformed correlations for the right temporal cortex (arrows indicate within-category correlations), and the map shows the topographical distribution of the difference of the Z scores for correlations within and across categories for the time interval from 170 to 210 ms after stimulus onset. The map in (b) shows the topographical distribution of the difference of the Z scores for correlations within and across categories for the time interval from 210 to 450 ms after stimulus onset. furn = furniture; cloth = clothes; anim = forest animals; flow = flowers.

left hemisphere, and was best reflected within the temporal lobe. In right-hemisphere areas, clustering resulted in occasional combinations of base-level concepts across superordinate categories. During the

early epoch from 170 to 210 ms, no coherent clustering was found in either hemisphere. A similar pattern emerged using SOM (Kohonen algorithm). As illustrated by Figure 3b, base-level concepts belonging

to the same superordinate category were located geometrically closer than concepts belonging to different categories.

DISCUSSION

The present results provide evidence for associations between the brain activities elicited by concepts within the same superordinate category as well as dissociations across categories. The time course of categorization suggests multistaged processing, probably subserved by different neural systems. Apparently, semantic categories are represented by activity in macroscopically separable neural networks, and differences between these representations are evident in the distribution of neuromagnetic sources of brain activity. The processing of perceptual categorization seems to develop across time, starting with initial perceptual categorization in the temporo-occipital cortex (probably

controlled primarily by right-hemisphere mechanisms), and continuing with a semantic-conceptual categorization (probably controlled by the left-hemisphere linguistic mechanisms).

The evidence for initial categorization observed in the occipito-temporal cortex is conceivably an MEG manifestation of the categorically organized activity elicited during an object's perception, as found in functional magnetic resonance imaging studies (for a recent demonstration, see Chao, Weisberg, & Martin, 2002). Furthermore, because all the stimuli were presented at fixation and none of the presented categories should have preferentially activated foveal retinal cells (cf. Malach, Levy, & Hasson, 2002), a recent "center-periphery" model (Levy, Hasson, Avidan, Hendler, & Malach, 2001) cannot account for the present findings. Also, there are no a priori reasons to assume that the participants in this study were particularly expert in processing pictures representing the 16 different base-level concepts

Super-Ordinate Category	Concept	Pass															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Furniture	table	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	chair	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1
	wardrobe	3	3	3	3	3	3	3	3	3	3	1	1	1	1	1	1
	sofa	4	4	4	4	4	3	3	3	3	3	1	1	1	1	1	1
Clothes	shoe	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1
	jacket	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	1
	shirt	7	6	6	6	6	6	6	6	6	6	6	6	5	5	5	1
	trousers	8	8	8	8	8	8	8	8	8	5	5	5	5	5	5	1
Animals	fox	9	9	9	9	9	9	9	9	9	9	9	9	9	1	1	1
	wolf	10	10	10	10	10	10	10	9	9	9	9	9	9	1	1	1
	deer	11	11	11	11	11	11	10	9	9	9	9	9	9	1	1	1
	bear	12	12	10	10	10	10	10	9	9	9	9	9	9	1	1	1
Flowers	rose	13	13	13	13	13	13	13	13	13	13	13	13	13	13	5	1
	tulip	14	14	14	14	14	14	14	14	14	14	14	13	13	13	5	1
	sunflower	15	15	15	15	14	14	14	14	14	14	14	13	13	13	5	1
	orchid	16	16	16	13	13	13	13	13	13	13	13	13	13	13	5	1

Fig. 4. Dynamic process of unsupervised hierarchical clustering of the data averaged between 210 and 450 ms over the left hemisphere. For illustration, each base-level concept was assigned a sequential number from 1 to 16. Each column within the matrix represents the ad hoc clustering at a given pass. This process starts with 16 different vectors and ends with one collapsed cluster. The shaded cells highlight the on-line clustering of base-level concepts within each superordinate category. Note that after 12 passes, when only four clusters are possible, the clustering accurately reflects the superordinate categories.

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included in the four superordinate semantic categories. Hence, neither familiarity (Chao et al., 2002) nor expertise (Gauthier & Tarr, 2002) could be a reasonable explanation for these findings.

This is not to say, however, that we necessarily opt for a modular organization of the perceptual-semantic system. Indeed, results of recent studies have led researchers to suggest that object categories have distributed representations, and that although all category-specific brain areas respond preferentially to one category, none responds exclusively to a given category (e.g., Ishai, Ungerleider, Martin, & Haxby, 2000; for supporting evidence from neuropsychological and connectionist perspectives, see Tyler & Moss, 2001). Furthermore, whereas previous research explored possible neuroanatomical dissociations between different superordinate categories, to our knowledge, this is the first study to demonstrate associations of base-level concepts within superordinate categories. It is tempting to speculate that the significant correlations between the activities elicited by concepts within a superordinate category reflect a higher degree of overlap of perceptual or semantic features of concepts belonging to the same superordinate category. It is also possible that the low positive correlations between concepts belonging to different superordinate categories reflect the activation of (semantic or perceptual) features that are common to different categories (Kraut, Moo, Segal, & Hart, 2002). However, the time course of the categorization process, as revealed by the present analyses of electromagnetic activity, suggests that these correlations reflect an advanced stage of visual processing rather than the overlap of low-level perceptual features represented in the early stages of visual processing.

Finally, it is interesting to consider the dynamics of the unsupervised dynamic clustering process. First, there was no tendency for faster clustering of animate versus man-made categories. This pattern does not support the idea that categories of natural objects are more stable or better clustered in the human brain (cf. Gerlach et al., 1999). Second, the response-based categorization of man-made versus natural categories was not reflected in the MEG data. This conspicuous result might suggest that semantic categorization in the neural system, at least during the time range explored in the present study, is limited to a priori defined categories, rather than task-determined (ad hoc) categories. In the present case, for example, the distinction between concepts denoting man-made and natural objects was probably based on temporary clustering of distributed representations, a clustering that might not be sufficiently well defined to be preserved by the neural system.

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REFERENCES

- Aguirre, G.K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to 'building' stimuli: Evidence and implications. *Neuron*, 21, 373–383.
- Allison, T., Puce, A., Spencer, D.D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex*, 9, 415–430.
- Chao, L.L., Haxby, J.V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, 2, 913–919.
- Chao, L.L., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cerebral Cortex*, 22, 545–551.
- Duda, R.O., Hart, P.E., & Stork, D.G. (2000). *Pattern classification* (2nd ed.). New York: John Wiley & Sons.
- Farah, M.J. (1990). *Visual agnosia: Disorders of object recognition and what they tell us about normal vision*. Cambridge, MA: MIT Press.
- Forde, E.M.E., & Humphreys, G.W. (1999). Category-specific recognition impairments: A review of important case studies and influential theories. *Aphasiology*, 13, 169–193.
- Freedman, D.J., Riesenhuber, M., Poggio, T., & Miller, E.K. (2001). Categorical representation of visual stimuli in the primate prefrontal cortex. *Science*, 291, 312–316.
- Gauthier, I., Anderson, A.W., Tarr, M.J., Skudlarski, P., & Gore, J.C. (1997). Levels of categorization in visual object studied with functional MRI. *Current Biology*, 7, 645–651.
- Gauthier, I., & Tarr, M.J. (2002). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 431–446.
- Gerlach, C., Law, I., Gade, A., & Paulson, O.B. (1999). Perceptual differentiation and category effects in normal object recognition. *Brain*, 122, 2159–2170.
- Hämäläinen, M.S., Hari, R., Ilmoniemi, R.J., Knuutila, J., & Lounasmaa, O.V. (1993). Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, 65, 413–497.
- Ishai, A., Ungerleider, L.G., Martin, A., & Haxby, J.V. (2000). The representation of objects in the human occipital and temporal cortex. *Journal of Cognitive Neuroscience*, 12(Suppl. 2), 35–51.
- Ishai, A., Ungerleider, L.G., Martin, A., Schouten, H.L., & Haxby, J.V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, USA*, 96, 9379–9384.
- Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, 3, 759–763.
- Kohonen, T. (2001). *Self-organizing maps*. Berlin: Springer-Verlag.
- Kraut, M.A., Moo, L.R., Segal, J.B., & Hart, J., Jr. (2002). Neural activation during an explicit categorization task: Category or feature-specific effects? *Cognitive Brain Research*, 13, 213–220.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, 4, 533–539.
- Malach, R., Levy, I., & Hasson, U. (2002). The topography of high-order human object areas. *Trends in Cognitive Sciences*, 6, 176–184.
- Martin, A., Wiggs, C.L., Ungerleider, L.G., & Haxby, J.V. (1996). Neural correlates of category-specific knowledge. *Nature*, 379, 649–652.
- Moore, C.J., & Price, C.J. (1999). A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain*, 122, 943–962.
- Newcombe, F., Metha, Z., & deHaan, E.H.F. (1994). Category specificity in visual recognition. In M.J. Farah & G. Ratcliff (Eds.), *The neuropsychology of high-level vision* (pp. 103–133). Hillsdale, NJ: Erlbaum.
- Puce, A., Allison, T., Asgari, M., Gore, J.C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional MRI study. *Journal of Neuroscience*, 16, 5205–5215.
- Pulvermüller, F., Assadollahi, R., & Elbert, T. (2001). Neuromagnetic evidence for early semantic access in word recognition. *European Journal of Neuroscience*, 13, 1–7.
- Schendan, H.E., Ganis, G., & Kutas, M. (1998). Neurophysiological evidence for visual perceptual categorization of words and faces within 150 ms. *Psychophysiology*, 35, 240–251.
- Smith, E.E. (1995). Concepts and categorization. In E.E. Smith & D.N. Osherson (Eds.), *An invitation to cognitive science: Vol. 3. Thinking* (pp. 3–33). Cambridge, MA: MIT Press.
- Tanaka, J.W. (2001). The entry point of face recognition: Evidence for face expertise. *Journal of Experimental Psychology: General*, 130, 534–543.
- Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, 19, 109–139.
- Thorpe, S.J., & Fabre-Thorpe, M. (2001). Seeking categories in the brain. *Science*, 291, 260–262.
- Tyler, L.K., & Moss, H.E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, 5, 224–252.
- Ultsch, A. (1993). Self-organizing neural networks for visualization and classification. In O. Opitz, B. Lausen, & R. Klar (Eds.), *Information and classification* (pp. 307–313). Berlin: Springer-Verlag.

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