

Experience-dependent Plasticity of Conceptual Representations in Human Sensory–Motor Areas

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Abstract

■ Concepts are composed of features related to different sensory and motor modalities such as vision, sound, and action. It is a matter of controversy whether conceptual features are represented in sensory–motor areas reflecting the specific learning experience during acquisition. In order to address this issue, we assessed the plasticity of conceptual representations by training human participants with novel objects under different training conditions. These objects were assigned to categories such that for one class of categories, the overall shape was diagnostic for category membership, whereas for the other class, a detail feature affording a particular action was diagnostic. During training, participants were asked to either make an action pantomime toward the detail feature of the novel object or point to it. In a

categorization task at test, we assessed the neural correlates of the acquired conceptual representations by measuring electrical brain activity. Here, we show that the same object is differentially processed depending on the sensory–motor interactions during knowledge acquisition. Only in the pantomime group did we find early activation in frontal motor regions and later activation in occipito-parietal visual–motor regions. In the pointing training group, these effects were absent. These results show that action information contributes to conceptual processing depending on the specific learning experience. In line with modality-specific theories of conceptual memory, our study suggests that conceptual representations are established by the learning-based formation of cell assemblies in sensory–motor areas. ■

INTRODUCTION

Conceptual knowledge about objects held in human semantic long-term memory plays an important role in information processing because it serves as cognitive basis for object recognition, goal-directed action, and verbal communication (Levelt, Roelofs, & Meyer, 1999; Humphreys, Riddoch, & Quinlan, 1988). Long before scientists started to investigate concepts empirically (e.g., Smith, Shoben, & Rips, 1974; Bruner, Goodnow, & Austin, 1956), Plato and classical philosophers had speculated about the nature of concepts: Are concepts innate and abstract? Or are they based on sensory–motor interactions with the environment? Cognitive neuroscience now addresses these fundamental questions about the nature of concepts by measuring brain activity in subjects engaged in conceptual processing. The spatial–temporal pattern of brain activity allows us to draw conclusions on the structure of concepts.

It is generally accepted that concepts are composed of features related to different sensory and motor modalities (vision, sound, action, etc.). However, it is contro-

versial as to whether conceptual knowledge is grounded in sensory–motor experiences. In modality-specific theories, it is proposed that functionally and neuroanatomically distinct subsystems store features derived from a particular sensory or motor channel (Pulvermüller, 2005; Barsalou, Simmons, Barbey, & Wilson, 2003; Humphreys & Forde, 2001; Kiefer & Spitzer, 2001; Martin & Chao, 2001; Warrington & Shallice, 1984). Concepts are assumed to be embodied (Gallese & Lakoff, 2005; Lakoff & Johnson, 1999) in the sense that interactions with objects form their conceptual memory traces in modality-specific brain areas, which typically process sensory or action-related object information. Accordingly, a concept is considered as a distributed activation pattern across one or several subsystems. The existence of an amodal or supramodal semantic subsystem is denied. Alternatively, it has been proposed that features of concepts are represented in an amodal format distinct from sensory and motor representations (Fodor, 2001; Tyler & Moss, 2001; Caramazza, Hillis, Leek, & Miozzo, 1994; Anderson, 1978). They are assumed to be distributed across the brain outside the sensory or motor areas. Hence, modality-specific theories are falsified and amodal theories are supported (i) if conceptual features referring to different modalities do not elicit differential brain activity at all or (ii) if they do not evoke

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differential activity in the corresponding sensory or motor areas of the brain, but in nonsensory areas (e.g., prefrontal, orbito-frontal, ventromedial-temporal areas).

Recently, a hybrid model (Simmons & Barsalou, 2003), the conceptual topography theory, combines elements of modality-specific and amodal theories by assuming modality-specific knowledge stores (modality-specific “convergence zones” in the sense of Damasio, 1989) in the sensory–motor areas as well as a cross-modality convergence zone located in the perirhinal cortex. The cross-modality convergence zone integrates conceptual features from the different modalities into a high-dimensional supramodal semantic space. According to the conceptual topography theory, conceptual knowledge is still modality-specific in its essence because representations in the cross-modality convergence zone do not contain the conceptual content themselves but act as pointer structures for activating conceptual features in lower-order modality-specific knowledge stores. As the present work focuses on the emergence of conceptual representations in the sensory–motor system as a result of the learning experience during concept acquisition, we do not distinguish in the remainder of the text between “pure” and “hybrid” modality-specific theories.

Evidence suggestive for a modality-specific view of conceptual knowledge comes from behavioral (Olseth Solomon, & Barsalou, 2004), neuropsychological (Warrington & McCarthy, 1987), and neuroimaging studies (Martin & Chao, 2001) as well as from computational modeling (Farah & McClelland, 1991). For instance, neuroimaging studies have revealed category-related brain activation in the sensory and motor cortex in several tasks such as object naming (Chao & Martin, 2000; Martin, Wiggs, Ungerleider, & Haxby, 1996), semantic verification (Phillips, Noppeney, Humphreys, & Price, 2002; Kiefer, 2001), and lexical decision (Kiefer, 2005). Artifact objects such as tools frequently activated brain areas involved in action (parietal and premotor areas) and action-related motion representation (middle temporal cortex) more strongly than objects from natural categories such as animals. Natural categories, in contrast, elicited stronger neurophysiological responses in visual areas of the occipito-temporal cortex. These effects have been observed with both pictures and words, suggesting a postperceptual, conceptual origin (Phillips et al., 2002; Kiefer, 2001). It has been proposed that action-related features are more relevant for representing manipulable artifacts, whereas visual features are more important for representing natural objects (Warrington & McCarthy, 1987). In support of this view, category-related activity was modulated by the task-relevance of object features (Sim & Kiefer, 2005; Phillips et al., 2002). Activity in regions implicated in the processing of manipulable artifacts has also been observed in language tasks such as listening to action-related sentences (Tettamanti et al., 2005). Furthermore, studies looking at fine-grained differences between subcategories of action-

related words (Hauk, Johnsrude, & Pulvermüller, 2004; Hauk & Pulvermüller, 2004) found that arm-, face-, and leg-related action words elicited a somatotopical activation pattern in cortical motor areas. These results suggest the learning-based formation of conceptual representations in sensory–motor areas (Pulvermüller, 2005).

However, there is also support for the notion of an amodal unitary conceptual system, in which conceptual features are represented outside the sensory or motor areas (Tyler & Moss, 2001; Caramazza et al., 1994). Firstly, category-related brain activity in sensory or motor areas was not replicated in some studies (Devlin et al., 2002; Tyler & Moss, 2001). Instead, category-related activity was only observed in the perirhinal cortex and related anterior ventromedial-temporal lobe structures (Bright, Moss, Stamatakis, & Tyler, 2005), an area presumably involved in the integration or binding of semantic features (see also its potential role as a supramodal convergence zone mentioned above). Secondly, patients with semantic dementia, in which the anterior temporal lobe is damaged, exhibited a general loss of semantic knowledge independent of category and knowledge type (Hodges, Patterson, Oxbury, & Funnell, 1992). Finally, other accounts suggested a role of the physical category structure for the emergence of category-related brain activity and deficits in brain-damaged patients (Tyler & Moss, 2001; Lloyd-Jones & Humphreys, 1997). Hence, the general principles underlying the cortical organization of conceptual knowledge remain to be resolved.

The assumption that concepts are represented in the sensory–motor areas through the learning-based formation of cell assemblies distinguishes modality-specific theories (in their pure or hybrid specification) from amodal theories. However, to date, the plasticity of conceptual representations attributable to specific sensory–motor learning experiences has not been directly investigated. Two training studies investigated the neural correlates of concept acquisition with functional magnetic resonance imaging (fMRI). In the first study by James and Gauthier (2003), participants learned associations between novel objects (“greebles”) and verbal labels of object features referring to a given modality (auditory and object motion). In a sequential matching task at test, the authors found stronger activity to objects associated with auditory words (“buzzes”) in the superior temporal gyrus, which responded to sounds in general. Activity in the superior posterior temporal sulcus, which was sensitive to motion processing, was greater for objects associated with motion words (“hops”). The observed activity in sensory areas is suggestive for the assumption of modality-specific theories that concepts are grounded in perception. However, as participants in the study of James and Gauthier only learned associations between objects and verbal labels, but did not interact with the objects,

a direct test for the experience-dependent plasticity of conceptual representations is missing so far. In the second study by Weisberg, van Turenhout, and Martin (2006), the learning of tool-like functions for novel objects was assessed. During training, participants had the opportunity to interact with the objects. In a sequential matching task with photographs of the objects, Weisberg et al. (2006) found after training, in comparison to a pretraining baseline, that there was increased activity in brain regions (left middle temporal gyrus, left intraparietal sulcus, and premotor) previously implicated in the processing of manipulable objects such as tools (Altmann et al., submitted; Noppeney, Price, Penny, & Friston, 2006; Kellenbach, Brett, & Patterson, 2003). Activity tended to be larger for trained than for not-trained control objects. Weisberg et al. suggested that as a result of training the novel objects have attained the conceptual status of “tools.” However, as the authors admit, their study has several limitations: The observed training-related activity differences in sensory–motor areas could be attributed to unspecific factors such as object familiarity or implicit naming. In order to be able to interpret training results unequivocally, the differential influence of *specific* learning experiences on the neural representation of objects has to be assessed. Furthermore and most importantly, due to the low temporal resolution of fMRI, it cannot be determined whether activity in sensory or motor regions reflects early access to conceptual object representations or later

postconceptual processing such as imagery, episodic associations, or decision-related processes.

The research reported here therefore tested the notion of experience-driven modality-specific object representations by training human participants with newly developed novel 3-D objects (which we have named “nobjects”) under two different training regimens (interaction with a functional vs. nonfunctional relation with the object). Exploiting the high temporal resolution of event-related potential (ERP) recordings, we asked whether the effects of the specific learning experience during training would emerge in a conceptual test task within early stages (100–200 msec after stimulus onset) of stimulus recognition (Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Thorpe, Fize, & Marlot, 1996). In order to assess the role of category structure (see Figure 1), in one class of categories (to which we refer as shape-defined categories), all nobjects of one category had the same overall shape (e.g., round, pyramidal), whereas in the other class of categories (to which we refer as function-defined categories), nobjects of one category showed the same detail feature (e.g., handle, point) affording a particular action, but varied in shape. This manipulation of the diagnosticity of features for category membership should affect the relevance of a given feature type (shape vs. detail feature/function) for the acquired concept. Most importantly, we varied the specific sensory–motor interactions of our participants with the detail feature of each nobject. In the pantomime

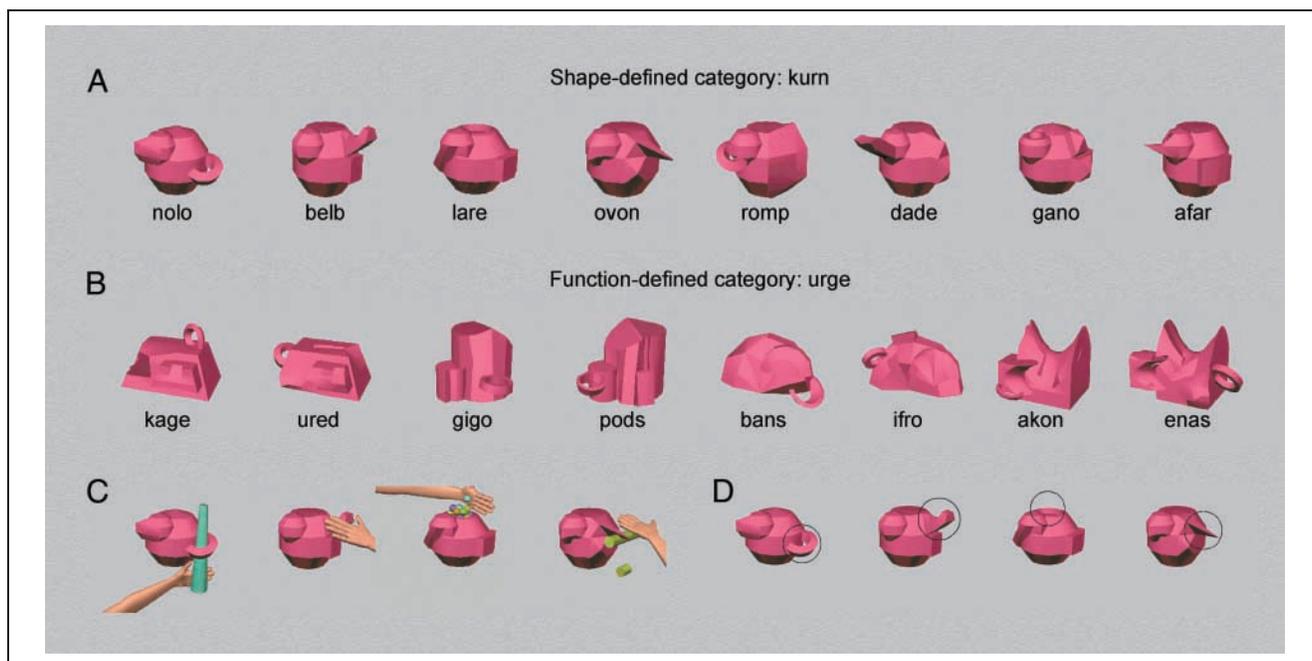


Figure 1. Example of the novel 3-D objects (“nobjects”). (A) Shape-defined category. For this type of category, all exemplars had the same overall shape, but varied in the detail feature. Therefore, the shape was diagnostic for category membership. (B) Function-defined category. For this class of category, exemplars showed the same detail feature, but varied in shape. Hence, the action afforded by the detail feature was diagnostic for category membership (C) Demonstration of the actions associated with the detail feature in the pantomime training group. (D) Pictures highlighting the detail feature to be pointed to in the pointing training group.

training group (*functional action*), participants had to learn and to perform a distinct action that exhibits a functional relation with the action affordance of the detail feature of each nobject (Tucker & Ellis, 1998). In this group, object representations of function-defined categories should strongly depend on action information in comparison to shape-defined categories because, for the former type of categories, the detail feature and its associated action are diagnostic for category membership. In the pointing training group (*nonfunctional action*), participants were instructed to uniformly point to the detail feature. In the context of the present experiment, pointing is not an action functionally associated with each detail feature because it does not depend on object-specific action affordances. Therefore, for the pointing group, acquired action information should be less relevant for function-defined categories, and category-related differences should be reduced. After successful completion of the training, the neurophysiological correlates of acquired object representations were determined by measuring ERPs during object verification tasks (object name and category verification). ERPs were subjected to distributed source analysis in order to estimate the brain areas involved in the corresponding processes. As stimuli were physically identical in both groups and only the specific motor interaction during training differed, group differences in spatial-temporal brain activation at test reflect training-related changes of object processing indexing experience-driven modulations of conceptual representations.

Here, we provide evidence that one and the same object is differentially represented depending on the sensory-motor interactions during acquisition. Only in the pantomime group did we find early visual and motor activation in response to shape- and function-defined categories, respectively. These effects were most pronounced in category verification and, to a lesser extent, in name verification. We expected this interaction between category, task, and training group because only for the category verification task was the action toward the detail feature crucial to solve the task (i.e., to determine category membership for an object from a function-defined category). In the name verification task, in contrast, action information was much less relevant for identifying a single object.

METHODS

Subjects

Twenty-six right-handed (according to Oldfield, 1971), native German-speaking students with normal or corrected-to-normal vision and without any signs of neurological or psychiatric disorders participated in the study for payment (€ 200). The data from one subject were excluded from analysis because of not meeting the training criterion (accuracy level of more than 90% at the end of training) and the data from another because

of excessive artifacts in the electroencephalogram (EEG) recordings. The 24 remaining subjects (13 women; 11 men) had a mean age of 24.0 years (range: 20–33 years). Half of the subjects were assigned to the action pantomime training condition and the other half to the pointing condition (for details, see below). All participants signed a written consent after the nature of the experiment had been explained. The study has been approved by the local Ethical Committee.

Stimuli

Training stimuli were 64 novel visual 3-D objects (“nobjects”) derived from eight polygonal prototypes (see Figure 1). From each prototype, eight nobject exemplars were created by blurring the prototypical shape to some degree and by attaching one out of four detail features (loop, trough, handle, point). Pictures of nobjects had an average width of 14 cm and an average height of 11 cm, which corresponds at a viewing distance of about 110 cm to a horizontal visual angle of 7.4° and a vertical visual angle of 5.7°. A meaningless, but pronounceable, four-letter nonsense name was assigned to each nobject (e.g., “avod”).

Eight nobject categories with eight members each were formed as following: For one type of four categories, all eight members were derived from the same shape prototype, but varied in the attached detail feature within and across categories (Figure 1A). As a consequence, the shape was diagnostic for determining category membership (*shape-defined categories*). For the other type of four categories, all eight category members had the same detail feature affording a particular action, but varied in prototypical shape within and across categories (Figure 1B). Hence, the detail feature/afforded action was diagnostic for determining category membership (*function-defined categories*). In order to rule out that possible effects of category type are compromised by visual properties of the nobject exemplars, the assignment of exemplars to each type of category was counterbalanced across subjects. Each category was labeled with a pronounceable four-letter nonsense word starting with a different letter. Each prototype shape also received a nonsense word label. In the action pantomime training condition, the detail feature was associated with a nonsense name whose last syllable grammatically resembled a German action verb (“lomen”), whereas in the pointing condition the name resembled a German adjective (“lomig”).

Training

Participants acquired conceptual knowledge on the nobjects at the individual exemplar and at the category level in a training regimen adopted from Gauthier, Williams, Tarr, and Tanaka (1998). The training consisted of 16 sessions lasting for about 1 hour each and

had to be completed within 3 weeks. In each session, one single participant was presented with a combination of 6 to 13 computerized training tasks in the presence of an experimenter (for a detailed description of the training tasks, see below and Appendix): The tasks required to name and to recognize individual nobject exemplars and nobject features. They also required learning category name and category membership (for the training schedule, see Table 1).

Two different training conditions were implemented, which differed only with respect to the training procedures related to the detail feature of the nobjects. In the *pantomime training condition*, each detail feature was associated with a distinct, functional action, which had to be pantomimed by the participants in some training tasks (functional action). Participants were familiarized on how to execute the pantomime as shown in the action demonstration (Figure 1C). In the *pointing training condition*, the detail features were not associated with distinct, functional actions in correspondence with

their action affordances (nonfunctional action). Instead, they were highlighted by a circle, and participants were requested to pay attention to them by pointing with their index finger to them (see Figure 1D). Thus, participants in both training groups attended comparably to the detail features but performed sensory–motor interaction with a different functional relation to the nobjects. The following types of tasks were used during training and task differences between training groups are explicitly mentioned:

Inspection tasks: Participants were visually presented with either all nobjects of one category or with one single nobject together with the visually and auditorily presented nobject or category name. Their task was to look carefully at the stimuli. In variants of the task depending on the training condition, they additionally either had to pantomime the action in response to the action demonstration picture or had to point to the encircled detail feature (see Figure 1C and D).

Table 1. Training Schedule

Training Session	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Task</i>																
Shape inspection with name	✓	✓	✓	✓	✓	✓	✓	✓	✓					✓	✓	✓
Introduction to action pantomimes/pointing	✓															
Inspection of action/detail feature names	✓	✓	✓	✓	✓	✓	✓	✓	✓					✓	✓	✓
Category inspection without category name	✓															
Category inspection with category name	✓															
Category inspection with category name and action pantomime/pointing	✓	✓	✓	✓												
Category naming—keyboard response with feedback	✓	✓	✓	✓	✓	✓	✓	✓								
Nobject inspection—nobject name–action/detail feature	✓	✓	✓	✓	✓	✓	✓	✓								
Nobject naming—new subset of nobjects with feedback	✓	✓	✓	✓	✓	✓	✓	✓								
Nobject naming—previously learned subsets with feedback		✓	✓	✓	✓	✓	✓	✓								
Nobject naming—all learned subsets with feedback		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Nobject naming—without feedback	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Category decision—pairs of nobject pictures with feedback		✓	✓	✓	✓	✓	✓	✓	✓		✓		✓		✓	
Category decision—pairs of nobject names with feedback					✓	✓	✓	✓		✓		✓		✓		✓
Category decision—pairs of nobject pictures without feedback	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Category decision—pairs of nobject names without feedback					✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Visual decision—pairs of nobject names with feedback									✓		✓		✓		✓	
Action/detail feature decision—pairs of nobject names with feedback										✓		✓		✓		✓
Action/detail feature and shape naming with feedback							✓	✓	✓					✓	✓	✓
Number of tasks per session	11	11	11	11	12	12	13	13	9	6	6	6	6	9	9	9

The table shows the specific combination of tasks used in the 16 training sessions.

Naming tasks: Participants were visually presented with either all nobjects of one category or with one single nobject and had to produce the correct category (category naming) or exemplar name (object naming). In other variants, they had to name the associated action (pantomime group) or the detail feature (pointing group). In some versions, they received feedback regarding the correctness of the response and, in case of an error, they were shown the correct name.

Decision tasks: Participants saw a pair of nobjects or a pair of nobject names. In variants of the task, they had to decide whether the nobjects belonged to the same category (category decision), had a similar shape (visual decision), or were associated with the same action (pantomime condition) or had the same detail feature (pointing condition). There were versions of these tasks with and without feedback.

Category membership and category names were trained for all 64 nobjects from the beginning. For learning the nobject names, the entire set was divided into eight subsets consisting of four nobjects from shape- and function-defined categories, respectively. In the first training session, participants started to learn nobject names for Subset 1, in the second session for Subset 2, and so forth. Nobjects names from previous sessions were repeated and learned together with new names. From Session 9 onward, names for all nobjects were trained. After completion of the training, participants had to answer a short questionnaire in which they were questioned whether they considered the pantomimed action as a functional, goal-directed action with the object and whether the action was conceived as an object part.

Test Task with ERP Recordings

On the following day after successful completion of the training, subjects participated in the test task, in which the neural correlates of the acquired object representations were assessed. All stimuli were shown in the center of the computer screen synchronous with the screen refresh against a black background. Subjects were first presented with a fixation cross for 750 msec. Thereafter, either a nobject name (name verification task) or a category name (category verification task) appeared for 900 msec as a probe. After an interstimulus interval of 500 msec, the target picture of a nobject was presented for 900 msec. In half of the trials, the target matched with the previously presented name (congruent condition), whereas in the other half it did not match (incongruent condition). Each nobject picture was shown four times in all task and congruency conditions. Incongruent probe–target pairings were constructed such that the target came from a different category than the probe, but always belonged to the same type of

category as the probe. The entire sequence of 256 trials was presented in randomized order. Subjects were instructed to decide as fast and as accurately as possible whether the probe name (nobject or category name) and the target picture matched or not. They had to respond by pressing two buttons with the index and middle fingers of their right hand. After the response, three hash marks appeared, which prompted the subjects to initiate the next trial with a button press.

The EEG recordings were performed in an electrically shielded, dimly lit sound-attenuating booth. Subjects were seated in front of the computer monitor on which the stimuli were presented and were instructed to restrict eye movements and blinking to the pauses between the trials. The entire experimental session required about 1 hour and 30 min to complete. Scalp potentials to the target pictures were collected using an equidistant montage of 64 sintered Ag/AgCl electrodes mounted in an elastic cap (EasyCap, Herrsching-Breitbrunn, Germany) referenced to an electrode between Cz and FCz (impedance below 5 k Ω). Eye movements were monitored with electrodes below and beside the eyes. Electrical signals were amplified with Synamps amplifiers (low-pass filter = 50 Hz, 24 dB/octave attenuation; 50 Hz notch filter), digitized at 250 Hz, digitally band-pass filtered (high cutoff: 16 Hz, 24 dB/octave attenuation; low cutoff: 0.1 Hz, 12 dB/octave attenuation), segmented (152 msec before to 1000 msec after target onset), and baseline-corrected to the 152 msec prestimulus interval. Artifact-free EEG segments to trials with correct responses were averaged with respect to the onset of the stimulus separately for each experimental condition. The average-reference transformation was applied to the ERP data (Bertrand, Perrin, & Pernier, 1985). EEG data analysis was performed with the BrainVision Analyzer (BrainProducts, Gilching, Germany).

Based on our previous studies with real objects (Sim & Kiefer, 2005; Kiefer, 2001, 2005) and our theoretical predictions, we statistically assessed ERP effects at occipitoparietal electrodes (electrode sites: O1/O2, P7/P8, TP7/TP8), at fronto-central electrodes (electrode sites: FC3/FC4, FC1/FC2, C1/C2), and at mid-prefrontal electrodes (Fp1/2, Fpz, Nz). Separate repeated-measures analyses of variance (ANOVAs) for each time window and scalp region were performed with the within-subject factors category type (shape- vs. function-defined categories), task (object name vs. category verification), hemisphere, and electrode site, and the between-subject factor training group (pantomime vs. pointing). For mid-prefrontal electrodes, only the topographical factor electrode site was included. When appropriate ($\epsilon < 1$), degrees of freedom were adjusted according to the method of Huynh-Feldt, and the Huynh-Feldt ϵ as well as the corrected significance levels are reported.

In order to determine the neural sources for significant group effects, we calculated maps of estimated cortical currents from the grand mean scalp voltages according to

the minimum-norm method. This method yields the unique solution that explains the data and does not contain components that are “silent,” that is, they do not produce any measurable surface signal by themselves (Hauk, 2004; Hamalainen & Ilmoniemi, 1994). Source estimates were computed for grand mean data in individual conditions using the approach described by Hauk (2004), and the resulting intensity distributions were then subtracted from each other. The regularization parameter (“ λ ”) was chosen such that the mean residual variance across datasets was 5%. Following the suggestion of Dale et al. (2000), the difference distributions were thresholded according to the signal-to-noise ratio (SNR) of the source strengths (SNR = 7) in order to focus on the most prominent effects. This threshold is more conservative than usual (SNR > 2). Talairach coordinates for the activation peaks were determined on the 2-D surface covering the cortex on which the source solution was computed. As we mainly expected cortical activation (e.g., in motor areas) and EEG is not very sensitive to the depth of a source, the 2-D solution does not result in a considerable loss of information. We report the nearest Brodmann’s areas (BA) to the peak activations located by the Talairach Daemon (<http://ric.uthscsa.edu/projects/talairachdaemon.html>).

RESULTS

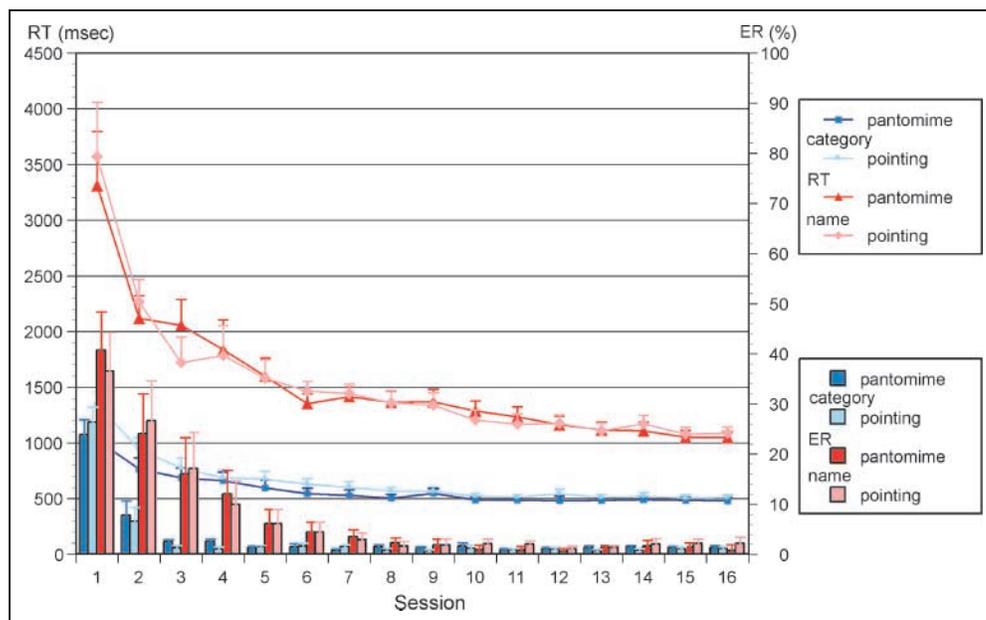
Behavioral Results

Figure 2 exemplarily illustrates the results of the category decision and object naming tasks during the course of training. Repeated-measures ANOVAs with task (naming vs. category decision), category type

(shape-defined vs. function-defined category), and session (1 to 16) as within-group factors and training group (pantomime vs. pointing) as between-group factor were carried out on median reaction time (RT) and error rate (ER). These analyses revealed an interaction of task and session for both RT [$F(15,330) = 17.6, p < .001$] and ER data [$F(15,330) = 5.6, p < .001$]. These effects indicated that category decision was faster and more accurate than object naming, particularly at the beginning of the training (Sessions 1–5). Later task differences disappeared (ER) or were reduced (RT). This shows that during the course of training, knowledge on the objects at both the individual exemplar and category level became similarly accessible. For RT, a main effect of category type indicated that objects from shape-defined categories were responded to faster than objects from function-defined categories [$F(1,22) = 22.7, p < .001$]. With regard to ER, the interaction of category type and session [$F(15,330) = 1.8, p < .05$] showed that function-defined categories were associated with higher ER only at the beginning of the training (Sessions 1 and 2). Most importantly, we did not observe an interaction with the factor training group (all $ps > .28$). Thus, participants in both groups learned the objects comparably. In the questionnaire after the training, the majority of the participants of the pantomime group indicated that they conceived the pantomime as a functional action with the object (70%) and as an integral object part (80%).

In the test task after training (Figure 3), we found faster and more accurate responses to shape- than to function-defined categories in the category verification, but not in the name verification task. This effect was more pronounced for congruent than for incongruent

Figure 2. Performance during the course of the training for the pantomime and pointing training groups. Shown are reaction time (RT) and error rate (ER) for the category decision and the object naming task without feedback. The small vertical bars indicate the standard error of means in this and the upcoming figures.



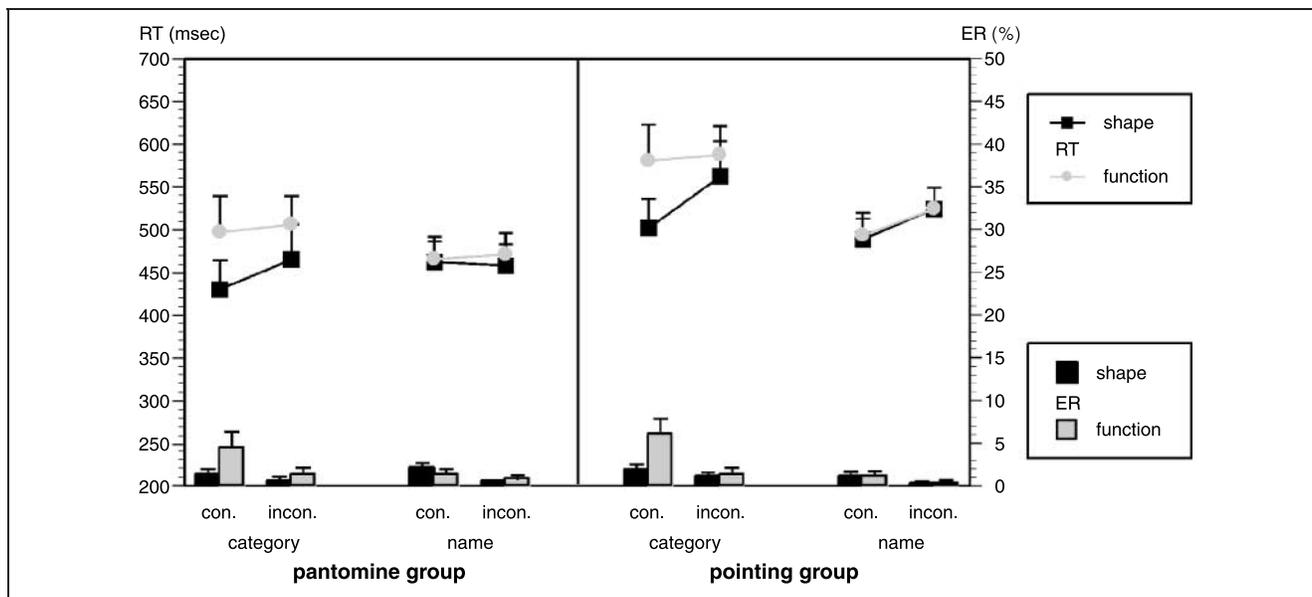


Figure 3. Reaction time (RT) and error rate (ER) in the test tasks as a function of training, type of task, category, and congruency.

trials [Task \times Category \times Congruency, $F(1,22) = 19.2$, $p < .001$]. However, both groups exhibited a similar performance pattern (all p s $> .65$) indicating that all participants had comparable access to the objects at test.

Electrophysiological Results

In the test task after the training, ERPs to the target object pictures were analyzed. Three ERP events were of theoretical interest (see Figure 4): The P1 (peaking at 117 msec) and the N1 (peaking at 160 msec) components, which are largest over the occipito-parietal scalp, reflect visual processes (Compton, Grossenbacher, Posner, & Tucker, 1991; Mangun & Hillyard, 1991) and are sensitive to stimulus category and expertise (Kiefer, 2001; Tanaka & Curran, 2001; Tanaka, Luu, Weisbrod, & Kiefer, 1999). The subsequent negative slow wave between 270 and 400 msec temporally coincided with a centro-parietal N400 component that indexes semantic processes (Kutas & Hillyard, 1980) and is sensitive to structural aspects of semantic memory (Kiefer, 2005; Kounios & Holcomb, 1994).

P1 Amplitude

P1 amplitude was defined as the most positive peak in the time window between 50 and 150 msec after stimulus onset at occipito-parietal electrode P7 as reference for all other electrodes (peak latency 117 msec). Over the occipito-parietal scalp, we observed large P1 amplitude differences between training groups over the right hemisphere [Group \times Task \times Congruency \times Hemisphere, $F(1,22) = 6.6$, $p < .05$]. Direct comparisons

showed that in the pointing training group P1 amplitude was larger than in the pantomime training group in all task and congruency conditions at right occipito-parietal electrodes ($p < .001$). The occipito-parietal P1 was accompanied by a simultaneous negative potential shift at fronto-central and mid-prefrontal electrodes. At fronto-central electrodes, this negative potential shift was greater for the pointing than for the pantomime group [$F(1, 22) = 6.3$, $p < .05$]. In order to determine the brain electrical sources of these overall group differences in scalp potentials, we compared source activity averaged across conditions between the two training groups. This analysis revealed for the pantomime group relatively greater activity in the left occipital, left inferior temporal, and most importantly, in superior frontal areas. The superior frontal activation peak was located close to premotor areas in the superior frontal cortex (BA 8). For the pointing group, greater activity in right occipital areas was observed (Figure 5A).

N1 Amplitude

N1 amplitude was defined as the most negative peak in the time window between 100 and 200 msec after stimulus onset at occipito-parietal electrode P7 as reference (peak latency 160 msec). The training regimen influenced occipito-parietal N1 amplitude differentially depending on task and category [Group \times Task \times Category type \times Congruency \times Hemisphere \times Electrode site, $F(2,44) = 4.1$, $p < .05$]. In order to explore this complex interaction, we performed separate analyses for the name and category verification tasks. In the name verification task, shape-defined categories elicited a larger N1 than feature-defined categories, particularly over the left hemisphere in the incongruent condition

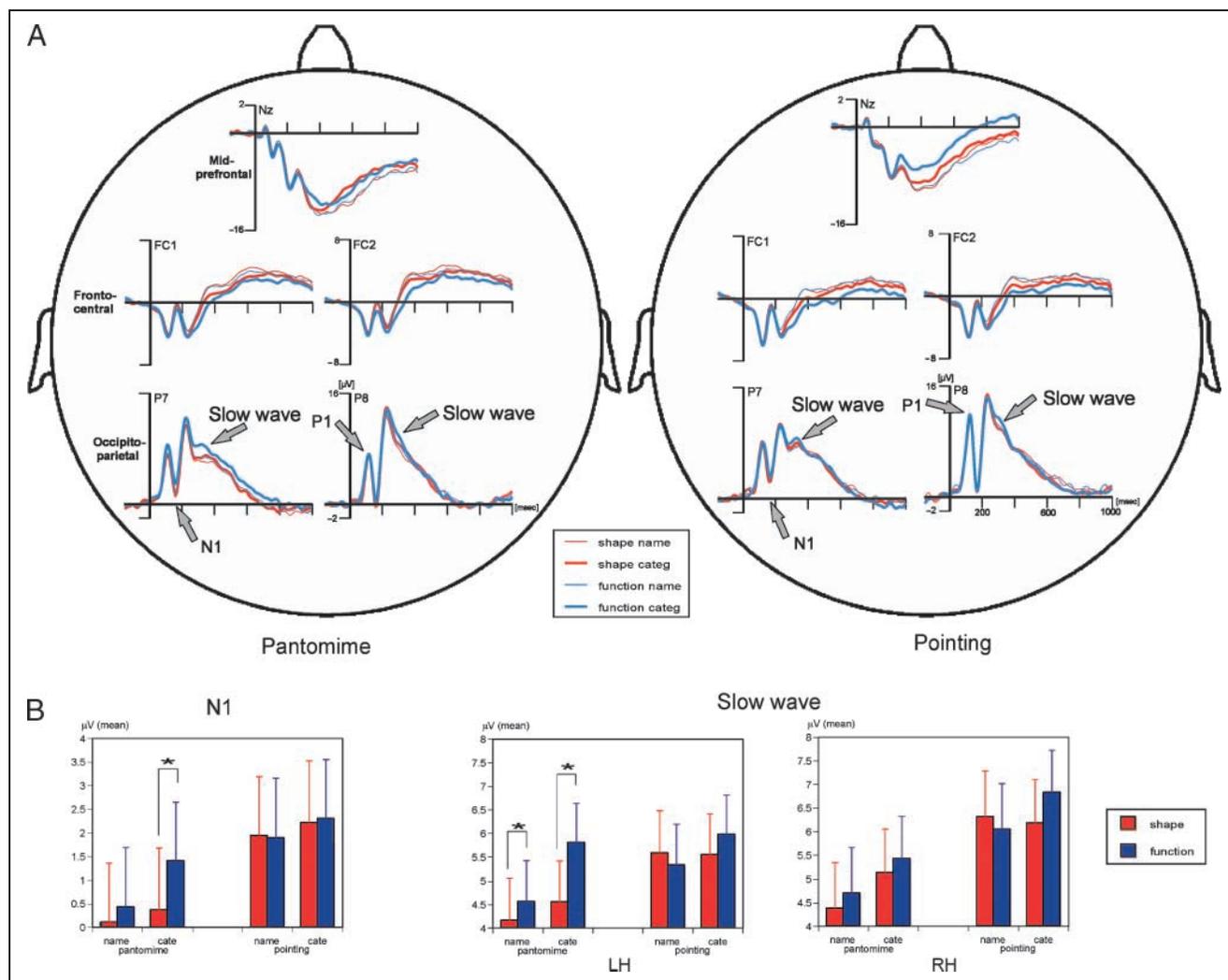


Figure 4. (A) Average-referenced grand-averaged ERP data ($n = 12$) in the pointing and the pantomime group as a function of category and task. Shown are representative electrode sites from each scalp region. Note the P1 effect of group at 117 msec and the greater category effects on the N1 and the later slow wave in the pantomime group (see arrows). (B) Category-related ERP effects at occipito-parietal electrodes as a function of training group differences on N1 peak amplitude (160 msec) and slow wave (270–400 msec). Shown is the mean potential averaged across electrode sites. Significant category effects are highlighted by an asterisk.

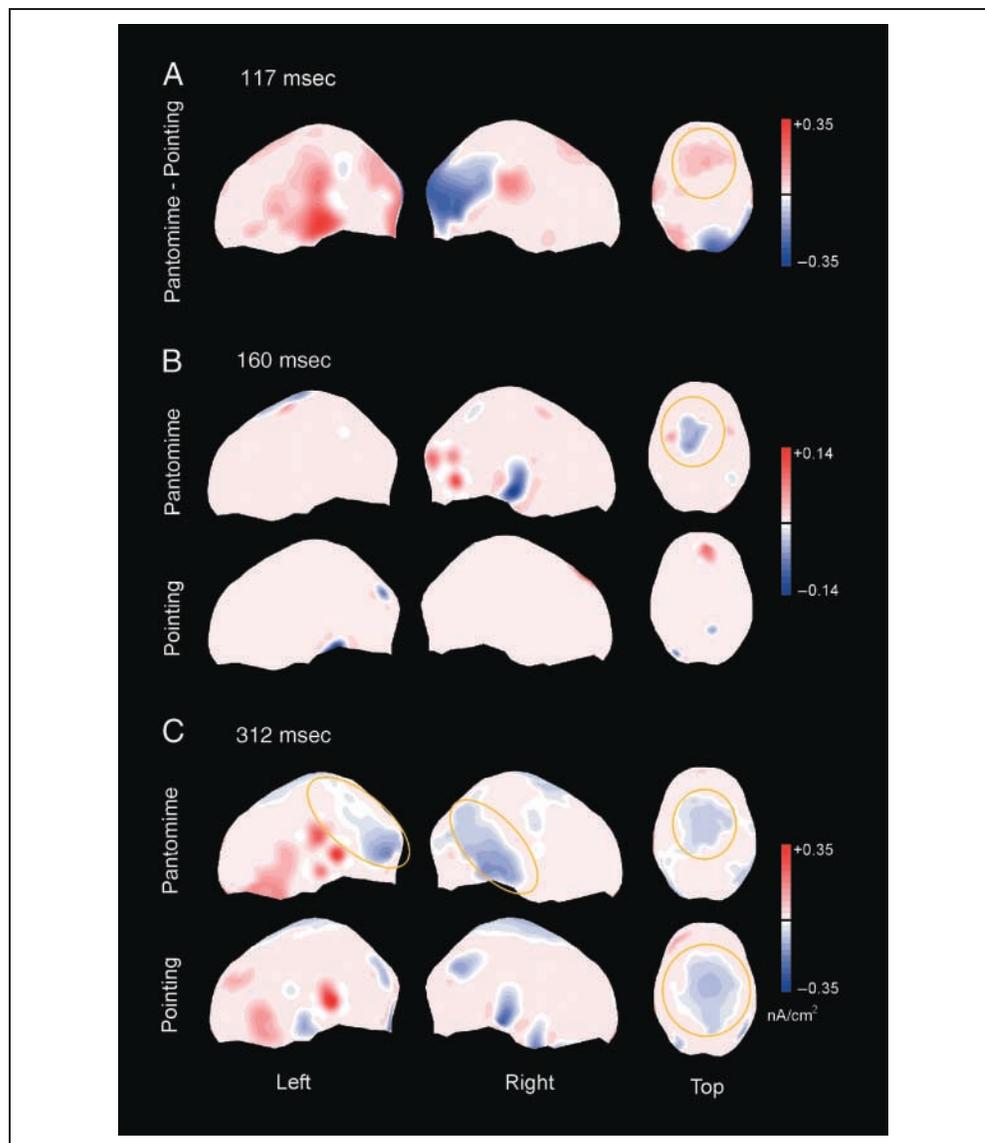
[Category type \times Congruency \times Hemisphere, $F(1,22) = 5.9$, $p < .05$]. However, we did not observe significant group differences ($p > .18$). In the category verification task, the Group \times Category type interaction indicated that effects of category type were confined to the pantomime training group [$F(1,22) = 4.5$, $p < .05$]. Direct comparisons revealed statistically reliable voltage differences between shape- and function-defined categories only in the pantomime ($p < .01$), but not in the pointing, training group ($p > .76$). We then determined the brain electrical sources for the ERP effects of category type in each group. We analyzed only the ERPs in the category verification task because the effects of category type were largest in this task. This source analysis revealed in the pantomime group greater activity to shape-defined categories in the right occipital cortex (Figure 5B). Function-defined categories, in contrast,

elicited greater activity in fronto-central areas somewhat more posteriorly than within the P1 window as well as activity in the right inferior temporal cortex. The fronto-central activation peak was located in the superior frontal cortex (BA 6), which corresponds to the premotor cortex. In the pointing group, only small spots of differential source activity were obtained (shape-defined categories: mid-prefrontal areas; function-defined categories: inferior temporal areas).

Time Window of 270–400 msec

Mean voltages within this time window were submitted to statistical analyses. The training regimen modulated effects of category type again at occipito-parietal [Group \times Task \times Category type \times Hemisphere, $F(1,22) = 4.5$, $p < .05$] and mid-prefrontal electrodes [Group \times Task \times

Figure 5. Minimum norm source estimates obtained from grand mean scalp ERPs. Shown are difference maps between conditions. (A) Difference between the pantomime and the pointing condition at 117 msec (P1 peak) averaged across categories. Greater activation for the pantomime group is indicated by red color, greater activation for the pointing group by blue color. (B and C) Difference maps between shape-defined (red) and function-defined (blue) categories at 160 msec (N1 peak) and 312 msec (slow wave), respectively. Note the activity close to the premotor region/supplementary motor area, SMA (A, B) and in the occipito-parietal region (C) in the pantomime group.



Category type \times Electrode site, $F(3,66) = 2.94, p < .05$. Separate ANOVAs for each verification task were performed in order to assess these interactions. In name verification, shape-defined categories evoked a more negative potential compared to function-defined categories at left occipito-parietal electrodes, particularly in the pantomime training group for congruent trials [Group \times Category type \times Congruency \times Hemisphere \times Electrode site, $F(1,22) = 3.3, p < .05$]. Over mid-prefrontal areas, effects involving the factors category type or group did not reach significance in name verification. In category verification, we observed group differences over occipito-parietal areas [Group \times Category type \times Hemisphere, $F(1,22) = 5.0, p < .05$]. Direct comparisons revealed a greater negativity to shape-defined than to function-defined categories in the pantomime training group only over the left hemisphere ($p < .01$). Over mid-prefrontal areas, in contrast, category-related

effects were greater in the pointing than in the pantomime group [Group \times Category type \times Electrode site, $F(3,66) = 3.5, \epsilon = .92, p < .05$].

Source analysis for ERPs in the category verification task was performed at 312 msec because voltage differences between shape- and function-defined categories were largest in this task and at this time point. This analysis yielded in both groups left inferior prefrontal and left temporal activity to shape-defined categories. Function-defined categories, in contrast, were associated with activity in fronto-central areas that were located more posteriorly than in the previous time segments, with bilateral occipito-parietal and right inferior temporal activity. The fronto-central activation peak was again located in the superior frontal gyrus (premotor cortex, BA 6). The peak of the occipito-parietal activation cluster was found in the left middle occipital gyrus (BA 19) and the right middle temporal gyrus (BA 21). As can be seen

in Figure 5C, occipito-parietal activity was stronger in the pantomime group.

DISCUSSION

In this study, we tested the plasticity of conceptual representations in sensory–motor areas by training participants with novel objects under different training regimens. We showed for the first time that specific sensory–motor interactions (functional action vs. non-functional pointing movement to detail features) with novel objects during knowledge acquisition modulate the spatial–temporal brain activation pattern in object verification tasks at test. Only in the participants who performed a distinct action pantomime during the training did function-defined categories elicit at test early activity in fronto-central areas close to the premotor cortex as well as later activity in occipito-parietal areas. Training-related ERP effects emerged as early as 117 msec after stimulus onset, suggesting modulation of object processing rather than postconceptual processes such as imagery or episodic memory associations. In our study, both training groups spent the same amount of time studying the objects during training and performed comparably in the verification tasks. The training procedure differed only with regard to the functional distinctiveness of the action toward the objects. Therefore, group differences in brain activation at test reflect training-related changes in object processing, most likely indexing experience-driven plasticity of conceptual representations.

Early Activity of the Premotor Cortex and the Occipital Cortex

The earliest differences between the training groups in the processing of nobjects were observed at 117 msec after stimulus onset in the time range of the P1 component. Source analysis revealed greater activity in left occipital, inferior temporal, and most importantly, in fronto-central areas close to the premotor cortex in the pantomime group. The activation of motor areas in this training group suggests that these subjects started to access action-related activation about the nobjects as early as 117 msec. In the pointing group, in contrast, we observed greater activity in the right occipital cortex. In accordance with previous studies (Compton et al., 1991), we relate this effect to early visual attribute analysis carried out in right occipito-temporal areas (Corbetta, Miezin, Fox, Dobmeyer, & Petersen, 1990). Probably, the detail features received a generally greater weight in the object representations in this group because their training tasks increased visual attention to this nobject part.

For the pantomime group only, category type affected ERPs starting at 160 msec after target onset in the time

range of the N1 component where shape-defined categories elicited a larger occipito-parietal N1 amplitude than function-defined categories. Similar effects on the N1 were previously observed during categorization tasks requiring careful assessment of the overall object shape (Kiefer, 2001; Tanaka & Curran, 2001). In the pantomime group, greater source activity to shape- than to function-defined categories was found in the right occipital cortex. Besides early visual attribute analysis, this region plays an important role in shape representation (Kosslyn et al., 1994). At the same time point in this group, function-defined categories were associated with greater activity of the right inferior temporal cortex and, most notably, with greater activity close to the premotor cortex. This activity in motor areas suggests that subjects in the pantomime group specifically retrieved action-related information for function-defined categories. For this type of categories, the action associated with the detail feature is diagnostic for category membership.

Later Activity of the Motor and Occipito-Parietal Cortex

The greater occipito-parietal negativity to shape-defined categories in the pantomime group continued into the time interval between 270 and 400 msec. Albeit much smaller, these category-related ERP effects in the pantomime group were not only present during category verification, but also during name verification, although the task required to individuate single nobjects, but not to distinguish between categories. Thus, the training regimen and category structure must have influenced acquired object representations in general, even when category information was not task-relevant. Source activity to shape-defined categories was obtained in both training groups in the left temporal and left inferior prefrontal cortex. Function-defined categories activated areas close to the premotor cortex in both the pantomime and the pointing groups. The focus of activity was somewhat more posteriorly than at the previous time points. This late activity of motor regions in both groups suggests that even execution of an unspecific movement (pointing) in the presence of an object suffices that action information becomes associated with the object representation to some extent.

However, we obtained in the pantomime group stronger occipito-parietal activity in comparison to the pointing group. The activated region comprised areas of the dorsal visual pathway. This pathway is involved in object-directed action and control of grasping movements (Milner & Goodale, 1995). The involvement of the dorsal pathway suggests that at about 300 msec after stimulus onset, participants in the pantomime group started to retrieve the precise action pantomime associated with each exemplar in function-defined categories. Interestingly, activity in frontal motor areas (117 msec) temporally preceded activity in occipito-parietal areas

(300 msec) and not vice versa, as one might have expected in conditions in which a visually presented object is grasped and manipulated. Possibly, the temporal sequence from anterior to posterior motor areas observed here reflects the fact that action representations associated with the objects are activated top-down in response to the semantic category decision (see also Noppeney et al., 2006) and are not driven by visual affordance (Tucker & Ellis, 1998).

The present results corroborate the importance of the physical and structural characteristics of categories for the formation of conceptual representations (Tyler & Moss, 2001; Lloyd-Jones & Humphreys, 1997; Rosch, 1973). In line with Lin and Murphy (1997), they emphasize that the relevance of an object attribute for category membership (here: shape vs. detail feature) determines its relative weighting in the object representation. More importantly, our results show that the weighting of object properties depends on the specific sensory–motor interactions during acquisition.

We are aware that conceptual knowledge on real objects is usually acquired more gradually over an extended period. Our study should be conceived best as “experimental model” for the influences of sensory–motor interactions on conceptual knowledge, rendering it likely that similar mechanisms are also active in real life. In fact, the activation pattern obtained with novel objects in the present study is similar to that observed with real concepts: Although the localizational value of ERPs has to be viewed with caution (Nunez, 1981), early and late action-related brain activity to function-defined categories in our pantomime group resembles the activity pattern found in frontal and temporo-parietal motor regions for manipulable objects from artifactual categories such as tools (Noppeney et al., 2006; Kellenbach et al., 2003; Chao & Martin, 2000; Martin et al., 1996) and action words (Hauk et al., 2004), that is, conceptual categories which crucially depend on action knowledge. Our source localizations are also in accordance with the results of the fMRI study by Weisberg et al. (2006), who observed that training the tool-like use of novel objects is accompanied by activity increases in frontal (dorsal premotor cortex, BA 6) and temporo-parietal (middle temporal cortex, BA 37/21; posterior parietal cortex, BA 7) sensory–motor regions. Our study confirms and extends these findings in several ways. Firstly, as we varied the specific learning experience during training and did not compare activity to trained and untrained objects as Weisberg et al. did, our results can unequivocally be referred to training-related modulations of object processing, and their interpretation is not compromised by other factors such as familiarity. Furthermore and even more importantly, the high temporal resolution of ERPs reveals that training-related activity emerges as early as 117 msec after stimulus onset. We therefore provide the first evidence that experience-dependent plasticity modulates early object processing rather than later strategic

postconceptual processes such as imagery or episodic associations.

Of course, due to the low spatial resolution of ERPs, it is difficult to unequivocally identify the precise locus of activity in the fronto-central motor cortex (premotor cortex or supplementary motor area, SMA). One might even be concerned that our source activity could originate from the frontal eye fields (FEFs) and not from the premotor cortex or SMA, reflecting training-related acquisition of implicit oculomotor programs instead of arm movements. However, this possibility is not very likely for the following reasons: (i) Pantomiming toward the objects in the training phase does not increase the necessity for eye movement planning compared to pointing. If anything, the probability of accompanying eye movements was much higher during the execution of the pointing movement: In the pointing training group, participants were explicitly instructed to attend to the encircled detail feature while pointing to it (see the Methods section). This fosters the probability of eye movements toward the detail feature. Hence, if activity in FEFs due to access to implicit oculomotor programs had produced our results in the categorization task at test, we would have expected greater motor activity in the pointing group. However, we exactly observed the opposite result. (ii) The fronto-central activation peaks of our source analyses in the different time windows were consistently located more superiorly than the FEFs and either close to (BA 8) or within the dorsal premotor cortex (BA 6) in agreement with the Weisberg et al. (2006) fMRI findings. We are aware that the functional relation between ERPs and the fMRI blood oxygen level-dependent (BOLD) signal is complex. Nevertheless, electrophysiological and BOLD responses are related and provide complementary measures of neural activity in terms of spatial and temporal resolution (Debener et al., 2005; Logothetis & Wandell, 2004; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001).

Does Activity in Sensory–Motor Areas Reflect Conceptual Processing?

We take training-related changes of activity in sensory–motor brain areas during object categorization as an index for plasticity of modality-specific conceptual representations. However, several alternative interpretations might be considered. Firstly, it might be argued that our results do not bear on the nature of conceptual *representations*, but simply demonstrate experience-related plasticity of neural *processes* during object categorization, which may or may not be accompanied by plasticity of representations. This criticism refers to the more general problem that mental representations (i.e., stored information structures about the environment) are theoretical entities which cannot be observed directly. Rather, they must be inferred from observable indicators such as behavioral measures or—as in the

present study—neural processes. We believe that it is warranted to refer to conceptual representations in the context of the present study instead solely to neural processes for the following reasons: (i) It is generally accepted that processes act on representations (for a discussion, see Rumelhart & McClelland, 1986). As a consequence, representations and processes are not independent of each other: Representations can only be empirically assessed when activated by a process and vice versa. (ii) The assumption is widely shared that neural activity in sensory or motor areas indexes activation of a sensory or motor representation, respectively (e.g., see Fries, Roelfsema, Engel, König, & Singer, 1997). Therefore, it seems sound to us to take neural activity in a sensory or motor area as an index for an activated sensory or motor representation. We admit that the neuroanatomical and functional distinction between sensory–motor and nonsensory motor areas might be sometimes debatable. This problem, however, is too general to be answered here and has to be resolved in future studies. (iii) A final argument refers to the fact that in both training groups, conceptual knowledge was tested under identical conditions differing only with respect to the prior sensory–motor experience with the trained objects. Therefore, it is difficult to explain why the differential temporal–spatial pattern of brain activity at test should reflect different task-related processes rather than experience-dependent plasticity of conceptual representations.

Secondly, it might be possible that activity in sensory or motor areas is purely *epiphenomenal* and does not essentially contribute to the conceptual representation. For instance, during learning, a sensory–motor interaction might get associated with the object. This association would simply be evoked (e.g., due to spreading activation) whenever the object is presented, but has no functional significance for the conceptual representation, which is stored elsewhere in the brain. Unfortunately, the issue of causality cannot be addressed with neurophysiological recording techniques such as ERPs or fMRI, which only provide correlational evidence for the relation between mind and brain. A causal relation can only be assessed with methods such as transcranial magnetic stimulation (TMS) or lesion studies showing that disruption of neural processes in a given brain area interferes with task performance. Although we cannot answer the issue of causality based on our data, the present study suggests at least a *functional relation* between activity in sensory–motor areas and conceptual processing. (i) Early activity in premotor areas and later activity of occipito-parietal areas in response to function-defined categories were only observed in the pantomime, but not in the pointing, training group. This suggests that the action must be functionally related with the object in order to achieve a strong link between motor and object representations. The mere existence of a pointing movement in the presence of an object

does not suffice. This result supports a conceptual account and renders a simple associative or episodic memory account unlikely (see also the discussion on the enactment effect below). (ii) Frontal motor activity emerged very early (117 msec, 160 msec) temporally concurrent with the ERP components (P1, N1) reflecting visual processing (e.g., Mangun & Hillyard, 1991). Hence, it is very unlikely that the observed premotor activity reflects imagery processes subsequent to conceptual processing. (iii) According to the postexperimental questionnaire, participants in the pantomime group considered the pantomimed actions to be meaningful uses of the novel objects. This shows that participants subjectively treated the action as an integral part of the object concept. (iv) The effect of category type (function- vs. shape-defined categories) in the pantomime group was larger in the category than in the name verification task. This interaction between category type and task reflects the fact that only for the category verification task was the action toward the detail feature crucial to solve the task (i.e., to determine category membership for an object from a function-defined category). In the name verification task, in contrast, action information was much less relevant for identifying a single object. This result pattern shows that sensory–motor regions are differentially recruited depending on the task demands, suggesting a functional role in conceptual processing. Finally, other studies are even suggestive for a causal role of action representations in conceptual processing. In a TMS study, stimulation of the arm or leg area of the motor cortex specifically facilitated lexical decisions on arm- and leg-related action words, respectively (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). Likewise, behavioral studies demonstrated that action representations facilitate object recognition (Helbig, Graf, & Kiefer, 2006) and language comprehension (Glenberg & Kaschak, 2002). Taking all these pieces together, there is accumulating evidence for the functional significance of sensory–motor representation in conceptual processing rendering an epiphenomenal role unlikely.

Thirdly, our finding of motor activity in the pantomime group resembles the well-documented *enactment effect in episodic memory* in some respect (e.g., Golly-Haring & Engelkamp, 2003): Verbal phrases about actions (“lift the pen”) are more efficiently memorized when participants are requested to perform the denoted movements during encoding than when they passively listened to the phrases. Previous ERP studies showed that recognizing action-encoded items among new items elicited a late fronto-central ERP effect starting at about 500 msec, suggesting that motor information associated with the learned items enhances performance during the memory test (Senkfor, Van Petten, & Kutas, 2002; Heil et al., 1999). However, our findings are novel and distinct from the enactment effect in episodic memory because our training effects emerged as early as 117 msec after stimulus

onset. Furthermore, our training paradigm fundamentally differs from these earlier studies with regard to the stimulus material, learning procedure, test task after learning, and the probed memory system. (i) The earlier studies on the enactment effect used well-known meaningful stimuli, which had to be learned and remembered within a single session. Our participants, in contrast, had to acquire conceptual knowledge on *novel unknown objects* across 16 training sessions. (ii) In the studies on the enactment effect, ERPs were recorded during a recognition test where participants had to distinguish between learned old items and new items. This task requires explicit retrieval of the learning episode held in episodic memory (Tulving, 1972). In our study, participants performed an object categorization task, which does not require recollection of a particular learning episode (e.g., performance of a particular action at a specific time point during training). Rather, this task affords access to acquired conceptual representations held in semantic memory (for a neuroanatomical distinction between episodic and semantic memory, see Tulving, 1999). Finally, it should be noted that unlike in the studies on the enactment effect, the pantomime and pointing groups of our study performed comparably during training and in the categorization tasks. Therefore, the present observation of motor activity to function-defined categories in the pantomime group most likely reflects rapid access to motor representations during conceptual processing rather than episodic retrieval processes.

In conclusion, this is the first study providing direct evidence that activity in motor areas during conceptual processing is determined by the specific sensory–motor experience during concept acquisition. We observed a distinct spatial–temporal brain activation pattern depending on the training regimen. Only participants who pantomimed an action functionally related with each detail feature exhibited early activity in frontal motor regions starting at 117 msec and later activity at about 300 msec in the dorsal visual pathway, which is involved in object-directed grasping movements. Participants who uniformly performed a pointing movement to the detail features (nonfunctional action) did not show this activity pattern. This suggests that only in the pantomiming participants were object representations strongly based on elaborated action information. In line with others (Gallese & Lakoff, 2005; Pulvermüller, 2005; Barsalou et al., 2003; James & Gauthier, 2003; Lakoff & Johnson, 1999), we propose that object concepts are essentially grounded in our sensory–motor interactions with the environment. Possibly, concepts are acquired through the learning-based formation of cortico-cortical cell assemblies in sensory–motor areas, for instance, through Hebbian learning (Pulvermüller, 2005). Our results are incompatible with the notion that the neural representation of concepts is amodal and distinct from the sensory–motor systems (Fodor, 2001), reflecting either the physical structure of the environ-

ment (e.g., Tyler & Moss, 2001) or an innate categorical specialization (e.g., Caramazza & Mahon, 2003). Consistent with modality-specific theories of semantic memory (Gallese & Lakoff, 2005; Pulvermüller, 2005; Barsalou et al., 2003; Simmons & Barsalou, 2003; Humphreys & Forde, 2001; Kiefer & Spitzer, 2001; Lakoff & Johnson, 1999), we show that experience-dependent conceptualizations recruit brain regions typically involved in sensory or motor processing. Of course, our results leave open the existence of a supramodal convergence zone, which integrates modality-specific conceptual features held in sensory–motor areas (Simmons & Barsalou, 2003).

APPENDIX

Description of the Training Tasks

Shape Inspection with Name

Subjects were sequentially presented with eight shape prototypes and with their corresponding names. The names were presented visually and auditorily. Each prototype was presented twice.

Introduction to Action Pantomimes/Pointing

Subjects in the pantomime group were shown each of the four possible actions which could be performed with the nobjects. The corresponding pantomimes were demonstrated by the experimenter and practiced with the subjects. In the pointing group, subjects were shown the four different detail features. Subjects were presented with the pictures where the detail feature was encircled and were told to point to it.

Inspection of Action/Detail Feature Names

In the pantomime group, subjects were first presented with a nobject picture and immediately thereafter with an action demonstration picture. The name of the action was subsequently presented visually and auditorily through headphones. Then subjects had to pantomime the action with the right hand. In the pointing group, the picture, where the detail feature was encircled, was shown instead of the action demonstration picture. Furthermore, the name of the detail feature was displayed. Then subjects had to point with their index finger of the right hand to the detail feature. Each nobject with action demonstration/detail feature was presented once.

Category Inspection without Category Name

Subjects were presented with one of the eight categories, with all eight members at once until subjects pressed a key (self-paced). Each category was presented eight times.

Category Inspection with Category Name

Subjects were presented with one category with all eight members at once until subjects pressed a key (self-paced). Simultaneously, the category name was presented visually on the computer screen and auditorily. Each category was presented three times.

Category Inspection with Category Name and Action Pantomime/Pointing

Subjects were first presented with one category with all eight members at once. Thereafter, the single category members were shown sequentially. For the pantomime group, the associated action was demonstrated on a picture, which prompted the subjects to pantomime the action. For the pointing group, the same features were highlighted by a black circle instead of demonstrating the associated action. The subjects in the pointing group were requested to point with the index finger to the highlighted features in each picture. Thereafter, subjects initiated the next trial with a button press. Each nobject was presented once.

Category Naming—Keyboard Response with Feedback

Subjects were presented with one category with all eight members at once. Subjects had to press a key on the keyboard corresponding to the first letter of the category name and speak the category name aloud. In case of an erroneous response, the word “error” and the correct category name were presented, whereas the word “correct” was presented when answered correctly. Each category was presented four times.

Nobject Inspection—Nobject Name—Action/Detail Feature

In this task, subjects learned for a subset of eight nobjects their names for the first time. In the pantomime group, one of eight unfamiliar nobjects was shown together with the picture demonstrating the action. Thereafter, the nobject name was presented visually and auditorily. Subjects had to pantomime the action in response to the action demonstration. In the pointing group, the sequence of events was the same except that no action demonstration was presented and subjects had to point with their index finger to the detail feature, which was highlighted by a black circle. After the action pantomime/pointing movement, subjects initiated the next trial with a button press. Each nobject was presented three times.

Nobject Naming—New Subset of Nobjects with Feedback

Subjects were shown the subset of eight nobject pictures for which the name was learned in the current session for

the first time. They were presented with a single nobject picture and were requested to name it. The experimenter classified the response as correct or false. In the case of a correct nobject name, the word “correct” was presented, whereas in case of an erroneous response, the word “error” and the correct nobject name were presented. Each nobject was presented three times.

Nobject Naming—Previously Learned Subsets with Feedback

This task was the same as the previous one except that only nobjects from subsets that were studied in the previous sessions were presented.

Nobject Naming—All Learned Subsets with Feedback

This task was the same as the previous one except that nobjects from all studied subsets were presented.

Nobject Naming—Without Feedback

This task was the same as the previous one except that except all 64 nobject pictures were presented and no feedback was given. If the nobject name had not been learned yet, subjects should press a nil-key for “name is unknown.” Each nobject was presented once.

Category Decision—Pairs of Nobject Pictures with Feedback

Subjects were sequentially presented with a pair of nobject pictures. In half of the trials, both nobjects belonged to the same category and in the other half they belonged to different categories. Subjects had to decide whether the first and second object pictures belong to the same category and had to indicate their decision with a key-press. In case of an erroneous response, both nobjects were sequentially presented together with the corresponding category name. Each nobject was presented three times.

Category Decision—Pairs of Nobject Names with Feedback

This task was the same as the one with pictorial stimuli except that pairs of nobject names were presented.

Category Decision—Pairs of Nobject Pictures without Feedback

This task was the same as the previous one except that there was no feedback.

Category Decision—Pairs of Nobject Names without Feedback

This task was the same as the previous one except that there was no feedback.

Visual Decision—Pairs of Nobject Names with Feedback

Subjects were sequentially presented with two nobject names and had to decide whether the corresponding nobjects have a similar shape (i.e., were derived from the same shape prototype) or not. In case of an erroneous response, the prototype shapes of the two nobjects with their names were sequentially shown as a feedback. Each nobject was presented three times.

Action/Detail Feature Decision—Pairs of Nobject Names with Feedback

Subjects were sequentially presented with two nobject names. In the pantomime group, subjects had to decide whether the same action can be performed with the objects or not. In case of an erroneous response, the pictures demonstrating the correct actions and the nobject names were shown. In the pointing group, subjects had to decide whether both nobjects have the same detail feature or not. In case of an erroneous response, the pictures demonstrating the correct detail features and the nobject name were shown. Each nobject was presented three times.

Action/Detail Feature and Shape Naming with Feedback

In the pantomime group, subjects were presented in half of the trials with a nobject picture and in the other half with the picture demonstrating the action. Subjects had to produce the name of the shape in response to the nobject picture and the name of the action in response to the picture with the action demonstration. The experimenter classified the response as correct or false. In the correct response, the word “correct” was presented, whereas in case of an erroneous response, the word “error” and the correct shape or action name was presented. In the pointing group, subjects were presented in half of the trials with a nobject picture and in the other half with the picture where the detail feature is encircled. Subjects had to produce the name of the shape in response to the nobject picture and the name of the detail feature in response to the picture with the encircled detail feature. Again, feedback was given. In both groups each nobject was presented once.

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