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How words get meaning: The neural processing of novel object names after sensorimotor training

Laura Bechtold [a,*,1], Marta Ghio [a,1], Gerald Antoch [b], Bernd Turowski [b], Hans-Jörg Wittsack [b], Marco Tettamanti [c], Christian Bellebaum [a]

[a] Institute for Experimental Psychology, Department of Biological Psychology, Heinrich Heine University Düsseldorf, Germany
[b] Department of Diagnostic and Interventional Radiology, Medical Faculty, Heinrich Heine University Düsseldorf, Germany
[c] CIMeC - Center for Mind/Brain Sciences, University of Trento, Italy

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ABSTRACT

The hypothesis that individual experience affects the formation and processing of conceptual representations is controversially debated. Previous training studies with novel tool-like objects have found experience effects on conceptual representations as measured in tasks requiring the processing of object pictures. This study instead explored the neural processing of training-induced word meaning of novel object names. We asked whether the type of experience gained during object concept formation specifically modulates object name processing. In three training sessions with novel tool-like objects, two groups of healthy participants gained either active or observational manipulation experience as well as purely visual experience, while learning pseudowords serving as object names. In an fMRI session after training, participants were presented with the learned novel object names in a lexical decision task. Results revealed that processing novel object names in comparison to meaningless pseudowords elicits a word-like activation pattern in frontal, parietal and temporal regions known to underlie lexical-semantic processing, thus suggesting word meaning formation. Experience-specific modulations did not emerge as regional activation effects. However, a post-hoc analysis revealed that the type of experience (manipulation versus visual) as well as the way, in which the manipulation was learned (active versus observational) led to specific functional connectivity increases between semantic regions and neuronal assemblies in brain areas coding for object manipulation and related visuospatial information. These results suggest that the emergence of conceptual processing for novel object names might be grounded in functional brain networks specifically coding for the experience with their referents.

1. Introduction

Our capability to convey meaning through language relies on the association of words with their referent's representations in semantic memory. There, knowledge we initially gained through experience is combined and stored in the form of concepts (Kiefer and Pulvermuller, 2012). Theoretical approaches differ concerning the role they ascribe to modality-specific areas involved in experience with the concepts' referents in conceptual-semantic neural representations (for a review see Meteyard et al., 2012). While amodal (Fodor, 1975, 1994) and domain-specific theories (Caramazza and Shelton, 1998; Mahon and Caramazza, 2009, 2011) postulate an independence of conceptual knowledge from modality-specific areas, embodied theories (Gallese and Lakoff, 2005; Glenberg and Kaschak, 2003) assume that conceptual processing recruits the same brain areas as the initial experience. Intermediate accounts (e.g., grounded cognition theory, Barsalou, 2008) assume a weaker form of embodiment and suggest that conceptual representations result from the interplay between modality-specific sensorimotor areas and one or multiple hubs, which mediate cross-modal integration (for recent reviews see Binder, 2016; Lambon Ralph et al., 2017).

The assumption of at least a certain degree of embodiment found broad support in neuroimaging research on manipulable objects, whose conceptual representations comprise information about their associated

* Corresponding author. Heinrich Heine University Düsseldorf, Institute for Experimental Psychology, Dpt. of Biological Psychology, Building 23.03., Universitätsstr. 1, D-40225, Germany.
E-mail address: Laura.Bechtold@hhu.de (L. Bechtold).
[1] co-first authors.

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perceptual features, actions and functions (for reviews see Cappa, 2008; Noppeney, 2008). For example, functional magnetic resonance imaging (fMRI) studies showed that the processing of tool pictures or names draws on an extensive left-hemispheric network including portions of the premotor, parietal, and posterior temporal cortices, which are involved in actual object-directed movements and object use (Beauchamp and Martin, 2007; Ishibashi et al., 2016; Martin, 2007). The comparable activation patterns elicited by the processing of pictures and written as well as spoken tool names suggest that conceptual representations can be accessed in different ways (Chao et al., 1999; Devlin et al., 2005). Furthermore, lesions in the left-hemispheric fronto-parietal tool-network lead to deficits in imitating tool-use (Buxbaum et al., 2014) and in the conceptual processing of action-related features in object identification (Lee et al., 2014), as well as a selectively impaired recognition of tool words (Dreyer et al., 2015). This evidence refutes a merely epiphenomenal nature of sensorimotor activations during conceptual tool (name) processing (but see Mahon, 2015). However, these studies only provided indirect evidence for the role of sensorimotor experience in the formation of novel concepts.

In order to directly control the quantity and quality of experiential information that forms the objects' conceptual representations, one line of research has employed training paradigms with novel tool-like objects (Bellebaum et al., 2013; Kiefer et al., 2007; Ruther et al., 2014b; Weisberg et al., 2007). Weisberg et al. (2007) found that after three training sessions, actively manipulated novel tool-like objects elicited activations in left-hemispheric brain areas involved in motion and manipulation processing for common tools. In a subsequent study, the left premotor and inferior parietal cortices were found to be recruited more strongly by the processing of manipulated than visually explored tools (Bellebaum et al., 2013). Comparable findings were obtained in a study with observational instead of active manipulation training, suggesting a common mechanisms for both types of experience in forming conceptual object representations (Ruther et al., 2014b).

In a previous electroencephalography (EEG) study, our working group tested if also lexical-semantic processing leads to a (re-)activation of recently acquired experiential information in modality-specific brain areas. We applied a variant of the novel objects training paradigm, in which participants additionally learned names for the objects, thereby acquiring novel word meanings (Bechtold et al., 2018). In an EEG measurement after training, processing the names of novel objects that were actively manipulated elicited a stronger beta and mu rhythm suppression than processing the names of visually explored objects, indicating an experience-dependent involvement of the sensorimotor cortex in the processing of novel tool names (Bechtold et al., 2018). The distinguishing characteristic of this study, namely presenting object names instead of pictures during the post-training task, made sure that the measured effects were unaffected by the object's perceptual qualities (Binder et al., 2009) such as affordances (Borghi and Riggio, 2015).

The present study aimed to further investigate the role of sensorimotor information in the formation of novel word meanings by exploring the specific spatial characteristics of training-induced neural representations with fMRI. Like in our previous EEG study (Bechtold et al., 2018), a group of participants gained manipulation and visual experience with novel objects in a training paradigm in which they also learned the novel objects' names. Another group of participants instead gained observational manipulation and visual experience. This between-groups distinction was introduced, since a direct comparison of active and observed manipulation has not been provided so far. In the fMRI session after training, participants processed the names of the novel objects in a lexical decision task (LDT).

Firstly, we aimed to examine neural correlates of training-induced word meaning. When compared to meaningless pseudowords (PWs), the processing of words leads to so-called lexicality effects as a result of accessing conceptual knowledge in semantic memory. Functional neuroimaging studies on lexicality effects, but also on the comparison of semantic and phonological processing of real words, revealed a left-lateralized brain network extending from heteromodal prefrontal to inferior posterior parietal areas and reflecting semantic processing (for a meta-analysis see Binder et al., 2009). We hypothesized that the training protocol would induce meaning in all novel object names by forming conceptual object representations associated with the novel word. Processing novel object names should thus show a word-like activation pattern in comparison to unfamiliar PWs (Binder et al., 2003; Mechelli et al., 2003). We expected this effect to arise to a comparable degree after (active and observational) manipulation as well as visual exploration training (Binder et al., 2009). The second aim was to investigate training-induced experience-specific effects by directly comparing the processing of novel object words from the different training conditions. We hypothesized that active as well as observational manipulation training leads to stronger activations in regions within the tool-related fronto-parietal network than the visual exploration training (Ishibashi et al., 2016; Noppeney, 2008). Additionally, active manipulation might lead to stronger effects than observed manipulation (Cannon et al., 2014; Macuga and Frey, 2012).

2. Method

2.1. Participants

Forty-six volunteers took part in this study. We excluded three participants due to artifacts in the imaging data, and two other participants due to a learning performance at chance level (see below for details in how learning was assessed). Of the remaining 41 participants, 20 (11 females) were part of the active (ACT) and 21 (15 females) of the observational (OBS) group. All were healthy adults aged from 18 to 35 years (ACT: $M = 23.30$ years, $SD = 4.93$ years; OBS: $M = 23.19$ years, $SD = 3.53$ years), with no significant difference in age between the two groups, $t(34.305) = 0.081$, $p = .936$. None of the participants had any history of psychiatric or neurological diseases. All had normal or corrected-to-normal visual acuity and were right-handed according to their scores in the Edinburgh Handedness Inventory (Oldfield, 1971; ACT: $M = 0.92$, $SD = 0.11$; OBS: $M = 0.82$, $SD = 0.22$). Mean handedness scores did not differ significantly between the two groups, $t(29.871) = 1.842$, $p = .075$. All participants gave their written informed consent prior to participation and subsequently received monetary compensation or course credit. Additionally, the five participants with the highest learning performance received a 30 € voucher of an internet-based retailer, which was announced for motivational purposes. The study received approval by the ethics committee of the Medical Faculty at Heinrich Heine University Düsseldorf, Germany, and the study procedures were in line with the declaration of Helsinki.

2.2. Stimulus material

2.2.1. Novel objects

Thirty-six novel tool-like objects were composed from a children's construction toy (K'NEX™, for an example see Fig. 1) and have already been used in previous studies by our group (Bechtold et al., 2018; Bellebaum et al., 2013; Ghio et al., 2016; Ruther et al., 2014a, 2014b). Each object had a specific tool-like function (i.e., transport, push, pull, move, destroy or separate) performed on small object-specific items (e.g., table tennis balls, paper cups, paper sheets). We divided the objects into two sets of 18 objects, including three objects for each function. The objects in the two sets were matched for visual complexity, singularity (i.e., how much an object "popped out" from the others) and similarity with real objects (see Ruther et al., 2014a for details on the rating procedure). For each object, a 640 × 360 pixel mp4 video served as non-verbal manipulation instruction. This video showed one full manipulation of the respective object, with a varying duration (17 s - 47 s, $M = 27.00$ s, $SD = 6.98$ s; see Fig. 1A and video V1 in supplementary online material), depending on the manipulation's complexity. For the observational manipulation training, an additional video existed for each object, which showed continuous manipulations for 60 s.

The supplementary video related to this article can be found at https://doi.org/10.1016/j.neuroimage.2019.04.069.

2.2.2. Verbal stimuli

2.2.2.1. Novel object names and pseudowords. We used the PW generator software *Wuggy* (Keuleers and Brysbaert, 2010) with the German language module to generate 36 PWs from real object names (see section 2.2.2.2). The output PWs were restricted to match the real object names with respect to the length of subsyllabic segments, word length (5–10 letters, $M = 6.61$, $SD = 1.46$), the transition frequencies between letters, and two out of three subsyllabic segments. Each novel object was uniquely assigned to one PW, which served as the novel object's name (e.g., *Zenkan*, *Tessen*). Novel object names were presented in association with the objects during the training and participants were asked to learn them. After the training, the novel object names served as stimuli for our experimental LDT (see section 2.3.3.1), referred to as LDT_{NOV} in the following. By applying the specified parameters in Wuggy, we created two additional sets of PWs, which served as non-trained material in the LDT_{NOV} and in the localizer task on real object names (see Table S1A in Supplementary Material 1).

2.2.2.2. Real object names. We used 36 German nouns describing real objects for a functional localizer task (see Table S1A in Supplementary Material 1). Eighteen nouns referred to manipulable objects (e.g., *hammer*), the remaining 18 to non-manipulable objects with mainly visual features (e.g., *pillow*). Manipulable and non-manipulable object names were matched for length and frequency of occurrence. Further, 13 independent raters rated all real object names on 1–7 Likert scales regarding the strength of their association with actions and manipulations and how easy it was to imagine a function or use-related gesture. Manipulable object names were rated significantly higher than non-manipulable object names on all scales, all $p < .001$ (see Table S1B in Supplementary Material 1 for descriptive and inferential statistics on the psycholinguistic variables). An LDT served as localizer task (referred to as LDT_{LOC} in the following).

2.3. Procedure

2.3.1. General procedure

Each subject underwent three training sessions and a subsequent fMRI session. The trainings were conducted in a laboratory room at Heinrich Heine University and the fMRI session took place at the University's medical center. For all participants, the intervals between sessions varied between one and five days, except for one participant of the ACT group, who completed the last training in the morning of the day the fMRI session took place. Of particular interest was the interval between the last training session and the fMRI session. This interval was significantly shorter in the ACT ($M = 0.95$ days, $SD = 0.22$ days) than in the OBS group ($M = 1.62$ days, $SD = 0.92$ days), $t(36) = -3.232$, $p = .004$. At the end of each training session and after the fMRI session, we applied a multiple-choice (MC) questionnaire, in which the participants were asked to assign each novel object name to its training condition (i.e., manipulation or visual, guessing would result in an average accuracy level of 50%). Notably, despite the longer interval before the fMRI session for the OBS than ACT group there was no group difference in MC test performance (see section 3.1.1).

2.3.2. Training procedure

The training sessions with the novel objects consisted of the manipulation condition (MAN), which was either active or observational for the participants of the two study groups, and the visual condition (VIS), which was identical for the participants of both groups. The assignment of the two object sets to the two training conditions was counterbalanced between and then held constant within participants. The order of conditions in each training session was counterbalanced within and between participants. The 18 objects within the MAN and VIS training conditions appeared in a randomized order. Note that, for any given participant, each object was only presented once, either in the VIS or in the MAN condition, according to the between-subjects counter-balanced object assignment to the two distinct sets. The software PsychoPy (version 1.81.03; Peirce, 2007) controlled the stimulus presentation in the training sessions on a Windows 10 PC with a 27' Ben Q LED monitor with 1920 × 1080 pixel resolution. All stimuli were presented on a black

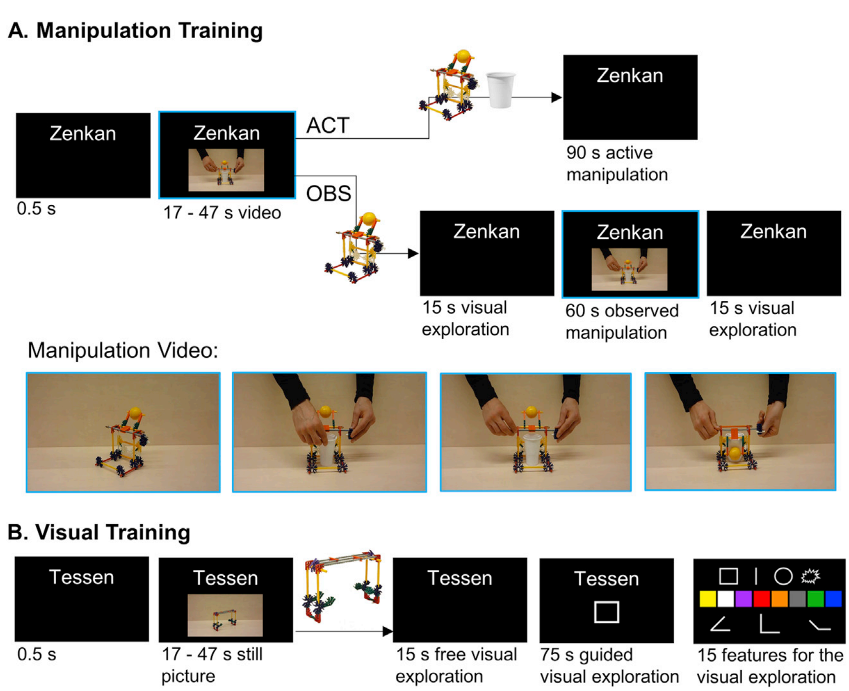

Fig. 1. *Procedure of the manipulation and visual training.* A. Displays the timing of the trials in the manipulation training in the active (ACT) and observational (OBS) learning group and four exemplary frames taken from a manipulation video. B. Displays trial timing in the visual non-manipulation training, which was the same for both groups.

background. Novel object names were presented in white (front: Arial, size: 72 pt). Each training session took about 90 min.

2.3.2.1. Manipulation training. In the MAN training (see Fig. 1A), the written name of one of the novel objects at a time appeared on the computer screen and the participants read the name aloud. After 0.5 s a video instruction started, showing one full manipulation of the object, while the name stayed on the screen. After the video, the experimenter placed the novel object in front of the participant. In the ACT group, the to-be-manipulated object-specific small items were additionally placed on the table and the participant was asked to manipulate the object for 90 s following the video instruction. The experimenter corrected the participant's manipulation if necessary. A beep tone and the written request to stop ended the manipulation time. In the OBS group, the MAN training continued with 15 s visual exploration of the novel object, which was prompted by a written request on the screen ("Please examine the object now"). Visual exploration took place twice, before and after the observational manipulation video, which lasted 60 s and showed continuous object manipulations (Fig. 1A). For each object, the duration of the MAN training in the OBS group was thus also 90 s. By this procedure, the participants gained a real-life three-dimensional experience with the novel object, while at the same time observationally learning about its function without any actual object-directed movement or haptic experience. A beep tone and the written request to stop ended the manipulation time.

2.3.2.2. Visual training. In the VIS training (see Fig. 1B), the name of one novel object at a time appeared and was read out aloud by the participant. After 0.5 s a still picture (extracted from the video instruction for the MAN training) was presented for the duration of the manipulation of the respective object. Then, the experimenter placed the novel object in front of the participant and the 90 s visual exploration time started, of which the first 15 s were dedicated to free visual exploration. Afterwards, the exploration was guided by the visual presentation of five features, which the participants were asked to look for in the novel object for 15 s each. Overall, there were 15 different features (eight different colors, four forms, three angles; see Fig. 1B), and five of these appeared for each novel object within each training session. Over the three training sessions, each feature appeared once for each novel object. The order was counterbalanced over the sessions. A beep tone and the written request to stop ended the exploration time.

2.3.3. fMRI session

The fMRI session included two runs of the LDT_{NOV}, which took 5 min each and were separated by a standardized alertness task for 4.5 min (Zimmermann and Fimm, 1993). The alertness task was introduced in order to reduce repetition effects in the second LDT_{NOV} run. Then, participants underwent the localizer task, consisting of one 5 min run, in which the participants performed the LDT_{LOC}. Before each run, the experimenter carefully instructed the participants about the task. The software Presentation (version 17.0, Neurobehavioral Systems Inc., Albany, CA, USA) controlled the stimulus presentation on a Dell Inspiron 15 7000 Series notebook. An LCD TFT Beamer (NEC, model MT1050, 1024 × 768 px resolution) projected the stimuli onto a translucent screen inside the scanner room. Participants could see the screen over a mirror construction attached to the birdcage coil. Responses were given on a Lumina Response Pad LS-PAIR for fMRI measurements (Cedrus Corporation, San Pedro, California, USA). The fMRI session ended with a T1-weighted anatomical image acquisition, which took about 11 min. The entire fMRI session lasted about 60 min.

2.3.3.1. Lexical decision task. In each LDT_{NOV} run, all 36 novel object names were presented intermixed with 36 meaningless PWs in white letters on a black background. The order was randomized once for each run, but then held constant across participants. Each object name and PW was shown for 1 s, preceded by a fixation cross for 0.45 s. The inter-trial-interval varied, with fixed durations of 1.7 s (42 times), 2.1 s (20 times) or 6 s (10 times). The participants responded by pressing one of two buttons with their left hand's index or middle finger. The participants were instructed to respond as fast as possible with the index finger to novel object names and with the middle finger to meaningless PWs. The same experimental paradigm was applied in the localizer task (LDT_{LOC}), in which 36 real object names were presented intermixed with a different set of 36 PWs.

2.3.3.2. fMRI data acquisition parameters. Images were acquired with a 12-channel head coil on a 3T Siemens scanner (MAGNETOM Trio, A TIM system). During the two LDT_{NOV} runs as well as the LDT_{LOC} run, whole-brain functional images were acquired with a T2*-weighted gradient echo, echo-planar imaging sequence using a blood-oxygenation-level dependent contrast (repetition time = 2000 ms, echo time = 30 ms, flip angle = 90°). The functional images consisted of 31 axial slices parallel to the anterior-posterior commissure (4.0 mm thick, in plane resolution = 2 × 2 mm, no gap, field of view = 192 × 192 mm, acquisition order = ascending interleaved, odd first). For each participant, one functional image sequence including 150 vol was gathered during both LDT_{NOV} runs and the LDT_{LOC} run, resulting in a total of 450 functional scans. Additionally, for each participant a T1-weighted anatomical image was acquired via three-dimensional spoiled-gradient-recalled sequences with a repetition time of 1850 ms and an echo time of 35 ms (240 slices, slice thickness = 0.7 mm, in plane resolution = 0.7 × 0.7 mm).

2.4. Data analysis

2.4.1. Behavioral data

We analyzed behavioral data with IBM SPSS Statistics (version 23, ©IBM). If the Mauchly test indicated a violation of the sphericity assumption, we applied the Greenhouse-Geisser correction and report corrected degrees of freedom and p-values. We considered an α-level of 0.05 as indicating statistical significance and applied the Bonferroni correction to post-hoc pairwise comparisons.

2.4.1.1. Learning performance. To assess learning performance, the percentage of object names that were correctly assigned to their training condition in the MC questionnaires after each session was determined for each participant, separately for the two training conditions. The percentage values of the MC performance were then analyzed with a 4 × 2 × 2 mixed ANOVA with the within-subjects factors Session (training session one, two, three; fMRI session) and Type of Word (MAN, VIS) and the between-subjects factor Learning Group (ACT, OBS).

2.4.1.2. LDT_{NOV}. For LDT_{NOV}, reaction times and accuracy (defined as the percentage of correct responses of all given responses) were analyzed via separate 3 × 2 ANOVAs. We included the within-subjects factor Type of Word (MAN, VIS and PW) and the between-subjects factor Learning Group (ACT, OBS). For the sake of completeness, we analyzed the LDT_{LOC} accordingly (results are displayed in Supplementary Material 2A).

2.4.2. fMRI data

We preprocessed the data with SPM8 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk/spm). The New Segment procedure was applied to the structural images of each participant, with registration to the Montreal Neurological Institute (MNI) standard space. Functional images were corrected for slice timing and spatially realigned. Subsequently, we normalized the images to the MNI space, using the New Segment procedure with the subject-specific segmented structural images as customized segmentation priors. Finally, the images were spatially smoothed with an 8-mm FWHM Gaussian kernel.

The data were further analyzed with SPM12 (version r7219). We adopted a two-stage random-effects statistical approach, and, at the second stage, we applied a partitioned error approach. The statistical analysis was restricted to an explicit mask including only the voxels with gray matter probability > .1 based on the segmented structural images of each participant. We corrected for multiple comparisons by applying the Gaussian random field theory as implemented in SPM12 to obtain clusters satisfying a cluster-level $p < .05$ family-wise error (FWE)-corrected threshold, with a $p < .001$ cluster-defining threshold.

At the first stage, we specified a general linear model (GLM) for each participant. We high-pass filtered each participant's time series at 128 s and modelled serial correlations by means of an autoregressive model AR(1). No global normalization was performed. We modelled the two LDT_{NOV} runs as two separate sessions, each including the conditions MAN, VIS, and PW as regressors of interest. These regressors contained the onsets of those novel object names and PWs, which were correctly identified in the LDT_{NOV}. Additionally, the MAN and VIS regressors contained only the onsets of those novel object names, which participants correctly assigned in the MC questionnaire after the last training session. This assured that only learned object names and correctly identified object names and PWs were considered as events of interest. If present, separate confounding regressors were modelled for unlearned object names (i.e., novel object names that participants did not correctly assign in the MC questionnaire after the last training session) and for trials in which participants gave erroneous LDT responses. Onset times for all these conditions were convolved with a canonical hemodynamic response function. We entered head movement realignment parameters into the model as covariates by implementing six regressors of no interest (three rigid-body translation, and three rigid-body rotation parameters).

2.4.2.1. Training-induced lexicality effects. In a first analysis, we aimed to examine the effects of training-induced lexicality by comparing the processing of novel object names (without distinguishing between MAN and VIS) and unfamiliar PWs. Although we did not expect differences between the ACT and OBS group, the factor Learning Group was entered into this analysis in order to control for group differences. We therefore applied a 2 × 2 factorial design with Lexicality as a within-subjects factor (Object Name [MAN + VIS], PW) and the between-subjects factor Learning Group (ACT, OBS). Within the estimated first-level GLM, we defined two first-level Student's *t*-test contrasts: (1) a contrast with a weight of +1 for MAN, +1 for VIS, −2 for PW and a weight of zero for all the other regressors; (2) a contrast with a weight of +1 for all the conditions of interest (MAN, VIS, PW) and a weight of zero for all the other regressors. In order to assess the main effect of the training-induced Lexicality, we used the contrast (1) to specify a second-level one-sample *t*-test design. To assess the main effect of Learning Group, we used the contrast (2) to create a second level two-sample *t*-test design (independence and unequal variances assumed between groups). Finally, we tested the Lexicality x Learning Group interaction by entering the contrast (1) into a two-sample *t*-contrast design (independence and unequal variances assumed between groups).

2.4.2.2. Training-induced experience-specific effects. The aim of the second analysis was to detect whether the specific type of training experience (manipulation vs. visual) with novel objects induced modulations of the activation patterns associated with novel object name processing, and whether these varied depending on whether the manipulation was learned actively or by observation. In this analysis, we thus omitted PWs and directly compared novel object names from the MAN and VIS training. We applied a 2 × 2 factorial design with Type of Word (MAN, VIS) as a within-subjects factor and the Learning Group (ACT, OBS) as the between-subjects factor. At the first stage, we defined two first-level Student's *t*-test contrasts: (1) a contrast with a weight of +1 for MAN and −1 for VIS and a weight of zero for all the other regressors; (2) a contrast with a weight of +1 for both MAN and VIS and a weight of zero for all the other regressors. In order to assess the main effect of Type of Word, we used the contrast (1) to specify a second-level one-sample *t*-test design. To assess the main effect of Learning Group, we used the contrast (2) to create a second level two-sample *t*-test design (independence and unequal variances assumed between groups). Finally, we tested the Type of Word x Learning Group interaction by entering the contrast (1) into a two-sample *t*-contrast design (independence and unequal variances assumed between groups). Additionally to the whole brain analysis, we applied a small volume correction ([SVC]; $p < .05$, FWE corrected; Poldrack et al., 2011) to the analyses of the main effect of Type of Word and the Type of Word x Learning Group interaction by using ROIs defined on the basis of the localizer task (see section 2.4.2.3). This aimed at testing the experience-dependent activation of specific brain regions involved in the representation of real manipulable object words.

2.4.2.3. Localizer fMRI data. The localizer task comprising real object names was analyzed at the first stage by modelling the session including three regressors of interest, one for the manipulable object names, one for the non-manipulable object names and one for PWs. These regressors included the onsets of the words and PWs for which participants gave correct LDT_{LOC} responses. Separate regressors were modelled for erroneous LDT_{LOC} responses (if present) and the six head movement realignment parameters.

The aim of the analysis of the localizer task was to identify the activation network for processing words referring to real manipulable vs. non-manipulable objects in order to specify regions of interest for the SVC analysis of the novel object names (see section 2.4.2.2). For this purpose, at the first stage, we defined a first-level Student's *t*-test contrast with a weight of +1 for manipulable and −1 for non-manipulable object names and a weight of zero for all the other regressors. We then used this contrast to specify a second-level one-sample *t*-test design. The main effect of Learning Group was not entered into the analysis. For the sake of completeness, we however also verified that when we additionally included the Learning Group factor as a covariate, we obtained the same pattern of results. Processing manipulable object names led to significantly stronger left-hemispheric activations in two clusters. One was located in the inferior frontal gyrus (pars triangularis) and the precentral gyrus (peak coordinates: $x = -42$, $y = 28$, $z = 20$, cluster size: 226 voxels, $p = .001$, $z = 4.08$). The second was located in the superior and inferior parietal lobule extending to the middle occipital gyrus (peak coordinates: $x = -30$, $y = -70$, $z = 40$, cluster size: 140 voxels, $p = .012$, $z = 3.92$). We applied an SVC of the training-induced experience-specific effects (see section 2.4.2.2) using 6 mm sphere ROIs around these clusters' peak coordinates.

3. Results

3.1. Behavioral data

3.1.1. Learning performance

Table 1 displays the descriptive statistics of the MC performance assessing the learning of the novel words. Session had a significant effect on the MC performance, $F(3, 117) = 28.526$, $p < .001$, $\eta_p^2 = 0.422$. The learning performance increased significantly from the first to the following sessions, all $p < .001$. From the second session to the third, there was a further marginally significant increase, $p > .062$, but not from the second to the fMRI session, $p = .797$. Indeed, the learning performance dropped significantly from the third training to the fMRI session, $p = .002$. Neither the main effects of Type of Word or Learning Group nor any of their interactions were significant, all $p > .132$.

3.1.2. LDT_{NOV}

Type of Word had a significant effect on reaction times, $F(1.492, 58.170) = 28.955$, $p < .001$, $\eta_p^2 = 0.426$. Participants reacted more slowly to PWs ($M = 724$ ms, $SE = 14$ ms) than to MAN ($M = 671$ ms, $SE = 12$ ms) and VIS ($M = 671$ ms, $SE = 11$ ms), both $p < .001$. MAN and VIS did not

Table 1
Learning performance in the multiple-choice questionnaire.

Group	Training	Session			
		T1	T2	T3	fMRI
		M (*SD*)	*M* (*SD*)	*M* (*SD*)	*M* (*SD*)
ACT	MAN	72.2 (18.0)	86.7 (11.9)	90.3 (10.3)	83.3 (16.0)
	VIS	71.1 (15.9)	87.2 (14.1)	89.7 (11.4)	86.1 (15.6)
OBS	MAN	68.5 (12.1)	79.4 (19.7)	88.9 (13.6)	76.2 (19.9)
	VIS	64.3 (13.9)	79.6 (20.7)	86.2 (11.6)	75.4 (23.6)

Note. Mean percentage of correct assignments in the multiple-choice questionnaire after the three training sessions (T1-T3) and the fMRI session for the active (ACT) and observational (OBS) group for novel object names from the manipulation (MAN) and visual (VIS) training condition.

differ significantly, $p > .999$. Neither the main effect of Learning Group nor its interaction with Type of Word were significant, both $p > .711$. The mean accuracy was very high in all experimental conditions (ACT-MAN: $M = 97.6\%$, $SE = 0.7\%$; ACT-VIS: $M = 97.6\%$, $SE = 0.9\%$; ACT-PW: $M = 97.7\%$, $SE = 0.7\%$; OBS-MAN: $M = 98.1\%$, $SE = 0.7\%$; OBS-VIS: $M = 97.5\%$, $SE = 0.9\%$; OBS-PW: $M = 96.7\%$, $SE = 0.7\%$). Neither the main effect of Type of Word nor Learning Group nor their interaction significantly affected LDT_{NOV} accuracy, all $p > .467$.

3.2. fMRI data

3.2.1. Training-induced lexicality effects

In order to investigate the effects of training-induced lexicality of the novel object names, we compared the activation elicited by the processing of object names (averaged across MAN and VIS) and PWs. The brain regions showing significantly higher activations for object names than PWs are displayed in Fig. 2A and listed in Table 2A. Processing object names elicited stronger activations in left-hemispheric frontal regions including the superior frontal gyrus, the middle frontal gyrus, the inferior frontal gyrus (pars triangularis), and different portions of the orbital frontal gyrus. Significant activations were also found in the parietal cortex, with one cluster extending from the left cuneus to the bilateral precuneus and middle cingulate cortex, and, bilaterally, two clusters from the inferior parietal lobule to the angular gyrus. Finally, significant activations were observed in the left middle and inferior temporal gyrus as well as in the parahippocampal gyrus.

The brain regions showing significantly stronger activations for PW than object name processing are displayed in Fig. 2b and listed in Table 2B. PWs led to significantly stronger activations in a large cluster extending from the right superior frontal gyrus, to the bilateral posterior-medial frontal gyrus, the left precentral and bilateral postcentral gyrus, and left inferior parietal lobule. Neither the analysis of the Learning Group main effect nor of the Lexicality by Learning Group interaction yielded any significant activation clusters.

3.2.2. Training-induced experience-specific effects

To investigate the experience-specific effects induced by the different kinds of training, we directly compared activations elicited by MAN and VIS object names. We found neither significantly stronger activations for processing MAN than VIS, nor for VIS than MAN. Neither the Learning Group main effect nor the Type of Word by Learning Group interaction yielded any significant activation clusters. Neither of these effects were significant, even when we applied an SVC approach using the two ROIs obtained by the functional localizer LDT_{LOC}.

3.2.3. Post-hoc analysis of training-induced functional connectivity

The examination of brain regions associated with the processing of novel object names vs. PW (i.e., the lexicality pattern) revealed a network that was highly consistent with the conceptual hub network identified by a quantitative meta-analysis on semantic processing (Binder et al., 2009, 2016). All nodes within this network have been identified as high-level multimodal areas, which are characterized by a dense pattern of connectivity with multiple modality-specific areas (Binder et al., 2016; Lambon Ralph et al., 2017). Hubs have been ascribed a key role in forming multimodal semantic representations by integrating experiential information from different modalities (Binder et al., 2016; Binder and Desai, 2011; Lambon Ralph et al., 2017). The lack of experience-specific effects in our data despite this significant lexicality effect brought us to formulate an additional post-hoc hypothesis. We assumed that experience-specific effects might be reflected by a differential functional connectivity between the high-level multimodal hub areas involved in processing the novel object names and neuronal assemblies in modality-specific areas (for a comparable line of thought, see Chow et al., 2014; Malone et al., 2016).

To investigate training-induced experience-specific functional

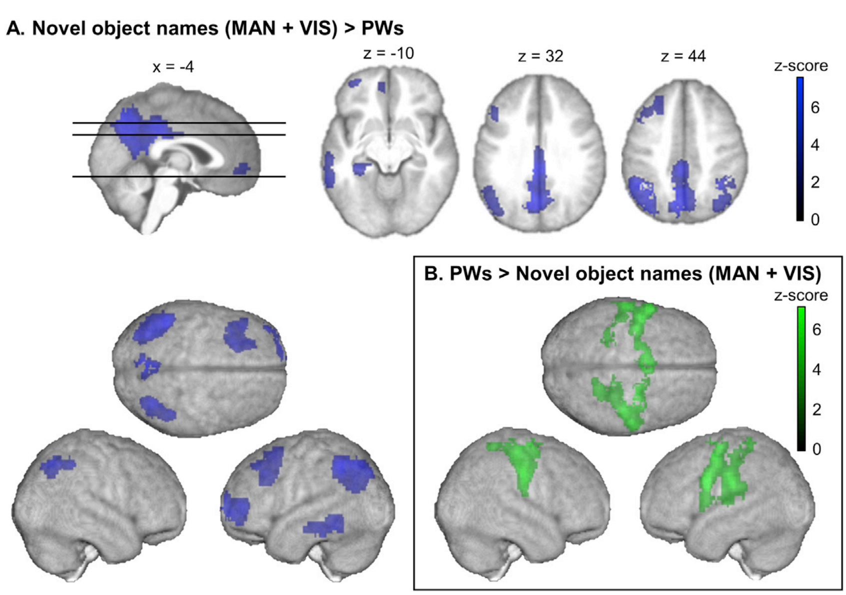

Fig. 2. *Training-induced lexicality effects*. A. Activations specific to novel object names (manipulation [MAN] and visual [VIS] training) compared to pseudowords (PWs) and B. vice versa. Clusters reaching the cluster-level $p < .05$ (FWE corrected) significance threshold, with a $p < .001$ cluster-defining threshold are displayed on the normalized T1-weighted anatomical image averaged across all participants ($n = 41$).

Table 2
Training-induced lexicality effects.

Cluster size	Brain Region	p	z-score	x	y	z
A. Object Names (MAN + VIS) > PWs						
550	L Superior Frontal Gyrus	<.001	5.12	−22	58	0
	L Superior Orbital Frontal Gyrus		5.07	−28	60	−4
	L Middle Frontal Gyrus		5.06	−38	50	8
	L Middle Orbital Frontal Gyrus		4.41	−32	54	−12
540	L Middle Frontal Gyrus	<.001	4.85	−26	18	52
	L Inferior Frontal Gyrus (pars Triangularis)		3.68	−50	30	28
124	L Medial Orbital Frontal Gyrus	.038	4.17	−6	44	−8
2142	L Precuneus	<.001	7.62	−4	−68	36
	L Middle Cingulate Cortex		6.76	−4	−36	40
	L Cuneus		5.46	−16	−58	20
	R Precuneus		4.86	16	−60	28
	R Middle Cingulate Cortex		3.55	14	−46	36
917	L Inferior Parietal Lobule	<.001	6.20	−46	−52	48
	L Angular Gyrus		5.38	−42	−64	48
388	R Inferior Parietal Lobule	<.001	5.54	36	−52	44
	R Angular Gyrus		5.26	36	−66	48
271	L Middle Temporal Gyrus	.001	4.74	−62	−46	−12
	L Inferior Temporal Gyrus		4.37	−50	−34	−24
201	L Parahippocampal Gyrus	.006	5.02	−30	−36	−12
	L Dentate Gyrus (Hippocampus)		4.91	−26	−36	−8
B. PWs > Object Names (MAN + VIS)						
2924	L Precentral Gyrus	<.001	6.95	−60	4	28
	R Postcentral Gyrus		6.28	52	−18	36
	L Postcentral Gyrus		5.87	−58	−22	28
	R Posterior-Medial Frontal Gyrus		5.63	4	0	56
	L Posterior-Medial Frontal Gyrus		5.33	−2	0	56
	R Superior Frontal Gyrus		5.32	30	−10	68
	L Inferior Parietal Lobule		4.99	−44	−28	40

Note. Activations for the lexicality analysis: A. stronger activation for the processing of novel object names (manipulation [MAN] and visual [VIS] training) than pseudowords (PWs). B. vice versa. The significance threshold was set to cluster-level $p < .05$ (FWE corrected), with a $p < .001$ cluster-defining threshold.

connectivity effects, we conducted a two-stage random-effects seed-to-voxel functional connectivity analysis, using the CONN toolbox (version 18b, Whitfield-Gabrieli and Nieto-Castanon, 2012, www.nitrc.org/projects/conn). As seed ROIs, we used the eight clusters of activation associated with the processing of novel object names vs. PWs (see Table 2A). For each participant, we imported the preprocessed structural and functional images and the specified first-level GLM (see section 2.4.2). We applied the default CONN denoising procedure and additionally specified first-order temporal derivatives as within-subject covariates. At the first level of the connectivity analysis, a correlation map for each condition (MAN, VIS) was generated. For this purpose, we applied a weighted GLM for computing bivariate Pearson's correlation coefficients of the condition-specific association between BOLD time series of the eight seed ROIs and each voxel in the brain. We applied Fisher's transformation to the resulting correlation coefficients to obtain normally distributed z-scores. We then entered the normalized connectivity maps of each participant into a second-level GLM. On the second level, we applied a 2×2 factorial design including the within-subjects factor Type of Word (MAN, VIS) and the between-subjects factor Learning Group (ACT, OBS). For each seed ROI, we tested the effect of Type of Word by applying a paired *t*-test (with a weight of +1 for MAN, −1 for VIS) and the effect of Learning Group by applying a two-sample *t*-test (with a weight of +1 for ACT, −1 for OBS), by always testing both the positive and the negative effect. We tested the Type of Word × Learning Group interaction by applying a mixed ANOVA interaction (with a weight of +1 for ACT, −1 for OBS, +1 for MAN and −1 for VIS). We report clusters satisfying a cluster-level false discovery rate (FDR)-corrected threshold of $p < .05$, with an uncorrected voxel-threshold of $p < .001$.

Table 3 provides a summary of the pattern of experience-specific functional connectivity. First, results revealed that the functional connectivity of two seeds was specifically influenced by the factor Type of Word (MAN, VIS; see Table 3A). Processing MAN words selectively increased the functional connectivity of the seed ROI in the left parahippocampal gyrus with two clusters in the left temporal pole (extending, respectively, into the left middle/inferior temporal gyrus and the left frontal orbital cortex) and with a cluster in the left frontal pole (extending into the left superior frontal gyrus). The MAN condition also selectively increased the connectivity between the seed in the left superior frontal gyrus and a cluster in the cerebellum (lobule VIIb). We found no specific increases in functional connectivity for processing VIS object names.

Second, we observed specific modulations of the functional connectivity with two other regions of the semantic network by the factor Learning Group (see Table 3B). Novel object name processing in the ACT group was specifically associated with increases in the functional connectivity of the right inferior parietal lobule seed with a cluster in the occipital pole and of the left inferior middle temporal gyrus seed with a cluster in the bilateral cerebellum (lobules VI-VIII). For the OBS group, in turn, we observed selective increases in the functional connectivity between the left medial orbital frontal gyrus seed and a cluster in the left cerebellum (lobules VIII-IX).

Finally, the results revealed a significant Type of Word x Learning Group interaction for two seed regions (see Table 3C). In the ACT (more than OBS) group, the precuneus showed specific increases in functional connectivity with a cluster in the left superior parietal lobule extending into the superior lateral occipital cortex when processing MAN words (more than VIS words). Additionally, in the ACT (more than OBS) group the functional connectivity of the left parahippocampal seed with the right putamen and insular cortex was increased by processing MAN words (more than VIS).

4. Discussion

In this study, we investigated the neural correlates of training-induced word meaning of novel object names and whether the type of sensorimotor experience gained during the object concept formation modulates object name processing. We applied a paradigm with novel objects and their names including active or observational learning in a manipulation training condition as well as a visual training condition. Participants successfully acquired the novel object names in all training conditions, which was also reflected in faster reaction times in response to novel object names than meaningless PWs and a generally very high accuracy in the LDT after the training. The fMRI data showed a general effect of training-induced lexicality for the novel object names (vs. PWs), which elicited a distinct activation pattern in a broad network of multimodal hub areas known to underlie semantic processing of real words. As hypothesized, this lexicality effect did not differ between the active and the observational learning group. Contradicting our hypotheses, the univariate analysis did not reveal any training-induced effects specifically associated with the type of sensorimotor experience gained with the objects (i.e., active or observed manipulation vs. visual) as well as the type of manipulation learning (i.e., active vs. observational). Experience-specific effects, however, appeared as selective functional connectivity increases between the semantic hub areas and cortical, cerebellar and striatal areas, as revealed by a post-hoc connectivity analysis. In the following, we first discuss the semantic network associated with the processing of novel object words, and then the identified connectivity patterns.

4.1. Training-induced lexicality effects

As for the training-induced lexicality effects, the activation in left-hemispheric fronto-temporo-parietal areas elicited by the processing of

Table 3
Post-hoc analysis of training-induced functional connectivity.

Cluster size	Seed ROIs	p	peak coordinates			Target region
			x	y	z	
A. Main Effect Type of Word						
MAN > VIS						
95	L Parahippocampal Gyrus	.017	−56	16	−16	L Temporal Pole
						L (anterior) Middle/Inferior Temporal Gyrus
75		.017	−36	36	−20	L Temporal Pole
						L Frontal Orbital Cortex
						L Frontal Pole
78		.017	−14	46	44	L Frontal Pole
						L Superior Frontal Gyrus
112	L Superior Frontal Gyrus	.008	−10	−78	−56	Cerebellum, Lobule VIIb
B. Main Effect Learning Group						
ACT > OBS						
64	R Inferior Parietal Lobule	.049	6	−100	8	Occipital Pole
101	L Inferior Middle Temporal Gyrus	.030	−4	−68	−28	Cerebellum, Lobules VI-VIII
OBS > ACT						
93	L Medial Orbital Frontal Gyrus	.013	−22	−58	−48	L Cerebellum, Lobules VIII-IX
C. Type of Word × Learning Group Interaction						
73	Precuneus	.049	−28	−56	60	L Superior Parietal Lobule
						L Superior Lateral Occipital Cortex
159	L Parahippocampal Gyrus	.001	28	−4	8	R Putamen
						R Insular Cortex

Note. Enhanced functional connectivity between seed ROIs (left) and target brain regions (right) for: A. Type of Word, B. Learning Group and C. Type of Word x Learning Group interaction. The significance threshold was set to cluster-level $p < .05$ (FDR corrected), with a $p < .001$ cluster-defining threshold.

the novel object names, in comparison to phonologically and orthographically matched PWs, largely overlaps with the network activated by real words in comparison to PWs in previous studies on lexical processing. This network has been associated with semantic processing (see e.g., Binder et al., 2009; Binder et al., 2003; Carreiras et al., 2007; Mechelli et al., 2003). Although the LDT is considered a rather implicit task, it has been shown to elicit semantic processing (Balota et al., 2004; Binder et al., 2003), with even stronger semantic effects when word-like PWs are used (Evans et al., 2012), as was the case in our study. Areas more strongly activated by PWs than novel object names included the precentral gyrus and supplementary motor area. This finding complements and further validates the lexicality effect described above, as it is consistent with findings on PW compared to real word processing in the literature (Binder et al., 2003; Carreiras et al., 2007) as well as in the present study (LDT_{LOC}, see Table S2 in Supplementary Material 2). Sensorimotor activations elicited by PWs have been interpreted as either reflecting phonological processing (Mechelli et al., 2005) or compensatory mechanisms if semantic processing cannot take place (Carreiras et al., 2007). Taken together, this word-like activation pattern suggests that the training successfully induced novel word meanings.

An alternative interpretation might be that differences in novel object name vs. PW processing reflect mere familiarity effects induced by repeated exposure throughout the trainings. This seems unlikely, however, as the brain network associated with processing novel object names (vs. PWs) largely overlaps with a semantic network identified in a meta-analysis on semantic processing (Binder et al., 2009; Binder, 2016). The inferior parietal cortex (including the angular gyrus), the precuneus, the middle and inferior temporal gyrus, the ventromedial temporal cortex (including the parahippocampal gyrus), the superior and middle frontal gyrus, the left inferior frontal and orbital frontal gyrus, which were involved in our lexicality effect, have been identified as semantic hubs (Xu et al., 2016). These regions have been shown to be connected with multiple modality-specific brain areas, and are considered to play a key role in integrating information from different modalities into multimodal high-level conceptual representations (Binder, 2016). The left inferior frontal and parietal regions as well as the left middle temporal gyrus involved in our lexicality effect have been shown to also be involved in processing tool-related information (for a review see Ishibashi et al., 2016) and showed training-induced activation specific for tool-related experience (Bellebaum et al., 2013; Malone et al., 2016; Weisberg et al., 2007).

Within the semantic hub network, nevertheless, differential functional roles of the nodes have been recognized. For example, the medial temporal lobe, including the dentate and parahippocampal gyri, has been interpreted as representing an interface between semantic and episodic memory (Binder et al., 2009). The parahippocampal gyrus might underlie strategical episodic retrieval, such as the recall of information about the training scene (Bird et al., 2010; Moscovitch et al., 2006; Yonelinas, 2013). Similarly, the precuneus has been linked to episodic retrieval and visuo-spatial imagery (Cavanna and Trimble, 2006). In previous studies, the left precuneus was more strongly activated when perceiving familiar than unfamiliar tools, reflecting automatically elicited processes of manipulation imagination (Vingerhoets, 2008). It has also been involved in willfully imagining the use of unfamiliar tools (Grezes and Decety, 2002). Notably, it has been shown that especially newly acquired semantic information strongly relies on strategic episodic memory retrieval (Smith and Squire, 2009). This result is particularly relevant for our findings on novel object representations, where we observed activations of the dentate and parahippocampal gyri and the precuneus. Activations of these brain regions have not been consistently observed in previous studies on real words with consolidated meaning (Mechelli et al., 2003). Compatibly, in our study they were absent in the LDT_{LOC} (see Table S2 in Supplementary Material 2). Medial temporal structures and the precuneus thus appear to serve the more effortful processing of novel object names by supporting the retrieval of episodic and/or spatial information (Hebscher et al., 2018).

4.2. Training-induced experience-specific effects

The second aim of this study was to examine experience-specific effects by directly comparing novel object names from the MAN and VIS training conditions and a potential influence of the type of manipulation learning (active vs. observational). However, we did not find the hypothesized stronger activation of MAN compared to VIS object names within the tool-related fronto-parietal network, neither in analyses on the whole brain level nor in regions specifically involved in the representation of manipulable objects identified in the functional localizer task. We also did not find any effect of the type of learning (active vs.

observational). Previous studies largely agree that active and observational tool-use draw on the same brain areas (for a meta-analysis see Lewis, 2006), a finding that is also consistent with our previous studies employing the novel object training paradigm (compare Bellebaum et al., 2013; Ruther et al., 2014b). However, the few studies directly comparing active and observed tool-use experience suggest a stronger involvement of the action-related brain areas during (Macuga and Frey, 2012) and after (Cannon et al., 2014) active experience, which contradicts our findings.

Previous research revealed that the involvement of experience-specific areas in conceptual processing is task- and context-dependent (Kiefer and Pulvermuller, 2012; Lebois et al., 2015). A more explicit task and/or context might thus have revealed experience-specific effects in our univariate analysis (see, e.g., Andres et al., 2013; Canessa et al., 2008). It seems very unlikely, however, that the chosen task was not appropriate to uncover experience-specific effects given the experience-specific effects for manipulation information in the LDT_{LOC}. Using object names instead of pictures might explain the discrepancy to previous fMRI studies, which revealed experience-specific effects after a comparable amount of training (Bellebaum et al., 2013; Ruther et al., 2014b). Indeed, a study with proficient children and adult readers suggests that it may take years of experience until reading written object names elicits modality-specific sensorimotor activations to a comparable degree as seeing object pictures (Dekker et al., 2014). Furthermore, the inclusion criterion for novel object names into the analyses based on the MC performance might not have guaranteed that only successfully established associations between the novel names and the respective objects entered the analyses. The performance in the multiple-choice test might be a more liberal criterion than, e.g. naming accuracy, which we did not assess.

It is, however, also conceivable that the differences in processing depending on the type of experience were more subtle in nature. As discussed above, processing the newly acquired object names in our study elicited a pattern, which was remarkably consistent with the semantic network identified for real word processing (Binder et al., 2009). As the nodes of this network are known to show a strong connectivity to modality-specific regions (Binder, 2016; Lambon-Ralph et al., 2017), we formulated the additional post-hoc hypothesis that experience-specific effects might be reflected by a differential functional connectivity between these high-level multimodal hub areas and neuronal assemblies in experience-specific areas. In a study on the processing of short stories, Chow et al. (2014) could show a functional connectivity of a content-independent language network with content-specific brain areas involved in action, perception and emotion processing. In the absence of areas showing modality-specific effects in our study, we relied on a seed-to-voxel analysis, exploring functional connectivity between areas involved in our lexicality pattern and potentially modality-specific brain areas post-hoc.

4.3. Post-hoc analysis of training-induced functional connectivity

The functional connectivity analysis revealed a complex pattern of experience-specific functional connectivity of nearly all regions involved in the lexicality pattern with neocortical, cerebellar, and striatal areas. Different effects emerged for the two experimental factors (Type of Word, Learning Group) as main effects, as well as for their interaction. As for the main effect of Type of Word, processing object names from the manipulation training selectively increased the functional connectivity of the left mediotemporal parahippocampal/dentate gyri seed ROI with two clusters in the left temporal pole, which is considered a transmodal semantic hub (Patterson et al., 2007). The first cluster extended into the left middle/inferior temporal gyrus, an area known to be involved in processing visual information (Visser et al., 2012) and concrete concepts (Hoffman et al., 2015). The second cluster extended into the frontal orbital cortex. In an fMRI study on motor imagery, Mizuguchi et al. (2018) showed that orbitofrontal activity was associated with the vividness of mental imagery. This pattern of functional connectivity between the parahippocampal gyrus, as an interface between episodic and semantic memory (see above), and the anterior temporal lobe extending into further modality-specific areas might reflect enriched, multimodal episodic information integrated into the conceptual representations of novel object names after manipulation compared to visual training. The functional connectivity of the parahippocampal seed ROI with the left frontal pole extending to the superior frontal gyrus was also selectively enhanced for MAN vs. VIS. The functional coupling of these regions has been previously described in the literature and interpreted as reflecting cognitively controlled episodic retrieval along the ventral path (Barredo et al., 2015). MAN object names further specifically increased the functional connectivity of the dorsal superior frontal gyrus seed ROI, which is involved in semantic retrieval (Binder et al., 2009), and the cerebellar lobule VIIb. O'Reilly et al. (2008) could show that lobule VII is involved in temporo-spatial judgments on observed movements (i.e., velocity vs. mere direction judgments, O'Reilly et al., 2008). The functional connectivity of the superior frontal seed ROI and the cerebellum might thus reflect the retrieval of sequences from the active and observed manipulation during the trainings.

As for the main effect of Learning Group (active vs. observational) the active learning group showed a stronger functional connectivity than the observational learning group between the left middle temporal seed ROI and the cerebellar lobules VI-VIII. This finding is in line with previous research showing a stronger activation of the cerebellar lobules V-VIII in actively performing than observing grasp movements (Casiraghi et al., 2019). Further, in a meta-analysis, Stoodley and Schmahmann (2018) showed that cerebellar lobules V-VII are strongly involved in motor tasks (see also Ghio et al., 2018). In the active learning group, we also found increased functional connectivity between the right inferior parietal lobule/angular gyrus seed ROI and the occipital pole. These areas are part of the dorsal visual stream involved in guiding goal-directed actions (Frey, 2007; Goodale and Milner, 1992). Brandi et al. (2014) could show that its ventro-dorsal part (i.e., the middle occipital gyrus and inferior parietal lobule) plays a role in processing familiar object manipulations. Further, the two seed ROIs involved in this functional connection spwcific for active learning are both part of the left-hemispheric network involved in processing tool-related information (for a review see Ishibashi et al., 2016). The pattern of stronger functional connectivity for ACT than OBS might thus reflect the retrieval of actual tool-use experience. The observational learning group instead showed a stronger functional connectivity between the medial orbital frontal gyrus seed ROI and the left cerebellar lobules VIII-IX. As described above, the orbitofrontal cortex is involved in motor imagery (Mizuguchi et al., 2018). The posterior cerebellum is part of the action-observation-network (Casiraghi et al., 2019; Sokolov et al., 2010) and the left cerebellar hemisphere is especially involved in visuo-spatial processing (Stoodley and Schmahmann, 2018). This functional connectivity might thus reflect the retrieval of the observed manipulation information. The fact that these learning group-specific effects occurred independently of the training condition probably reflects a generalization of manipulation information. If participants spontaneously engaged in manipulation imagery during the visual exploration, this might have led to functional manipulation information available also for VIS objects, albeit probably leading to less vivid mental imagery (see above). In line with this idea, Vingerhoets (2008) found that seeing pictures of tools with unknown function leads to activation in the left hemispheric tool-network.

Lastly, the Type of Word and Learning Group also interacted in their effects on the functional connectivity originating in two regions involved in our lexicality effect. There was a specific increase in functional connectivity for MAN vs. VIS object names in the active, but not the observer group in the precuneus seed ROI, which was more strongly connected with a cluster in the left superior parietal lobule extending into the superior lateral occipital cortex. The left superior parietal lobule is involved in spatial attention (Molenberghs et al., 2007) and is, together with the superior lateral occipital cortex, part of the dorso-dorsal pathway involved in the online control and selection of complex, goal-directed actions (Brandi et al., 2014). Notably, this target region marginally overlaps with the parieto-occipital ROI for real manipulable object processing identified with the functional localizer task. A further interaction effect was found for the left parahippocampal seed ROI, which showed a stronger cross-hemispherical connectivity with the right putamen and insular cortex (again selectively for MAN in the ACT group). Previous research showed that the putamen and insula are involved in the episodic retrieval of temporal sequences (Hsieh and Ranganath, 2015) and egocentric spatial representations (Kenzie et al., 2015; Mijovic-Prelec et al., 2004). The right hemispheric involvement of the putamen and the insula may be consistent with the right hemispheric dominance for processing spatial information, as shown by (virtual) lesion studies (Fierro et al., 2000; Schintu et al., 2014). Overall, these interaction effects might reflect episodic retrieval of manipulation and (egocentric) visuospatial information supporting the conceptual processing of actively manipulated objects.

Taken together, the results revealed a complex pattern of functional connectivity between, on the one side, multimodal semantic hub areas involved in the lexicalization and, on the other side, distributed cortical, cerebellar and striatal areas known to contribute to the processing of object-specific manipulation, functional and visuospatial information. The results cannot be interpreted in terms of top-down vs. bottom-up influences, as the seed-to-voxel functional analysis does not allow such directional inferences. A further caveat is that these results emerge from a post-hoc analysis that was introduced to cope with the unexpected lack of significant experience-specific activation in the more conventional functional specialization analysis. They nevertheless might be interpreted in favor of a certain degree of experience-specific grounding of the lexicalization of novel object names.

5. Conclusion

The present study in healthy adult human subjects provides evidence that a short training promoting novel object name learning induces functional brain changes that reflect both lexical and semantic processes associated with the encoding of novel concepts in linguistic form. In particular, the processing of the novel names engages brain areas identified to serve as semantic hubs, mirroring real word lexicality effects, as well as brain areas underlying strategic episodic memory processes. To a limited extent, the short training seems to also induce experience-specific brain activity modulations involving sensorimotor areas, as previously observed for processing real words referring to objects for which we already have a consolidated experience. These experience-specific modulations do not appear to emerge as regional activation effects, but rather as functional connectivity increases between semantic hub regions and distributed neocortical, cerebellar and striatal areas coding for object manipulation and related visuospatial information. The emergence of conceptual processing for novel words thus appears to be grounded in functional brain networks specifically coding for the experience with the referred objects.

Declarations of interest

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Appendix A. Supplementary data

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