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# The sensory-motor specificity of taxonomic and thematic conceptual relations: A behavioral and fMRI study

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## ABSTRACT

Previous behavioral data suggest that the salience of taxonomic (e.g., hammer-saw) and thematic (e.g., hammer-nail) conceptual relations depends on object categories. Furthermore, taxonomic and thematic relations would be differentially grounded in the sensory-motor system. Using a picture matching task, we asked adult participants to identify taxonomic and thematic relations for non-manipulable and manipulable natural and artifact targets (e.g., animals, fruit, tools and vehicles, respectively) inside and outside a 3 T MR scanner. Behavioral data indicated that taxonomic relations are identified faster in natural objects while thematic relations are processed faster in artifacts, particularly manipulable (e.g., tools). Neuroimaging findings revealed that taxonomic processing specifically activate the bilateral visual areas (cuneus, BA 18), particularly for non-manipulable natural objects (e.g., animals). On the contrary, thematic processing specifically recruited a bilateral temporo-parietal network including the inferior parietal lobules (IPL, BA 40) and middle temporal gyri (MTG, BA 39/21/22). Left IPL and MTG activation was stronger for manipulable than for non-manipulable artifacts (e.g., tools vs. vehicles) during thematic processing. Right IPL and MTG activation was greater for both artifacts compared to natural objects during thematic processing (manipulable and non-manipulable ones, e.g., tools and vehicles). While taxonomic relations would selectively rely on perceptual similarity processing, thematic relations would specifically activate visuo-motor regions involved in action and space processing. In line with embodied views of concepts, our findings show that taxonomic and thematic conceptual relations are based on different sensory-motor processes. It suggests that they may have different roles in concept formation and processing depending on object categories.

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## Introduction

Growing behavioral and neuroimaging evidence suggest that concepts are grounded in sensory-motor subsystems (Barsalou, 2008; Borghi, 2005; Gallese and Lakoff, 2005). According to embodied views of concepts, our knowledge about objects would not be amodal but would remain highly linked to our previous sensorial and motor experience with these objects (Barsalou et al., 2003). The role of concepts would be therefore to support our on-line interactions with objects through the re-activation of the neural pattern activated during previous interactions with these objects. For example, the concept "knife" would re-activate perceptual and motor experience with knives and help to deal with the current knife, namely to recognize it quickly, to grasp it, to move it, and to use it an appropriate way.

Most arguments in this direction come from studies contrasting knowledge for different object categories (e.g., animals, tools) since

the weighting of perceptual/visual and functional/motor features differs across object categories. Feature norms in adults (Cree and McRae, 2003; McRae et al., 2005) demonstrate that natural kinds such as animals, are mainly defined by perceptual/visual attributes, while artifacts such as tools are mostly characterized by functional/motor features. The idea that object knowledge is organized around sensory and functional features, i.e. the sensory/functional hypothesis (Humphreys and Forde, 2001; Warrington and Shallice, 1984) has been initially proposed to account for semantic category-specific deficits in brain-damaged patients (Capitani et al., 2003). In this view, semantic deficits for animals would result from damage in brain regions involved in perceptual/visual knowledge while semantic deficits for artifacts would be linked to lesions in areas involved in functional/motor knowledge. Therefore, knowledge about objects would depend on the brain areas involved in the processing of their main features, visual/perceptual or functional/motor features. In the last decade, neuroimaging studies in normal adults have provided new empirical data supporting the sensory-motor feature-based hypothesis. They reveal that conceptual processing of objects recruits similar brain

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areas as those involved in perception and action, and thus depends on object categories (Martin, 2007). Retrieving both knowledge about tools and actions activates areas of the visuomotor action system, i.e. premotor, parietal and posterior temporal cortices, predominantly in the left hemisphere (Assmus et al., 2007; Beauchamp and Martin, 2007; Johnson-Frey, 2004; Kable et al., 2005; Kellenbach et al., 2003; Noppeney, 2008; Weisberg et al., 2007). On the contrary, knowledge about living things such as animals appears closely linked to perceptual knowledge (e.g., form, color). Both perceptual knowledge and natural object concepts rely on brain areas involved in visual processing, i.e. ventro-temporal and occipital cortices (Goldberg et al., 2006a,b; Kan, Barsalou et al., 2003; Marques, 2006; Sim and Kiefer, 2005; Simmons et al., 2007). Taken as a whole, neuroimaging findings indicate that concepts of artifact/manipulable objects (e.g., tools) and of natural/non-manipulable objects (e.g., animals) specifically activate brain regions involved in action and visual processing, respectively.

Considering that object knowledge is organized around sensory/functional features may result in distinctions between object categories. We further assume that grounding concepts in sensory-motor experience may also lead to distinctions between conceptual relations. The distinction between taxonomic and thematic conceptual relations is of major interest since (a) they are both highly relevant for adult conceptual organization (Lin and Murphy, 2001; Murphy, 2001; Sachs et al., 2008a), (b) they have both been considered at the origin of concepts (Nelson, 1983, 1985; Quinn and Eimas, 1996, 2000) and (c) they refer to different types of knowledge. On the one hand, taxonomic conceptual relations define relations between objects of the same kind (e.g., dog–bear, saw–hammer). Objects of the same taxonomic category usually share a common name and similarity-based relations. They have similar perceptual properties (e.g., have eyes, have a handle) and similar non-perceptual properties (e.g., breathe, repair things). On the other hand, thematic conceptual relations rely on contextual/functional relations between objects that are not of the same kind (e.g., dog–doghouse, saw–wood) but that could be met in the same event schema (Nelson, 1983). Therefore, thematic relations involve temporo-spatial relations between objects and action experience.

In line with the sensory/functional hypothesis and more generally with embodied view of concepts, we suggest that taxonomic conceptual relations may rely more on perceptual processing while thematic conceptual relations may rely more on action processing, even though both taxonomic and thematic relations assess some aspects of conceptual knowledge. Indirect evidence of the specificity of taxonomic and thematic conceptual processing has already been found in behavioral studies in children and adults. Taxonomic and thematic relations appear more or less relevant in concept formation and processing depending on object categories. We recently observed a distinction between natural and artifact object concepts (Bonthoux and Kalénine, 2007), consistently with category-specific semantic deficits (Capitani et al., 2003) and features norms in normal adults (Cree and McRae, 2003; McRae et al., 2005). More specifically, similarity-based relations (i.e. taxonomic relations) are more helpful to categorize natural objects, while contextual/functional relations (i.e. thematic relations) are more useful to categorize artifact objects. For example, the ability of young children to categorize natural and artifact objects at the superordinate level, (tools, clothes, fruits, animals, etc.) depends on their greater sensitivity towards similarity-based relations (e.g., tennis shoe–shoe) or contextual/functional relations (e.g., tennis shoe–foot ball) (Kalénine and Bonthoux, 2006). Furthermore, recent data indicate that taxonomic and thematic conceptual processing depends on object domain (natural vs. artifact objects) but also on object manipulability (Kalénine and Bonthoux, 2008). In this study, we demonstrated that both children and adults were faster to identify taxonomic conceptual relations for non-manipulable objects (e.g., armchair–sofa, poodle dog–shepherd) but

they were faster to identify thematic relations for manipulable objects (e.g. spoon–yoghurt, tulip–vase). Overall, these findings suggest that taxonomic conceptual relations seem to be more relevant for object categories mainly defined by perceptual/visual attributes, i.e. natural objects, and particularly non-manipulable ones such as animals. On the contrary, thematic conceptual relations would be more relevant for object categories mainly characterized by contextual/functional attributes, i.e. artifacts, and particularly manipulable ones such as tools.

The aim of the present study was to specify the cognitive and neural mechanisms underlying taxonomic and thematic conceptual processing in adults for different object categories. While the distinction between taxonomic and thematic knowledge is well described in the literature in terms of concepts, it has rarely been investigated in terms of neuroanatomical substrate. The cerebral correlates of taxonomic and thematic conceptual relations have been explored for the first time by Sachs and colleagues in two fMRI studies (Sachs et al., 2008a,b). Thematically related words (e.g., car–garage) and taxonomically-related words (e.g., car–bus) for target words denoting artifact concepts (e.g., car) were used in a matching task and a priming task. In the matching task (Sachs et al., 2008a), participants were presented a target word (e.g., car) and had to decide which one of two words of choice (e.g., bus/eraser in the taxonomic matching condition; garage/brush in the thematic matching condition) matched best with the target word. In the priming task (Sachs et al., 2008b), participants had to perform a lexical decision task on a target word that was taxonomically related to the prime (e.g., car–bus), thematically related to the prime (e.g., car–garage), non-related to the prime (e.g. car–spoon) or a non-word (e.g., car–derf). In both studies, Sachs and colleagues showed that taxonomic and thematic conceptual processing recruits similar neural networks, suggesting that both relations are important for adult conceptual organization. However, when they directly contrasted taxonomic and thematic conditions, they failed to observe substantial differences between taxonomic and thematic processing in terms of activated regions. In the present study, using a picture-matching task with target pictures belonging to different categories, we assume that taxonomic and thematic conceptual processing may specifically recruit different sensory-motor components reflected by different sensory-motor network regions. If taxonomic conceptual relations rely on similarity-based relations, then we expect that the identification of taxonomic relations a) would be faster for natural objects than artifacts, particularly for non-manipulable ones such as animals and b) would selectively activate brain areas involved in perceptual processing. Enhanced activation in visual areas for taxonomic conceptual relations might be stronger for natural objects, particularly non-manipulable ones. Similarly, if thematic conceptual relations rely on contextual/functional relations, then the identification of thematic relations a) would be faster for artifacts than for natural objects, particularly for manipulable ones such as tools and b) would selectively recruit brain areas involved in action processing. Enhanced activation for thematic conceptual relations in areas of the visuo-motor system linked to action processing might be stronger for artifacts, particularly for manipulable ones. The specificity of taxonomic and thematic conceptual processing for objects from different categories was assessed in the present behavioral and fMRI experiments.

## Behavioral experiment

### Materials and methods

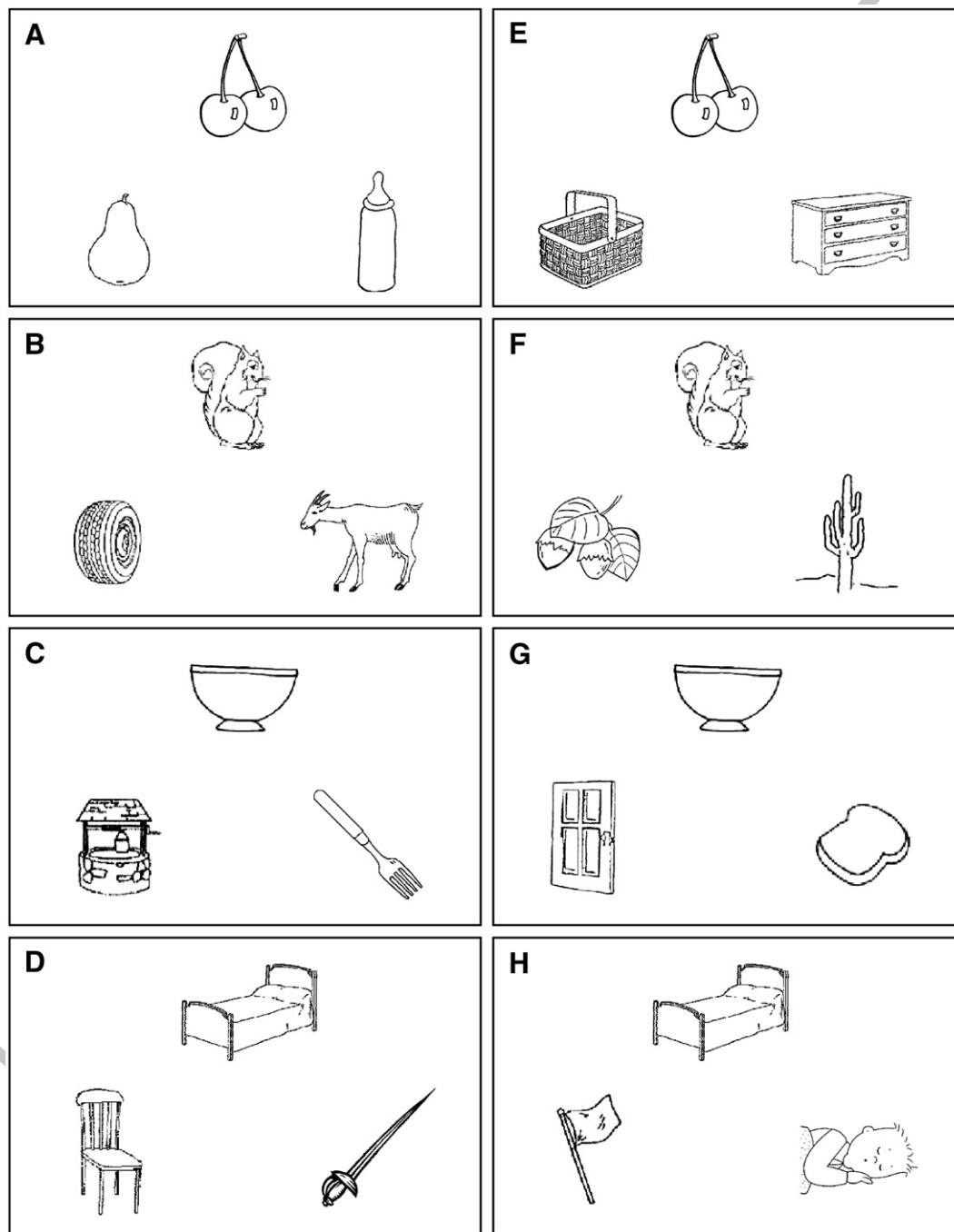
#### Participants

Forty-eight adults (age range 17–47, mean age 22±SD 6.5; 39 females, 6 males) participated in the behavioral experiment. They were undergraduate psychology students from the University Pierre Mendès France and they received course credit for their participation.

## 199 Stimuli

200 Stimuli were 240 black-and-white drawings selected from  
 201 different French picture data bases (e.g., [http://webu2.upmf-](http://webu2.upmf-grenoble.fr/Banque_images/index.php)  
 202 [grenoble.fr/Banque\\_images/index.php](http://webu2.upmf-grenoble.fr/Banque_images/index.php); [http://leadserv.u-](http://leadserv.u-bourgogne.fr/bases/pictures/)  
 203 [bourgogne.fr/bases/pictures/](http://leadserv.u-bourgogne.fr/bases/pictures/)). Forty-eight were target pictures, 96 were  
 204 semantically related to target pictures, either thematically or  
 205 taxonomically, and 96 were neither semantically nor perceptually  
 206 related to target pictures. Among target pictures, 24 represented  
 207 natural (Nat) object concepts and 24 represented artifact (Art)  
 208 object concepts. Twelve target pictures represented manipulable  
 209 natural object concepts (Nat/Manip target pictures; i.e. plants, fruit/  
 210 vegetables and body parts), 12 represented non-manipulable  
 211 natural object concepts (Nat/Nonmanip target pictures; i.e. ani-

212 mals), 12 represented manipulable artifact object concepts (Art/  
 213 Manip target pictures; i.e. tools, kitchen utensils and clothes) and  
 214 12 non-manipulable artifact object concepts (Art/Nonmanip target  
 215 pictures; i.e. vehicles, furniture and habitat). For each target picture,  
 216 a taxonomic and a thematic associate were selected. Ninety-six  
 217 triads including a target picture, a related picture and a non-related  
 218 picture were designed. In 48 triads, the related picture was  
 219 taxonomically (Taxo) linked to the target. In the other 48 triads,  
 220 the related picture was thematically (Them) related to the target.  
 221 This resulted in 8 experimental conditions: Taxo/Nat/Manip, Taxo/  
 222 Nat/Nonmanip, Taxo/Art/Manip, Taxo/Art/Nonmanip, Them/Nat/  
 223 Manip, Them/Nat/Nonmanip, Them/Art/Manip and Them/Art/Non-  
 224 manip (see Fig. 1 for examples of stimuli).



**Fig. 1.** Example of stimuli used in each experimental condition. Figures from A to D correspond to the 4 taxonomic conditions. Figures from E to H correspond to the 4 thematic conditions. (A) Taxo/Nat/Manip: cherry-pear; (B) Taxo/Nat/Nonmanip: squirrel-goat; (C) Taxo/Art/Manip: bowl-fork; (D) Taxo/Art/Nonmanip: bed-chair; (E) Them/Nat/Manip: cherry-basket; (F) Them/Nat/Nonmanip: squirrel-hazelnuts; (G) Them/Art/Manip: bowl-slice of bread; (H) Them/Art/Nonmanip: bed-person asleep.

The Domain and Manipulability factors always referred to the semantic domain and manipulability of the target pictures. Note however that when considering the whole item (i.e. the target picture, the related picture and the non-related picture), most triads were mixed in terms of domain and manipulability. The domain (natural vs. artifact objects) and manipulability (manipulable vs. non-manipulable objects) of the pictures of choice (related and non-related) were also controlled. Regarding taxonomic triads, taxonomically-related pictures were by definition similar in terms of domain and manipulability (e.g., dog–bear). The domain and manipulability of non-related pictures were counterbalanced in each Domain × Manipulability condition. Thus, 50% of the taxonomic triads involved 3 similar pictures in terms of domain or manipulability. Regarding thematic triads, the domain of the related and non-related pictures was counterbalanced in each Domain condition. Thus, 25% of the thematic triads involved 3 pictures from the same domain. The limited number of potential thematic associates did not allow us to strictly counterbalance the manipulability of the pictures of choice in the thematic condition. Nevertheless, the proportion of thematically-related pictures which referred to manipulable objects was equivalent between the Manipulable and Non-manipulable conditions (about 66%). Overall, 15% of the thematic triads were composed of 3 object pictures from the same manipulability.

Two lists of 48 triads were elaborated. Each target picture appeared twice, with a taxonomic associate in one list and with a thematic associate in the other. Eight additional triads with different pictures involving different semantic categories were designed for practice trials.

Since several studies have demonstrated that thematic relations are generally more strongly associated than superordinate taxonomic relations in adults and children (Osborne and Heath, 2003; Pennequin et al., 2006; Scheuner et al., 2004), we controlled the associative strength (AS) of taxonomic and thematic triads. In a pilot work, 10 adults that did not participate in the present behavioral experiment rated on a 10-point scale (from 0 “not associated at all” to 10 “very strongly associated”) the AS between target and related pictures on the one hand, and between target and non-related pictures on the other hand, independently of the type of semantic relation, taxonomic or thematic. For each triad, a measure of AS was obtained by subtracting the AS between the target and the unrelated picture to the AS between the target and the related picture. This final score of AS was entered into a 2 × 2 ANOVA with Semantic relation (taxonomic vs. thematic), Domain (natural vs. artifact objects) and Manipulability (manipulable vs. non-manipulable objects) as between-items factors. The analysis confirmed that the mean score of AS did not differ between thematic ( $M=6.0$ ) and taxonomic triads ( $M=5.65$ ), [ $F(1,88)=1.5$ ,  $p=.22$ ]. The only significant effect was a 3-way interaction between Semantic relation, Domain and Manipulability [ $F(1,88)=6.07$ ,  $p<.05$ ] resulting from the fact that taxonomic triads for manipulable natural objects were more associated than taxonomic triads for non-manipulable natural objects [ $F(1,88)=6.47$ ,  $p<.05$ ].

#### Procedure

Triads were displayed on a computer monitor using E-prime software (E-prime Psychology Software Tools Inc., Pittsburgh, USA). Each trial began with a fixation point for 500 ms immediately followed by a picture triad. Target pictures appeared in the top center of the screen. Related and non-related pictures were presented either in the bottom left or bottom right of the screen, their relative position being counterbalanced across trials. Participants were asked to decide which one of the two bottom pictures was semantically related to the target picture. They were instructed to press either key 1 or 2 with their right index and middle finger, 1 for the bottom left picture and 2 for the bottom right picture. They were told to respond as quickly and accurately as possible. The triad

was displayed until participant's response. Each participant performed 8 practice trials and then underwent the two lists of 48 trials each. The order of lists presentation was counterbalanced between subjects. Reaction times and accuracy were recorded for the 96 experimental trials.

#### Behavioral results

Participants were correct on most trials ( $M=95.6\%$ ,  $SD=2.6\%$ ). A 2 × 2 × 2 analysis of variance (ANOVA) with Semantic relation (taxonomic vs. thematic), Domain (natural things vs. artifacts) and Manipulability (manipulable vs. non-manipulable) as within-subjects factors was conducted on mean correct reaction times (mRT) after logarithmic transformation of mRT to ensure variances homogeneity. The ANOVA on mRT indicated a main effect of the kind of Semantic relation [ $F(1,44)=12.79$ ,  $p<.001$ ] with faster reaction times for taxonomic relations ( $M=1478$  ms) than for thematic relations ( $M=1512$  ms). More important, we observed the expected interaction between Semantic relation and Domain [ $F(1,44)=79.85$ ,  $p<.001$ ]. Planned comparisons revealed that participants were faster to identify taxonomic relations for natural concepts than for artifacts [ $F(1,44)=46.60$ ,  $p<.001$ ]. On the contrary, they were faster to recognize thematic relations for artifacts than for natural concepts [ $F(1,44)=16.22$ ,  $p<.01$ ]. As predicted, thematic relations were identified more quickly for manipulable artifacts than for non-manipulable ones [ $F(1,44)=8.68$ ,  $p<.01$ ], although the 3-way interaction between Semantic relation, Domain and Manipulability was not significant [ $F<1$ ]. For taxonomic relations, the advantage of non-manipulable natural objects over manipulable ones did not reach significance [ $F(1,44)=1.63$ ,  $p=.20$ ]. Results are reported on Fig. 2.

A similar 2 × 2 × 2 ANOVA was also conducted on mean accuracy rates (mACC) to ensure that there was no speed-accuracy trade-off in the data. The ANOVA on mACC revealed a main effect of the kind of Semantic relation consistent with mRT [ $F(1,44)=6.23$ ,  $p<.005$ ], with more correct responses for taxonomic relations ( $M=98.5\%$ ) than for thematic relations ( $M=96\%$ ). The interaction between Semantic relation and Domain was also significant on mACC [ $F(1,44)=13.82$ ,  $p<.001$ ]. Planned comparisons revealed an advantage for identifying thematic relations for artifacts in comparison to natural kinds [ $F(1,44)=22.07$ ,  $p<.0001$ ]. However, participants did not identify better taxonomic relations for natural object than for artifacts [ $F<1$ ]. The 3-way interaction between Semantic relation, Domain and Manipulability reached significance in the analysis on mACC [ $F(1,44)=2.32$ ,  $p<.05$ ]. However, taxonomic relations were not more accurately identified for non-manipulable natural objects than for manipulable ones [ $F<1$ ], and thematic relations were not more accurately

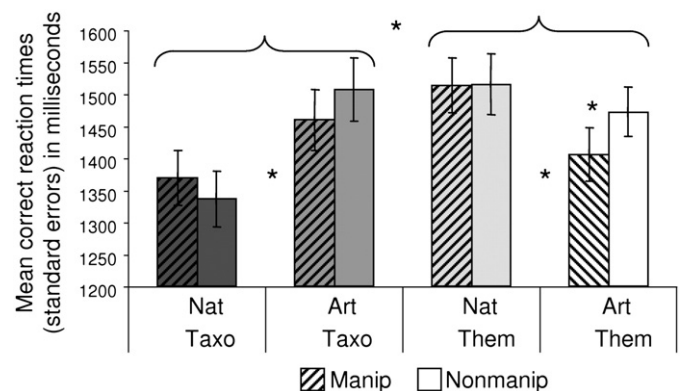


Fig. 2. Mean correct reaction times and standard errors (milliseconds) in the behavioral study for identifying conceptual relations as a function of Semantic relation (taxonomic vs. thematic), Domain (natural vs. artifact objects) and Manipulability (manipulable vs. non-manipulable objects). \*Highlights significant differences at  $p<0.05$ .

334 identified for manipulable artifacts than for non-manipulable ones  
335 [ $F(1,44)=1.54, p=.22$ ].

## 336 fMRI experiment

### 337 Materials and methods

#### 338 Participants

339 Sixteen healthy adults were examined (age range 21–52, mean age  
340  $28.5 \pm 7.5$ ; 9 females, 7 males). All participants were right-handed  
341 according to the Edinburgh Handedness Inventory (Oldfield, 1971),  
342 had normal or corrected-to-normal vision and no history of  
343 neurological or psychiatric disorders. They gave their informed  
344 written consent for the experiment and the study was approved by  
345 the local ethic committee.

#### 346 Stimuli and task

347 The picture stimuli were those used in the behavioral experiment  
348 and consisted of two lists of 48 triads. The task and instructions was  
349 identical, excepted for the duration of each triad display that was fixed  
350 to 2000 ms in the scanner. Stimuli were transmitted into the magnet  
351 by means of a video projector (Epson EMP 8200), a projection screen  
352 situated behind the magnet and a mirror centered above the  
353 participant's eyes. As in the behavioral experiment, participants  
354 responded with their index and middle finger of their right hand.  
355 Reaction times and accuracy were recorded.

#### 356 Event-related fMRI experimental design

357 Pseudo-randomized ER-fMRI paradigms were used optimizing the  
358 onset of each type of stimuli (Friston et al., 1999). Each participant  
359 performed the two lists of 48 triads twice, leading to 4 ER-fMRI  
360 consecutive sessions. The order of fMRI sessions was counterbalanced  
361 across participants. Each session included 8 experimental conditions  
362 (containing 6 events each) by crossing the Semantic relation  
363 (taxonomic vs. thematic), Domain (natural vs. artifact objects) and  
364 Manipulability (manipulable vs. non manipulable objects) variables.  
365 This resulted in 24 events for each experimental condition. In  
366 addition, 17 null-events (5 of them at the end of the session) were  
367 included in each session in order to provide an appropriate baseline  
368 measure (Friston et al., 1999). Null-events were composed of a white  
369 screen and a black fixation dot displayed at the center of the screen.

370 For each functional session, six initial dummy scan were performed  
371 in order to stabilize the magnetic field. After dummies, 78 functional  
372 volumes were acquired during each session. The averaged inter-  
373 stimulus interval was 3 s. The total duration of each functional session  
374 was 3'15". Before the experiment, participants underwent the 8  
375 practice trials outside the scanner.

#### 376 MR acquisition

377 A whole-body 3 T MR scanner was used (Bruker MedSpec S300)  
378 with 40 mT/m gradient strength. For functional scans, the manufac-  
379 turer-provided gradient-echo/T2\* weighted EPI method was used.  
380 Thirty-nine adjacent axial slices parallel to the bi-commissural plane  
381 were acquired in interleaved mode. Slice thickness was 3.5 mm. The  
382 in-plane voxel size was  $3 \times 3$  mm ( $216 \times 216$  mm field of view acquired  
383 with a  $72 \times 72$  pixels data matrix; reconstructed with zero filling to  
384  $128 \times 128$  pixels). The main sequence parameters were: TR=2.5 s,  
385 TE=30 ms, flip angle =  $77^\circ$ . To correct images for geometric distortions  
386 induced by local  $B_0$ -inhomogeneity, a  $B_0$  fieldmap was obtained from  
387 two gradient echo data sets acquired with a standard 3D FLASH  
388 sequence ( $\Delta TE=9.1$  ms). The fieldmap was subsequently used during  
389 data processing. Finally, a T1-weighted high-resolution three-  
390 dimensional anatomical volume was acquired, by using a 3D Modified  
391 Driven Equilibrium Fourier Transform (MDEFT) sequence (field of  
392 view =  $256 \times 224 \times 176$  mm; resolution:  $1.333 \times 1.750 \times 1.375$  mm; ac-  
393 quisition matrix:  $192 \times 128 \times 128$  pixels; reconstruction matrix:  $256 \times$

128  $\times$  128 pixels). During fMRI scanning, eye position was monitored  
394 on-line by an infrared eye-tracker (ASL Model 504, Applied Science  
395 Group) on 15 participants (data from one participant were lost due to  
396 technical reasons). Repeated-measure ANOVAs on mean eye position  
397 data recorded along the vertical and horizontal axes during stimulus  
398 presentation ( $\sim 2000$  ms) did not show significant differences in eye  
399 movements during the processing of triads displaying either taxo-  
400 nomic or thematic relations (vertical axis:  $F(1,15)=1.49, p=.24$ ;  
401 horizontal axis:  $F < 1$ ).  
402

#### Data processing

403 Data analysis was performed by using the general linear model  
404 (Friston et al., 1995) as implemented in SPM2 (Wellcome Department of  
405 Imaging Neuroscience, London, UK, [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) where  
406 each event is modelled using a hemodynamic function model. Data  
407 analysis started by applying several spatial pre-processing steps. First,  
408 functional volumes were time-corrected with the 19th slice as  
409 reference, in order to correct effects caused by the different  
410 acquisition time of each slice. Subsequently, all volumes were  
411 realigned to correct head motion using rigid body transformations.  
412 The first volume of the first ER-fMRI session was taken as reference  
413 volume. Unwarping was performed by using the individually  
414 acquired fieldmaps, to correct for interaction between head move-  
415 ments and EPI distortions (Andersson et al., 2001). T1-weighted  
416 anatomical volume was co-registered to mean images created by the  
417 realignment procedure and was normalized to the MNI space using a  
418 trilinear interpolation. The anatomical normalization parameters  
419 were subsequently used for the normalization of functional volumes.  
420 Finally, each functional volume was smoothed by an 8-mm FWHM  
421 (Full Width at Half Maximum) Gaussian kernel. Time series for each  
422 voxel were high-pass filtered (1/128 Hz cutoff) to remove low-  
423 frequency noise and signal drift.  
424

425 After pre-processing steps, statistical analysis was first performed  
426 on functional images for each task separately. The 8 conditions of  
427 interest (Taxo/Nat/Manip, Taxo/Nat/Nonmanip, Taxo/Art/Manip, Taxo/  
428 Art/Nonmanip, Them/Nat/Manip, Them/Nat/Nonmanip, Them/Art/  
429 Manip and Them/Art/Nonmanip) were modelled as 8 regressors  
430 convolved with a canonical hemodynamic response function (HRF).  
431 Movement parameters derived from realignment corrections (3  
432 translations and 3 rotations) were also entered in the design matrix  
433 of each experiment as additional factors. The general linear model was  
434 then used to generate parameter estimates of activity at each voxel, for  
435 each condition, and each participant. Statistical parametric maps were  
436 generated from linear contrasts between the HRF parameter estimates  
437 for the different experimental conditions. The spatial resolution of the  
438 statistical parametric maps was the same as the spatial resolution of  
439 the functional MR acquisition ( $3 \times 3 \times 3.5$  mm).  
440

441 At the individual level, we first assessed the whole network of  
442 cerebral areas involved in the processing of each semantic relation by  
443 contrasting taxonomic and thematic categorization conditions to the  
444 baseline. Then, we identified brain correlates associated with each  
445 specific categorization process by contrasting taxonomic vs. thematic  
446 conditions on the one hand, and thematic vs. taxonomic conditions  
447 on the other hand. We then performed a random-effect group  
448 analysis on the contrast images from the individual analyses (Friston  
449 et al., 1998), using one-sample  $t$  tests. Clusters of activated voxels  
450 were then identified, based on the intensity of the individual  
451 response ( $p < 0.05$ , FWE corrected for multiple comparisons for  
452 contrasts calculated relative to the baseline and  $p < 0.001$  uncorrected  
453 for contrasts between conditions of interest). An extended threshold  
454 of 15 voxels was determined empirically and then used for all  
455 contrasts). Lastly, the regions specifically involved in each semantic  
456 categorization process were defined as regions of interest (ROI) and  
457 ROIs activity was compared between conditions. Brain regions were  
458 reported according to the stereotaxic atlas of Talairach and Tournoux  
459 (1988).  
460

459 *fMRI results*460 *Behavioral data*

461 In the scanner, participants were correct on most trials ( $M=92.4\%$ ,  
 462  $SD=4.1\%$ ). As in the behavioral study, a  $2 \times 2 \times 2$  ANOVA (Semantic  
 463 relation\*Domain\*Manipulability) was conducted on mRT. Again, the  
 464 main effect of Semantic relation [ $F(1,15)=6.10$ ,  $p<.05$ ] as well as the  
 465 interaction between Semantic relation and Domain [ $F(1,15)=10.05$ ,  
 466  $p<.005$ ] was observed. Taxonomic relations were more quickly  
 467 identified for natural objects ( $M=1195$  ms) than for artifacts  
 468 ( $M=1218$  ms), [ $F(1,15)=13.32$ ,  $p<.005$ ]. For thematic relations, the  
 469 difference between artifacts and natural objects was not significant  
 470 [ $F<1$ ]. As in the behavioral study, thematic relations were identified  
 471 more quickly for manipulable artifacts than for non-manipulable  
 472 artifacts [ $F(1,15)=25.75$ ,  $p<.0005$ ], although the 3-way interaction  
 473 between Semantic relation, Domain and Manipulability was not  
 474 significant [ $F<1$ ]. For taxonomic relations, the advantage of non-  
 475 manipulable natural objects over manipulable ones did not reach  
 476 significance [ $F<1$ ]. The  $2 \times 2 \times 2$  ANOVA conducted on mACC did not  
 477 show any significant effect.

478 *Imaging data*

479 *Taxonomic and thematic categorization vs. baseline.* Comparing the  
 480 activation corresponding to the taxonomic and the thematic categor-  
 481 ization conditions vs. baseline ( $p<.05$  corrected), we observed the  
 482 recruitment of a very similar neural network. For both taxonomic and  
 483 thematic conditions, the largest cluster of activation was found in the  
 484 middle occipital gyrus, bilaterally ( $>2000$  voxels, BA 17/18/19/37).  
 485 Other areas of activation included the bilateral superior parietal lobule  
 486 (BA 7/19), the left inferior parietal gyrus (BA 40) extending to the left  
 487 pre- and post-rolandic region (BA 1/2/3, BA 4), the right superior  
 488 frontal gyri (BA 6) and the thalamus.

489 *Posterior occipital regions specific to taxonomic vs. thematic*  
 490 *categorization.* The only regions specifically activated during taxo-  
 491 nomic categorization (taxonomic vs. thematic conditions,  $p<.001$   
 492 uncorrected) were situated bilaterally in the posterior occipital cortex  
 493 (cuneus/lingual gyrus, BA 18), more strongly in the right (50 voxels)  
 494 than in left (19 voxels) hemisphere (Table 1, Fig. 3A). To further  
 495 investigate the specific role of posterior occipital areas in taxonomic  
 496 vs. thematic categorization of different categories of objects, we  
 497 extracted the parameter estimates from the clusters activated within  
 498 the right and left cuneus/lingual gyri (RCu, LCu). These values were

submitted to two separate repeated-measure ANOVAs with Semantic  
 relation (taxonomic vs. thematic), Domain (natural objects vs. artifact  
 objects) and Manipulability (manipulable vs. non-manipulable  
 objects) as within-subjects factors, one examining the parameter  
 estimates from the right cuneus/lingual gyrus and the other one from  
 the left cuneus.

ANOVAs showed that activation in these two regions during  
 taxonomic categorization was modulated by object categories.  
 Although no interaction was significant in the RCu and LCu, we  
 observed the expected advantage of non-manipulable natural objects  
 over manipulable ones in the taxonomic condition in both regions  
 [RCu:  $F(1,15)=15.79$ ,  $p<.005$ ; LCu:  $F(1,15)=6.66$ ,  $p<.05$ ]. For thematic  
 relations, there were no difference between manipulable artifacts  
 and non-manipulable ones [RCu:  $F(1,15)=1.60$ ,  $p=.22$ ; LCu:  $F<1$ ], see  
 Fig. 3A.

*Temporo-parietal regions specific to thematic vs. taxonomic cate-*  
*gorization.* The reverse contrast (thematic vs. taxonomic conditions,  
 $p<.001$  uncorrected) showed that thematic categorization specifically  
 activated temporo-parietal regions bilaterally including the right and  
 left posterior middle temporal gyri (BA 39, BA 21/22) and the right and  
 left inferior parietal lobule (BA 39/40) centered around the supramar-  
 ginal gyrus in the left hemisphere (Table 1, Fig. 3B). Increased activation  
 was also observed in the right precuneus (BA 19) and the right middle  
 frontal gyrus (BA 8) extending to the right anterior cingulate gyrus  
 (BA 32). In order to investigate the role of the temporo-parietal cortex  
 in thematic vs. taxonomic categorization of different categories of  
 objects, we extracted parameter estimates from the clusters activated  
 within the right and left posterior middle temporal gyri (RMTG, LMTG),  
 and within the right and left inferior parietal lobule (RIPL, LIPL).

We conducted four separate repeated-measure ANOVAs on these  
 values with Semantic relation (taxonomic vs. thematic), Domain  
 (natural vs. artifact objects) and Manipulability (manipulable vs. non-  
 manipulable objects) as within-subjects factors. ANOVAs revealed  
 significant interactions between the type of Semantic relation  
 (taxonomic, thematic) and object categories (Fig. 3B).

In the RIPL, the type of Semantic relation interacted with Domain  
 [ $F(1,15)=5.44$ ,  $p<.05$ ]. Specifically, the RIPL was more activated when  
 participants identified thematic relations for artifacts than for natural  
 objects [ $F(1,15)=7.25$ ,  $p<.05$ ]. On the contrary, the RIPL was more  
 activated when participants identified taxonomic relations for natural  
 objects than artifacts [ $F(1,15)=8.83$ ,  $p<.005$ ]. In addition, the 3-way  
 interaction between Semantic Relation, Domain and Manipulability  
 was significant in the RIPL. However, the activation in the RIPL did not  
 differ neither between Taxo/Nat/Manip and Taxo/Nat/Nonmanip  
 conditions [ $F<1$ ] nor between Them/Art/Manip and Them/Art/Non-  
 manip conditions [ $F(1,15)=3.27$ ,  $p=.09$ ]. In the RMTG, the type of  
 Semantic relation interacted also with Domain [ $F(1,15)=14.83$ ,  
 $p<.005$ ]. However, planned comparisons between natural and artifact  
 objects for taxonomic relations and for thematic relations failed to  
 show any significant difference of activation in the RMTG. The 3-way  
 interaction between Semantic relation, Domain and Manipulability  
 was almost significant [ $F(1,15)=4.38$ ,  $p=.054$ ] due to a marginally  
 advantage of manipulable artifacts over non-manipulable ones for  
 thematic relations [ $F(1,15)=4.39$ ,  $p<.053$ ]. For taxonomic relations, no  
 difference was observed between non-manipulable and manipulable  
 natural objects [ $F<1$ ].

In the LMTG and the LIPL, the type of Semantic relation did not  
 interact with Domain aside [LMTG and LIPL:  $F<1$ ], but the 3-way  
 interaction between Semantic relation, Domain and Manipulability  
 was significant [LMTG:  $F(1,15)=5.22$ ,  $p<.05$ ; LIPL:  $F(1,15)=6.06$ ,  
 $p<.05$ ]. As predicted, in both the LMTG and the LIPL, this 3-way  
 interaction was due to a greater activation for the thematic  
 categorization of manipulable artifacts in comparison to non-  
 manipulable ones [LMTG:  $F(1,15)=19.91$ ,  $p<.0005$ ; LIPL:  $F(1,15)=$   
 $6.62$ ,  $p<.05$ ]. For taxonomic relations, there was no difference

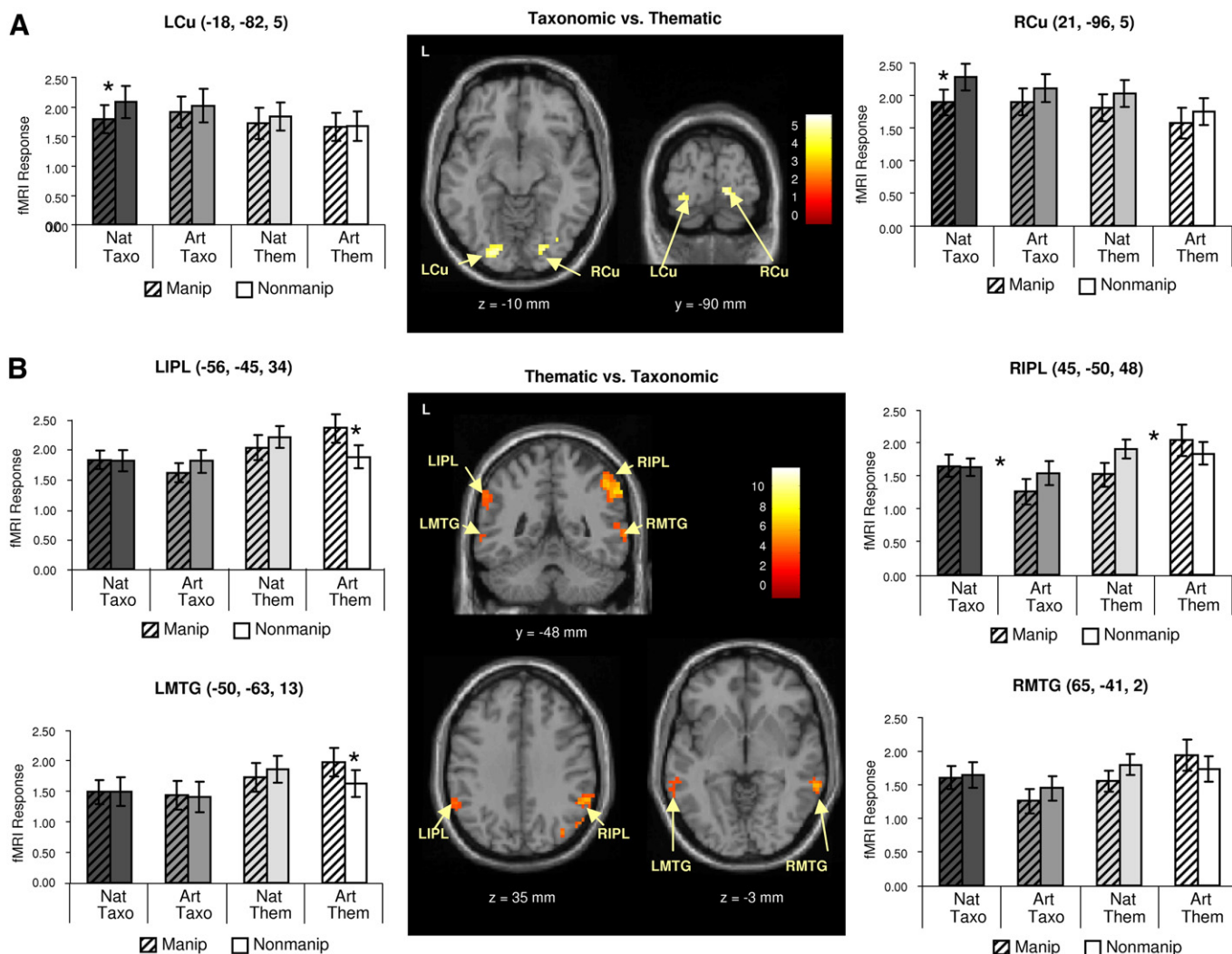
t1.1 **Table 1**

t1.2 Cerebral regions specifically activated during taxonomic and thematic processing

Contrasts	Area	Side	BA	k	x	y	z	T
<i>Specific taxonomic processing</i>								
[Taxo>Them]	Cuneus	R	18	50	21	-96	5	5.07
	[Lingual gyrus]	R	18		15	-87	-2	4.68
	Cuneus/Lingual gyrus	L	18	19	-18	-82	-5	4.61
<i>Specific thematic processing</i>								
[Them>Taxo]	Inferior parietal lobule	R	40	183	45	-50	48	11.57
	[Middle temporal gyrus]	R	39		53	-63	29	4.78
	Middle temporal gyrus	R	21	80	65	-41	2	8.12
	[Superior temporal gyrus]	R	22		59	-49	12	4.93
	Precuneus	R	19	23	36	-71	42	6.41
	Middle temporal gyrus	L	39	103	-50	-63	13	6.13
	[Middle temporal gyrus]	L	37/21		-62	-52	3	4.59
	Middle frontal gyrus	R	8	17	36	23	44	5.19
	[Anterior cingulate gyrus]	R	32		30	19	38	4.35
	Inferior parietal lobule	L	40	28	-56	-45	34	4.69

For each cluster, the region showing the maximum  $t$  value is listed first, followed by the other regions belonging to the cluster [between brackets]. The Talairach coordinates ( $x$ ,  $y$ ,  $z$ ) are indicated.

Abbreviations: R = right hemisphere; L = left hemisphere; BA = Brodmann area; k = number of voxels in the cluster.



**Fig. 3.** (A) Cerebral regions of the occipital cortex specifically activated for taxonomic vs. thematic conceptual relations. Results of the statistical analysis on parameter estimates for the right cuneus (RCu) and left cuneus (LCu) are presented on the associated graphs. In the taxonomic condition, the fMRI response was more important for non-manipulable natural objects than for manipulable ones in both the RCu and LCu. (B) Cerebral regions of the temporo-parietal network specifically activated for thematic vs. taxonomic conceptual relations. Results of the statistical analysis on parameter estimates for the left and right middle temporal gyri (LMTG and RMTG respectively) and the left and right inferior parietal lobules (LIPL and RIPL respectively) are presented on the associated graphs. In the LIPL and LMTG, the fMRI response was more important during thematic processing of manipulable artifacts than non-manipulable ones. In the RIPL, thematic processing elicited a greater fMRI response for artifacts than for natural objects while taxonomic processing elicited a greater fMRI response for natural objects than for artifacts. In the RMTG, these differences failed to reach significance. \*Highlights significant differences at  $p < .05$

564 between non-manipulable and manipulable natural objects [LMTG  
565 and LIPL:  $F < 1$ ].

## 566 Discussion

567 Overall, our behavioral results showed that taxonomic and  
568 thematic conceptual relations were more or less available as a  
569 function of object categories. The fMRI results showed that contrasting  
570 appropriate conditions, taxonomic and thematic conceptual processing  
571 selectively activates different cerebral networks including regions of  
572 occipital, temporal and parietal cortices. The analysis of parameter  
573 estimates within the regions of interest selected from these contrasts  
574 indicated significant differences according to Semantic relation  
575 (taxonomic vs. thematic), Domain (natural vs. artifact objects) and  
576 Manipulability (manipulable vs. non-manipulable).

### 577 Taxonomic and thematic salience as a function of object categories

578 The behavioral results indicate that a) taxonomic conceptual  
579 relations are identified faster and more accurately than thematic

conceptual relations, b) taxonomic relations are more salient for  
580 natural objects and c) thematic relations are more salient for artifacts,  
581 particularly manipulable ones. In both the behavioral and fMRI  
582 experiments, participants were faster and more accurate to identify  
583 taxonomic than thematic relations. As we controlled the picture  
584 associative strength (kept equivalent between taxonomic and thematic  
585 triads), the global advantage observed for taxonomic relations  
586 cannot be explained by the choice of stimuli. In addition, the  
587 taxonomic advantage was not due to the failure to identify thematic  
588 relations. Participants were accurate and quick to process both  
589 relations (around 95% accuracy and 1500 ms in the behavioral  
590 experiment; around 92% accuracy and 1200 ms in the scanner).  
591 Whereas both taxonomic and thematic relations appear relevant for  
592 adult conceptual organization (Lin and Murphy, 2001; Murphy, 2001),  
593 taxonomic relations seem to be more easily processed. We assumed  
594 that taxonomic relations would specifically rely on perceptual  
595 similarity while thematic relations would specifically involve con-  
596 textual/functional processing. Detecting perceptual similarity  
597 between objects would be therefore easier than detecting context-  
598 tual/functional relations. From a developmental perspective, 599

perceptual similarity is the first cue used by young infants to form taxonomic categories (Quinn et al., 1993). Since infants perceive their environment before being able to directly act upon it, all developmental models concede that object categories are first perceptually-based, at least during the first months of life (Mandler, 2000; Nelson, 1983, 1985; Quinn and Eimas, 1996, 2000). In adulthood, this may result in a global advantage to process the cues that have been acquired first, i.e. perceptual similarity cues, which would facilitate taxonomic conceptual processing in comparison to thematic conceptual processing.

Beyond the main advantage of taxonomic relations, we observed the expected interaction between the type of semantic relation (taxonomic vs. thematic) and the domain of objects (natural vs. artifact objects) in both the behavioral and neuroimaging experiment. Participants were faster to identify taxonomic relations for natural objects than for artifacts. On the contrary, they were faster and more accurate to identify thematic relations for artifacts than for natural objects. This second specific comparison failed to reach significance in the neuroimaging experiment. However, the lack of statistical power in the analysis on reaction times in the neuroimaging experiment (only 16 participants vs. 45 during the behavioral study) may partially account for the small disparities we observed between the two experiments for a few fine-grained comparisons. Overall, results show that taxonomic and thematic processing differs according to object domain (natural vs. artifact objects). In line with sensory/functional accounts of conceptual organization (Humphreys and Forde, 2001; Warrington and Shallice, 1984) and embodied views of concepts (Barsalou, 2008; Borghi, 2005; Gallese and Lakoff, 2005), conceptual processing would depend on the congruency between the cues used to categorize objects (perceptual similarity vs. contextual/functional relations) and object main features (perceptual vs. functional features). Taxonomic conceptual processing was assumed to be specifically based on perceptual similarity and was facilitated for objects mainly defined by perceptual features, i.e. natural objects (Cree and McRae, 2003; Marques, 2002; McRae et al., 2005). On the contrary, thematic conceptual processing would specifically rely on contextual/functional relations and was facilitated for objects mainly defined by functional features, i.e. artifacts (Cree and McRae, 2003; McRae et al., 2005). These findings confirm that taxonomic and thematic relations have a different role in natural and artifact concept formation and processing. In addition, we found the expected advantage of manipulable artifacts (e.g., tools, utensils) over non-manipulable ones (e.g., vehicles, furniture) in thematic processing in both experiments. This result supports previous findings showing that thematic processing could also be modulated by object manipulability (Kalénine and Bonthoux, 2008). Since thematic relations are extracted from event schemas (Nelson, 1983, 1985), they may involve several components of action experience: contextual information (e.g., the bowl and the slice of bread are found in the kitchen during breakfast time), functional knowledge (e.g., both are used to eat for breakfast) and manipulation knowledge (e.g. grasping the bowl/the slice of bread). Whereas contextual and functional links would characterize thematic relations for all artifacts, only manipulable artifacts would be directly concerned by manipulation knowledge. Thematic relations may be particularly easy to identify when they convey contextual, functional and manipulation information, namely when they concerned manipulable artifacts. This finding emphasizes the importance of thematic relations in the formation and processing of manipulable artifact concepts such as tools or utensils. However, the symmetric advantage of non-manipulable natural objects (e.g., animals) over manipulable ones (e.g., fruit/vegetables) was not significant. The relevance of perceptual features would not be reduced to animals but may be extended to all natural objects (Goldberg et al., 2006a). In the present study, stimuli were black and white drawings. Perceptual similarity may have been detected through shape properties. This would mean that shape is a highly relevant property for all natural

concepts. However, the possibility of a floor effect for taxonomic processing of non-manipulable natural objects (i.e. animals) has to be considered. The Taxo/Nat/Nonmanip condition leads to the shortest reaction times ( $M=1418$  ms) and may correspond to participants' highest identification speed. Thus, a difference between non-manipulable and manipulable natural objects in taxonomic processing may not have been detected. An alternative explanation would be that taxonomic conceptual relations rely on multi-modal perceptual similarity relations (Goldberg et al., 2006a,b). Beyond shape similarity processing, color, smell and taste properties that often characterized manipulable natural object concepts such as fruit and vegetables may also have been reactivated during taxonomic processing. Thus, taxonomic conceptual relations would be easily available for all natural objects, those predominantly defined by shape perceptual properties (i.e. animals) and those strongly characterized by other perceptual properties such as color, smell and taste (i.e. fruit and vegetables, plants).

#### *Taxonomic processing specificity in the occipital visual cortex* 683

In comparison to thematic conceptual processing, we found that taxonomic conceptual processing specifically activated visual association areas bilaterally (cuneus and lingual gyrus, BA 18). Taxonomic conceptual relations specifically recruit the occipital areas involved in the earliest stages of visual processing. In addition, the analysis of parameter estimates extracted from the clusters activated within the occipital cortex showed that the recruitment of the visual areas during taxonomic processing was particularly strong for non-manipulable natural object concepts, i.e. animals. Such occipital activations are commonly reported in perceptual tasks involving the processing of visual features such as shape, color or texture (Cant and Goodale, 2007; Chao and Martin, 1999; Humphreys and Riddoch, 2006; Marques et al., 2008). Lesions within these regions are responsible for several forms of visual agnosia in which visual object recognition is impaired and attributable to simple visual sensorial information processing deficits (for a review, see Heider, 2000). More important, similar occipital areas are activated during conceptual processing of objects mainly defined by perceptual features such as animals. The medial and lateral occipital cortex has been found out to respond specifically to animal concepts during naming (Chao et al., 2002; Martin et al., 1996; Whatmough et al., 2002) and semantic tasks (Chao et al., 1999; Gerlach, 2007; Grossman et al., 2002; Perani et al., 1999b; Sim and Kiefer, 2005; Wheatley et al. 2005). Note that in these studies, animal-selective activations within the occipital cortex were observed when participants directly perceived their visual features, i.e. using picture stimuli (Chao et al., 1999, 2002; Martin et al., 1996; Perani et al., 1999b; Whatmough et al., 2002) but also when animal visual features were not directly available, i.e. using word stimuli (Grossman et al., 2002; Perani et al., 1999b; Wheatley et al., 2005).

In keeping with the sensory/functional theory (Humphreys and Forde, 2001; Warrington and Shallice, 1984) and embodied views of concepts (Barsalou, 2008), we argue that the activation observed in visual association areas reflects perceptual similarity processing between taxonomically related objects. Consistent with this claim, the occipital activation reported during taxonomic processing appeared more strongly associated with non-manipulable natural concepts, i.e. animal concepts. However, the recruitment of the medial occipital cortex in response to animal conceptual processing has been alternatively linked to extra visual processing demands rather than to animal concepts *per se* (e.g., Moore and Price, 1999; Tyler et al., 2003a). Since the intra-categorical similarity would be maximum for animals, Moore and Price (1999) suggest that additional processing may be required to differentiate an animal from another one. Although this explanation may be relevant in semantic tasks assessing concepts at the basic-level (e.g., naming animal exemplars or matching different pictures of the same animal exemplar), it can be

ruled out in the present study. In our experiment, taxonomic relations were identified at the superordinate level (e.g., animals). Therefore, participants did not need to discriminate basic-level exemplars as it can be the case in a naming task. Instead, processing the perceptual features shared by basic-level exemplars (e.g., squirrel, goat) should have helped them to access the superordinate taxonomic categories (e.g., animals). In keeping with this interpretation, we observed the shortest reaction times in the Taxo/Nat/Nonmanip condition. This behavioral result corroborates the idea that processing perceptual similarity between exemplars has facilitated animal taxonomic categorization and was reflected by a stronger occipital activation in this condition.

Finally, our findings are consistent with data from neuropsychology and developmental studies that suggest a perceptual basis of taxonomic conceptual relations. In neuropsychology, Davidoff and Roberson (2004) reported the case of an aphasic patient (LEW) who was strongly impaired for both perceptual and taxonomic categorization while his performance in thematic categorization was preserved, suggesting a specific overlap between perceptual and taxonomic neural processing networks. In the developmental field, several experiments using visual preference methods have demonstrated that young infants are able to form taxonomic categories of animals and artifacts at the basic-level (e.g., cats and chairs respectively) and at the superordinate level (e.g., animals and furniture respectively) on a purely perceptual basis (Behl-Chadha, 1996; Quinn et al., 1993). In both studies, three-month-olds could categorize objects taxonomically using the similarity and the distinctivity between the perceptual features of the picture exemplars they have been exposed to during a familiarization phase. Whereas the perceptual basis of taxonomic categories in older children and adults was still a matter of debate in the behavioral literature (Mandler, 2000; Mareschal et al., 2003; Quinn et al., 1993) the present findings clearly demonstrate that in adulthood, taxonomic conceptual relations are grounded in the perceptual system.

#### 764 Thematic specificity in the temporo-parietal cortex

In comparison to taxonomic conceptual processing, we showed that thematic conceptual processing specifically activated bilateral areas in the posterior middle temporal cortex (BA 39/21/22) and inferior parietal lobules (BA 40). In addition, the parameter estimates analysis showed that these regions were differentially activated during thematic processing depending on object categories. Two patterns could be distinguished, one in the left temporo-parietal cortex and the other one in the right homologue region.

In the left temporo-parietal network (LMTG and LIPL), thematic conceptual relations elicited greater activation when they concerned manipulable (e.g., tools, utensils) than non-manipulable artifacts (e.g., furniture, vehicles). The specific activation of LMTG and LIPL during thematic processing, particularly important for manipulable artifacts, provides the first direct evidence for a strong involvement of the visuo-motor system during the identification of thematic conceptual relations. Indeed, the LMTG and LIPL are considered two key regions in which the neural systems underlying action execution and observation, action semantics and tool-selective knowledge overlap (for a recent review, see Noppeney, 2008). First, processing action words or pictures depicting actions is associated with reliable activation of posterior LMTG and, to a lower extent, of LIPL (Grezes and Decety, 2001; Kable et al., 2005; Liljestrom et al., 2008; Noppeney et al., 2005; Perani et al., 1999a; Tyler et al., 2003b). The proximity of the LMTG to the visual motion area MT would account for its crucial role in action semantics (Beauchamp and Martin, 2007). Second, tool-selective knowledge consistently rely on LMTG and LIPL functioning. In the last decade, tool-selective responses in the LMTG and LIPL have been generalized to various semantic tasks (e.g., naming, matching, semantic judgments) and different stimuli (e.g., pictures, words)

(Cappa et al., 1998; Chao et al., 1999, 2002; Devlin et al., 2002; Grossman et al., 2002; Martin et al., 1996; Moore and Price, 1999; Noppeney et al., 2006; Perani et al., 1999b; Phillips et al., 2002; Weisberg et al., 2007; Wheatley et al., 2005). However, to what extent LMTG and LIPL activation refers to function vs. manipulation knowledge remains a central issue. Regarding the present study, it would allow specifying the basis of thematic conceptual relations, which were assumed to convey both functional and manipulation information in the case of manipulable artifacts (e.g., hammer-nail; bowl-slice of bread). Several neuroimaging studies attempted to answer this question by contrasting functional and manipulation semantic judgments for manipulable objects (e.g., “does a key involve a twisting action?” vs. “is a stapler used to attach objects together?”). Enhanced activation of the LIPL for manipulation knowledge conditions has been found (Boronat et al., 2005; Canessa et al., 2008; Kellenbach et al., 2003), while both function and manipulation knowledge conditions recruited the LMTG (Ebisch et al., 2007; Kellenbach et al., 2003). Nevertheless, the relative role of the LMTG and LIPL in the function/manipulation dissociation is not so clear-cut. For example, the LMTG involvement in manipulation knowledge does not seem equivalent for all manipulable objects. Phillips et al. (2002) have contrasted manipulation and perceptual knowledge conditions for natural and artifact manipulable objects (i.e. fruit and tools, respectively). They reported greater activation within LMTG for tools with respect to fruit in the manipulation knowledge condition, while both categories are composed of manipulable objects. Thus, the LMTG and LIPL response for manipulation knowledge may be particularly important when action is closely linked to object use (i.e. function), that is specifically the case of tools. Contrary to non-manipulable artifacts (e.g., furniture) and other manipulable objects (e.g., fruit), manipulable artifacts (e.g., tools) associate specific manipulation and functional information. Recent imaging studies investigating the neural substrate of object use support this assumption (Vingerhoets, 2008; Weisberg et al., 2007). For example, Weisberg et al. (2007) showed the emergence of neural activity in the LMTG and LIPL when participants processed invented manipulable objects after having being trained to use them for a specific goal. Thus, the left temporoparietal cortex could be related to specific object use, namely to manipulation-for-function.

Overall, the specific involvement of the left temporo-parietal network during thematic processing, particularly for manipulable artifacts (e.g., tools, utensils), indicates that thematic conceptual relations are grounded in the visuo-motor system. They would specifically rely on object use experience that associates functional and manipulation knowledge.

In the right temporo-parietal network (RMTG and RIPL), the analysis of parameter estimates showed that thematic conceptual relations elicited greater activation for artifacts (e.g., tools, furniture) than for natural objects (e.g., animal, fruit). Even if this difference failed to reach significance in the RMTG, the activation patterns observed in RIPL and RMTG were almost similar. The specific recruitment of the RMTG and RIPL during thematic conceptual processing was particularly strong for artifacts, whether they were manipulable or not. Bilateral activations within the temporo-parietal network during thematic processing are not surprising. Neuroimaging studies focusing on tool-selective conceptual processing frequently report bilateral activations of the temporoparietal cortex (Cappa et al., 1998; Chao et al., 1999, 2002; Damasio et al., 2004; Martin et al., 1996), even if activations are usually more important in the left hemisphere. However, one interesting finding of our study is that contrary to the left temporo-parietal network, the involvement of RMTG and RIPL during thematic processing was stronger for both manipulable and nonmanipulable artifacts. Thus, we suggest that activation observed within the right temporo-parietal network would correspond to the processing of spatial relations between objects, since contextual links were assumed to be an important component of thematic conceptual relations (e.g., bowl-slice of bread; bed-person asleep). Indeed, the

role of the RIPL is central for spatial coding and spatial relation processing (Colby and Goldberg, 1999; Committeri et al., 2004; Husain and Nachev, 2007; Jeannerod and Jacob, 2005). Several spatial disorders (e.g., unilateral spatial neglect) followed damage of the RIPL (Vallar, 2007). Spatial relation processing is essential to perform object-directed actions (e.g. grasping the bowl) but also to orient oneself in a complex environment in order to achieve more general actions (e.g. moving to the bed). Therefore, spatial relation processing would be specifically recruited during thematic processing of objects that elicited specific actions (i.e. manipulable artifacts such as tools or utensils) and more general actions (i.e. non-manipulable artifacts such as furniture or vehicles). Consistent with this interpretation, our RMTG activation extended closely to the right superior temporal sulcus (59x, -49y, 12z), a region involved in biological motion processing (Beauchamp et al., 2002) responding selectively to whole body movements, in comparison to hand movements (Noppeney et al., 2005). Embedded in action event schemas (Nelson, 1983, 1985), thematic conceptual relations may specifically convey information about the spatial context in which more general actions (e.g., walking, driving, cleaning) would take place and would be therefore particularly relevant for artifacts, even non-manipulable ones (e.g., vehicles, furniture).

To sum up, our findings indicate that thematic conceptual relations specifically activate a bilateral temporo-parietal cortical network and are therefore grounded in the visuo-motor system. Furthermore, the recruitment of the brain areas involved in action (LIPL, LMTG) and space processing (RIPL, RMTG) was particularly strong during thematic processing of artifact concepts. The more fine-grained distinctions between manipulable and non-manipulable artifacts during thematic processing might result from a greater involvement of the left temporo-parietal network in the case of manipulable artifacts (e.g., tools).

## Conclusion

The present findings highlight the sensory-motor specificity of the neural substrates underlying taxonomic and thematic conceptual processing. Our results a) provide additional support in favor of embodied views of concepts, b) show that taxonomic and thematic conceptual processing differs depending on object categories at the cognitive and neural levels, c) suggest that taxonomic and thematic relations could play different complementary roles in concept formation and finally d) point out the necessity to distinguish taxonomic and thematic knowledge when investigating conceptual processing.

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