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Article

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The tool-use cortical network contributes to semantic neural representations

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Abstract

Tool use and language are two highly refined human abilities which may have co-evolved, thus resulting in neural commonalities. We recently provided evidence for shared neural resources between tool use and syntax. However, the debate is still open on whether semantics and phonology also recruit neurofunctional supplies common to tool use. Here we tested the hypothesis that activity within the tool-use network contributes to semantic and phonological neural representations. To this aim, we identified the tool-use network with fMRI while participants used pliers. The same participants underwent, a semantic and a phonological task to evidence the underlying networks. Through a series of representational similarity analyses we tested whether activity in tool-use clusters contributed to neural representations of semantic and phonological stimuli. The results revealed that semantic activity patterns within the left inferior frontal gyrus and left occipitotemporal cortex, activated by tool use, displayed significant similarity between nouns belonging to the same semantic category. Activity in tool-use related areas therefore contributes to semantics. By contrast, no significant relationship was observed for the activity patterns elicited by phonological stimuli. These findings suggest that semantics is grounded within the tool-use network, reinforcing the hypothesis of a functional link between semantics and tool use.

Main Text

Tool use and language are advanced human abilities which might have co-evolved¹. Their potential co-evolution predicts that tool use and linguistic processes may rely on common neural and cognitive resources². Recently, we revealed that tool use and syntax share cognitive processes and neural substrates within the basal ganglia (BG)³. The fundamental question therefore opens of whether tool use also shares other crucial components with language. Tool use relies on a left fronto-parietal network, encompassing the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL)^{4,5}, as well as subcortical structures, like the BG⁶. This left fronto-parietal stream supports the planning and execution of tool-use movement⁵, while the BG may support the sequential and hierarchical aspects of tool use^{3,6}. Furthermore, activity in the occipito-temporal cortex (OTC) contributes to the visual recognition of tools^{7,8}, the observation⁴ and actual execution of tool-use actions⁵. The aforementioned left IFG⁹⁻¹², left OTC^{8,12,13} and left IPL¹⁴⁻¹⁶ are also critical for processing the semantic content of action-related words. Similarly, both the left IPL and IFG are essential for phonology, the first playing a role in neural amplification for categorical perception of speech sounds¹⁷, and the second in phoneme perception, especially in noisy contexts¹⁸. Although encouraging, these findings often refer to different participant groups and assume a co-localization of sensorimotor and linguistic computations even though the sensorimotor network was not directly assessed. For semantic processing, this issue has been in part addressed recently in studies involving the observation of various actions^{13,16}. However, observing actions is not strictly parallel to their execution and all actions do not require the use of tools¹⁹. Here we tested the hypothesis that activity in specific nodes of the tool-use network allows to decode word semantic categories or phonemes, through

multivariate pattern analyses (i.e. representational similarity analyses - RSA) within the same participants. This would be proof that the neural signal in tool-use-related areas contributes to semantics and phonology.

Results

Tool-use, semantic and phonological neural networks

We identified the tool-use network by assessing brain activations with fMRI in healthy participants (N=20, 10 females) while preparing to use a tool in order to move a peg from a position to another on a board. As a control, they executed the same task with the bare hand (Fig.1a). Planning an action with the tool, rather than the hand, recruited a network (Fig.1f and Table S1) encompassing bilaterally the BG, the OTC and the IPL ($p < 0.05$ family-wise error (FWE) cluster corrected, $p < 0.001$ cluster forming threshold) in addition to the bilateral IFG ($p > 0.05$ FWE cluster corrected on the right and $p < 0.001$ uncorrected on the left hemisphere). To assess semantic processing in the same participants, we used a semantic priming paradigm. Prime-target French word pairs, semantically related or not, were presented and participants had to make a lexical decision on the target (i.e., whether it is a word or a pseudoword, Fig.1b). The words belonged to two distinct semantic categories: animal and tool nouns. Pseudowords, which were orthographically legal in French, were only presented as targets. Participants responded faster to semantically primed as compared to unprimed words, irrespective of their category ($[\chi^2_{(1)}=25.78, p<0.001]$; Fig.1d). Furthermore, responses were slower $[\chi^2_{(1)}=14.35, p<0.001]$, and tended to be less accurate $[\chi^2_{(1)}=3.79, p=0.051]$, for tool than for animal nouns. The general

semantic priming effect, irrespective of the semantic category, elicited significant activity in a cluster of the left IFG ($p < 0.05$ FWE cluster corrected, $p < 0.001$ cluster forming threshold; Fig.1g top and Table S2A). Regardless of the priming condition, tool nouns, as compared to animal nouns, activated the IFG bilaterally, the right superior frontal gyrus (SFG) extending to the left hemisphere as well ($p < 0.05$ FWE cluster corrected, $p < 0.001$ cluster forming threshold), and the left OTC ($p < 0.001$ uncorrected; Fig.1g bottom and Table S2B). No significant cluster resulted from the opposite contrast meant to identify activations specifically induced by processing animal nouns. The same participants also underwent a phonological identification task of isolated syllables extracted from a continuum between unambiguous /ba/ and /da/, whose intermediate steps were progressively ambiguous instances of the two phonemes. The same syllable was presented three consecutive times in each trial and participants were instructed to identify it as quickly as possible at the end of the third repetition (Fig.1c). The proportion of /ba/ responses better followed a sigmoid rather than a linear model as quantified by the root mean square error (RMSE, Sigmoid RMSE=0.025 vs. Linear RMSE=0.109, $p=0.01$; Fig.1e), indicating a categorical perception process. Such a process has been previously described^{17,20,21} and reflects the ability of the brain to assign a phoneme to a given category, while irrelevant acoustic differences are ignored. Then we used this individual behavioral performance in the phonological task to weight neuroimaging contrasts¹⁷. One contrast aimed at characterizing the neural network for speech sounds perceived unambiguously (i.e. proportion of /ba/ responses near extremums), while the other aimed to highlight the neural network for speech sounds perceived as ambiguous (i.e. proportion of /ba/ responses near chance level). The perception of unambiguous syllables activated the left angular

gyrus of the IPL ($p < 0.05$ FWE cluster corrected, $p < 0.001$ cluster forming threshold; Fig.1h top and Table S3A). Conversely, ambiguous speech sounds induced bilateral activations within the IFG and SFG ($p < 0.05$ FWE cluster corrected, $p < 0.001$ cluster forming threshold; Fig.1h bottom and Table S3B). A series of conjunction analyses testing for co-localization of tool-use activity with either semantic or phonological processes did not reveal any significant overlap of the activation.

Semantic but not phonological categories are decoded within the tool-use network

To test our prediction that activity within the tool-use network contributes to semantic processing, we conducted representational similarity analyses in the left IFG, left IPL and left OTC, three crucial nodes of the tool-use network with a documented role in language, as described above. We reasoned that if tool-use-related regions contribute to semantics, primed and unprimed tool nouns should elicit similar neural representations in this network. The same rationale should apply for primed and unprimed animal nouns. By contrast, as a proof for a representation of semantic categories, tool and animal nouns should elicit dissimilar neural activities. This assumption was tested with RSA: the distance between the neural patterns elicited by each pair of semantic conditions (Tool primed, Tool unprimed, Animal primed and Animal unprimed) was estimated as $1 - \text{the Pearson's correlation between the respective patterns}$. This step resulted in a neural representational dissimilarity matrix (RDM) that was then correlated with a model-based RDM (RDM, Fig.2a) aiming to test how well the model fitted with the neural data. The model-based RDM assumed a stronger neural patterns similarities within each semantic condition rather

than between them. Crucially, this model-based RDM significantly represented the neural activations recorded within the tool-use neural network for both the left IFG (mean $r=0.17 \pm 0.09$; $p=0.04$) and left OTC (mean $r=0.14 \pm 0.7$; $p=0.03$) but not for the left IPL (mean $r = 0.01 \pm 0.13$; $p = 0.48$; $p=0.68$; Fig. 2c-e). By contrast, the neural activity elicited in these regions when processing tool nouns was dissimilar from the one elicited by animal nouns (i.e. different semantic category). In other words, the neural activity within the left IFG and left OTC clusters activated by tool use, allows to decode words semantic categories. Using an analogous approach, we then tested whether the left IFG and IPL clusters activated by tool use, could decode the phonological input based on the neural activity elicited by the speech perception task within those regions. The RDM consisted to test whether the phonological categorical perception phenomenon can be reflected within the left IFG and IPL (Fig.2b for the group mean). This RDM was defined for each subject individually based on their categorical boundary between /ba/ and /da/. Syllables perceived by the participants as belonging to the same phonemic category (i.e. /ba/ or /da/) should elicit more similar neural representations in the targeted regions than when pertaining to different categories. Results showed that the IPL (mean $r=- 0.03 \pm 0.07$) and IFG (mean $r=0.08 \pm 0.06$; $p=0.11$) clusters of the tool-use network however did not significantly contribute to the phonological decoding (Fig.2c and e).

Discussion

Our findings show that neural activity within the inferior frontal and occipito-temporal regions of the tool-use network contributes to semantic decoding. So far, the available evidence was limited to the co-localization of semantic processing and tool-use, however

without critically assessing the two functions in the same participants^{8,14,15}. To overcome this limitation, we identified the clusters activated by tool-use actions in comparison to the same actions performed without a tool. The same participants also solved a semantic task with tool and animal nouns. The recorded neural activity allowed to identify distinct neural representations for each semantic category within the inferior frontal and occipito-temporal clusters activated by tool use. Both primed and unprimed nouns pertaining to the same semantic category elicited similar neural patterns in these regions, while the cross-category neural patterns between tool and animal nouns were distinguishable. This provides evidence that neural activity for semantics is supported by neural resources shared with tool use. This finding empirically supports the language embodiment theory^{22–26} predicting that semantic representations are grounded within modality-specific systems for action and perception. More generally, it comes in support of the idea that semantic representations are supported by a multimodal representations built on previous sensorimotor experiences²⁷.

In the motor domain, neuroimaging studies previously reported contribution of the left IFG and left OTC to tool-use behaviors^{4,5}. More generally these cortical areas are part of the dorsal stream coding for goal-directed movements of the upper limbs^{28,29} and have been recently proposed to represent a gradient from abstract to more concrete motor representations³⁰. The OTC would encode conceptual information of action that does not depend on the movement kinematics, the context or the object manipulated (e.g. hammering is a back and forth movement regardless of the direction of object involved)^{30,31}. Interestingly, the OTC appears to store an abstract representation of a movement well beyond action production or observation¹³. Indeed, the neural patterns for

action observation have been found to be similar to those elicited when the participants read a sentence describing the same action, revealing the crucial role of the OTC in holding an action concept across different modalities¹³. On the contrary, the IFG is thought to underlie more concrete processes by selecting the relevant kinematic parameters (e.g. grip aperture) required by the task³¹. Our findings suggest that the IFG is indeed involved in a skillful action involving a tool and may store concrete action representations that are crucial for semantics. This result corroborates previous observations that single pulse TMS applied to the left IFG inhibits the semantic priming effect for tool but not for animal nouns¹¹. Finally, we did not find evidence for semantic processing in the left IPL cluster activated by tool use contrarily to the assumptions made by previous work^{14,15}. This observation suggests that semantic processing of object categories within the IPL might occur outside of the tool-use network. The contribution of the left IPL to semantic processing previously found may also be explained because this area encodes more specific semantic information such as knowledge about the tool that has to be manipulated^{14,32}, and this parameter was not critically assessed in our experiment, which may at least partly account for the discrepant results.

Unlike semantics, our findings show that phonological perception instead is supported by activity in cortical regions that are contiguous to - but not part of - the tool-use network, in particular in the left IPL and IFG. This possibly reflects different neural resources for tool use and phonology. More generally this observation might suggest that tool use and phonological computations – even though relying both on fine grained sensory information – are subserved by specific cortical representations that do not generalize across effectors (see² for a similar assumption). Nonetheless, it does not prevent the existence of shared

neural resources between these two functions especially when considering speech production rather than perception, a question that remains to be addressed in future experiments.

Shared neural substrates might originate from the co-evolution of tool use and language¹. Experimental support for this assumption has been provided by previous studies³³⁻³⁵. Our study however underlines that a better understanding of this functional link requires to capture the specificity of each linguistic function rather than studying language as a whole. Indeed, the co-evolution processes between tool use and language may not have affected each linguistic function equally. Accordingly, the neural circuits devoted to tool use might have been exapted³⁶⁻³⁸ for specific language functions only. This specificity might depend on the degree of similarity between the computations performed by given neural structures (i.e. IFG and OTC for conceptual processing and BG for hierarchical processing³).

Finally, the finding of common neuro-functional resources between semantics and tool use predicts potential reciprocal impact of one function over the other at the behavioral level^{3,39}. Coherently, the use of novel tools that received a label, which may have sharpened their semantic representation, is facilitated in comparison to unlabeled tools⁴⁰. We also predict the so far untested reverse influence, namely that tool use may benefit semantic processing, in line with the reciprocal impact more generally documented between action and action-related language⁴¹. Accordingly, shared neural resources between tool use and semantics may open new strategies for rehabilitation of brain-damaged patients⁴².

Figures and Tables

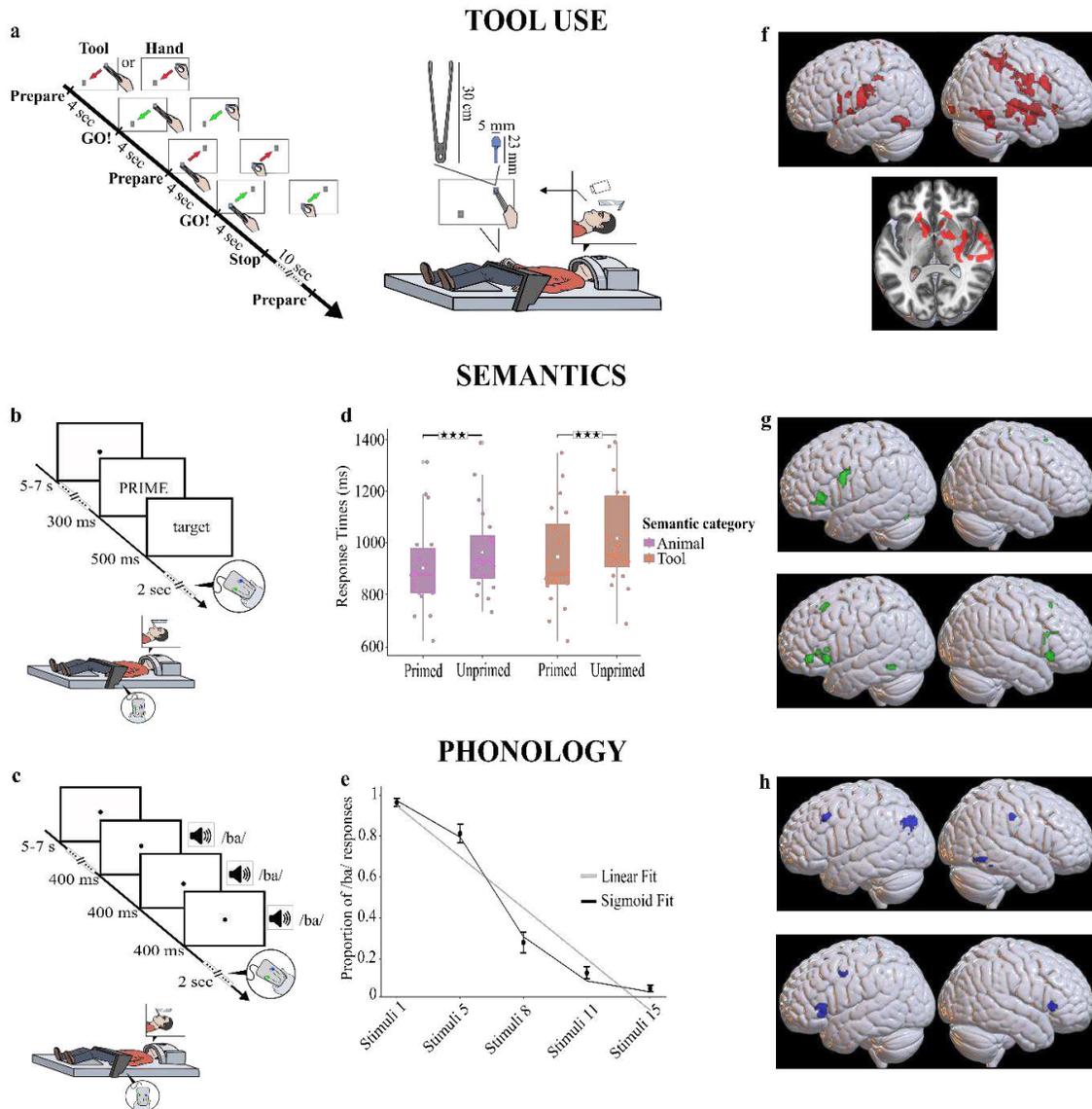


Figure 1. Brain networks for tool use, semantics and phonology.

a-c. Set-up and timing of the events for the motor (a), the semantic (b) and the phonological (c) tasks in the scanner. **d.** Semantic priming effect. Irrespective of word category, responses were faster for semantically primed compared to unprimed targets (main effect of priming [$\chi^2_{(1)}=25.78$, $p<0.001$]). Tool Primed= 945 ± 43 ms vs. Tool Unprimed= 1017 ± 43 ms, [$\chi^2_{(1)}=21.25$, $p<0.001$]; Animal Primed= 901 ± 38 ms vs. Animal Unprimed= 962 ± 37 ms, [$\chi^2_{(1)}=20.04$, $p<0.001$]). Tool nouns were processed more slowly than animal nouns (main effect of the semantic category: Tool nouns= 981 ± 31 ms vs. Animal nouns= 931 ± 27 ms,

[$\chi^2_{(1)}=14.35$, $p<0.001$]). The response accuracy only revealed a trend for the effect of semantic category: participants tended to be less accurate for tool than for animal nouns (Tool nouns= 96.3 ± 0.9 % vs. Animal nouns= 99.1 ± 0.4 %, [$\chi^2_{(1)}=3.79$, $p=0.051$]). **e.** Categorical perception of phonemes. The sigmoid rather than the linear model better fitted the identification performance (Sigmoid RMSE= 0.025 vs. Linear RMSE= 0.109 , $p=0.01$). **f-h.** Brain activations for tool-use compared to free-hand planning (f), semantic priming (g), and phonological perception (h), uncorrected maps at $p < 0.001$ (see Tables S1-S3 for clusters passing the family-wise error correction at the cluster level).

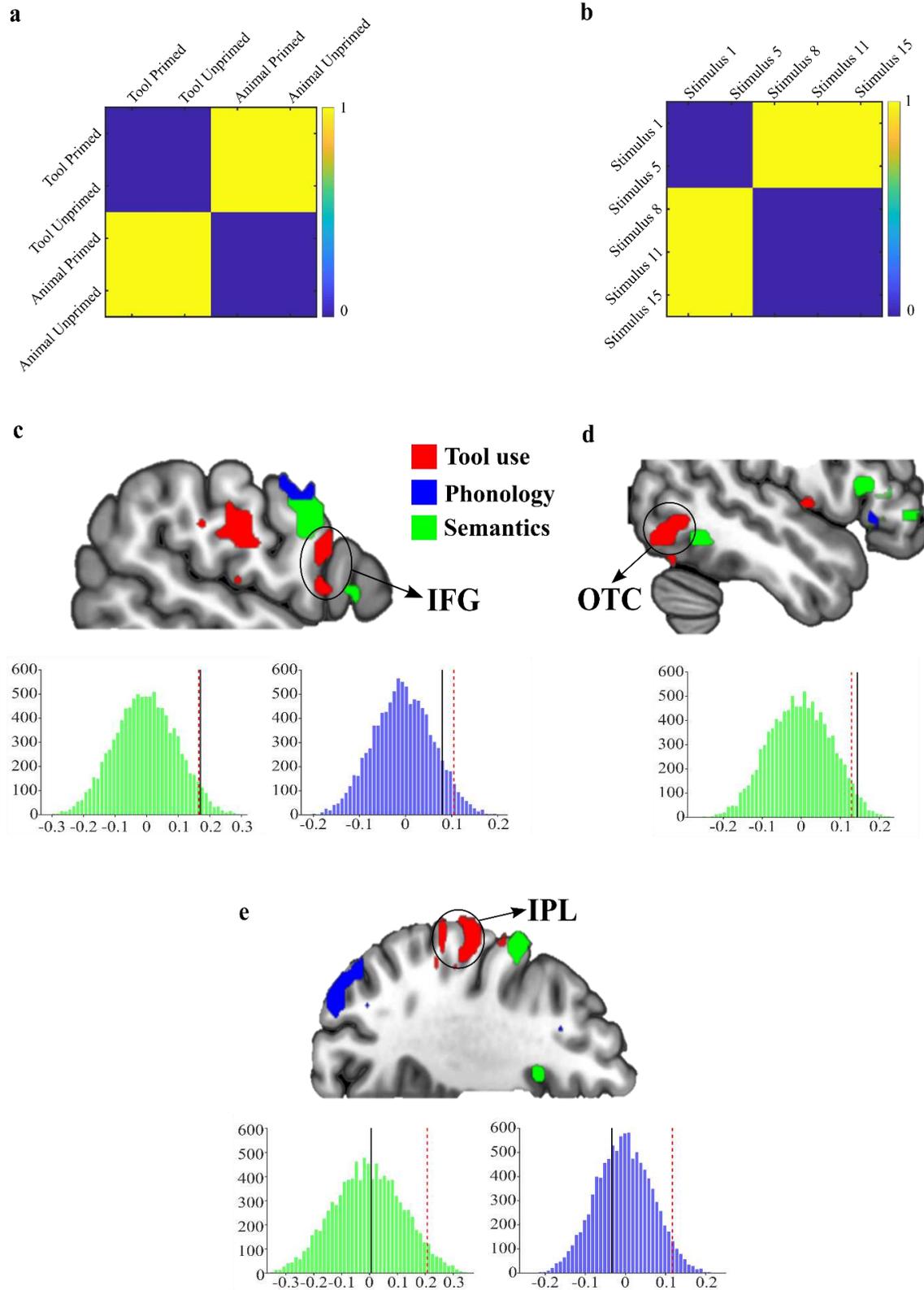


Figure 2. Semantic decoding in the left IFG and OTC within the tool-use network.

a. The model for semantics tested for dissimilarity between words belonging to different semantic categories (i.e. tool vs. animal nouns, in yellow) and for similarity for words belonging to the same semantic category (in blue). **b.** The model for phonology tested for dissimilarity between speech stimuli crossing the category boundary (in yellow) and similarity for stimuli lying on the same side of the boundary (in blue). **c.** Significant semantic (in green) but not phonological (in blue) decoding in the left IFG (for semantics: mean $r=0.17 \pm 0.09$; $p=0.04$, for phonology: mean $r=0.08 \pm 0.06$; $p=0.11$) of the tool-use network (brain left sagittal view). **d.** Significant semantic (in green) decoding in the left OTC (semantics: mean $r=0.14 \pm 0.07$; $p=0.03$) of the tool-use network (brain left sagittal view). **e.** Non-significant decoding for semantics (green; mean $r = 0.01 \pm 0.13$; $p = 0.48$) and phonology (blue; mean $r=- 0.03 \pm 0.07$; $p=0.68$) in the left IPL (brain left axial view). The green and blue plots represent the distribution obtained after 10,000 permutations with the value of *Pearson correlation score* represented on the x-axes and the number of occurrences of these scores on the y-axes.

Materials and Methods

Participants

The sample of participants, the motor task and fMRI acquisition parameters for this dataset have been described in a previous publication³. fMRI acquisition included 24 (11 females and 13 males) right-handed, French native participants. All had normal or corrected-to-normal vision, and they reported no history of neurological, auditory, language or sensorimotor deficits. Four participants were excluded, two did not fulfill the familiarization performance requirements before any neuroimaging acquisition, one dropped out after the inclusion phase and one was removed from analyses due to substantial head movements (several runs with movements above 1.5 mm). Hence, we analyzed the data of 20 participants with the following sociodemographic characteristics and manual preference: 10 females and 10 males; mean age \pm SD: 24 ± 4 years old; higher education level: 3 ± 2 years; mean score on the Edinburgh handedness inventory⁴³: 0.93 ± 0.09 . The protocol conformed to the Helsinki declaration and was approved by a national ethical committee (46/17, OUEST IV). All participants gave their written consent prior to the study and received compensation of 110 euros.

Tasks

Tool-use task

The motor task employed here has been previously described³. The participants were asked to use a pair of 30-cm-long pliers with their right hand in order to move a peg on a plastic board (Quercetti, Torino, Italy) where two fixed visual landmarks, separated by a 9-cm distance, indicated the start and end points (Fig. 1a). The participants were lying in a resting

position and were instructed to wait for a pure tone signal delivered through a MRI compatible device (Optoacoustics OptoACTIVE-two way noise cancellation communication system, Mazor, Israel). A single pure tone required the participant to prepare the movement, while a double presentation 4s later indicated the Go for the action. In order to perform the requested movements, the described sequence was repeated twice: grasping the peg to displace it from the start to the end point and then grasping it again to move it back to its initial position. The whole sequence (4-s planning – 4-s execution – 4-s planning – 4-s execution – 10-s rest) was repeated 15 times in a single run. The participants had to press a button with their left index finger if a peg fell (i.e. to indicate the missed sequence) and then grab a new peg from the left side of the plastic board. The few missed trials (lower than 0.5%) were modeled separately. As a control, in a distinct run, the same task was performed with the free hand. This allowed to define the contrast aimed to identify the tool-specific neural network. The motor task device was placed at a reachable distance in front of the participants and made visible with a double mirror mounted onto the head coil. To minimize elbow and shoulder movements, the participants' right upper arm was strapped to the trunk. The scripts controlling the audio sequence of instructions in the scanner were delivered with Presentation software (NBS, Berkeley, USA).

Semantic Priming Task

A semantic priming paradigm with a lexical decision task allowed to assess semantic processing. In such a paradigm, prime-target word pairs that are semantically related or not are presented and participants have to make a lexical decision on the target. Stimuli used

as primes and targets were French words belonging to two distinct semantic categories: animal and tool nouns. Pseudowords were created by changing two letters from tool and animal nouns while following the French phonotactic rules (i.e. they remained pronounceable and orthographically legal). Pseudowords were only presented as targets, never as primes. The selection of word stimuli was based on an anonymized online survey. A total of 574 French native participants (mean age \pm SD=23.92 \pm 4.39) judged the imageability and manipulability of a subset of a larger sample of 374 object nouns, on a 7-point Likert scale. They could also report whether a word was unknown to them. Additional 246 participants (mean age \pm SD=26.59 \pm 6.01) judged the imageability of a subset of 220 animal nouns. Because the participants received only a subset of words (i.e., 52 for object nouns and 74 for animal nouns) and not the full list, each word was quoted 82 times (i.e. by 82 participants).

Overall, 147 object nouns with manipulability and imageability scores equal or above five (out of seven) were selected as tool nouns. Furthermore, 172 animal nouns with an imageability score equal or above five were retained. Words from the two semantic categories were selected to obtain two lists of 70 tool nouns and 70 animal nouns matched for psycholinguistic variables (written and oral frequencies, numbers of syllables, letters and orthographic neighbors) as verified with the Lexique 3.80 database⁴⁴ (Table S4). The two lists of animal and tool nouns were then each divided into 5 lists of 14 words each. The resulting 10 lists (5 animal nouns and 5 tool nouns) were matched for the aforementioned psycholinguistic variables (Table S4). Each list was uniquely assigned to a function in the priming paradigm (either prime or target) so as to create five experimental

conditions: Tool Primed, Tool Unprimed, Animal Primed, Animal Unprimed and Pseudowords.

For words, primes and targets were associated by pairs in four conditions: a prime could be followed by a target either from the same semantic category (i.e. Tool Primed and Animal Primed) or from a different semantic category (i.e. Tool Unprimed and Animal Unprimed). In case of primed conditions, the words belonging to the same semantic category were always different. In a fifth condition, the target was a Pseudoword, following either an Animal or a Tool prime. The prime-target pairs were the same for all participants. During the experiment, following a fixation dot presented for 500 ms, a prime word was visually presented in uppercase for 300 ms and immediately followed by a target word in lowercase for 500 ms (Fig.1b). Participants were instructed to indicate as quickly and correctly as possible whether the target was a word or a pseudoword by pressing one of two buttons with their left index and middle fingers. They had a maximum of 2 seconds after the target onset to respond. The button-response association was counterbalanced across participants. The intertrial period was jittered between 5 and 7 seconds.

Overall, participants underwent 84 trials across the five experimental conditions: 14 prime-target pairs were presented for each of the four word conditions and 28 prime-target pairs for pseudowords (Table S5). The stimuli were visible through the mirror and the task script was programmed onto *Psychtoolbox* (PTB-3) running on MATLAB (Mathworks, Natick, USA).

Phonological identification Test

A two-alternative forced choice (2-AFC) phonological identification task was designed to assess phonological processing. Stimuli were isolated syllables synthesized with Praat (<https://www.fon.hum.uva.nl/praat/>) and varied by stepwise transformations in the second and third formants over 15 steps spanning a continuum between the syllables /ba/ and /da/. Each stimulus had a duration of 343 ms.

Five stimuli out of the 15 of the continuum (i.e. stimuli 1, 5, 8, 11 and 15) were selected for presentation to the participants. One trial consisted in the presentation of the same syllable three consecutive times with a stimulus onset asynchrony (SOA; time interval between the onsets of the stimuli) of 400 ms. The participants had a maximum of 2 seconds after the onset of the third repetition to identify the stimulus as /ba/ or /da/. They were instructed to wait for the third repetition to give their response as quickly and correctly as possible via a button press using their left index and middle fingers. The button-response association was counterbalanced across participants. All syllables were delivered through the same MRI compatible device as the one used for the tool-use task. Each stimulus was presented 11 times (11 trials), resulting in a total of 55 trials (11 × 5 stimuli) presented in a randomized order during the experiment. The intertrial period was jittered between 5 and 7s (Fig. 1c). To warn participants of an upcoming trial, a fixation dot was presented 500 ms beforehand and remained during stimulus presentation until the response interval. The dot was visible through the mirror oriented towards the screen placed on the back of the scanner bore. The task script was programmed onto Psychtoolbox (PTB-3) running on MATLAB (Mathworks, Natick, USA).

Procedure

The experiment consisted of an inclusion session to familiarize participants with the tasks and to ensure that the individual level of performance met the inclusion criteria. Short versions of the semantic and phonological tasks and of the motor task were proposed. The requirements to perform the fMRI session were at least 6 correct responses in the lexical decision task (over 9 trials including 6 words and 3 pseudo-words) and at least 5 correct categorizations of the syllables located at the continuum extremums (over 8 repetitions). This procedure aimed to maximize the chances of collecting a sufficient number of correct and analyzable trials in each task during the neuroimaging acquisition. The motor task for inclusion consisted of performing two blocks with each effector (two tool-use blocks and two free-hand block). In each block, the participants performed the task on the Grooved Pegboard test and were instructed to insert ten pegs as quickly as possible on the two first rows. To be included in the experiment, they were required to insert the 10 pegs for the two tool-use blocks in less than 5 minutes on average and the two free-hand blocks in less than 1 minute on average. The participants took part in two different fMRI sessions separated by two days. For each session, the participants performed an anatomical acquisition (T1-weighted), followed by motor (tool-use and free-hand) and linguistic runs in a counterbalanced order. The phonological and semantic tasks were presented on the same session, while two additional tasks, one assessing syntactic processing and the other working memory were performed in the other session. The session order was counterbalanced between participants. The results for the additional tasks, together with an analysis of the data relative to the motor task, are presented in a separate report³. Here, we present novel and unpublished results for the neuroimaging data of the motor runs,

reanalyzed using a different pipeline for the preprocessing, as well as of the semantic and phonological runs.

Functional and anatomical MRIs were acquired with a Siemens Prisma 3T scanner (Siemens Medical systems, Erlangen, Germany) with a gradient echo EPI sequence, with TE=30 ms and TR=2400 ms. Volumes were acquired with 44 interleaved slices of 3.3 mm thickness ($3 \times 3 \times 3.3$ mm voxel size) aligned to the AC-PC plane. Overall, 171 volumes were acquired for each motor block, 303 for the semantic task and 215 for the phonological task. T1-weighted images were acquired with a 1-mm isotropic voxel and a GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) acceleration factor of 2 (TE=3.8 ms, TR=3000 ms).

Analyses

Behavioral analyses

For the semantic task, response times (RTs; i.e. time interval from the display of the target word to the participant's response) and response accuracy were measured to index semantic performance. Statistics on these data were run in R-studio with the *afex* package⁴⁵. A linear mixed model (LMM) was used on RTs and included *Semantic Category* (Tool nouns vs. Animal nouns) and *Priming* (Unprimed vs. Primed) as fixed-effect within-subject factors. These factors were also included as random slopes in addition to the random intercept for *Subjects*⁴⁶. Planned comparisons of RTs between semantically primed and unprimed conditions for each semantic category were performed with LMMs including *Priming* as fixed-effect within-subject factor and *Subjects* as random intercept. The *Priming* factor was also added as random slope only for the animal nouns. This difference between the two

LMMs is explained because random effects and their impact on model fit were introduced and assessed sequentially, so that the one with significantly better fitting was chosen (see⁴⁷ for a similar procedure). A generalized linear mixed model (GLMM) with a binomial law was performed on response accuracy. Both *Semantic Category* and *Priming* were used as fixed-effect within-subject factors, *Semantic Category* was considered as random slope and *Subjects* as random intercept. All results are reported as the mean \pm SEM.

For the phonological identification task, the proportion of /ba/ responses was quantified for each of the five stimuli of the continuum going from /ba/ to /da/. We then calculated the average proportion at the group level and reported it as mean \pm SEM. We quantified the goodness of fit of both linear and sigmoidal models on these data by computing the root mean square error (RMSE). The fitting of the two models were statistically compared with the R built-in function *anova*.

fMRI preprocessing.

For preprocessing of the fMRI data, we used fMRIPrep (<https://fmriprep.org/en/stable/>), a pipeline aiming to conduct robust and reproducible preprocessing of fMRI data⁴⁸. The fMRIPrep pipeline generates a file describing the preprocessing procedure applied that is available for downloading (<https://osf.io/yr394/>).

fMRI univariate analyses.

The Statistical Parametric Map 12 (SPM12, <https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>) was used for the univariate analysis.

Data were smoothed with a Gaussian kernel of $8 \times 8 \times 8$ mm. At the first level, each participant's hemodynamic responses were modeled by the convolution of the canonical hemodynamic response with a box-car function. Each motor block was designed with planning, execution, rest and missed trials and head movements. Both directions of the movements (back and forth) were taken into consideration together. For the semantic priming task, we modeled the prime - target association (i.e. 0.8s from the prime onset) separately for Tool Primed, Tool Unprimed, Animal Primed, Animal Unprimed and Pseudowords. The head movements, incorrect trials as well as the remaining time allotted to give a response (i.e. 1.5s) were modeled in separate regressors. For the phonological identification task, we modeled together the three consecutive repetitions of the same syllable (i.e. 1.2s from the onset of the first repetition), and separately for each of the five syllable stimuli from the continuum. The remaining response time (i.e. 1.6s) was modeled apart, as the same was done for head movements.

At the second level, we conducted within-subjects ANOVAs to identify the general network underlying the motor task. To do so, we entered the parameter estimates (i.e. beta) against baseline obtained for each condition of interest and each subject. We computed the interaction contrast highlighting the specific tool-use planning neural network with respect to free-hand planning and the overall execution network:

$$\text{Tool-use Planning Network} = [(\text{Tool-use}_{\text{Planning}} - \text{Free-Hand}_{\text{Planning}}) - (\text{Tool-use}_{\text{Execution}} - \text{Free-Hand}_{\text{Execution}})].$$

To assess the semantic neural network, we conducted within-subjects ANOVAs to identify the general network underlying the semantic task. As for the motor task, we entered the parameter estimates against baseline obtained for each condition of interest and each subject. To identify the main effect of semantic priming, given that primed paired may induce a repetition suppression effect^{49,50}, we considered the voxels more activated for unprimed in comparison to primed nouns:

$$\text{Semantic Priming Network}=[\text{Unprimed nouns} - \text{Primed nouns}]$$

Then we studied the main of effect semantic category by considering separately tool and animal nouns, to evidence the network supporting each category irrespective of the priming manipulation:

$$\text{Semantic Tool Category Network}=[\text{Tool nouns} - \text{Animal nouns}]$$

and

$$\text{Semantic Animal Category Network}=[\text{Animal nouns} - \text{Tool nouns}]$$

To assess the phonological network, we used a different strategy. We weighted the contrasts on the individual behavioral performance in the phonological identification task, similar to a previous study of phonological perception¹⁷. We aimed to uncover the brain regions specifically activated for processing speech sounds. Identifying the brain regions involved in speech categorical perception requires testing for neural differences between speech sounds that are perceived either unambiguously or ambiguously. To do so, we used the proportion of /ba/ responses during the phonological identification task: ambiguous syllables are stimuli with a proportion of /ba/ responses tending towards the chance level

at 50%. Conversely, unambiguous sounds correspond to stimuli with a proportion of /ba/ responses tending towards 100% or 0%, the latter case meaning that participants categorized the syllable unambiguously as /da/. Thus, for each participant, we defined a contrast weighted on their individual performance and then we used it for the first level analyses. To identify brain regions specifically responding to unambiguously perceived speech sounds, we needed to estimate signal changes displaying a U-shape relation with the interval of stimuli. Such a contrast would therefore attribute the maximum weight to the categorization performance at the extremes (i.e. 100%, namely unambiguously perceived /ba/, and 0%, unambiguously perceived /da/), and, at the opposite, the minimum weight to stimuli producing a performance at chance level (50%). To this aim, we performed a calculation over the proportion of /ba/ responses for each of the five stimuli presented (Equation1).

$$abs(stimuli_categoriation - chance_level) \text{ (Equation 1)}$$

Equation 1. Stimuli categorization is the proportion of /ba/ responses recorded for each of the five speech stimuli of the continuum. We subtracted the chance level and transformed the resulting value in absolute value.

To identify brain regions that better responded to ambiguous phonemes, we needed to obtain the reverse relation, that is an inverted U-shape curve. Thus, we obtained the relative weighted contrast by computing the inverse of Equation 1 (Equation 2). The scores obtained were then normalized in order to have a contrast centered on zero.

$$-abs(stimuli_categoriation - chance_level) \text{ (Equation 2)}$$

Equation 2. The same calculation as in Equation 1 was applied and transformed to a negative value.

To guarantee the reliability of the results, for each analysis, we reported each cluster at the whole brain level, containing more than 10 contiguous voxels, with a *p-value* below the 0.001 threshold uncorrected for multiple comparisons. Furthermore, the motor contrast was submitted to an exclusive mask defined at 0.05 uncorrected for multiple comparisons aiming to rule out the contribution of the interaction second component (i.e., for Tool-use Planning Network, the contribution Free-Hand Execution > Tool-use Execution was masked). Clusters passing the family-wise error (FWE) correction for multiple comparisons at the cluster level are highlighted with a ^{FWE} mention (Tables S1-S3). To test the existence of shared neural resources between tool use and, separately, the two linguistic processes under investigation, we performed series of conjunction analyses between the tool-use network and each of the linguistic contrasts.

fMRI multivariate representational similarity analysis (RSA)

We selected regions of interest (ROIs) from the tool-use related neural activity. To this aim, we saved a mask of all the significant voxels ($p < 0.001$ uncorrected) for clusters of interest. Overall, we retained three ROIs of the tool-use planning network also known for their involvement either in phonology or semantics, or in both. The three tool-use clusters were the left IPL (size =150 voxels), left OTC (size=76 voxels) and left IFG (size=28

voxels). For the two linguistic tasks, first-level analyses were run again on non-smoothed data and included the same regressors as for the univariate analyses. We used the CoSMoMVPA toolbox⁵¹ to extract, for each participant, the *t*-value at each voxel within a given ROI. The RSA consists of testing whether the representational similarity hypothesized in a model fits with the neural activity patterns recorded across various stimuli types⁵². The neural dissimilarity (i.e. $1 - \text{Pearson's correlation score}$) is tested across a set of conditions.

For the semantic priming task, we considered four conditions of interest (i.e. Tool Primed, Tool Unprimed, Animal Primed, Unprimed Animal). Similarly, at the neural level, a distance was calculated across these four conditions and entered in a representational dissimilarity matrix (RDM). We tested an *a priori* model assuming that primed and unprimed tool nouns were similarly represented, the same rationale was applied for primed and unprimed animal nouns. The two semantic categories were on the other hand expected to be dissimilarly represented. In others words, we tested a model assuming stronger similarity of neural activity patterns within semantic categories but dissimilarity between each semantic category (Fig.2a).

For the phonological identification task, we considered a model aiming to test whether the speech category boundary is represented at the neural level. The model was designed at the individual level, to take into account interindividual differences of the categorical perception boundary. The model assumed that stimuli whose proportion of /ba/ is above the chance level (i.e. 50%) would be similarly represented at the neural level; the same holds for stimuli whose proportion of /ba/ responses is under the chance level. On the

contrary, neural activity elicited by sounds perceived as belonging to different sides of the boundary would be considered dissimilar (Fig. 2b).

To assess if the model fitted with the RDM, we computed a Pearson's correlation for each participant. To test the significance of the mean correlation score, we performed 10,000 permutations by randomly flipping the sign of the participant's correlation scores in order to obtain a null distribution. The probability for observing a significant effect under the null hypothesis was thresholded at 0.05 right-tailed and calculated from the proportion of values of the null distribution superior to the observed *Pearson's correlation score*. Thus, if this proportion is smaller than 0.05, the observed *Pearson's correlation score* is considered significant and different from the chance level set at zero.

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Region	BA	Peak MNI coordinates			Cluster size (k)	Z-value
		x	y	z		
Tool-use Planning Network: (Tool-use_{Planning} – Free-Hand_{Planning}) - (Tool-use_{Execution} – Free-Hand_{Execution})						
L Postcentral Gyrus (extending onto Inferior Parietal Lobule)^{FWE}	BA1, 2, 3, 40	-66	-16	27	150	4.64
L Caudate (extending onto Globus Pallidus) ^{FWE}	-	-18	20	-13	112	4.31
L Occipitotemporal Cortex^{FWE}	BA19, 37	-54	-72	-9	76	4.53
L Putamen	-	-28	-4	-6	46	4.03
L Inferior Frontal Gyrus (Precentral Sulcus)	BA6	-58	12	27	28	3.99
L Intraparietal Sulcus	BA40	-36	-36	44	26	4.18
L Putamen	-	-24	8	-16	21	4.34
L Insula	BA13	-42	-4	4	19	3.74
L Ventral Anterior Cingulate Cortex	BA24	-10	30	11	17	4.40
L Inferior Frontal Gyrus (Ventral Premotor Cortex)	BA6	-64	0	30	11	4.15

R Putamen (cluster extending onto Globus Pallidus and Caudate Nucleus) ^{FWE}	-	26	-13	-3	772	5.21
R Inferior Frontal Gyrus (extending onto Postcentral and Supramarginal Gyri) ^{FWE}	BA1,2,3,4,6,40	62	6	30	177	4.37
R Occipitotemporal Cortex ^{FWE}	BA19, 37	50	-58	-9	140	4.72
R Intraparietal Sulcus	BA7	36	-42	47	130	4.55
R Secondary Visual Area	BA18	26	-100	-6	13	3.65
R Cerebellum Crus I	-	26	-46	-39	11	3.65

Table S1. Brain areas activated for tool-use planning. All presented clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}. The three regions highlighted are the ROIs used for the RSA focusing on the neural activity elicited by the phonological identification and semantic priming tasks.

Region	BA	Peak MNI coordinates			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		
(A) Unprimed nouns - Primed nouns						
L Inferior Frontal Gyrus (<i>Pars Triangularis</i>) ^{FWE}	BA45	-30	30	4	54	4.30
L Inferior Frontal Gyrus (<i>Pars Opercularis</i>)	BA44	-48	20	14	26	4.02
L Superior Frontal Gyrus	BA8	-6	20	53	19	3.44
L Superior Frontal Gyrus (Supplementary Motor Area)	BA6	-10	12	57	12	3.47
(B) Tool nouns - Animal nouns						
L Inferior Frontal Gyrus (<i>Pars Orbitalis</i>) ^{FWE}	BA47	-42	42	1	50	3.88
L Anterior Insula	BA13	-34	20	-3	34	4.60
L Occipitotemporal Cortex	BA37	-48	-52	-13	17	4.14
R Superior Frontal Gyrus (Supplementary Motor Area, extending bilaterally) ^{FWE}	BA6	8	14	50	89	4.66
R Inferior Frontal Gyrus (<i>Pars Orbitalis</i>) ^{FWE}	BA47	36	24	-6	44	4.89
R Middle Frontal Gyrus	BA9	42	30	24	21	3.57
R Caudate Nucleus	-	2	0	17	11	3.87

Table S2. Brain areas activated for the main effect of semantic priming (A), the main effect of the tool semantic category (B). All reported clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the

cluster level are indicated with the mention ^{FWE}. No significant voxel was found for the main effect of the animal semantic category (i.e. Animal nouns – Tool nouns)

Region	BA	Peak MNI coordinates			Cluster size (<i>k</i>)	Z-value
		<i>x</i>	<i>y</i>	<i>z</i>		
(A) Unambiguous Speech Sounds - Ambiguous Speech Sounds						
L Angular Gyrus ^{FWE}	BA39	-40	-84	37	74	4.37
L Parahippocampal Gyrus	BA36	-30	-40	-13	21	4.04
L Middle Frontal Gyrus	BA8	-28	18	44	20	3.84
R Parahippocampal Gyrus	BA36	32	-40	-13	24	4.46
R Inferior Temporal Gyrus	BA47	60	-54	-9	18	3.85
R Supramarginal Gyrus	BA40	62	-22	40	16	3.95
R Caudate Nucleus	-	2	0	17	11	3.87
(B) Ambiguous Speech Sounds - Unambiguous Speech Sounds						
L Inferior Frontal Gyrus (<i>Pars Orbitalis</i>) ^{few}	BA47	-46	26	-3	55	4.33
L Middle Frontal Gyrus (Dorsal Premotor Cortex)	BA6	-58	2	44	16	3.36
R Superior Frontal Gyrus (Supplementary Motor Area, extending bilaterally) ^{FWE}	BA6	8	12	50	128	4.28
R Inferior Frontal Gyrus (<i>Pars Triangularis</i>) ^{FWE}	BA45	36	24	4	34	4.39

Table S3. Brain areas activated for ambiguous (A) and unambiguous syllable-embedded phonemes (B). All presented clusters contain more than 10 contiguous voxels and are below the statistics threshold $p < 0.001$, unc. Clusters passing the family-wise error correction with $p < 0.05$ at the cluster level are indicated with the mention ^{FWE}.

	Tool Nouns	Animal Nouns	Semantic Categories Statistics	Word Lists Statistics
Written Frequency	7.27 ± 8.98	6.82 ± 6.23	$W=2720.5, p=0.26$	$F_{(9,130)}=1.18, p=0.31$
Oral Frequency	4.65 ± 7.42	5.45 ± 6.53	$t_{(138)}=1.57, p=0.12$	$F_{(9,130)}=1.12, p=0.35$
Letters	6.76 ± 1.86	6.26 ± 1.98	$W=2109.5, p=0.15$	$F_{(9,130)}=0.87, p=0.56$
Syllables	1.96 ± 0.81	1.86 ± 0.82	$W=2277.5, p=0.44$	$\chi^2_{(9)}=9.79, p=0.37$
Orthographic Neighbors	3.40 ± 4.21	2.60 ± 4.02	$W=2045, p=0.08$	$\chi^2_{(9)}=8.91, p=0.45$
Unknown Words	0.59 ± 0.92	0.34 ± 0.74	$W=2080, p=0.06$	$\chi^2_{(9)}=12.83, p=0.17$
Imageability	6.59 ± 0.30	6.44 ± 0.60	$W=2313.5, p=0.57$	$\chi^2_{(9)}=9.80, p=0.37$
Manipulability	5.90 ± 0.35	×	×	$F_{(4,65)}=0.69, p=0.60$

Table S4. Statistics for tool and animal nouns. Means ± SD are reported respectively for tool and animal nouns on several psycholinguistic variables: written and oral frequencies (occurrences per million), number of letters, number of syllables, number of orthographic neighbors, the times a word is reported unknown, imageability and, for tool nouns, manipulability. Statistics are reported for the comparison between the two semantic categories (i.e. 2 levels, animals vs. tools; two-sample t-test or Wilcoxon sum rank test) as well as between the 10 lists of words used either as primes or targets across the five experimental conditions (i.e. 10 levels; ANOVA or Kruskal-Wallis test performed according to the residuals normality).

Prime	Target	Prime (translation)	Target (translation)	Condition
pieuvre	dauphin	octopus	dolphin	Animal Primed
cafard	araignée	cockroach	spider	Animal Primed
boeuf	vache	beef	cow	Animal Primed
chèvre	bouc	goat	goat	Animal Primed
pie	mouette	magpie	seagull	Animal Primed
crabe	oursin	crab	sea urchin	Animal Primed
libellule	papillon	dragonfly	butterfly	Animal Primed
lion	panthère	lion	panther	Animal Primed
cerf	biche	stag	doe	Animal Primed
rhinocéros	zèbre	rhinoceros	zebra	Animal Primed
corbeau	oie	crow	goose	Animal Primed
paon	autruche	peacock	ostrich	Animal Primed
guêpe	abeille	wasp	bee	Animal Primed
grenouille	vipère	frog	viper	Animal Primed
craie	stylo	chalk	pen	Tool Primed
javelot	raquette	javelin	racket	Tool Primed
brosse	peigne	brush	comb	Tool Primed
fouet	lasso	whip	lasso	Tool Primed
aspirateur	balai	vacuum	broom	Tool Primed
gomme	crayon	rubber	pencil	Tool Primed
équerre	compas	square	compass	Tool Primed
feutre	pinceau	felt	brush	Tool Primed
seringue	pipette	syringe	pipette	Tool Primed
décapsuleur	louche	bottle opener	ladle	Tool Primed
rame	pagaie	oar	paddle	Tool Primed
hache	machette	chopped	machete	Tool Primed
tronçonneuse	scie	chain saw	saw	Tool Primed
briquet	allumette	lighter	matche	Tool Primed
tortue	manivelle	turtle	crank	Animal Unprimed
mouche	agrafeuse	fly	stapler	Animal Unprimed
taureau	spatule	taurus	spatula	Animal Unprimed
cygne	stylet	swan	stylus	Animal Unprimed
mouton	cisaille	sheep	shears	Animal Unprimed
hippocampe	rasoir	seahorse	razoe	Animal Unprimed
coccinelle	batte	ladybug	bat	Animal Unprimed

lynx	chalumeau	lynx	blowtorch	Animal Unprimed
daim	arrosoir	deer	watering can	Animal Unprimed
âne	éplucheur	donkey	peeler	Animal Unprimed
canard	télécommande	duck	remote control	Animal Unprimed
perroquet	clef	parrot	key	Animal Unprimed
bourdon	canne	bumblebee	cane	Animal Unprimed
lézard	ponceuse	lizard	sander	Animal Unprimed
pelle	brebis	shovel	ewe	Tool Unprimed
tournevis	fourmi	screwdriver	ant	Tool Unprimed
épée	girafe	sword	giraffe	Tool Unprimed
lime	panda	lime	panda	Tool Unprimed
scalpel	puma	scalpel	puma	Tool Unprimed
pioche	koala	pickaxe	koala	Tool Unprimed
poignard	brochet	dagger	pike	Tool Unprimed
pince	écrevisse	pliers	crayfish	Tool Unprimed
hachoir	mésange	chopper	tit	Tool Unprimed
tamis	hippopotame	sieve	hippopotamus	Tool Unprimed
fourche	gorille	fork	gorilla	Tool Unprimed
aiguille	rat	needle	rat	Tool Unprimed
balayette	coq	brush	rooster	Tool Unprimed
crosse	loup	butt	wolf	Tool Unprimed
sanglier	tupou	boar	tupou	Pseudowords
aigle	telcite	eagle	telcite	Pseudowords
escargot	crapal	snail	crapal	Pseudowords
guenon	celnar	monkey	celnar	Pseudowords
hérisson	soricame	hedgehog	soricame	Pseudowords
écureuil	paceton	squirrel	paceton	Pseudowords
renard	létupien	fox	létupien	Pseudowords
grillon	fulet	cricket	fulet	Pseudowords
veau	gralut	calf	gralut	Pseudowords
crevette	permoriteur	shrimp	permoriteur	Pseudowords
huître	faurmeau	oyster	faurmeau	Pseudowords
ours	paindon	bear	paindon	Pseudowords
limace	granpoir	slug	granpoir	Pseudowords
salamandre	greplin	salamander	greplin	Pseudowords
râteau	cruine	rake	cruine	Pseudowords

marteau	ladontin	hammer	ladontin	Pseudowords
sabre	majot	saber	majot	Pseudowords
râpe	tranon	grated	tranon	Pseudowords
cutter	panton	cutter	panton	Pseudowords
massue	carporan	club	carporan	Pseudowords
canif	bimette	penknife	bimette	Pseudowords
sécateur	solaie	shears	solaie	Pseudowords
couteau	orunel	knife	orunel	Pseudowords
épuisette	rinot	net	rinot	Pseudowords
truelle	bafin	trowel	bafin	Pseudowords
perceuse	daillot	drill	daillot	Pseudowords
soufflet	pimeau	bellows	pimeau	Pseudowords
levier	riploir	lever	riploir	Pseudowords

Table S5. List of Prime-Target pairs of stimuli in French with their English translation and the underlying condition for the semantic task.