

The Role of Reward in Word Learning and Its Implications for Language Acquisition

Pablo Ripollés,^{1,2,*} Josep Marco-Pallarés,^{1,2}
Ulrike Hielscher,³ Anna Mestres-Missé,⁴
Claus Tempelmann,⁵ Hans-Jochen Heinze,⁵
Antoni Rodríguez-Fornells,^{1,6,8} and Toemme Noesselt^{3,7,8,*}

¹Cognition and Brain Plasticity Group, Bellvitge Biomedical Research Institute (IDIBELL), L'Hospitalet de Llobregat, Barcelona 08097, Spain

²Department of Basic Psychology, University of Barcelona, Campus Bellvitge, L'Hospitalet de Llobregat, Barcelona 08097, Spain

³Department of Biological Psychology, Otto von Guericke University Magdeburg, P.O. Box 4120, Magdeburg 39106, Germany

⁴School of Psychological Sciences, The University of Manchester, Zochonis Building, Brunswick Street, M13 9PL Manchester, UK

⁵Department of Neurology, Otto von Guericke University, Leipziger Straße 44, Magdeburg 39120, Germany

⁶Catalan Institution for Research and Advanced Studies (ICREA), Barcelona 08010, Spain

⁷Center for Behavioral Brain Sciences, Magdeburg 39120, Germany

Summary

The exact neural processes behind humans' drive to acquire a new language—first as infants and later as second-language learners—are yet to be established. Recent theoretical models have proposed that during human evolution, emerging language-learning mechanisms might have been glued to phylogenetically older subcortical reward systems [1], reinforcing human motivation to learn a new language. Supporting this hypothesis, our results showed that adult participants exhibited robust fMRI activation in the ventral striatum (VS)—a core region of reward processing [2]—when successfully learning the meaning of new words. This activation was similar to the VS recruitment elicited using an independent reward task. Moreover, the VS showed enhanced functional and structural connectivity with neocortical language areas during successful word learning. Together, our results provide evidence for the neural substrate of reward and motivation during word learning. We suggest that this strong functional and anatomical coupling between neocortical language regions and the subcortical reward system provided a crucial advantage in humans that eventually enabled our lineage to successfully acquire linguistic skills.

Results and Discussion

An important source of pleasure in our life depends on interpersonal communication [3, 4], and language is the most

effective cognitive device developed to this end. From our very first years, we are intrinsically motivated to learn new words and their meanings based on few incidental exposures [5]. Moreover, this motivation to learn is preserved throughout the lifespan, helping adults to acquire a second language [6, 7]. However, the exact mechanism behind the human drive to acquire communicative linguistic skills is yet to be established [8, 9].

It has been proposed at the theoretical level that an anatomical link between subcortical reward mechanisms and cortical learning systems might be essential to the development of language and communication [1]. Extending this rationale to the level of functional neuroanatomy, we hypothesized that human adults would show enhanced activity within subcortical reward and motivational circuitries when successfully learning new words. Moreover, enhanced anatomical and functional connectivity between cortical language and subcortical reward-related structures should also be observed. To test this hypothesis, we studied 36 adult participants by means of fMRI while performing two different tasks: a monetary gambling task [10], used to independently localize subcortical reward-related structures (Figure 1A), and a language-learning paradigm in which participants were requested to learn the meaning of new words from context [11] (Figure 1B; Figure S1 available online).

During the word-learning paradigm, participants were presented with two sentences ending in the same “new-word.” Participants were instructed to learn the new-word and its meaning only if both sentences lead to a congruent meaning (M+ condition) and to reject the new-words in which meaning between sentences was not congruent (M– condition). Non-readable (NR) sentences (meaningless strings of false font) were also presented as a visual control condition (Figure S1). Meaning acquisition was measured after each learning run was completed, and no feedback was given during fMRI data collection. Overall word learning was 60% ± 15.51% (mean, SD; chance level was 33%; see Supplemental Information) in the M+ condition; for the M– condition, the absence of coherent meaning was correctly reported in 61% ± 21.63% of the cases. To assess the persistence of learning, we performed the test again 30 min after the end of the scanning session. Participants still recognized the correct meaning of 68.02% ± 14.78% of M+ new-words previously learned (correct meaning associated during the test inside the scanner) and correctly rejected 67.78% ± 22.98% of M– new-words correctly rejected during the previous test.

The crucial whole-brain fMRI comparison between learned and nonlearned words during the congruent condition (M+ correct > M+ incorrect, taken at the second presentation of the new-word during the learning phase) yielded robust activations in subcortical bilateral ventral striatum (VS), confirming our hypothesis. Enhanced fMRI signals were also found in language-related cortical areas, including the left inferior frontal gyrus (IFG, Brodmann area [BA] 47), left inferior parietal gyrus (IPG, BA 40), and superior and middle frontal areas (BA 8; Figure 2, red-yellow regions; Table S1). In addition, we directly tested whether the VS regions engaged in successful language learning were also modulated by monetary gains, which are

⁸Co-senior author

*Correspondence: pabloripollesvidal@gmail.com (P.R.), toemme@med.ovgu.de (T.N.)

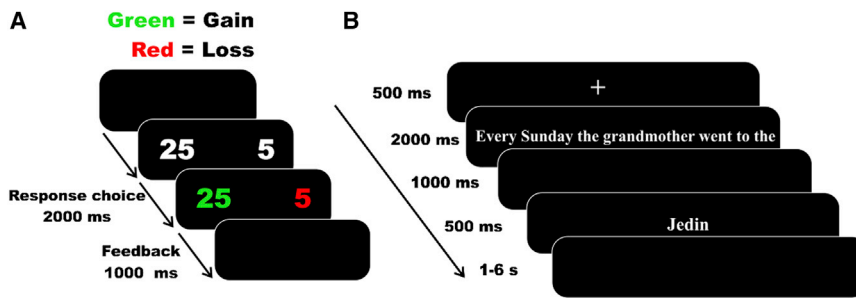


Figure 1. Experimental Setup

(A) Graphic depiction of a trial in the gambling task. Each trial started with the presentation of two numbers ([25 5] or [5 25]) for 2 s. Participants selected one of the two numbers, which then turned red (indicating a loss) or green (indicating a gain).

(B) Schematic overview of trials and condition in the word-learning paradigm. Each trial started with a fixation cross lasting 500 ms, followed by the first six German words of the sentence for 2 s and 1 s of dark screen. Finally, the new word was presented for 500 ms. Before the next trial, the screen remained dark for a variable

period between 1 s and 6 s (see also [Figure S1](#)). Participants completed ten fMRI sessions. Four pairs of sentences of each condition (M+, M−, NR) were presented per session (see [Figure S1](#)). Note that first sentences for each condition are always presented prior to and in a different order than second sentences.

well known to enhance VS fMRI activity [10]. Critically, a large overlap within the VS was found between the brain modulations related to the independent reward localizer task (gains > losses; blue areas in [Figures 2, 3](#), and [S2](#); [Table S2](#)) and to the successful meaning acquisition of a new-word. A subsequent conjunction analysis between both tasks further confirmed this conjoint activation (154 voxels within left VS, maximum $x = -10$, $y = 2$, $z = -12$; 45 voxels within right VS, maximum $x = 12$, $y = 4$, $z = -6$; $p < 0.05$, family-wise error (FWE) corrected). In order to demonstrate that new-words also activated the classical language network, we compared whole-brain fMRI activity for the learned new-words from the congruent condition against the nonreadable sentences (M+ correct > NR, taken at the second presentation of the new-word). This comparison yielded enhanced fMRI signals within the left IFG, left middle temporal lobe (using a $p < 0.001$ false discovery rate (FDR)-corrected threshold, the left hippocampus was also active), left IPG ([Table S3](#); [Figure S2](#)), and bilateral VS (conjunction analysis: left VS, $x = -12$, $y = 10$, $z = 0$, 119 voxels; right VS, $x = 10$, $y = 6$, $z = 0$, 70 voxels; $p < 0.05$, FWE corrected). Therefore, these results show how, during word learning, human adults recruited the VS—a key reward-related structure [2]—along with canonical neocortical language areas.

Subcortical reward-related areas, especially the VS, are activated by a wide range of rewarding stimuli, including money, odors, liquid reward, food, or sex [12]. In addition, the human reward system is also active in response to other high-order rewards (e.g., intellectual, artistic, or altruistic pleasures [13]), activities which are often mediated by language. Although our hypothesis postulates reward-related processes as the mental function behind the VS activity elicited during word learning, other possible interpretations must be accounted for: several reward-related structures are also activated by the novelty or salience of the stimuli [14–16], by attentional processes, by task difficulty, or by exertion of effort [17, 18]. Crucial to our interpretation, the design of our paradigm allows us to rule out these alternative explanations by including the incongruent (M−, no meaning extraction) condition: participants were equally prompted to complete the task for both M+ and M− conditions, and in both cases, a correct result could be reached (for M+, correct meaning assignment; for M−, correct rejection of the new-word, i.e., no meaning is graspable). Importantly, regarding the possible effort-related interpretation of the VS activation, previous studies using a similar paradigm have shown that incongruent conditions (M−) are more difficult and effortful to resolve than congruent

ones (M+), especially during the processing of the second sentence [19]. In order to rule out the aforementioned possible explanations, further region-of-interest (ROI) analyses focusing on the VS and including the M− condition were calculated. For these, independent VS ROIs defined by results from the independent monetary gambling task (gains > losses) were used to avoid circularity. The interaction between condition (M+ and M−) and type of response (correct and incorrect) during the presentation of the second sentence also yielded enhanced activation of the left VS (contrast: M+ correct – M+ incorrect > M− correct – M− incorrect; 63 voxels, maximum $x = -12$, $y = 12$, $z = 0$; $p < 0.05$, FWE corrected). The decomposition of this interaction ([Figure 3A](#), top row) revealed that the effects were driven solely by M+ correct responses: the VS was only engaged when participants learned the meaning of the new-word (no response was driven by correctly completing the M− condition). Moreover, when comparing brain activity for the correctly learned words of the M+ congruent condition with the correctly rejected new-words of the incongruent M− condition (contrast: M+ correct > M− correct, second presentation of the new-word), 584 voxels in the left VS (maximum $x = -10$, $y = 12$, $z = -4$) and 526 voxels in the right VS (maximum $x = 12$, $y = 4$, $z = -12$; [Figure 3A](#), bottom row; $p < 0.05$, FWE corrected) showed enhanced fMRI activation. These results strongly suggest that an explanation based on effort, attention, or difficulty seems unlikely.

As mentioned above, the VS is also related to novelty processing [14–16]. However, [Figures S2](#) and [3A](#) show that the second presentation of M− correct new-words or NR characters did not enhance fMRI signals within the VS, although both types of stimuli were also novel to the participants. Moreover, first presentation of a particular new-word (during first M+ and M− sentences) also failed to elicit activity within the VS: contrast estimates for first and second sentences in [Figure 3B](#) show that the VS only responded to second presentation of M+ correct trials, when the subject successfully learned the meaning of the new-word. All these further comparisons support our initial idea that the observed activation in the VS during word learning cannot be attributed to correct responding (around 60% in both M+ and M− conditions), novelty of the new-words, or attention-effort factors but rather to reward-related effects. Finally, one possible limitation of our interpretation could be related to the problem of reverse inference (inferring cognitive states solely from the activation of a particular brain area [20]). However, previous meta-analyses have shown that VS activation is linked to reward-related processes with a posterior probability of 0.90 [21].

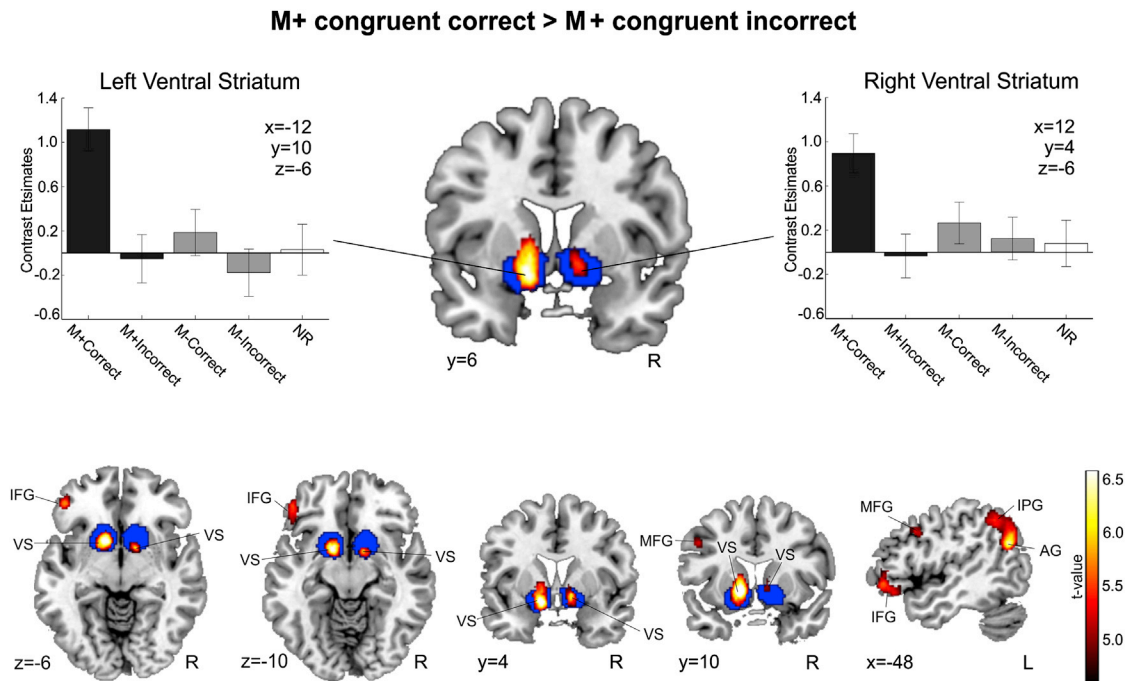


Figure 2. Whole-Brain fMRI Results: M+ Correct versus Incorrect Trials

In red-yellow, enhanced group-level fMRI signal for the learned versus nonlearned new-words during the congruent condition (M+ correct > M+ incorrect, trials taken at the second presentation of the new-word; $p < 0.05$, FWE corrected; see also Figure S2). The results for the gambling task (gain > loss, $p < 0.05$, FWE corrected) are overlaid in blue. Bar graphs indicate contrast estimates with 90% confidence intervals (proportional to percent signal change; black: M+, gray: M-, white: NR). Contrast estimates for M+ correct trials were significantly higher than for any other condition for both left and right VS (all $p < 0.001$). Neurological convention is used, with Montreal Neurological Institute (MNI) coordinates at the bottom left of each slice.

M+, congruent meaning extraction possible; M-, congruent meaning extraction impossible; NR, nonreadable sentences; VS, ventral striatum; IFG, inferior frontal gyrus; IPG, inferior parietal gyrus; AG, angular gyrus; MFG, middle frontal gyrus.

Following this rationale, we used NeuroSynth, a platform for large-scale, automated meta-analysis of fMRI data [22], to assess which was the most probable mental process behind the VS activation elicited during word learning. Using the maximum peaks in the left and right VS from all the comparisons, the meta-analysis tool showed that the term most associated with the majority of our peak activations was reward (see Supplemental Information).

Another important question in the present study is to what extent the observed activation in the VS is directly linked to the neocortical language regions engaged during word learning. To answer this, we conducted a whole-brain functional connectivity analysis using the VS as a seed point. This analysis revealed enhanced coupling of the left VS with the left IFG (including Broca's area; BA 44, 45, and 47), the left caudate nucleus, and the supplementary motor area in the context of learned versus nonlearned new-words during the congruent condition (M+ correct > M+ incorrect, taken at second sentence presentation; Figure 4A; Table S4). In accord with these observations, a recent study evaluating music and reward reported that increased functional connectivity between the VS and cortical regions (including the auditory cortex) predicted how music gained reward value [23]. Moreover, it has also been shown that atypical functional connectivity between speech and subcortical reward regions could underlie the reduced capacity of autistic children to experience speech as a rewarding episode, which ultimately might influence the correct development of their communicative skills [24].

Finally, using diffusion tensor imaging (DTI) in the same subjects, we also found evidence for the predicted anatomical link between cortical language and subcortical reward-related areas [1]: the strength of microstructural white matter anatomical connectivity within the VS predicted participants' language-learning success. Specifically, we found a correlation between the percentage of learned new-words during the M+ condition with the radial diffusivity (RD) and mean diffusivity (MD) values (DTI indices measuring white matter integrity) of the white matter pathways reaching the VS, as well as with the left uncinate fasciculus and the inferior fronto-occipital fasciculus (IFOF); see Figures 4B for RD and S3A for MD; Table S5). Decreases in RD are likely to reflect increased axonal diameter or increased myelination, which is correlated with enhanced action potential conduction and increased synchronization of information across connected regions, whereas MD is more related to tissue density [25, 26]. The uncinate fasciculus, which connects the anterior temporal pole with orbitofrontal cortex and also conveys information to the VS, has been linked to reward-related brain activity [10] and to the integration of emotion with behavior [27], whereas the IFOF has been linked to semantic processing [28]. Thus, both the anatomical and the functional connectivity provide converging evidence for a critical connection between subcortical reward-related areas and cortical regions during word learning.

Taken together, our results demonstrate that a crucial linguistic ability—i.e., creating a link between a new word and its meaning—also relies on subcortical networks, which are

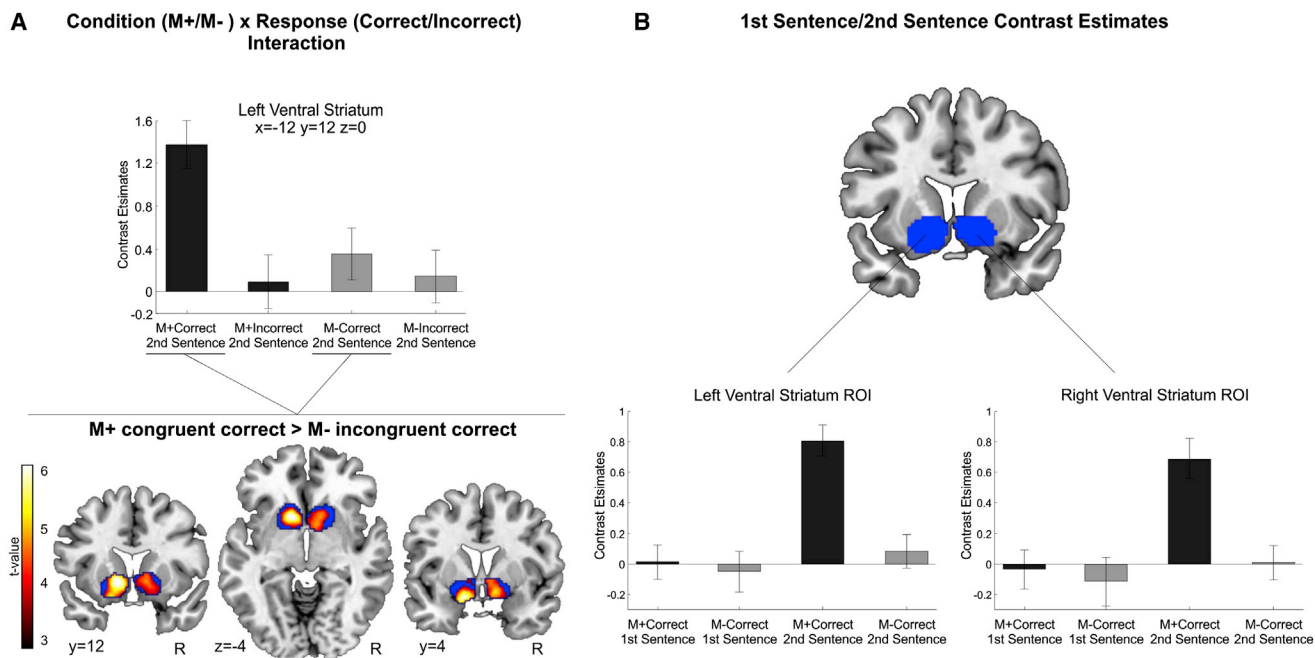


Figure 3. ROI Analysis Centered on the VS

The independent VS functional localizer (extracted from the gains > losses contrast of the independent monetary gambling task) was used for the ROI analyses in the word-learning task, and its activations are depicted in blue.

(A) Top row: contrast estimates (proportional to percent signal change; 90% confidence intervals are included; black: M+, gray: M-) of the peak voxel in the left VS cluster, which shows a significant interaction between condition (M+ and M-) and type of response (correct and incorrect) during second sentence presentation. Contrast estimates for M+ correct 2nd sentence trials were significantly higher than for any other condition (all $p < 0.001$). Bottom row: enhanced group-level fMRI signals for the learned new-words during the congruent condition versus the correctly rejected new-words from the incongruent condition (M+ correct > M- correct trials, taken at the second presentation of the new-word).

(B) No significant voxels within the VS were found when comparing the first sentence presentation against the second sentence presentation of correctly learned new-words during the congruent condition (M+ correct 1st sentence > M+ correct 2nd sentence) or of correctly rejected new-words during the incongruent condition (M- correct 1st sentence > M- correct 2nd sentence). Therefore, mean contrast estimates (proportional to percent signal change; 90% confidence intervals are included; black: M+, gray: M-) of first sentence presentation and second sentence presentation for both M+ and M- trials are presented (calculated by computing the mean signal within the whole left and right VS ROIs; blue areas). Once again, contrast estimates for M+ correct 2nd sentence trials were significantly higher than for any other condition in both left and right VS (all $p < 0.001$). Neurological convention is used, with MNI coordinates at the bottom left of each slice. All images are reported at a FWE-corrected $p < 0.05$ threshold, with 30 voxels of spatial extent.

M+, congruent meaning extraction possible; M-, congruent meaning extraction impossible.

instrumental in regulating adaptive behavior [29]. Indeed, some forms of communication in other species (e.g., songbird learning) seem to be specifically connected to mesolimbic dopaminergic reward signals [30]. Moreover, songbirds possess area X, a striatal nucleus analog to the human basal ganglia, which is crucial for song learning in both young and adult birds [31]. In addition, area X receives midbrain dopaminergic projections [31] and shows increased FoxP2 (a gene associated in humans with language and speech) expression during periods of learning [32]. Thus, consistent with the songbird's instinct to learn to sing [30], human beings also display an urge to acquire language [9], and both adaptive behaviors might be driven by similar, phylogenetically older, reward-related circuits.

Following an evolutionary perspective, the initial development of a “protolanguage” in human ancestors was probably crucial for sharing information and emotions, improving success on reward-seeking behaviors, bonding social groups, and increasing the chances of group survival in competitive environments [8]. This protolanguage might have been naturally selected and reinforced by interlinking it with ancient brain mechanisms involved in hedonic reward processing [3, 4]. This hypothesis favors current perspectives, which emphasize that language was an evolutionary innovation

built on different preexisting cognitive capabilities, probably “hijacking” old evolutionary solutions as reward-reinforcement mechanisms. Language learning could then rely on the interaction between general-domain cognitive abilities (e.g., theory of mind, associative learning, analogical processing, or joint attention) and more-specific linguistic ones [4, 6, 7, 33].

In conclusion, we provide compelling evidence for the recruitment of nonlinguistic subcortical reward mechanisms during word learning, which might support one of our primal urges: the desire to acquire language and to communicate.

Experimental Procedures

Meaning Acquisition fMRI Experiment

Stimuli consisted of 80 pairs of seven-word-long German sentences ending in a new-word that stood for a noun. New-words respected the phonotactic rules of German and were built by changing one or two letters of an existing word. The current experiment disambiguated the multiple meanings—therefore enabling the acquisition of the meaning of the new-word—in only half of the pairs of sentences (M+ condition; e.g., sentence 1: “Every Sunday the grandmother went to the jedin.” Sentence 2: “The man was buried in the jedin.” *Jedin* means graveyard and is congruent with both the first and second sentence; Figure S1, first row). For the other

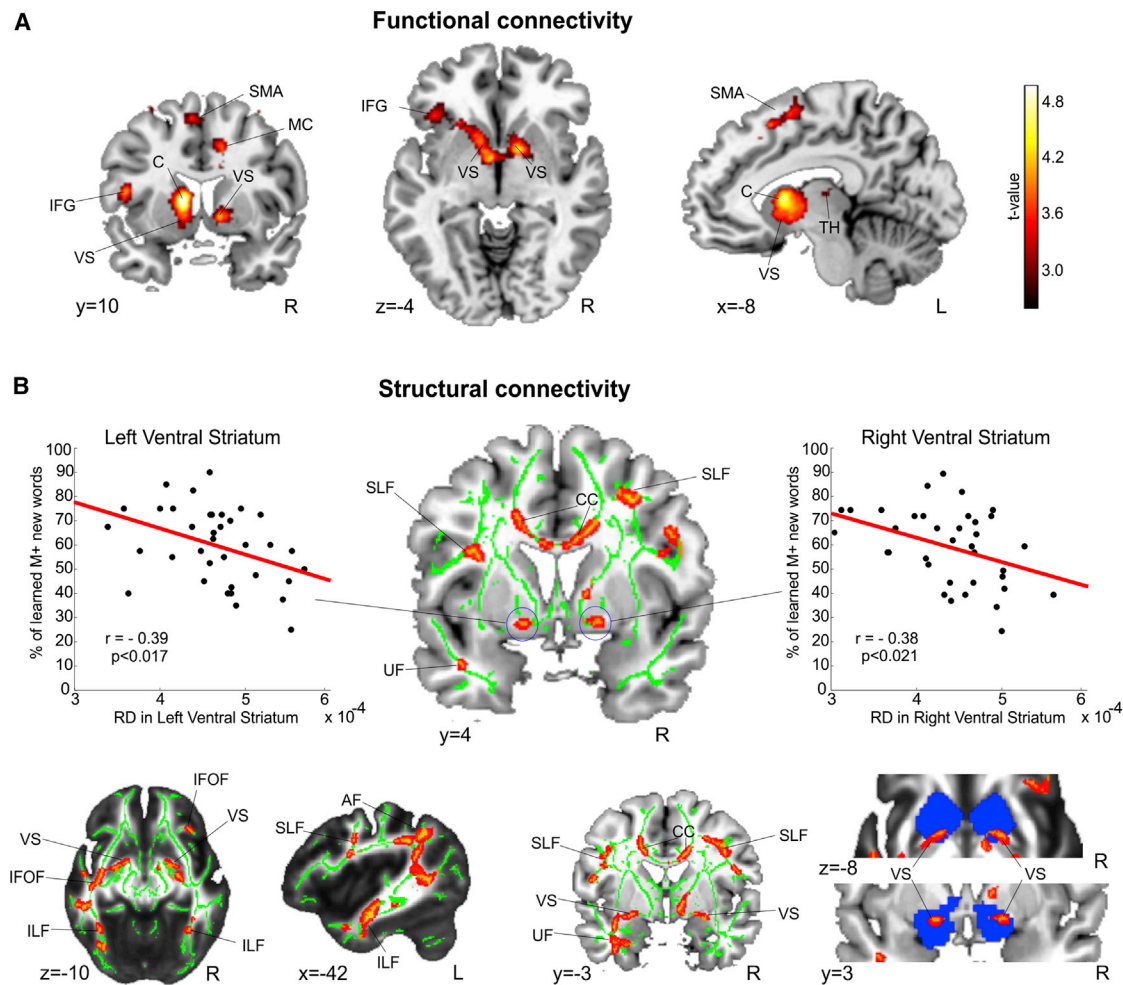


Figure 4. Connectivity Results

(A) Higher coupling (red-yellow) with the left VS in the context of learned versus nonlearned new-words during the congruent condition (M+ correct > M- incorrect; $p < 0.05$, FWE corrected at the cluster level, plus $p < 0.005$ at the voxel level).

(B) White matter pathways correlating with the percentage of learned words for the congruent condition (red-yellow, $p < 0.05$, FWE corrected) over the mean group skeleton depicted in green (see also Figure S3). The results for the gambling task (gain > loss) are overlaid in blue. In coronal slices, results are displayed on a canonical T1-weighted template for improved localization of the basal ganglia. For axial and sagittal slices, the FMRIB58_FA template is used for better visualization of the white matter pathways. The scatterplots display the correlation between the mean RD value of the voxels entering the left and right VS and the percentage of learned words. Neurological convention is used in both images, with MNI coordinates at the bottom left of each slice.

VS, ventral striatum; IFG, inferior frontal gyrus; C, caudate; TH, thalamus; SMA, supplementary motor area; MC, middle cingulum; SLF, superior longitudinal fasciculus; UF, uncinate fasciculus; IFOF, inferior fronto-occipital fasciculus; ILF, inferior longitudinal fasciculus; AF, arcuate fasciculus; CC, corpus callosum.

40 pairs, second sentences were scrambled so that they no longer matched their original first sentences. In this case, the new-word was not associated with a congruent meaning across the sentences (M- condition; e.g., sentence 1: "Every night the astronomer watched the heutil." Moon is one possible meaning of *heutil*. Sentence 2: "In the morning break co-workers drink heutil." Coffee is now one of the possible meanings of *heutil*, which is not congruent with the first sentence; Figure S1, second row). These constituted the M- condition in which meaning acquisition was not possible. In addition, NR sentences created from the M+ and M- stimuli by converting each letter into a symbol were also presented as a control (Figure S1, third row).

After finishing the meaning-acquisition task, participants completed two runs of a standard event-related gambling task [10], which was used to independently localize subcortical reward-related brain structures [34] (see Supplemental Information). DTI images were acquired during a second session on a different scanner better equipped for DTI acquisition (see Supplemental Information).

This study was approved by the Ethics Committee of the Hospital Universitari de Bellvitge, Barcelona.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, three figures, and five tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.09.044>.

Author Contributions

P.R., J.M.-P., A.M.-M., A.R.-F., and T.N. designed the research. P.R., U.H., and C.T. performed the research. P.R. analyzed the data. P.R., J.M.-P., A.M.-M., U.H., C.T., H.-J.H., A.R.-F., and T.N. wrote the manuscript.

Acknowledgments

We thank T. Pohl, D. Scheermann, and K. Moehring for their help scanning the participants and A. Waite for editing the language of this manuscript. The present project has been funded by the Spanish government (Ministry of Economy and Competitiveness [MINECO] Grant PSI2011-29219 to A.R.-F., MINECO Grant PSI2012-37472 to J.M.-P., and Formación

Profesorado Universitario program AP2010-4179 to P.R.) and by the Deutsche Forschungsgemeinschaft (SFB-TR31/TPA8 to T.N and SFB-779/TPA11 to H.-J.H).

Received: July 9, 2014

Revised: September 3, 2014

Accepted: September 17, 2014

Published: October 23, 2014

References

1. Syal, S., and Finlay, B.L. (2011). Thinking outside the cortex: social motivation in the evolution and development of language. *Dev. Sci.* **14**, 417–430.
2. Haber, S.N., and Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology* **35**, 4–26.
3. Panksepp, J. (1998). *Affective Neuroscience: The Foundations of Human and Animal Emotions* (Oxford: Oxford University Press).
4. Tommasello, M. (2003). *Constructing a Language: A Usage-Based Theory of Language Acquisition* (Cambridge: Harvard University Press).
5. Carey, S., and Bartlett, E. (1978). Acquiring a single new word. *Proceedings of the Stanford Child Language Conference* **15**, 17–29.
6. Davis, M.H., and Gaskell, M.G. (2009). A complementary systems account of word learning: neural and behavioural evidence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 3773–3800.
7. Rodríguez-Fornells, A., Cunillera, T., Mestres-Missé, A., and de Diego-Balaguer, R. (2009). Neurophysiological mechanisms involved in language learning in adults. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 3711–3735.
8. Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex* (London: John Murray).
9. Fitch, W.T. (2010). *The Evolution of Language* (Cambridge: Cambridge University Press).
10. Camara, E., Rodríguez-Fornells, A., and Münte, T.F. (2010). Microstructural brain differences predict functional hemodynamic responses in a reward processing task. *J. Neurosci.* **30**, 11398–11402.
11. Mestres-Missé, A., Rodríguez-Fornells, A., and Münte, T.F. (2010). Neural differences in the mapping of verb and noun concepts onto novel words. *Neuroimage* **49**, 2826–2835.
12. Schultz, W. (2007). Behavioral dopamine signals. *Trends Neurosci.* **30**, 203–210.
13. Berridge, K.C., and Kringelbach, M.L. (2008). Affective neuroscience of pleasure: reward in humans and animals. *Psychopharmacology (Berl.)* **199**, 457–480.
14. Guitart-Masip, M., Bunzeck, N., Stephan, K.E., Dolan, R.J., and Düzel, E. (2010). Contextual novelty changes reward representations in the striatum. *J. Neurosci.* **30**, 1721–1726.
15. Zaehle, T., Bauch, E.M., Hinrichs, H., Schmitt, F.C., Voges, J., Heinze, H.J., and Bunzeck, N. (2013). Nucleus accumbens activity dissociates different forms of salience: evidence from human intracranial recordings. *J. Neurosci.* **33**, 8764–8771.
16. Rauschecker, J.P., Leaver, A.M., and Mühlau, M. (2010). Tuning out the noise: limbic-auditory interactions in tinnitus. *Neuron* **66**, 819–826.
17. Maunsell, J.H. (2004). Neuronal representations of cognitive state: reward or attention? *Trends Cogn. Sci.* **8**, 261–265.
18. Boehler, C.N., Hopf, J.M., Krebs, R.M., Stoppel, C.M., Schoenfeld, M.A., Heinze, H.J., and Noesselt, T. (2011). Task-load-dependent activation of dopaminergic midbrain areas in the absence of reward. *J. Neurosci.* **31**, 4955–4961.
19. Mestres-Missé, A., Münte, T.F., and Rodríguez-Fornells, A. (2014). Mapping concrete and abstract meanings to new words using verbal contexts. *Second Lang. Res.* **30**, 191–223.
20. Poldrack, R.A. (2011). Inferring mental states from neuroimaging data: from reverse inference to large-scale decoding. *Neuron* **72**, 692–697.
21. Ariely, D., and Berns, G.S. (2010). Neuromarketing: the hope and hype of neuroimaging in business. *Nat. Rev. Neurosci.* **11**, 284–292.
22. Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., and Wager, T.D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nat. Methods* **8**, 665–670.
23. Salimpoor, V.N., van den Bosch, I., Kovacevic, N., McIntosh, A.R., Dagher, A., and Zatorre, R.J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science* **340**, 216–219.
24. Abrams, D.A., Lynch, C.J., Cheng, K.M., Phillips, J., Supekar, K., Ryali, S., Uddin, L.Q., and Menon, V. (2013). Underconnectivity between voice-selective cortex and reward circuitry in children with autism. *Proc. Natl. Acad. Sci. USA* **110**, 12060–12065.
25. Zatorre, R.J., Fields, R.D., and Johansen-Berg, H. (2012). Plasticity in gray and white: neuroimaging changes in brain structure during learning. *Nat. Neurosci.* **15**, 528–536.
26. López-Barroso, D., Catani, M., Ripollés, P., Dell'Acqua, F., Rodríguez-Fornells, A., and de Diego-Balaguer, R. (2013). Word learning is mediated by the left arcuate fasciculus. *Proc. Natl. Acad. Sci. USA* **110**, 13168–13173.
27. Catani, M., Dell'acqua, F., and Thiebaut de Schotten, M. (2013). A revised limbic system model for memory, emotion and behaviour. *Neurosci. Biobehav. Rev.* **37**, 1724–1737.
28. Friederici, A.D., and Gierhan, S.M. (2013). The language network. *Curr. Opin. Neurobiol.* **23**, 250–254.
29. O'Connell, L.A., and Hofmann, H.A. (2011). The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. *J. Comp. Neurol.* **519**, 3599–3639.
30. Margoliash, D., and Nusbaum, H.C. (2009). Language: the perspective from organismal biology. *Trends Cogn. Sci.* **13**, 505–510.
31. Mooney, R. (2009). Neurobiology of song learning. *Curr. Opin. Neurobiol.* **19**, 654–660.
32. Scharff, C., and Haesler, S. (2005). An evolutionary perspective on FoxP2: strictly for the birds? *Curr. Opin. Neurobiol.* **15**, 694–703.
33. Bloom, P. (2000). *How Children Learn the Meanings Of Words* (Cambridge: MIT Press).
34. Kriegeskorte, N., Simmons, W.K., Bellgowan, P.S., and Baker, C.I. (2009). Circular analysis in systems neuroscience: the dangers of double dipping. *Nat. Neurosci.* **12**, 535–540.

Current Biology, Volume 24

Supplemental Information

**The Role of Reward in Word Learning
and Its Implications
for Language Acquisition**

**Pablo Ripollés, Josep Marco-Pallarés, Ulrike Hielscher, Anna Mestres-Missé, Claus
Tempelmann, Hans-Jochen Heinze, Antoni Rodríguez-Fornells, and Toemme Noesselt**

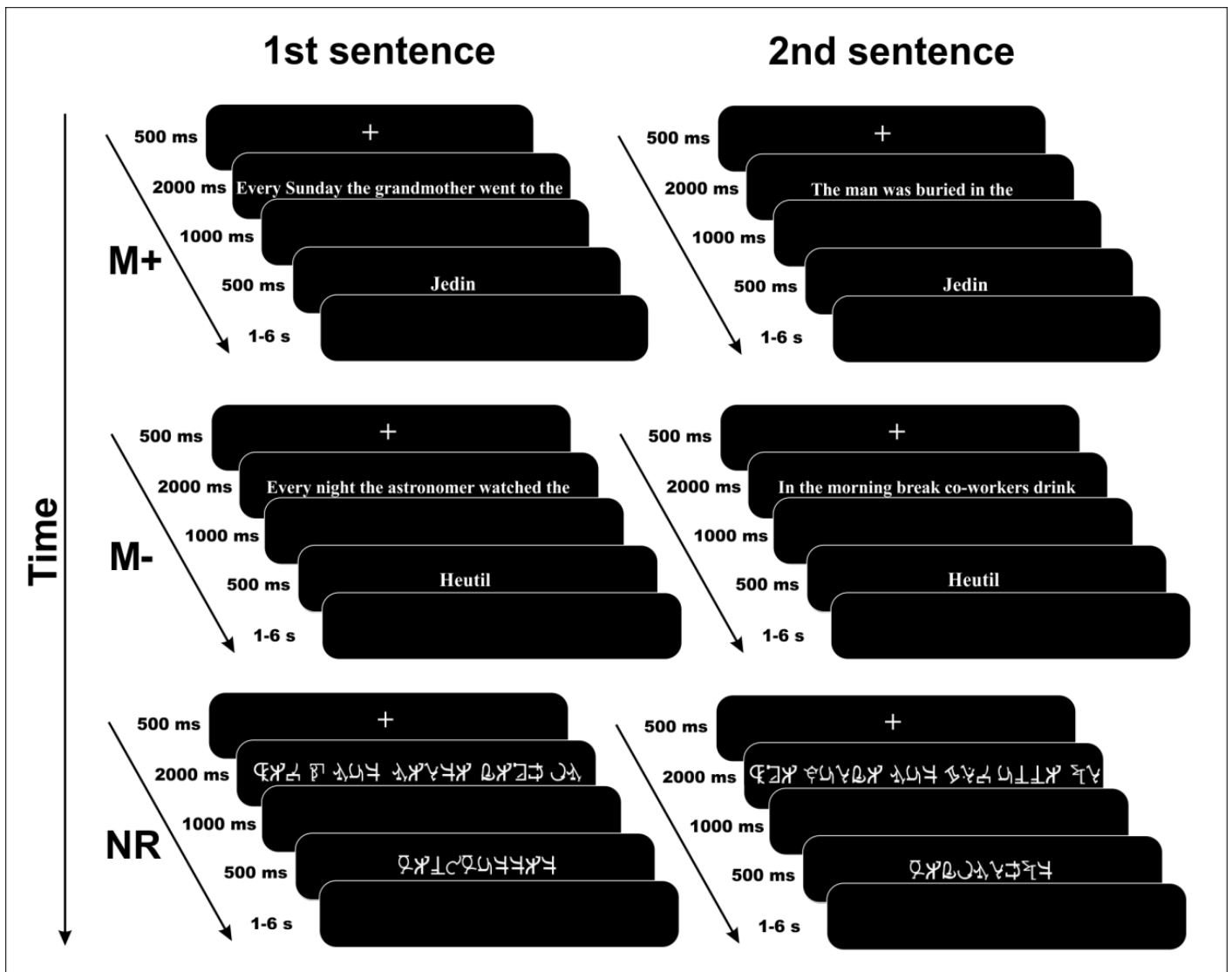


Figure S1 (Related to Figure 1b). Schematic overview of trials and conditions in the word-learning paradigm. Each trial started with a fixation cross lasting 500 ms followed by the 6 first German words of the sentence for 2 seconds and 1 second of dark screen. Finally, the new-word was presented for 500 ms. Before the next trial, the screen remained dark for a variable period between 1 and 6 seconds. Note that first sentences for each condition are always presented prior to and in a different order than second sentences. M+ sentences (congruent meaning acquisition possible during second presentation); M- sentences (congruent meaning acquisition impossible during second presentation); NR sentences (no meaning acquisition possible).

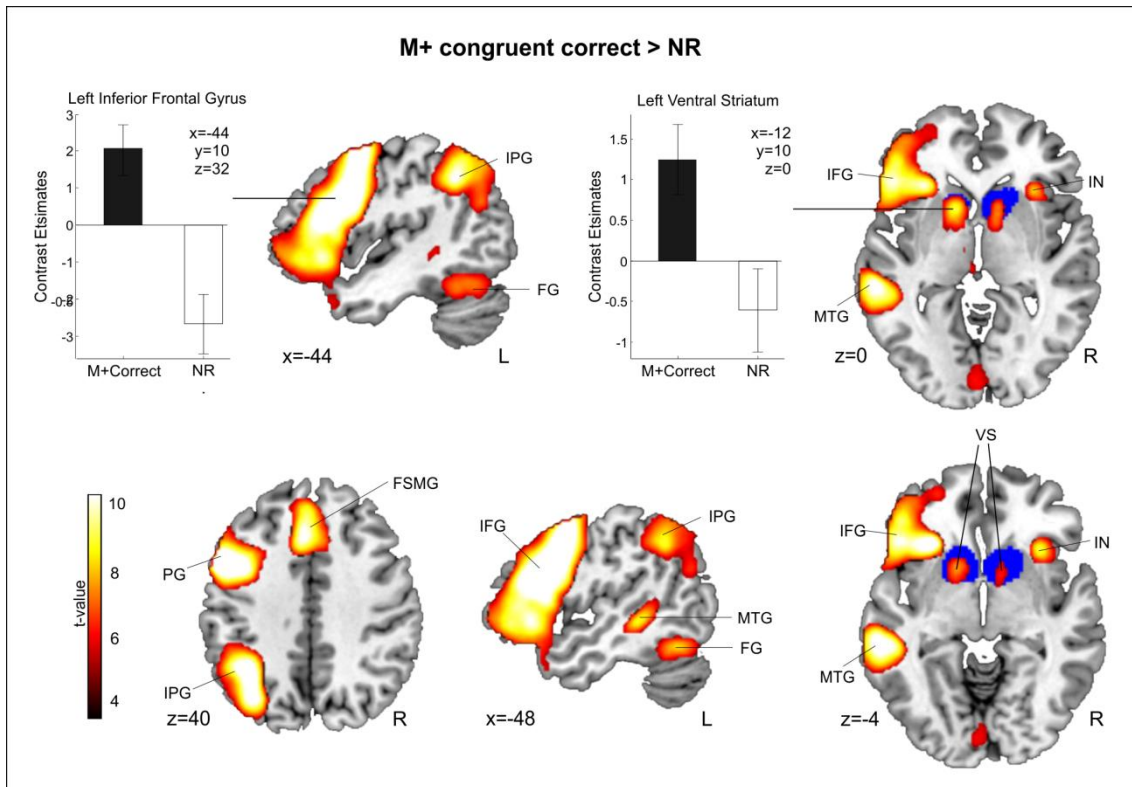


Figure S2 (Related to Figure 2). Whole brain group fMRI results: M+ correct versus NR trials. In red-yellow, enhanced group-level fMRI-signals for the learned new-words from the congruent condition versus the non-readable sentences (M+ correct > NR trials taken at the second presentation of the new-word, $p < 0.05$ FWE-corrected). Bar graphs indicate contrast estimates with 90% confidence intervals (proportional to percent signal change) for the maximum peak in the left inferior frontal and left VS (black for M+, white for NR). Contrast estimates for M+ correct trials were significantly higher than NR trials in both left VS and left IFG, including Broca's area (all $p < 0.001$). Neurological convention is used with MNI (Montreal Neurological Institute) coordinates at the bottom left of each slice. M+, congruent meaning extraction possible; NR, Non-Readable sentences; IFG, Inferior Frontal Gyrus; IPG, Inferior Parietal Gyrus; MTG, Middle Temporal Gyrus; FG, Fusiform Gyrus. PG, Precentral Gyrus; IN, Insula; FSMG, Frontal Superior Medial Gyrus.

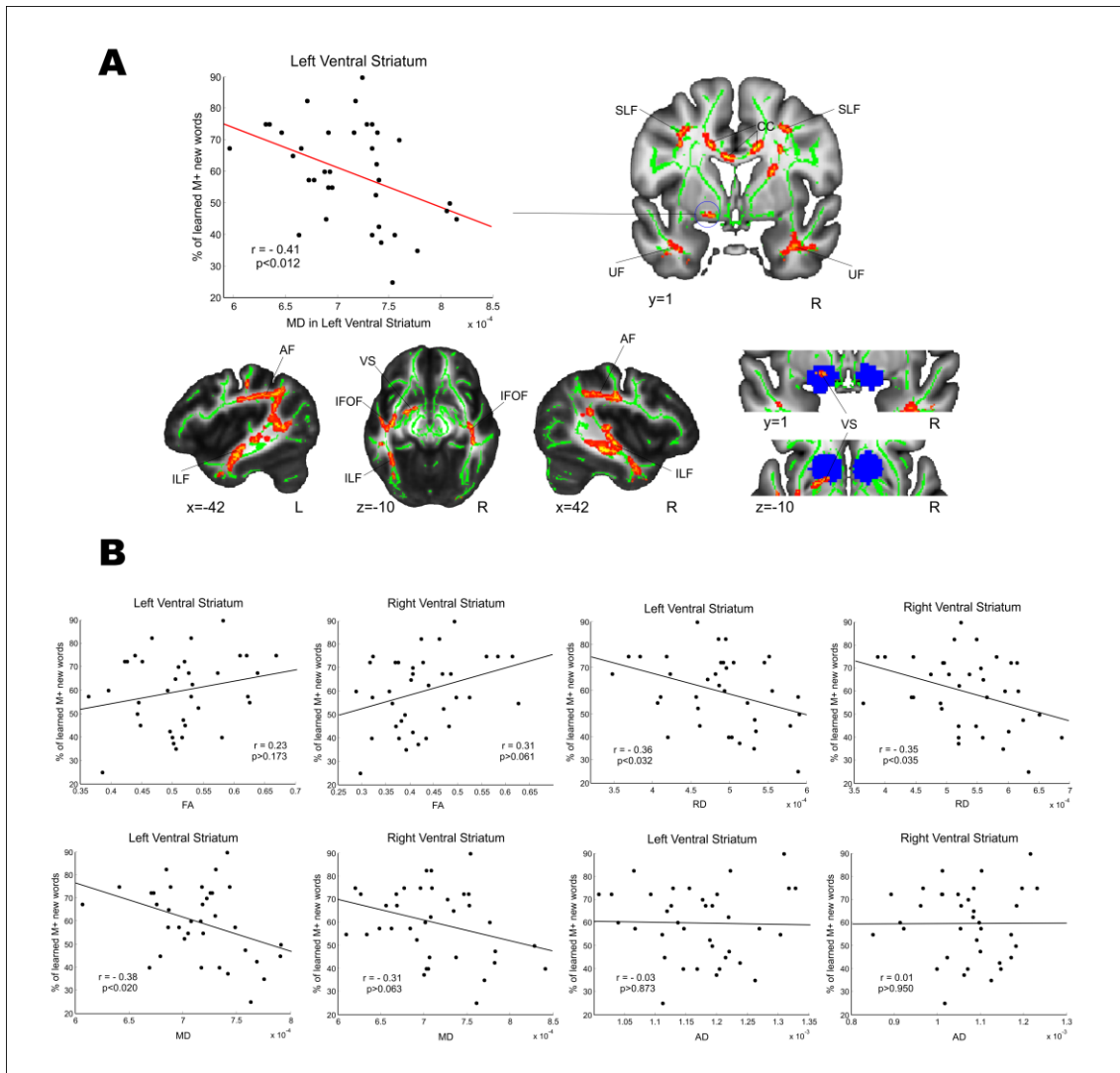


Figure S3 (Related to Figure 4b). Supplemental Connectivity results. **A.** Mean Diffusivity white matter pathways correlating with the percentage of learned words for the congruent condition (red-yellow, $p < 0.05$ FWE-corrected) over the mean group skeleton (green). The results for the gambling task (gain > loss) are overlaid in blue. The scatter plot displays the correlation between the mean MD value of the voxels entering the left VS and the percentage of learned words. Neurological convention is used with MNI coordinates at the left bottom of each slice. **B.** Results for the ROI-DTI analysis focusing on the TBSS tracks entering the VS. Scatter plots show the correlations between mean RD, MD, AD and FA of voxels entering the left and right VS and the percentage of learned words for the M+ condition. Voxels in VS were independently identified using the results from the gambling task. MD, Mean Diffusivity; FA, Fractional Anisotropy; RD, Radial Diffusivity; AD, Axial Diffusivity; VS, Ventral Striatum; SLF, Superior Longitudinal Fasciculus; UF, Uncinate Fasciculus; IFOF, Inferior Fronto-Occipital Fasciculus; ILF, Inferior Longitudinal Fasciculus; AF, Arcuate Fasciculus; CC, Corpus Callosum.

Table S1 (Related to Figure 2). Whole brain effects of meaning acquisition on fMRI-signal: M+ correct versus M+ incorrect trials. Group-level fMRI local maxima for the learned vs. non-learned new-words in the congruent condition (M+ correct > M+ incorrect trials taken at the second presentation of the new-word; see also red-yellow regions in Figure 2). Results are reported at $p < 0.05$ threshold (FWE-corrected, extent threshold: $k > 30$ voxels) using MNI coordinates. BA, Brodmann Area.

M+ congruent correct > M+ congruent incorrect for 2nd presentations

Anatomical area	Coordinates	Cluster Size	t-value
Left Ventral Striatum	-12 10 -6	591	7.11
Left Angular Gyrus (BA 39); Left Inferior Parietal Gyrus (BA 40)	-48 -64 26 -36 -70 50	1350	6.52 5.26
Left Superior Medial Frontal Gyrus (BA 8)	-6 42 42	273	6.30
Right Ventral Striatum	12 4 -6	204	6.18
Left Inferior Frontal Gyrus (BA 47)	-46 40 -8	269	5.82
Left Precuneus (BA 23)	-2 -56 12	63	5.69
Left Superior Frontal Gyrus (BA 9,10)	-12 60 32	263	5.68
Left Thalamus	-2 -20 2	33	5.37
Left Middle Frontal Gyrus (BA 9)	-46 10 36	88	5.32

Table S2 (Related to Figures 2 and 3). Whole brain effects of reward on fMRI-signal. Enhanced group level fMRI-signals for the gain && boost-gain > loss && boost-loss contrast (see also blue regions in Figures 2, 3 and S2) thresholded at a $p < 0.05$ (FWE-corrected, extent threshold: $k > 30$ voxels) using MNI coordinates. BA, Brodmann Area.

Effects of gains > losses

Anatomical area	Coordinates	Cluster Size	t-value
Left Ventral Striatum	-12 10 -8	708	10.62
Right Ventral Striatum	12 10 -6	715	9.55
Right Cerebellum	42 -72 -44	58	6.41
Right Middle Occipital Gyrus (BA 19)	30 -86 6	67	6.38

Table S3 (Related to Figures 2 and S2). Whole brain effects of meaning acquisition on fMRI signal: M+ correct versus NR trials. Group-level local maxima for the learned new-words from the congruent condition versus the non-readable sentences (M+ correct > NR comparison, taken at the second presentation of the new-word; see also red-yellow regions on Figure S2) using a $p < 0.05$ (FWE-corrected, extent threshold: $k > 30$ voxels) and MNI coordinates. BA, Brodmann Area.

M+ congruent correct > NR for 2nd presentations

Anatomical area	Coordinates	Cluster Size	t-value
Left Precentral Gyrus (BA 9);	-44 10 32	11167	13.93
Left Inf. Frontal Gyrus (including Broca's area; BA 44,45,46,47);	-50 22 22		13.83
Left Middle Frontal Gyrus (BA 8);	-46 10 36		13.64
Supplementary Motor Area (BA 6);	-2 18 50		11.78
Left Insula (BA 13);	-32 24 -4		11.67
Left Superior Medial Frontal Gyrus (BA 8)	-2 22 42		11.02
Right Cerebellum	10 -74 -28	2997	12.24
Left Inferior Parietal Gyrus (BA 40);	-34 -60 42	3007	11.91
Left Angular Gyrus (BA 39);	-36 -60 42		11.70
Left Superior Parietal Gyrus (BA 7)	-32 -62 44		10.95
Left Middle Temporal Gyrus (BA 21,22)	-60 -34 -2	1540	11.40
Left Ventral Striatum;	-12 10 0	854	8.96
Left Caudate;	-12 4 10		7.15
Left Thalamus;	-4 -18 4		6.01
Left Putamen;	-18 4 6		5.96
Left Globus Pallidum	-14 -2 2		5.29
Right Insula (BA 13)	32 22 -4	390	8.70
Left Inferior Temporal Gyrus (BA 20);	-48 -58 -18	632	7.92
Left Fusiform Gyrus (BA 37)	-38 -38 -24		5.07
Right Ventral Striatum;	12 10 2	341	7.19
Right Caudate	12 8 10		6.66
Right Inferior Frontal Gyrus (BA 9,46);	56 28 28	424	6.86
Right Middle Frontal Gyrus (BA 9)	54 30 32		6.40
Left Calcarine (BA 30)	-2 -58 10	82	5.81
Left Calcarine (BA 18)	0 -92 2	249	5.80

Table S4 (Related to Figure 4a). Changes in interregional functional connectivity of the fMRI-data: local maxima for the functional coupling with the VS seed specifically testing for higher coupling in the context of the learned vs. non-learned new-words during the congruent condition (M+ correct > M+ incorrect trials, taken at the second presentation of the new-word; see also red-yellow regions of Figure 4a). Results are reported at $p < 0.05$ FWE corrected threshold at the cluster level with an auxiliary threshold of $p < 0.005$ at the voxel level. BA, Brodmann Area.

Anatomical area	Coordinates	Cluster Size	t-value
Left Ventral Striatum;	-12 6 6	2007	5.36
Left Caudate;	-12 8 10		4.97
Right Ventral Striatum;	12 6 -2		4.70
Left Inferior Frontal Gyrus (including Broca's area; BA 44,45,47);	-46 8 14		4.09
Left Thalamus	-14 -6 6		4.09
Bilateral Supplementary Motor Area (BA 6);	-8 16 54	945	4.46
Right Middle Cingulum (BA 32)	12 10 40		4.21

Table S5 (Related to Figure 4b and S3a). Relationship of subject-specific structural connectivity strength with subject-specific behavioral effect: summary of local maxima (radial and mean diffusivity and fractional anisotropy) of white matter pathways significantly correlated with the percentage of learned new-words during the congruent condition (M+) in the whole brain TBSS analysis (see also red-yellow areas in Figures 4b and S3a). The correlations with axial diffusivity yielded no significant results. Results are shown at a FWE-corrected $p < 0.05$ value using threshold-free cluster enhancement and a nonparametric permutation test with 5000 permutations. MNI coordinates are used.

Radial Diffusivity	Coordinates	p-value	Mean Diffusivity	Coordinates	p-value
Right body of corpus callosum	18 -26 35	0.010	Right body of corpus callosum	10 -30 24	0.009
Left body of corpus callosum	-15 -10 33	0.011	Left body of corpus callosum	-11 -36 24	0.009
Left Ventral Striatum	-16 1 -10	0.012	Left Superior Longitudinal fasciculus/Arcuate fasciculus	-42 -34 32	0.010
Left Uncinate fasciculus	-35 -5 -13	0.012	Right Superior Longitudinal fasciculus/Arcuate fasciculus	44 -16 30	0.012
Left Superior Longitudinal fasciculus/Arcuate fasciculus	-37 -36 31	0.012	Right Inferior Fronto-Occipital fasciculus	39 -18 -9	0.040
Left Inferior Longitudinal fasciculus	-43 -18 -17	0.012	Right Uncinate fasciculus	37 -1 -21	0.042
Right Inferior Fronto-Occipital fasciculus	33 -25 2	0.027	Left Inferior Fronto-Occipital fasciculus	-38 -33 1	0.043
Right Inferior Longitudinal fasciculus	33 -53 -11	0.029	Left Inferior Longitudinal fasciculus	-48 -23 -18	0.043
Right Superior Longitudinal fasciculus	49 -9 24	0.033	Left Uncinate fasciculus	-38 -9 -17	0.043
Left Inferior Fronto-Occipital fasciculus	-36 -11 -10	0.034	Right Inferior Longitudinal fasciculus	41 -2 -26	0.043
Right Ventral Striatum	17 3 -8	0.049	Left Ventral Striatum	-16 1 -9	0.048
Fractional Anisotropy	Coordinates		p-value		
Right body of Corpus Callosum	17 -17 34		0.031		

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Participants

Forty German speakers (mean age, $SD = 24.78 \pm 4.7$, 18 women) were recruited from the student population at Otto-von-Guericke University (Magdeburg, Germany). All participants were right handed, gave written consent, and were paid or received course credits for their participation in accord with local ethics. Four subjects were later excluded due to extensive head movements (see below for details).

Meaning acquisition fMRI experiment

Stimuli were presented using the Psychophysics Toolbox 3.09 [S1] and Matlab version R2011b (7.13.0.564, 32 bit). The nouns to be learned were selected from the CELEX database (mean frequency 46.5 per million, standard deviation 22.85 [S2]). Two sentences for each noun were built with an increasing degree of contextual constraint [S3-S7]. Mean cloze probability (the proportion of people who complete a particular sentence fragment with a particular word) was $14.88 \pm 7.6\%$ for the first sentence (low constraint), and $89.1 \pm 9.2\%$ for the second (high constraint). These cloze probability patterns were assessed by presenting each sentence in isolation to 150 participants [S3]. Before entering the scanner, participants were instructed to learn the meaning of a new-word only if both sentences lead to a congruent meaning (M+) and to reject the new-words in which learning was not possible (M-). To ensure that both stimulus types were equally comparable, participants were told that it was just as crucial to learn the words of the M+ condition as it was to correctly reject the new-words from the M- condition. For the NR conditions, participants were asked to look at the symbols and try to “read” them. No motor responses were required during the learning runs. Participants were aware that they would complete a test after each learning run and were

instructed on how to answer it. It was made explicit that they would assess both M+ and M- new-words during these test phases. However, only after the fMRI task ended were they told that they had to complete an additional recognition test. All participants completed a training block before entering the scanner in order to familiarize them with the task and the recognition test.

To allow for equilibration, each run started with a fixation cross lasting for 8 seconds. Each of the 20 trials of a run (10 first sentences, 10 second sentences) started with a fixation cross lasting 500 ms, continued with the 6 first German words of the sentence presented for 2 seconds, and were followed by a 1 second duration dark screen (Figure 1b). Finally, the new-word was presented for 500 ms. All words were placed in the middle of a black screen with a font size of 22 and in white color. Before the next trial started, the screen remained dark for a variable period between 1 and 6 seconds (Poisson distribution [S8]).

Participants performed 10 consecutive fMRI runs of an event-related design in each of which 4 pairs of M+, 4 pairs of M- and 2 pairs of NR conditions were presented. Therefore, a total of 40 new-words from the M+ and 40 from the M- conditions were presented during the whole experiment. In order to achieve an ecologically valid paradigm, presentation of the first and second sentences with the same new-word at the end were separated in time. First, the 4 first sentences of each of the M+ and M- conditions (a total of eight new-words) plus 2 ‘sentences’ of the NR condition were presented in a pseudo-randomized order (e.g., M+1A, M-1A, M-1B, NR1A, M-1C, M+1B, M+1C, NR1B, M+1D, M-1D). Then, the second ‘pair’ sentences of both M+ and M- conditions were presented (i.e. second presentation of the identical eight new-words), again in a pseudo-randomized order (Figure 1b) including 2 ‘sentences’ of the NR condition (e.g., M-2C, M-2B, NR2A, M+2B, M+2D, M-2D, M+2C, M+2A, M-2A,

NR2B). The temporal order of the different new-words during first sentence presentation was not related in any systematic way to the order of presentation of the same new-words for their second sentence.

After each of the 10 learning runs, participants had to complete a short recognition test. Participants were presented with a new-word at the centre of the screen with two possible meanings below, one on the left and one on the right. In each test, all 4 M+ and 4 M- new-words presented during a learning run were tested in a pseudo-randomized order. If the new-word tested did not have a congruent meaning associated between the first and the second sentence, and thus learning was not possible (M- condition), participants had to press a button located in their left hand. In this case, the two possible meanings offered in the test served as foils: one was the meaning evoked by the second sentence of the M- new-word being tested (e.g., "coffee" when testing "Heutil", following the example on Figure S1); the other word shown was the meaning evoked by another second sentence presented in the same run as the new-word being tested. Instead, if the new-word tested had a consistent meaning through the first and second sentence, and thus learning was possible (M+ condition), participants had to select the correct meaning using a two-button pad placed on their right hand. In this case, one of the two possible meanings was correct and the other, which served as a foil, was the meaning of another new-word presented in the same run. Therefore, chance level was at 33% as for both M+ and M- conditions three response options were available (no meaning, meaning on the left, meaning on the right).

As stated in the main text, overall word learning was $60 \pm 15.51\%$ in the M+ condition. For M+ new words, in $31 \pm 14.06\%$ of the cases participants incorrectly pressed the button in their left hand (mistakenly indicating that the new-word being tested had no congruent meaning). In the remaining $9 \pm 7.98\%$ of the test trials, they

chose the incorrect meaning that served as a foil (it was the meaning evoked by another second sentence not related to the new-word being tested). For the M- condition, the absence of coherent meaning was correctly reported in 61 ± 21.63 % of the cases. In 29 ± 17.32 % of the cases participants incorrectly selected the meaning evoked by the second sentence of the new-word being tested (e.g., "coffee" when testing "Heutil", following the example on Figure S1). In the remaining 10 ± 9.50 % of M- test trials, they chose the other incorrect meaning that also served as a foil but that was not related to the new-word being tested (it was the meaning evoked by another second sentence of the run).

Approximately 30 minutes after the meaning acquisition task ended, i.e. after finishing the gambling task (see below) and once outside the scanner, participants had to complete another recognition test. In this last task, participants were presented with all the 40 M+ and 40 M- new-words used in the experiment. They were instructed to proceed exactly as in the previous test. The only difference was that the pairings between true meanings and foils were different than those tested inside the scanner. In this case, we calculated the percentage of learned M+ new-words (correctly paired with their meaning during the test inside the scanner) whose meaning was still correctly recognized during this second test. In the same vein, we also calculated the percentage of M- new-words correctly rejected during the test inside the scanner, which were still correctly rejected during the test outside the scanner.

Gambling fMRI experiment

Stimuli were presented using the Psychophysics Toolbox 3.09 [S1] and Matlab version R2011b (7.13.0.564, 32 bit). Each trial of this task started with the presentation of two numbers ([25 5] or [5 25]) for 2 seconds. Participants were instructed to select one of the two numbers by pressing the spatially corresponding button with their right

hand. After this, one of the numbers turned red and the other green (see Figure 1a). If the number selected by the participant turned green, the participant gained the corresponding amount of money in Euro cents. The number turning red indicated a loss (if a subject had selected 25 he/she won/lost 25 cents of euro; if she/he had selected 5 he won/lost 5 cents of euro). In order to take into account unexpected gains or losses, two more conditions were created (boost gain and boost loss). In these trials, instead of earning or losing 5 or 25 cents, participants gained or lost 25 or 125 cents, respectively. Thirty gain trials, thirty loss trials, fifteen boost gain and fifteen boost loss trials were presented in each of the two runs of the task. Additionally, 30 trials of a 3 second-long fixation cross were also presented per run. The inter-trial time varied between 0 and 2 seconds. After each run, the amount of money earned or lost was presented, in the middle of the screen, to the participant.

Unknown to the participants, the characteristics of the trial and its result (gain or loss) were decided by the computer program before the start of the experiment. Therefore, participants could not learn any particular pattern or make any effective predictions to gain larger amounts of money. Participants started the gambling task with 0 Euros and were instructed to earn as much money as possible. The amount of money won by a participant was paid to him/her at the end of the scanning session. All participants completed a training block before entering the scanner in order to familiarize them with the gambling task.

Participants responded using a two button pad on their right hand which enabled them to select the number presented on the left (left button, right hand) or on the right of the screen (right button, right hand). This was the same button pad they held in their right hand during the meaning acquisition experiment. The left-hand button-pad was not used in this task.

Scanning parameters

MRI data was collected on a 3T scanner (Siemens Magnetom Trio) using an eight-channel phased-array coil (Siemens, Erlangen, Germany). The session started with the acquisition of an inversion recovery prepared echo-planar imaging sequence (IR-EPI; TR=15000 ms, TE=21 ms, TI=1450 ms, flip angle=90°, slice thickness=3.8 mm, 3 mm in plane resolution, 34 slices, matrix size=80×80) in order to allow precise coregistration with functional data. After this, 10 runs of 92 sequential whole-brain volumes of EPI images sensitive to blood-oxygenation level-dependent contrast (Gradient Echo EPI; TR=2000 ms, TE=30 ms, flip angle=80°, slice thickness=3.8 mm, 3 mm in plane resolution, 34 slices, matrix size=80×80) were acquired for the meaning acquisition task. The same parameters were used to acquire the two runs of 260 sequential images of the gambling task.

A Diffusion Tensor MRI scanning session (DT-MRI) was run on a different 3T scanner (Siemens Magnetom Verio, software syngo MR B17) with a 32-channel phased-array head coil that was better suited for DTI-imaging. Images were obtained from the same 36 participants who properly ended the fMRI session (see below fMRI preprocessing for exclusion criteria). DTI-scans were acquired with a spin-echo EPI sequence fully optimized for DT-MRI of white matter [S9] (72 axial slices, TR: 10400 ms, TE: 86 ms, PAT-modus: GRAPPA acceleration factor 3, slice thickness: 2.0 mm, acquisition matrix: 128 × 128, voxel size: 2.0 × 2.0 × 2.0 mm³). Two runs with one non-diffusion weighted volume (using a spin-echo EPI sequence coverage of the whole head) and 30 diffusion weighted volumes (non-collinear diffusion gradient directions from Siemens MDDW mode, b-values of 1000 s/mm²) were acquired.

fMRI preprocessing and statistical analysis

Data were preprocessed using Statistical Parameter Mapping software (SPM8, Wellcome Trust Centre for Neuroimaging, University College, London, UK, www.fil.ion.ucl.ac.uk/spm/). Functional runs were first realigned and a mean image of all the EPIs was created. Four participants were rejected due to excessive head movements during the MRI session (abrupt head motion exceeding 4 mm within one run). The rest of the functional analysis was carried out with the remaining 36 participants. The inversion recovery image was coregistered to the mean EPI image and then segmented into grey and white matter (GM; WM) by means of the Unified Segmentation algorithm [S10]. After an initial 12-parameter affine transformation of the GM tissue probability map to the GM MNI template included with SPM8, the resulting normalization parameters were applied to the whole functional set. Finally, functional EPI volumes were re-sampled into $2 \times 2 \times 2$ mm voxels and spatially smoothed with an 8 mm FWHM kernel.

For both the meaning acquisition experiment and the gambling task, an event-related design matrix was specified using the canonical hemodynamic response function. For the meaning acquisition task, trial onsets were modeled at the moment of the presentation of the new-word. M+ and M- conditions were classified as correct or incorrect using the test performed after each learning run. Hence, ten different conditions were specified: M+ correct first sentence, M+ incorrect first sentence, M- correct first sentence, M- incorrect first sentence, NR first sentence, M+ correct second sentence, M+ incorrect second sentence, M- correct second sentence, M- incorrect second sentence, and NR second sentence. Data were high-pass filtered (to a maximum of 1/128Hz) and serial autocorrelations were estimated using an autoregressive (AR(1)) model. Remaining motion effects were minimized by also including the estimated

movement parameters in the model. First-level contrasts were specified for all participants using each condition against the implicit baseline. These contrast images were introduced into a second-level repeated-measures ANOVA that also modeled the subject-specific constants.

First, a whole brain contrast for the learned versus the non-learned new-words during the congruent condition was calculated ($M+$ correct > $M+$ incorrect, taken at the second presentation of the new-word; see Figure 2 and Table S1). In order to confirm that the new-words presented activated classical language areas [S11], whole brain fMRI-responses were compared for the learned new-words from the congruent condition against the non-readable sentences ($M+$ correct > NR comparison, taken at the second presentation of the new-word; see Figure S2 and Table S3).

After these previous contrasts showed modulations within the VS, a region of interest analysis (ROI)—using the results from the functional localizer obtained for the VS by means of the gambling task (gain>loss contrast, see below)—was calculated. For this, the toolbox WFU PickAtlas for ROI analysis [S12,S13] was used. In order to control for effort, difficulty and attentional effects, the interaction (see Figure 3a, top row) between condition ($M+/M-$) and type of response (correct/incorrect) was first calculated (contrast: $M+$ 2nd sentence correct - $M+$ 2nd sentence incorrect > $M-$ 2nd sentence correct - $M-$ 2nd sentence incorrect). Further contrasts for the ROI analysis included the comparison between correctly learned new-words during the congruent condition versus correctly rejected new-words during the incongruent condition ($M+$ correct > $M-$ correct, taken at the second presentation of the new-word; see Figure 3a, bottom row). One final analysis, to control for possible novelty effects, was conducted. The interaction between correct condition ($M+$ correct/ $M-$ correct) and order of presentation (first sentence/second sentence) was calculated (contrast: $M+$ 1st sentence

correct - M+ 2nd sentence correct > M- 1st sentence correct - M- 2nd sentence correct). Further, paired t-tests for 1st sentence against 2nd sentence presentation of correctly learned new-words during the congruent condition (M+ correct 1st sentence > M+ correct 2nd sentence) and for correctly rejected new-words during the incongruent condition (M-correct 1st sentence > M-correct 2nd sentence) were calculated. However, none of these analyses yielded any activations within the VS ROIs ($p < 0.05$ FWE-corrected, $k > 30$). Note that when calculating the interaction between correct condition and order of presentation, but comparing second sentences against first (contrast: M+ 2nd sentence correct - M+ 1st sentence correct > M- 2nd sentence correct - M- 1st sentence correct), VS activation was detected (128 voxels at the left VS, peak coordinate $x = -12$, $y = 12$; $z = -8$; 108 voxels in the right VS, peak coordinate $x = 8$, $y = 6$, $z = 0$). Additionally, for each participant, mean contrast estimates (proportional to percent signal change) were calculated by averaging the mean signal within the whole left and right VS ROIs for each contrast of interest (M+ correct 1st sentence, M- correct 1st sentence, M+ correct 2nd sentence, M- correct 2nd sentence, see Figure 3b; the only contrast showing significant VS activity was M+ correct 2nd sentence, when subjects correctly learned the meaning of new-words).

For the gambling task, trial onsets were modeled at the moment in which participants received the feedback. For each participant, the contrast gain && boost gain versus loss && boost loss was computed. These contrasts were taken into a second level random effects analysis (one-sample t-test) that was used to locate the areas of the brain that respond to monetary gains (blue areas in Figures 2, 3 and S2 and Table S2). The VS activations were used as an independent mask for the ROI analysis.

A repeated measures ANOVA including M+ correct second sentence, M+ incorrect second sentence, NR second sentence, gain && boost gain and loss && boost

loss contrasts was also built to conduct a conjunction analysis between the VS activation elicited by the correct learning of a new-word and the monetary gains. We used the minimum statistic compared to the conjunction null, testing for a true logical AND between M+ correct word-learning and monetary gains [S14].

Unless otherwise noted, all statistics are FWE-corrected at the voxel level for multiple comparisons at $p < 0.05$ with a minimal cluster size of 30 voxels. Maxima and all coordinates are reported in MNI space. Anatomical and cytoarchitectonical areas were identified using the Automated Anatomical Labeling [S15] and the Talairach Daemon database atlases [S16] included in the xjView toolbox (<http://www.alivelearn.net/xjview8/>).

Functional connectivity analysis

For the functional connectivity analysis, a 4 mm radius ROI was defined around the peak value of the white matter tract entering the left ventral striatum (VS) that significantly correlated with the percentage of learned words (for Radial Diffusivity, see below for DTI-analysis). Individual time-courses from this ROI were extracted, and an extended model was built. This model included the ten conditions previously defined for the language acquisition task plus the extracted VS time-course and the derived *psychophysiological interaction* (PPI) within the standard PPI approach [S17] as regressors. In particular, we used PPIs to test for higher inter-regional coupling with the VS during the congruent condition, when meaning is successfully extracted and a word is learned (M+ correct second sentence) versus when it is not learned (M+ incorrect second sentence). The computed first level PPI results were taken to a second level random effect analysis (one-sample t-test) to assess group effects (see Figure 4a and Table S4). Results are reported at $p < 0.05$ (FWE-corrected) at the cluster level, with an auxiliary $p < 0.005$ threshold at the voxel level.

DTI-MRI analysis

Diffusion data processing started by correcting for eddy current distortions and head motion using FMRIB's Diffusion Toolbox (FDT), which is part of the FMRIB Software Library (FSL 5.0.1, www.fmrib.ox.ac.uk/fsl/ [S18]). Subsequently, the gradient matrix was rotated to provide a more accurate estimate of diffusion tensor orientations [S19]. Following this, brain extraction was performed using the Brain Extraction Tool [S20], which is also part of the FSL distribution. Analysis continued with the reconstruction of the diffusion tensors using the linear least-squares algorithm included in Diffusion Toolkit 0.6.2.2 (Ruopeng Wang, Van J. Wedeen, trackvis.org/dtk, Martinos Center for Biomedical Imaging, Massachusetts General Hospital). Finally, Fractional Anisotropy (FA), Radial Diffusivity (RD), Mean Diffusivity (MD) and Axial Diffusivity (AD) maps for each participant were calculated using the eigenvalues extracted from the diffusion tensors.

Voxel based analysis of FA, RD, MD and AD maps were performed using Tract Based Spatial Statistics (TBSS [S21]). Briefly, FA maps from all participants were registered to the FMRIB58_FA template (MNI152 space and $1 \times 1 \times 1 \text{ mm}^3$) using the nonlinear registration tool FNIRT [S22,S23]. These registered FA maps were first averaged to create a mean FA volume. Then a mean FA skeleton was derived, which represents the centers of all tracts common to all participants in the study. Each participant's aligned FA data were then projected onto this skeleton by searching for the highest FA value within a search space perpendicular to each voxel of the mean skeleton. This process was repeated for the RD, MD and AD maps by applying the transformations previously calculated with the FA maps. Finally, correlations between each of the RD, MD, AD and FA skeletons and the percentage of learned words were carried out at a second level analysis. Results are reported at a FWE-corrected $p < 0.05$

value using threshold-free cluster enhancement [S24] and a nonparametric permutation test with 5000 permutations [S25]. Correlations for RD and MD were filled to make the presentation of results easier to follow and are shown on Figure 4b and Figure S3a, respectively. Results for FA, MD and RD values are reported on Table S5. RD describes microscopic water movements perpendicular to the axon tracks [S26] and it has been proposed to reflect myelin quality along the axon with demyelination being associated with increased RD [S27-S30]. MD is more related to tissue density [S31].

In addition, a complementary ROI-DTI analysis was carried out. Using the independent VS ROI from the gambling task (gain>loss contrast) the TBSS tracks entering the VS were a priori selected. Correlations were calculated between mean RD, MD, AD and FA values of the aforementioned voxels entering the left and right VS and the percentage of learned words for the M+ condition. Scatter plots for these correlations are shown on Figure S3b.

Meta-analysis of language related VS peak voxels

Due to the fact that our interpretation might be at risk of *reverse inference* (inferring cognitive states solely from the activation of a particular brain area [S32]) we used NeuroSynth ([www. http://neurosynth.org/](http://neurosynth.org/) [S33]) to carry out a large-scale, automated meta-analysis of fMRI data. The main objective was to calculate, based on previous publications, the most probable mental process behind the VS activation elicited during word learning. Given a particular voxel coordinate, NeuroSynth uses information from more than three thousand studies to return a list of related terms (i.e., *reward, novelty, incentive...*). Each term is accompanied by a posterior probability (PP, related to effect size) and a z-score (related to the confidence in the statistical association between the given activity and the mental process in question). Both variables serve as a measure of how strong is the probability of the term taking place when activation in the specified

voxel occurs. All of the maximum peaks in left and right VS were used to carry out this meta-analysis.

Specifically, *reward* was the term most associated to the peak voxel in the left VS extracted from the correctly learned versus non-learned words contrast in the congruent condition (Figure 2; M+ correct > M+ incorrect, taken at the second presentation of the new-word; x=-12 y=10 z=-6), with a posterior probability of 0.90 and a z-score of 16. Using the peak coordinate at the right VS from this same contrast (x=12 y=4 z=-6), *reward* was again the term most associated to the peak activation (PP=0.88, z-score=12.59). Regarding the VS peaks reported for the correctly learned new-words against the NR trials (Figure S2; M+ correct > NR, taken at the second presentation of the new-word) *reward* was again the term most associated to the right VS peak (x=12 y=10 z=2; PP=0.79, z-score=8.45) and the second (the first was *incentive*, PP=0.91, z-score=10.54) most related term to the left VS peak (x=-12 y=10 z=0; PP=0.82, z-score=10.33). *Monetary* was the term most associated to the left peak reported for the condition (M+/M-) x type of response (correct/incorrect) interaction (x=-12 y=12 z=0; PP=0.90, z-score=11.32), followed by *reward* (PP=0.89, z-score=10.77). Finally, regarding the VS peaks reported for the correctly learned new-words from the congruent condition against the correctly rejected new-words from the incongruent condition (Figure 3a, bottom; M+ correct > M- correct, taken at the second presentation of the new-word) *reward* was also the term most associated to the left (x=-10 y=12 z=4; PP=0.90, z-score=17.10) and right VS peak (x=12 y=4 z=-12; PP=0.91, z-score=12.20). In contrast, the term *novelty* achieved very low posterior probabilities and z-scores for all the peaks assessed (x=-12 y=10 z=-6, PP=0.56, z-score=0.43; x=12 y=4 z=-6, PP=0.58, z-score=0.31; x=12 y=10 z=2, PP=0.64, z-score=0.54; x=-12 y=10 z=0, PP=0.48, z-score=-0.78; x=-12 y=12 z=0, PP=0.51, z-score=0.61; x=-10 y=12 z=4,

PP=0.64, z-score=0.27; x=12 y=4 z=-12; PP=0.84, z-score=2.59).

SUPPLEMENTAL REFERENCES

- S1. Brainard D.H. (1997). The Psychophysics Toolbox. *Spat. Vis.* 10: 433-436.
- S2. Baayen R.H., Piepenbrock R., and Gulikers L. (1995). The CELEX Lexical Database (CD-ROM). Linguistic Data Consortium, University of Pennsylvania).
- S3. Mestres-Missé A., Rodriguez-Fornells A., and Munte T.F. (2010). Neural differences in the mapping of verb and noun concepts onto novel words. *Neuroimage.* 49: 2826-2835.
- S4. Mestres-Missé A., Munte T.F., and Rodriguez-Fornells A. (2014). Mapping concrete and abstract meanings to new words using verbal contexts. *Second Language Research* 30: 191-223.
- S5. Mestres-Missé A., Rodriguez-Fornells A., and Munte T.F. (2007). Watching the brain during meaning acquisition. *Cereb. Cortex* 17: 1858-1866.
- S6. Mestres-Missé A., Camara E., Rodriguez-Fornells A., Rotte M., and Munte T.F. (2008). Functional neuroanatomy of meaning acquisition from context. *J. Cogn Neurosci.* 20: 2153-2166.
- S7. Mestres-Missé A., Munte T.F., and Rodriguez-Fornells A. (2009). Functional neuroanatomy of contextual acquisition of concrete and abstract words. *J. Cogn Neurosci.* 21: 2154-2171.
- S8. Hinrichs H., Scholz M., Tempelmann C., Woldorff M.G., Dale A.M., and Heinze H.J. (2000). Deconvolution of event-related fMRI responses in fast-rate experimental designs: tracking amplitude variations. *J. Cogn Neurosci.* 12 Suppl 2: 76-89.
- S9. Reese T.G., Heid O., Weisskoff R.M., and Wedeen V.J. (2003). Reduction of eddy-current-induced distortion in diffusion MRI using a twice-refocused spin echo. *Magn Reson. Med.* 49: 177-182.
- S10. Ashburner J. and Friston K.J. (2005). Unified segmentation. *Neuroimage.* 26: 839-851.
- S11. Rodriguez-Fornells A., Cunillera T., Mestres-Missé A., and de Diego-Balaguer R. (2009). Neurophysiological mechanisms involved in language learning in adults. *Philos. Trans. R. Soc. Lond B Biol. Sci.* 364: 3711-3735.
- S12. Maldjian J.A., Laurienti P.J., Kraft R.A., and Burdette J.H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage.* 19: 1233-1239.
- S13. Maldjian J.A., Laurienti P.J., and Burdette J.H. (2004). Precentral gyrus discrepancy in electronic versions of the Talairach atlas. *Neuroimage.* 21: 450-455.
- S14. Nichols T., Brett M., Andersson J., Wager T., and Poline J.B. (2005). Valid conjunction inference with the minimum statistic. *Neuroimage.* 25: 653-660.
- S15. Tzourio-Mazoyer N., Landeau B., Papathanassiou D., Crivello F., Etard O., Delcroix N., Mazoyer B., and Joliot M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage.* 15: 273-289.
- S16. Lancaster J.L., Woldorff M.G., Parsons L.M., Liotti M., Freitas C.S., Rainey L., Kochunov P.V., Nickerson D., Mikiten S.A., and Fox P.T. (2000). Automated Talairach atlas labels for functional brain mapping. *Hum. Brain Mapp.* 10: 120-131.

- S17. Friston K.J., Buechel C., Fink G.R., Morris J., Rolls E., and Dolan R.J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage*. *6*: 218-229.
- S18. Jenkinson M., Beckmann C.F., Behrens T.E., Woolrich M.W., and Smith S.M. (2012). FSL. *Neuroimage*. *62*: 782-790.
- S19. Leemans A. and Jones D.K. (2009). The B-matrix must be rotated when correcting for subject motion in DTI data. *Magn Reson. Med*. *61*: 1336-1349.
- S20. Smith S.M. (2002). Fast robust automated brain extraction. *Hum. Brain Mapp*. *17*: 143-155.
- S21. Smith S.M., Jenkinson M., Johansen-Berg H., Rueckert D., Nichols T.E., Mackay C.E., Watkins K.E., Ciccarelli O., Cader M.Z., Matthews P.M. et al. (2006). Tract-based spatial statistics: voxelwise analysis of multi-subject diffusion data. *Neuroimage*. *31*: 1487-1505.
- S22. Andersson J.L.R., Jenkinson M., and Smith S.M. (2007). Non-linear optimisation. FMRIB technical report TR07JA1 (<http://www.fmrib.ox.ac.uk/analysis/techrep/tr07ja1/tr07ja1.pdf>).
- S23. Andersson J.L.R., Jenkinson M., and Smith S.M. (2007). Non-linear registration, aka Spatial normalisation. FMRIB technical report TR07JA2 (<http://www.fmrib.ox.ac.uk/analysis/techrep/tr07ja2/tr07ja2.pdf>).
- S24. Smith S.M. and Nichols T.E. (2009). Threshold-free cluster enhancement: addressing problems of smoothing, threshold dependence and localisation in cluster inference. *Neuroimage*. *44*: 83-98.
- S25. Nichols T.E. and Holmes A.P. (2002). Nonparametric permutation tests for functional neuroimaging: a primer with examples. *Hum. Brain Mapp*. *15*: 1-25.
- S26. Klawiter E.C., Schmidt R.E., Trinkaus K., Liang H.F., Budde M.D., Naismith R.T., Song S.K., Cross A.H., and Benzinger T.L. (2011). Radial diffusivity predicts demyelination in ex vivo multiple sclerosis spinal cords. *Neuroimage*. *55*: 1454-1460.
- S27. Fields R.D. (2008). White matter in learning, cognition and psychiatric disorders. *Trends Neurosci*. *31*: 361-370.
- S28. Zatorre R.J., Fields R.D., and Johansen-Berg H. (2012). Plasticity in gray and white: neuroimaging changes in brain structure during learning. *Nat. Neurosci*. *15*: 528-536.
- S29. Lopez-Barroso D., Catani M., Ripolles P., Dell'Acqua F., Rodriguez-Fornells A., and de Diego-Balaguer R. (2013). Word learning is mediated by the left arcuate fasciculus. *Proc. Natl. Acad. Sci. U. S. A* *110*: 13168-13173.
- S30. Song S.K., Sun S.W., Ramsbottom M.J., Chang C., Russell J., and Cross A.H. (2002). Demyelination revealed through MRI as increased radial (but unchanged axial) diffusion of water. *Neuroimage*. *17*: 1429-1436.
- S31. Sagi Y., Tavor I., Hofstetter S., Tzur-Moryosef S., Blumenfeld-Katzir T., and Assaf Y. (2012). Learning in the fast lane: new insights into neuroplasticity. *Neuron* *73*: 1195-1203.
- S32. Poldrack R.A. (2011). Inferring mental states from neuroimaging data: from reverse inference to large-scale decoding. *Neuron* *72*: 692-697.
- S33. Yarkoni T., Poldrack R.A., Nichols T.E., Van Essen D.C., and Wager T.D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nat. Methods* *8*: 665-670.