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

8 authors, including:

Some of the authors of this publication are also working on these related projects:

Recreational Drug Use & Addiction View project

Anatomical correlates of word-learning View project

Report

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,*]

[1]Cognition and Brain Plasticity Group, Bellvitge Biomedical Research Institute (IDIBELL), L'Hospitalet de Llobregat, Barcelona 08097, Spain
[2]Department of Basic Psychology, University of Barcelona, Campus Bellvitge, L'Hospitalet de Llobregat, Barcelona 08097, Spain
[3]Department of Biological Psychology, Otto von Guericke University Magdeburg, P.O. Box 4120, Magdeburg 39106, Germany
[4]School of Psychological Sciences, The University of Manchester, Zochonis Building, Brunswick Street, M13 9PL Manchester, UK
[5]Department of Neurology, Otto von Guericke University, LeipzigerStraße 44, Magdeburg 39120, Germany
[6]Catalan Institution for Research and Advanced Studies (ICREA), Barcelona 08010, Spain
[7]Center 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

[8]Co-senior author
*Correspondence: pabloripollesvidal@gmail.com (P.R.), toemme@med.ovgu.de (T.N.)
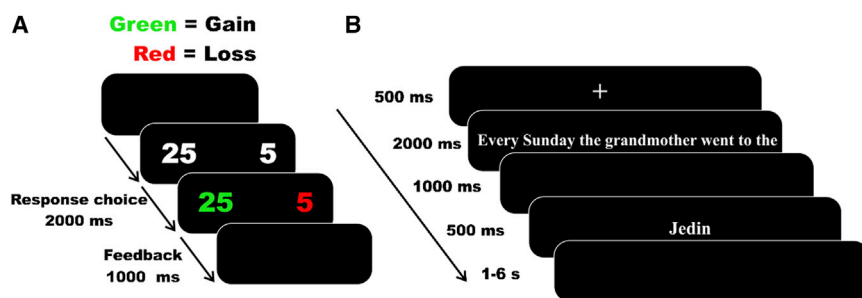
Figure 1. Experimental Setup

(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].

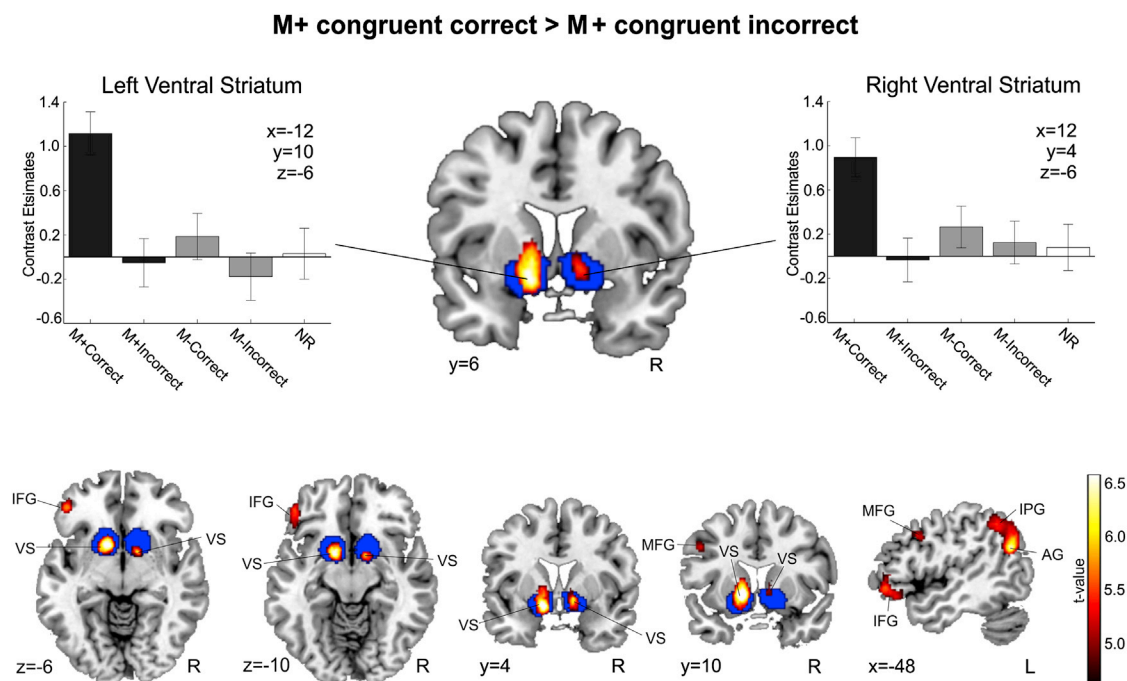## M+ congruent correct > M + congruent incorrect

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
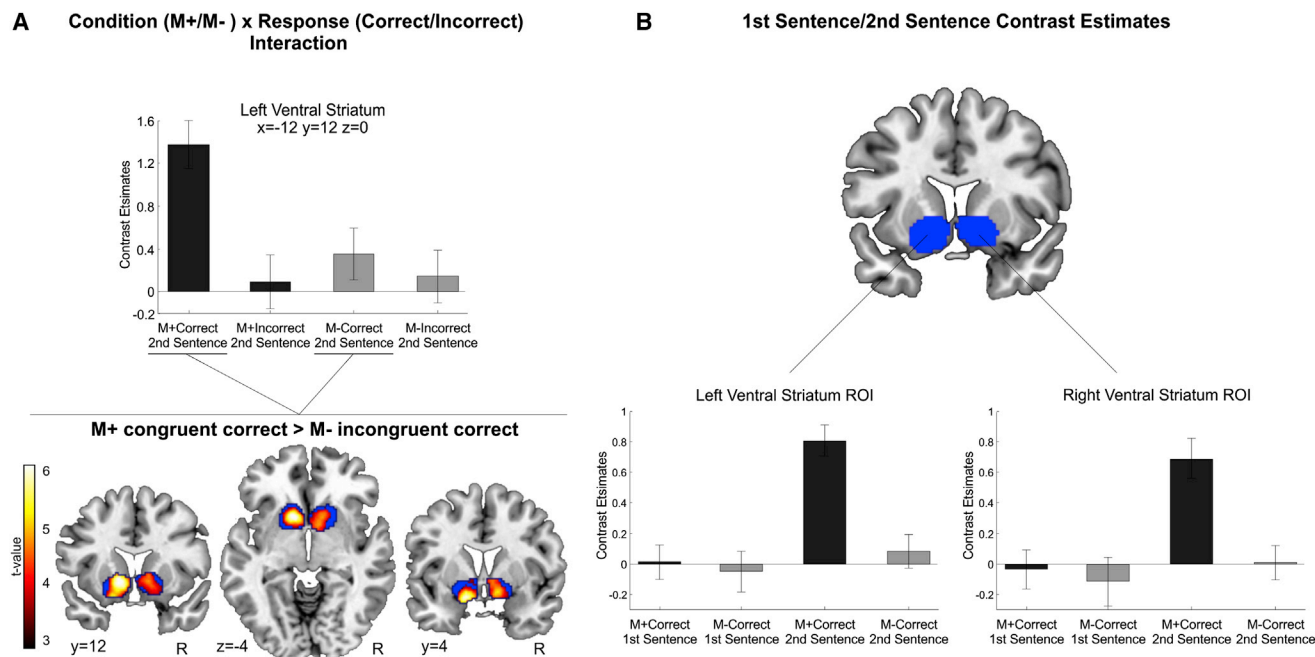
A Condition (M+/M-) x Response (Correct/Incorrect) Interaction

M+ congruent correct > M- incongruent correct

B 1st Sentence/2nd Sentence Contrast Estimates

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
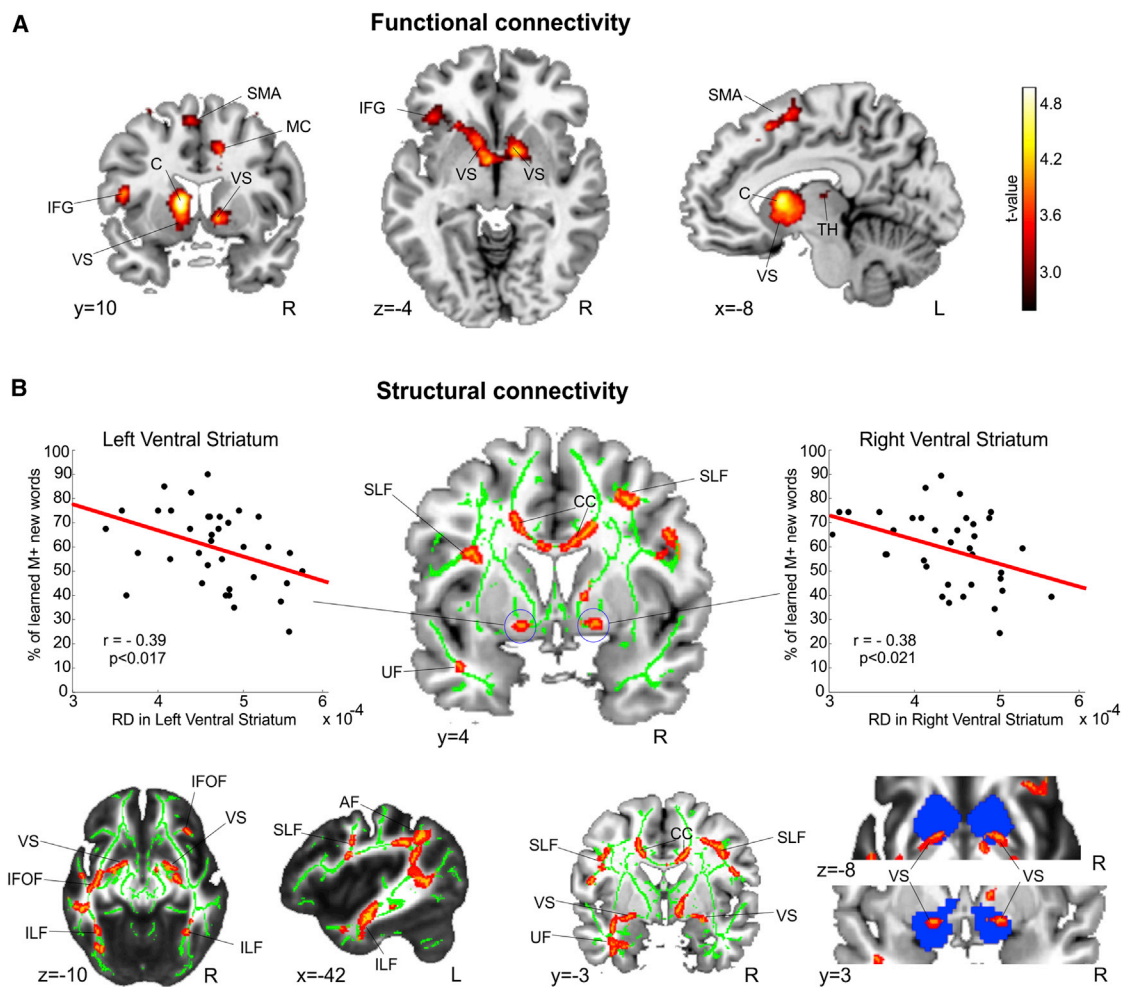
Figure 4. Connectivity Results

(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 callossum.

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.

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., Rodriguez-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., Rodriguez-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., Munte, T.F., and Rodriguez-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.