A functional role for the motor system in language understanding: Evidence from theta burst TMS

Journal:	*Psychological Science*
Manuscript ID:	PSCI-10-0942.R3
Manuscript Type:	Research report
Date Submitted by the Author:	n/a

Complete List of Authors:	Willems, Roel; UC Berkeley, Helen Wills Neuroscience Institute Labruna, Ludovica; UC Berkeley, Helen Wills Neuroscience Institute D'Esposito, Mark; UC Berkeley, Helen Wills Neuroscience Institute Ivry, Richard; UC Berkeley, Helen Wills Neuroscience Institute Casasanto, Daniel; Max Planck Institute for Psycholinguistics

Keywords:	Language, Cognitive Neuroscience, Psycholinguistics

A functional role for the motor system in language understanding: Evidence from theta burst TMS

Roel M. Willems[1], Ludovica Labruna[1,2,3], Mark D'Esposito[1], Richard Ivry[1,2] & Daniel Casasanto[4,5,6]

[1]Helen Wills Neuroscience Institute, University of California Berkeley, USA

[2]Department of Psychology, University of California, Berkeley, USA

[3]Department of Health Science, University of Molise, Campobasso, Italy

[4]Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

[5]Donders Institute for Brain, Cognition & Behaviour, Nijmegen, The Netherlands

[6]Department of Psychology, The New School for Social Research, New York, USA

For correspondence:

Roel Willems; Helen Wills Neuroscience Institute

University of California Berkeley; 132 Barker Hall

Berkeley CA 94720-3190, USA

roelwillems@berkeley.edu; +1 510-642-2839

Abstract

Does language comprehension depend, in part, on neural systems for action? In previous studies, motor areas of the brain were activated when people read or listened to action verbs, but it remains unclear whether this activation was functionally relevant for comprehension. Here we used off-line theta burst transcranial magnetic stimulation (TBS) to investigate a causal relationship between activity in premotor cortex and action language understanding. Right-handed participants performed lexical decisions on verbs describing manual actions typically performed with the dominant hand (e.g., throw, write) and on non-manual verbs (e.g., earn, wander). Responses to manual verbs (but not to non-manual verbs) were faster after stimulation of the hand area in left premotor cortex than after stimulation of the right premotor hand area. These results suggest a functional role for premotor cortex in action language understanding.

According to theories of embodied cognition, word meaning is constituted in part by activity in brain areas involved in perception and action (e.g. Barsalou, 2008; Zwaan, 2004). Consistent with this proposal, studies using functional magnetic resonance imaging (fMRI) have demonstrated effector-specific activity in the brain's motor system during action language processing (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermuller, 2004; Tettamanti, et al., 2005; Willems, Hagoort, & Casasanto, 2010; but see Kemmerer & Gonzalez-Castillo, 2010; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008). On the embodied view, this activity in cortical motor areas is part of the verb's semantics.

Yet, these data are also consistent with an alternative proposal (Mahon & Caramazza, 2008). Motor activity cued by action language could be a downstream consequence of 'true' semantic processing (see discusscion in Willems & Hagoort, 2007). In an effort to demonstrate a functional role for motor areas in understanding action language, researchers have tested how rapidly motor areas are activated in response to language. Differences between the premotor correlates of leg, arm, or face words emerge around 200 ms after word presentation (Hauk & Pulvermuller, 2004; Pulvermuller, Shtyrov, & Ilmoniemi, 2005). Such rapidity argues against the possibility that language-related motor activity is only a consequence of explicit motor imagery (Farah, 1989; Willems, Toni, Hagoort, & Casasanto, 2010). However, these correlational data do not speak to the functional significance of motor activity for meaning construction (Mahon & Caramazza, 2008).

To investigate a causal role for the motor system, researchers have applied single-pulse transcranial magnetic stimulation (TMS) to motor areas and measured motor-evoked potentials (MEPs) in participants' hands or feet while they processed language about hand or foot actions (Buccino, et al., 2005; Papeo, Vallesi, Isaja, & Rumiati, 2009). MEPs were modulated in the relevant body parts, demonstrating a causal link between activation of motor cortex and excitability of muscles in the limbs, which is mediated by language. Still, these studies do not imply that the motor system is involved in language processing, per se. Contracting muscles in the limbs is most easily interpreted as an *effect* of language comprehension, not as a *constituent* of language processing.

Does sensorimotor activity contribute to language comprehension? Here we used 'theta-burst' TMS (see below), to test whether modulating activity in the motor system causes a change in performance on a language processing task. Specifically, participants performed a lexical decision task (Meyer & Schvaneveldt, 1971), after theta-burst stimulation (TBS) was applied over the hand area of left premotor cortex in one experimental session and over right premotor hand area in another session. We compared the effects of stimulation on reaction times to verbs describing manual actions associated with dominant hand movements (e.g., *to throw*, *to write*) and on non-manual verbs (e.g., *to wander*, *to earn*).

In right-handers, manual action verbs preferentially activate the premotor hand area in the left hemisphere, which mainly controls actions performed by the right hand (Tettamanti, et al., 2005; Willems, Hagoort, & Casasanto, 2010). Therefore, we predicted that TBS applied over this region would modulate reaction times more strongly for manual action verbs than for non-manual verbs and that the strength of this effect would depend on whether TBS was applied over the left or right premotor cortex.

METHODS

Participants Twenty participants took part in the experiment and data from two participants were discarded because of experimental error. Data from eighteen right-handed, healthy participants were analyzed (11 female; mean age 23.5 years, range 19-35; Edinburgh Handedness Inventory: mean 93, median 100, range 67-100; no history of psychiatric or neurological illness; not taking medication at time of test). Eight participants (of which six were included in analysis of the main study) took part in a control experiment (see below; 4 female; mean age 23.6, range 20-35, mean EHI 92, median 94, range 82-100). **All participants took part in two sessions, one session with rTMS over left premotor cortex, and one with rTMS over right premotor cortex (see below).** The institutional review board at UC Berkeley approved the experiment.

Materials Stimuli were 192 English verbs describing concrete actions (see supplemental materials). Half of the stimuli referred to actions mainly performed with the hand (manual; e.g. *to throw*, *to write*), whereas the other half of the stimuli referred to actions not involving concrete actions (non-manual; e.g. *to wander*, *to earn*). The stimuli were matched for lexical frequency (Brysbaert & New, 2009; Coltheart, 1981) and word length (Coltheart, 1981; t<1). We created 96 pronounceable pseudowords (e.g. *to barst*, *to wunger*), matched in length to the action verbs. Manual verbs referred to actions typically performed with the dominant hand (Willems, Hagoort, & Casasanto, 2010).

The manual action verbs differed from the non-manual verbs not only in their effector-specificity but also in concreteness, and, presumably, in imageability. Our previous fMRI studies show selective activation of hand areas even when manual versus non-manual action verbs were equated for imageability. Furthermore, hand area activation cued by verbs could not be attributed to conscious motor imagery (Willems, et al., 2010).

We included a control experiment to directly assess the effect of concreteness, drawing on the database of Coltheart (1981). For this experiment participants performed lexical decision to nouns naming non-manipulable entities with either high or low concreteness (557 vs. 313, **t(190)=45.14, p<0.0001)** and high or low imageability (**567 vs. 355; t(190)=36.85, p<0.0001)**. There were 96 concrete nouns (e.g. *the moon*, *the farm*), 96 non-concrete nouns (e.g. *the topic*, *the mercy*), and 96 pseudowords. Stimuli were matched for lexical frequency (Brysbaert & New, 2009; Coltheart, 1981), as well as for word length |t|<1).

Experimental set-up Stimuli were presented in the middle of a computer monitor, on a white background with 18 point black font. Participants were seated approximately 25 cm from the screen. They indicated whether a visually presented string of letters was a real English word or not (lexical decision task) by pressing a button with the left or right index finger. We used a flexible response mapping scheme such that response side (left or right) varied unpredictably with respect to the response option ('yes' or 'no'). The response mapping for a given trial was presented below the verb, 4.5 cm to the left or right from the middle of the screen. Stimuli were presented until the response. Participants were instructed to respond as quickly and accurately as possible.

Stimuli were presented together with 'to' to signal that it was a verb. Stimulus presentation was randomized with 1 sec intertrial interval. There were 48 trials per condition per session and materials were not repeated over sessions. The order of stimulation site (left premotor, right premotor) was counterbalanced across subjects.

There were 18 practice trials which were not used in the remainder of the experiment. The control experiment always followed the main experiment.

Data acquisition A Magstim 'Rapid' figure of eight coil (Magstim, Whitland, UK) was used to generate the theta burst stimulation (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Six hundred pulses were administered in bursts of 3 pulses at 5Hz (total stimulation duration 40 sec.). When applied over motor cortex, this procedure changes the excitability of cortical tissue for up to 60 minutes (Huang, et al., 2005; Huang, et al., 2009). Participants remained silent and did not move ten minutes after stimulation, and the two test sessions were separated at least one week, in accordance with safety guidelines (Huang, et al., 2005; Rossi, Hallett, Rossini, & Pascual-Leone, 2009).

For each participant we first determined the stimulation level required to elicit MEPs in the first dorsal interosseous muscle on five out of ten trials, while the participant maintained a contraction level at 20% of maximum force. The stimulation intensity for TBS was 80% of this threshold (Huang, et al., 2005; Huang, et al., 2009; Rossi, et al., 2009). This was done for each stimulation site separately. No difference in stimulation intensity for the two hemispheres was observed (left: mean 40.5% of maximum stimulation output, s.d. 4.94; right: mean 41.7%, s.d. 4.79; $|t|<1$).

Location of stimulation was determined on the basis of our previous fMRI experiment (involving a separate group of participants, Willems, Hagoort, & Casasanto, 2010). Comparing manual versus non-manual action verb reading, we had observed dorsal premotor cortex activation at MNI coordinates [x y z] [-35, -1, 53] and [34, 0, 53], for left and right dorsal premotor cortex, respectively (supplementary Fig. S1). We targeted these areas in the current experiment in each individual, using a T1-weighted anatomical scan. Brainsight software (Rogue Research, Canada) was used to determine correspondence between the location at the skull and the site of stimulation on the scan. The normalized regions were taken as a guideline, stimulation sites were determined in **'native space' based upon visual inspection of landmarks on each individual's MRI. The locations were not normalized to a standardized template**.

Data analysis Incorrect responses were excluded and outliers were removed by excluding values three standard deviations above or below **the overall mean per subject.** Analysis involved repeated measures analysis of variance employing a mixed-effects linear model with factors HEMISPHERE (left premotor TBS, right premotor TBS) and VERB (Manual, Non-manual) as fixed effects, and SUBJECTS and ITEMS as random effects[1]. This procedure effectively combines analysis over subjects and items, allowing generalization to the general subject and language population (Baayen, Davidson, & Bates, 2008). All main effects and interactions were tested and post hoc comparisons involved two-sided t-tests.

Analysis of the control experiment data was similarly done using a model with factors HEMISPERE (left premotor TBS, right premotor TBS) and NOUN (concrete, non-concrete) as fixed effects and SUBJECTS and ITEMS as random effects.

RESULTS

Main experiment Results showed a HEMISPHERE x VERB interaction ($F(1,3152)=5.97$, $r=0.09$, ste=11.7, $p=0.015$; Fig. 1; Table 1). Responses to manual verbs were faster after stimulation of left premotor cortex than after stimulation of the right premotor cortex (M=-34.1 ms; $t(3159)=4.36$, $r=0.11$, ste=8.2, $p<0.001$). This was not observed for the non-manual verbs (M=-5.8 ms, $|t|<1$). There was a main effect of HEMISPHERE ($F(1,3152)=13.46$, $r=0.08$, ste=8.3, $p<0.001$), but not of VERB ($F<1$). Response times for pseudowords showed no effect of HEMISPHERE ($F(1,1393)=1.72$, $r=0.02$, ste=8.2, $p=0.19$).

Error rates were low (mean 4.6%, ste 0.21%). There was no HEMISPHERE x VERB interaction in the error rates (Wald $X^2<1$), and no statistically significant main effects of VERB (Wald $X^2<1$) or HEMISPHERE (Wald $X^2=2.98$, $p=0.084$).

Control experiment There was no HEMISPHERE x NOUN interaction (F<1; Fig. 2; Table 1). Neither were there statistically significant main effects (Fs<1). Results to concrete and non-concrete nouns did not differ after stimulation of left, nor right premotor cortex (M_{left}=4.2 ms; |t|<1; M_{right}=-7.5 ms; |t|<1). A direct comparison showed an EXPERIMENT x VERB/NOUN x HEMISPHERE interaction (F(4,4330)=3.04, ste=17.89, r=0.07, p=0.016), confirming that the MAN and NONMAN verbs were differentially influenced by left or right premotor TMS, but Concrete and Non-concrete nouns were not.

DISCUSSION

We investigated whether action language understanding depends in part on activity in the brain's motor system. Lexical decisions for manual action verbs (compared to non-manual verbs) were faster following TBS of left premotor cortex compared to TBS of right premotor cortex. This effect was not found for non-manual verbs or in the control task with concrete and non-concrete nouns. This dissociation is consistent with fMRI data showing selective activation of left premotor cortex when right-handers read verbs for actions typically performed with their dominant hand (Willems, Hagoort, & Casasanto, 2010). Beyond showing a correlation between brain and behavior, the present data show that specific changes in premotor activity cause corresponding changes in action language processing. These data suggest a functional role for premotor cortex in action language understanding.

This TBS study provides a more direct test of the motor system's functional contributions to language understanding than previous single-pulse TMS studies, which have used motor evoked potentials in limbs as a dependent measure. Lexical decision is a classic index of semantic processing, *per se*, as opposed to a TMS-induced response in hand or foot muscles that occurs downstream of language processing (Buccino, et al., 2005). An earlier paper reported modulation of lexical decision reaction times for action verbs following single-pulse TMS (Pulvermuller, Hauk, Nikulin, & Ilmoniemi, 2005). Crucially, however, these results did not show the predicted specificity of the arm area for processing arm-related verbs. Our results are consistent with the predictions from this earlier study.

Furthermore, our results are consistent with findings from a study showing effects of use-induced motor plasticity on **understanding of concrete as well as abstract motion sentences** (Glenberg, Sato, & Cattaneo, 2008). Participants moved objects toward or away from their body. Following this, participants were slower to respond to sentences indicating motion in the same direction, suggesting a functional link between language comprehension and motor activity. The present data provide additional information about both the automaticity and specificity of the link between the motor system and language. First, whereas the Glenberg et al. study involved sensibility judgments on full sentences, and thus required 'deep' semantic processing, we show that modulating motor system activity can influence even a 'shallow' processing task like lexical decision, in which the meanings of verbs are only activated incidentally. Second, behavioral manipulations of motor activity cannot specify the location of an interaction between language comprehension and action production. Glenberg and colleagues speculated their effect was due to changes "primarily located in the left inferior frontal and parietal regions" (p. R291). The present results implicate premotor cortex.

The finding that left-hemisphere stimulation resulted in faster reaction times may seem surprising since theta burst stimulation over motor cortex decreases MEPs, suggesting a depression of excitability (Huang, et al., 2005). One might assume that depression of premotor activity would disrupt action language processing. Instead, we observed a facilitatory effect at the behavioral level. It is difficult to infer how modulation at the neural level is manifest behaviorally. TBS may have caused inhibition at the neural level that resulted in disinhibition at the behavioral level. Indeed, movement-related cells in premotor cortex exhibit inhibition during action observation (e.g. Kraskov et al., 2009). TBS of left premotor cortex may also facilitate processing hand words by reducing irrelevant background processing within a part of the language comprehension network (see Landau, Aziz-Zadeh, & Ivry, 2010).

We previously found that participants preferentially activate premotor cortex contralateral to their preferred hand when reading manual action verbs (Willems, Hagoort & Casasanto, 2010). We did not observe a hand effect in the present study: the facilitation effect following premotor TBS was observed for both right and left hand responses (see footnote 1). We note that this null effect is based on a limited amount of trials per cell (< 24). Nonetheless, future work is required to explore how modulation of the motor system may influence linguistic processing of body-specific actions.

We conclude that processing an action verb depends in part on activity in a motor region that contributes to planning and executing the action named by the verb. Premotor cortex is functionally involved in understanding action language. It is a challenge for future research to characterize the neural mechanisms that underlie this functionality. Furthermore, it remains an open question to what extent premotor representations are necessary for ordinary language understanding, and how changes in premotor activity are related to changes in a verb's meaning from one instantiation to the next.

ACKNOWLEDGEMENTS

Supported by grants from the Dutch Science Foundation (NWO Rubicon 446-08-008) and the Niels Stensen foundation to RW and by a James S. McDonnell Scholar Award to DC.

NOTES

1) The factor RESPONSE HAND was included in the initial analyses of the data. Given that this factor was not significant, nor involved in any interactions, we present simplified analyses in which the RTs were collapsed over response hand.

REFERENCES

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology, 16*(18), 1818-1823.

Baayen, R.H., Davidson, D.J. and Bates, D.M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language, 59*, 390-412.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology, 59*, 617-645.

Brysbaert, M., & New, B. (2009). Moving beyond Kucera and Francis: a critical evaluation of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behavior Research Methods, 41*(4), 977-990.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Research Cognitive Brain Research, 24*(3), 355-363.

Coltheart, M. (1981). The MRC Psycholinguistic Database. *Quarterly Journal of Experimental Psychology, 33A*, 497-505.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorial in Quantitative Methods for Psychology*, *1*(1), 42-45.

Farah, M. J. (1989). The neural basis of mental imagery. *Trends in Neurosciences, 12*(10), 395-399.

Glenberg, A. M., Sato, M., & Cattaneo, L. (2008). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current Biology, 18*(7), R290-R291.

Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*(2), 301-307.

Hauk, O., & Pulvermuller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping, 21*(3), 191-201.

Huang, Y. Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. *Neuron, 45*(2), 201-206.

Huang, Y. Z., Rothwell, J. C., Lu, C. S., Wang, J., Weng, Y. H., Lai, S. C., et al. (2009). The effect of continuous theta burst stimulation over premotor cortex on circuits in primary motor cortex and spinal cord. *Clinical Neurophysiology, 120*(4), 796-801.

Kemmerer, D., & Gonzalez-Castillo, J. (2010). The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain and Language, 112*(1), 54-76.

Kraskov A., Dancause N., Quallo M.M., Shepherd S., & Lemon R.N. (2009). Corticospinal neurons in macaque ventral premotor cortex with mirror properties: a potential mechanism for action suppression? *Neuron, 64*(6): 922-930.

Landau, A., Aziz-Zadeh, L., & Ivry, R. B. (2010). The influence of language on perception: Listening to sentences about faces affects the perception of faces. *Journal of Neuroscience, 30*(45), 15254-15261.

Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology Paris, 102*(1-3), 59-70.

Meyer, D. E., & Schvaneveldt, R. W. (1971). Facilitation in recognizing pairs of words: Evidence of a dependence between retrieval operations. *Journal of Experimental Psychology, 90*, 227-234.

Papeo, L., Vallesi, A., Isaja, A., & Rumiati, R. I. (2009). Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS ONE, 4*(2), e4508.

Postle, N., McMahon, K. L., Ashton, R., Meredith, M., & de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *Neuroimage, 43*(3), 634-644.

Pulvermuller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience, 21*(3), 793-797.

Pulvermuller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience, 17*(6), 884-892.

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology, 120*(12), 2008-2039.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience, 17*(2), 273-281.

Willems, R. M., & Hagoort, P. (2007). Neural evidence for the interplay between language, gesture, and action: A review. *Brain and Language, 101*(3), 278-289.

Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: Neural evidence from right- and left-handers. *Psychological Science, 21*(1), 67-74.

Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2010). Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience, 22*(10), 2387-2400.

Zwaan, R. A. (2004). The immersed experiencer: toward an embodied theory of language comprehension. In B. H. Ross (Ed.), *The Psychology of Learning and Motivation, Vol. 44*. New York: Academic Press.

Fig. 1. Results from the main experiment. A) Reaction time difference between left premotor and right premotor TBS for manual verbs (grey) and non-manual verbs (black). The left-right difference was stronger for manual verbs than for non-manual verbs. **B)** Reaction times. Displayed are the mean reaction times for manual (left bars) and non-manual (right bars) verbs after TBS to left (grey) or right (black) dorsal premotor cortex. Error bars represent standard error of the mean, corrected for individual subject means (Cousineau, 2005). Asterisk denotes statistical significance at the $p<0.05$ level; n.s. non-significant.

Fig 2. Results from the control experiment (concrete and non-concrete nouns). A) Reaction time difference between left premotor and right premotor TBS for concrete nouns (grey) and non-concrete nouns (black). No differences between conditions were found. **B)** Reaction times. Displayed are the mean reaction times for concrete (left bars) and non-concrete (right bars) nouns after TBS to left (grey) or right (black) dorsal premotor cortex. Error bars represent standard error of the mean, corrected for individual subject means (Cousineau, 2005); n.s. non-significant.

Main exp.	**MAN left TBS**	**MAN right TBS**	**NONMAN left TBS**	**NONMAN right TBS**	**Nonword left TBS**	**Nonword right TBS**
Mean	663.4	697.5	683.7	689.5	789.3	802.6
s.d.	168.8	206.8	178.9	180.9	175.6	193.0
Control exp.	**CONC left TBS**	**CONC right TBS**	**NONCONC left TBS**	**NONCONC right TBS**	**Nonword left TBS**	**Nonword right TBS**
Mean	606.3	610.5	606.4	613.9	751.9	787.6
s.d.	151.0	172.7	153.4	155.1	218.6	251.9

Table 1. Descriptive statistics. Means and standard deviations for all conditions; see Figs. 1B and 2B for bar graphs. MAN=Manual, NONMAN=Non-manual, CONC=concrete, NONCONC=non-concrete.

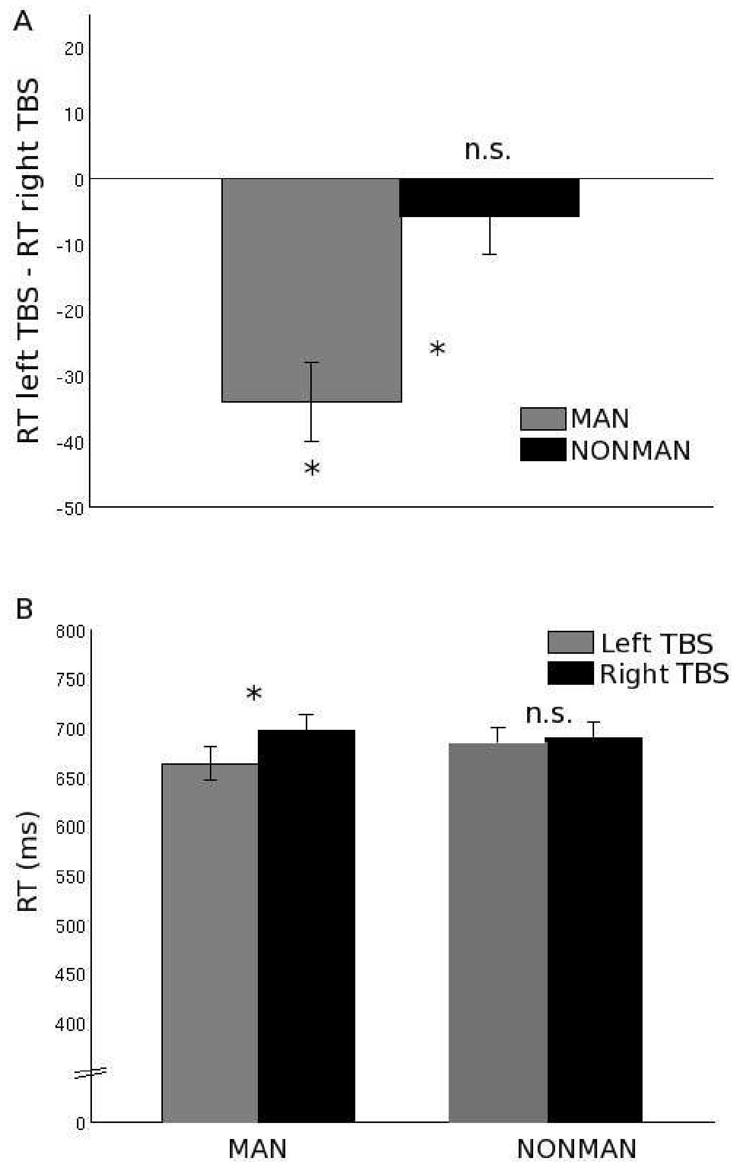


Fig. 1. Results from the main experiment. A) Reaction time difference between left premotor and right premotor TBS for manual verbs (grey) and non-manual verbs (black). The left-right difference was stronger for manual verbs than for non-manual verbs. B) Reaction times. Displayed are the mean reaction times for manual (left bars) and non-manual (right bars) verbs after TBS to left (grey) or right (black) dorsal premotor cortex. Error bars represent standard error of the mean, corrected for individual subject means (Cousineau, 2005). Asterisk denotes statistical significance at the $p<0.05$ level; n.s. non-significant.
184x278mm (75 x 75 DPI)

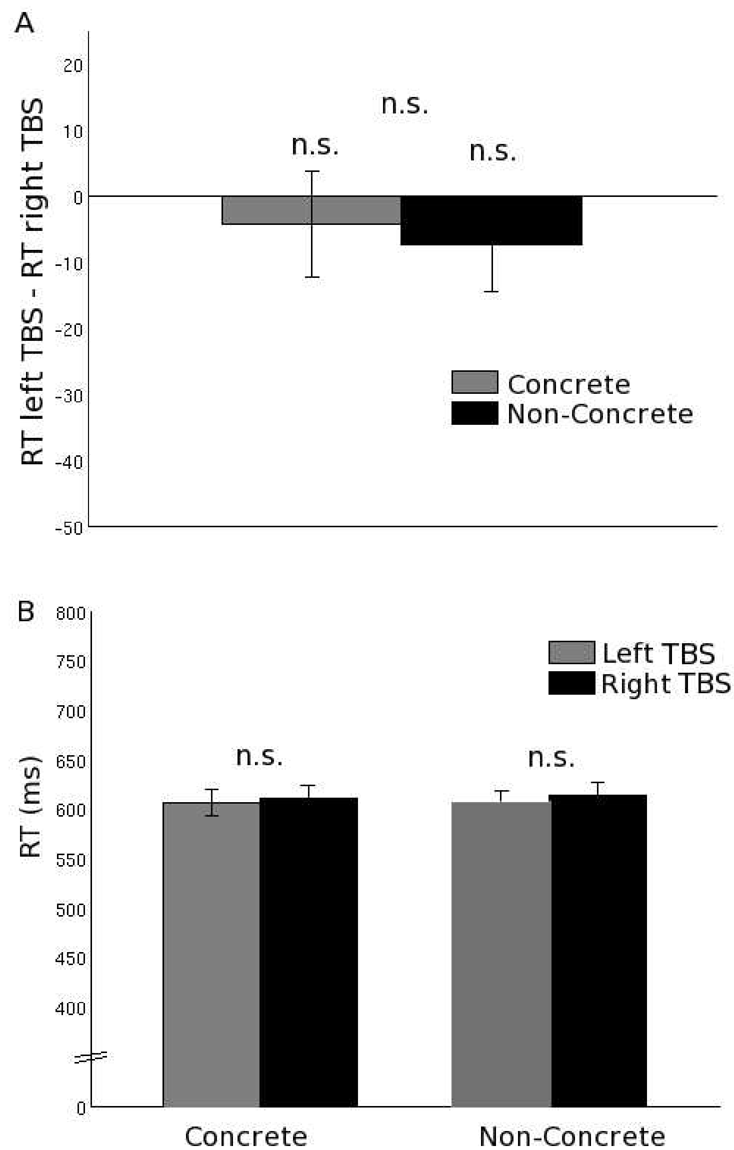


Fig 2. Results from the control experiment (concrete and non-concrete nouns). A) Reaction time difference between left premotor and right premotor TBS for concrete nouns (grey) and non-concrete nouns (black). No differences between conditions were found. B) Reaction times. Displayed are the mean reaction times for Concrete (left bars) and Non-concrete (right bars) nouns after TBS to left (grey) or right (black) dorsal premotor cortex. Error bars represent standard error of the mean, corrected for individual subject means (Cousineau, 2005); n.s. non-significant.
185x288mm (72 x 72 DPI)

Supplementary materials Willems, Labruna, D'Esposito, Ivry & Casasanto

Materials and their characteristics

Displayed are the materials used in the main experiment (A) and in the control experiment (B) and scores for these materials and concreteness (CONC, Coltheart, 1981), number of letters (NLET), Thorndike and Lorge lexical frequency (T-L FREQ; Coltheart, 1981) and Subtlex lexical frequency (Subtlex; Brysbaert & New, 2009). For the nouns in the control experiment also imageability score is provided (IMG; Coltheart, 1981).

A) MAIN EXPERIMENT

MANUAL

Word	CONC	NLET	T-L freq	Subtlex
to autograph		9	2.639	2.619
to brush	589	5	6.001	2.859
to caress		6	4.317	1.839
to carry	364	5	7.313	3.526
to carve		5	4.407	2.199
to catch		5	6.129	3.840
to chisel	597	6	3.401	1.653
to chop	555	4	4.990	2.841
to clasp	498	5	4.691	1.716
to cleave		6	1.099	1.000
to clench		6	4.489	1.301
to clutch		6	5.118	2.104
to comb		4	4.564	2.490
to cut	430	3	6.849	4.069
to dial	537	4	3.761	2.655
to draw	442	4	6.059	3.314
to engrave		7	3.296	1.176
to erase		5	3.178	2.501
to etch		4	2.708	1.000
to fiddle	582	6	3.219	2.267
to finger		6	6.755	3.272
to flick		5	3.871	2.410
to fling		5	4.043	2.255
to flog		4	1.946	1.176
to fondle		6	2.708	1.398
to gesture	403	7	5.642	2.579
to grab		4	5.308	3.558
to grasp	330	5	5.333	2.367
to grip	490	4	5.730	2.694
to hammer	605	6	4.663	2.803
to handle		6	5.852	3.743
to hit		3	6.040	4.147
to hold	416	4	6.729	4.348
to inscribe		8	3.135	0.954
to jab		3	2.565	2.233

to knead		5	2.303	0.954
to knock		5	5.919	3.518
to manipulate		10	3.091	2.248
to massage		7	3.258	2.752
to paddle		6	3.611	2.281
to paint	577	5	7.005	3.273
to pat	400	3	5.652	2.970
to pet	557	3	5.088	3.012
to pick	502	4	6.894	4.005
to pinch		5	4.454	2.494
to pluck		5	3.761	2.072
to point	464	5	7.228	4.081
to poke		4	4.094	2.474
to pound	515	5	6.534	2.850
to pour	356	4	6.321	2.887
to press		5	6.498	3.487
to pull	360	4	6.842	3.873
to punch	548	5	4.357	3.180
to push		4	6.297	3.556
to reach	368	5	7.284	3.463
to rub		3	5.517	2.897
to salute	471	6	4.331	2.568
to scoop		5	3.664	2.461
to scratch	523	7	4.754	2.983
to scrawl		6	3.584	1.079
to scribble		8	3.045	1.505
to scrub		5	4.691	2.502
to shake		5	5.338	3.306
to shave		5	4.127	2.846
to shove		5	4.700	2.829
to shovel	581	6	3.850	2.543
to sketch	535	6	5.371	2.401
to slap	511	4	4.771	2.803
to slash		5	4.205	2.086
to slice	443	5	5.872	2.638
to smack	451	5	3.807	2.686
to smash	402	5	4.615	2.624
to snap	420	4	5.832	2.948
to snip		4	2.773	2.033
to spar		4	2.708	1.556
to spear	584	5	2.944	2.365
to squeeze		7	4.796	2.886
to stab		4	3.638	2.650
to stir		4	6.242	2.479
to strike		6	5.787	3.366
to stroke	463	6	5.252	2.824
to tap	538	3	4.913	2.876
to throw	400	5	5.802	3.818
to tickle	473	6	3.497	2.389

to topple		6	3.091	1.505
to toss		4	5.505	2.801
to touch	417	5	6.924	3.877
to trace	371	5	5.403	2.995
to tug		3	4.543	2.146
to twist	423	5	5.638	2.808
to wave	492	4	6.170	3.035
to whack	409	5	3.091	2.658
to whip	570	4	5.553	2.827
to whittle		7	2.398	1.322
to write	446	5	6.863	3.811
to yank		4	3.367	2.380

NONMANUAL

Word	**CONC**	**NLET**	**T-L freq**	**Subtlex**
to acknowledge	290	11	4.754	2.496
to admire	296	6	5.549	2.859
to aid	372	3	5.737	2.851
to aim	324	3	4.700	2.880
to amuse	321	5	5.323	2.124
to assent	311	6	3.989	0.602
to assist	342	6	4.522	2.602
to bargain	399	7	4.920	2.787
to bid	364	3	4.466	2.808
to blow	397	4	5.823	3.697
to boast	295	5	4.796	1.732
to bother	267	6	5.659	3.536
to bury	372	4	5.628	3.023
to cheat	329	5	4.625	2.955
to clash	399	5	3.611	1.833
to condemn	314	7	4.489	2.083
to cope	347	4	4.143	2.220
to crush	381	5	5.613	2.933
to cure	352	4	5.389	3.027
to curse	363	5	5.204	2.968
to debate	375	6	4.331	2.676
to decay	370	5	4.248	2.021
to defeat	363	6	5.112	2.763
to deliver	393	7	5.303	3.160
to despise	314	7	4.317	2.362
to earn	349	4	5.628	2.894
to ease	305	4	5.493	2.989
to flow	311	4	5.394	2.846
to flutter	386	7	4.700	1.643
to gain	346	4	5.864	2.845
to gleam	391	5	5.278	1.699
to halt	345	4	5.004	2.760

to hang	397	4	5.844	3.877
to harm	244	4	5.545	3.210
to haul	369	4	4.654	2.558
to hush	396	4	4.500	2.589
to ignore	320	6	5.263	2.978
to import	320	6	4.454	2.045
to incline	376	7	4.898	1.279
to insult	375	6	4.615	2.806
to leap	389	4	5.717	2.531
to lease	371	5	4.277	2.505
to marvel	293	6	4.466	1.996
to measure	366	7	5.215	2.730
to nag	392	3	4.007	2.045
to offend	321	6	4.205	2.425
to pardon	307	6	4.718	3.518
to pat	400	3	5.652	2.970
to peep	388	4	4.060	2.354
to pledge	360	6	4.248	2.545
to plot	379	4	4.852	2.772
to plunge	396	6	5.425	2.057
to praise	354	6	4.754	2.683
to pray	372	4	5.595	3.266
to prime	360	5	4.174	2.970
to punish	344	6	4.025	2.693
to quicken	380	7	3.912	1.146
to recall	319	6	5.690	3.001
to recruit	393	7	3.611	2.274
to refrain	325	7	3.932	2.017
to refresh	362	7	3.738	2.104
to regret	260	6	5.425	3.141
to repair	394	6	4.736	2.653
to restore	275	7	4.852	2.403
to retain	308	6	4.956	2.083
to review	388	6	5.043	2.878
to revolt	400	6	4.357	1.898
to reward	396	6	5.037	2.963
to risk	290	4	5.606	3.398
to scare	380	5	5.328	3.234
to scorn	290	5	4.543	1.771
to scowl	386	5	4.277	1.415
to shock	395	5	5.841	3.167
to slumber	386	7	4.060	2.146
to smother	377	7	4.159	1.778
to sneer	371	5	4.511	1.580
to soar	366	4	3.807	1.892
to span	352	4	3.611	2.004
to spare	313	5	5.521	3.197
to spell	376	5	5.220	3.272
to steal	363	5	5.130	3.435

to stifle	292	6	4.220	1.176
to succeed	304	7	5.576	2.683
to tempt	283	5	4.543	2.111
to tidy	311	4	3.738	2.276
to toil	386	4	4.317	1.708
to torment	288	7	4.111	2.143
to trace	371	5	5.403	2.995
to trick	391	5	5.817	3.382
to trim	388	4	5.247	2.338
to unite	309	5	5.591	2.188
to upset	282	5	5.106	3.580
to vow	329	3	5.081	2.441
to wander	320	6	5.416	2.476
to weigh	363	5	5.069	2.560
to win	364	3	5.710	3.837

AVERAGE	**CONC**	**NLET**	**T-L freq**	**Subtlex**
MANUAL	475.7333333	5.0625	4.729	2.640
NONMANUAL	348.9375	5.270833333	4.861	2.550
T	12.12768607	1.100928648	0.823	0.869
p-value	1.93228E-25	0.272320496	0.411	0.386

B) CONTROL EXPERIMENT

Concrete

Word	**CONC**	**IMG**	**NLET**	**T-L Freq**	**Subtlex**
the air	518	450	3.000	2.986	3.851
the aisle	509	528	5.000	1.857	2.579
the arch	512	557	4.000	1.886	2.274
the audience	515	555	8.000	2.505	3.112
the avenue	539	564	6.000	2.505	2.935
the bank	573	560	4.000	2.922	3.637
the bar	565	596	3.000	2.505	3.642
the barn	614	589	4.000	2.246	2.841
the battle	564	597	6.000	2.487	3.333
the bay	580	570	3.000	2.276	3.092
the beam	502	539	4.000	2.104	2.648
the bedroom	615	629	7.000	2.583	3.272
the blade	584	568	5.000	1.924	2.822
the blood	613	620	5.000	2.702	3.977
the bloom	520	524	5.000	2.248	2.449
the blossom	559	618	7.000	2.230	2.265
the brain	556	572	5.000	2.603	3.594
the branch	583	548	6.000	2.405	2.711
the breeze	500	560	6.000	1.982	2.613
the bubble	563	604	6.000	1.954	2.611
the bush	585	549	4.000	2.204	2.857

the cabin	596	582	5.000	2.666	3.001
the camp	571	588	4.000	2.776	3.417
the canal	598	588	5.000	1.875	2.513
the carriage	576	529	8.000	2.045	2.581
the ceiling	606	557	7.000	2.248	2.629
the cell	542	590	4.000	2.477	3.443
the cellar	572	572	6.000	2.146	2.679
the cement	646	578	6.000	1.892	2.369
the channel	527	508	7.000	1.968	3.095
the circle	515	591	6.000	2.589	3.040
the circus	535	586	6.000	2.041	2.940
the cloud	554	595	5.000	2.565	2.777
the coast	562	588	5.000	2.446	3.134
the colony	511	481	6.000	1.964	2.480
the column	520	491	6.000	2.233	2.747
the coral	572	561	5.000	2.201	2.083
the court	509	552	5.000	2.846	3.711
the dawn	501	586	4.000	2.377	3.114
the deck	566	539	4.000	2.519	3.084
the dirt	564	547	4.000	2.134	3.117
the disease	504	487	7.000	2.512	3.125
the dock	570	559	4.000	1.987	2.696
the doorway	578	548	7.000	2.401	2.215
the dot	530	556	3.000	2.248	2.529
the dust	550	549	4.000	2.491	3.085
the earth	580	580	5.000	2.651	3.705
the estate	541	474	6.000	2.292	3.032
the farm	565	560	4.000	2.917	3.185
the fat	540	574	3.000	2.709	3.608
the feast	542	610	5.000	1.826	2.534
the fleet	520	510	5.000	1.839	2.732
the flood	553	598	5.000	2.512	2.464
the flora	557	472	5.000	1.869	2.057
the fog	556	606	3.000	2.029	2.683
the forest	609	633	6.000	2.320	2.984
the fort	580	559	4.000	1.940	2.896
the frost	608	595	5.000	1.978	2.389
the gallery	569	566	7.000	2.064	2.637
the gas	554	532	3.000	2.517	3.539
the grove	538	470	5.000	1.820	2.294
the harvest	535	562	7.000	2.079	2.290
the hill	588	607	4.000	2.525	3.282
the lobby	532	462	5.000	1.863	2.811
the meadow	594	622	6.000	1.845	2.064
the moisture	545	513	8.000	1.820	1.792
the moon	581	585	4.000	2.455	3.406
the mountain	616	629	8.000	2.459	3.256
the ocean	593	623	5.000	2.068	3.189
the parade	523	578	6.000	2.000	2.818

the port	531	546	4.000	2.179	2.870
the prairie	575	569	7.000	1.973	2.155
the prison	570	593	6.000	2.412	3.527
the railroad	579	596	8.000	2.565	2.802
the rain	600	618	4.000	2.571	3.397
the ridge	547	543	5.000	2.045	2.558
the road	583	609	4.000	2.961	3.757
the sea	596	606	3.000	2.775	3.485
the shore	574	624	5.000	2.380	3.006
the sky	542	618	3.000	2.540	3.359
the smoke	541	615	5.000	2.736	3.523
the song	514	578	4.000	2.595	3.679
the square	516	610	6.000	2.758	3.210
the stable	562	537	6.000	2.045	2.828
the star	574	623	4.000	2.722	3.618
the station	572	554	7.000	2.787	3.606
the storm	527	587	5.000	2.592	3.197
the sun	617	639	3.000	2.780	3.551
the sunset	525	633	6.000	1.857	2.721
the thunder	547	554	7.000	2.140	2.832
the tide	516	530	4.000	2.093	2.574
the tribe	504	515	5.000	1.863	2.512
the troop	509	498	5.000	2.155	2.471
the valley	575	600	6.000	2.461	3.106
the village	576	578	7.000	2.590	3.234
the wind	552	535	4.000	2.818	3.481

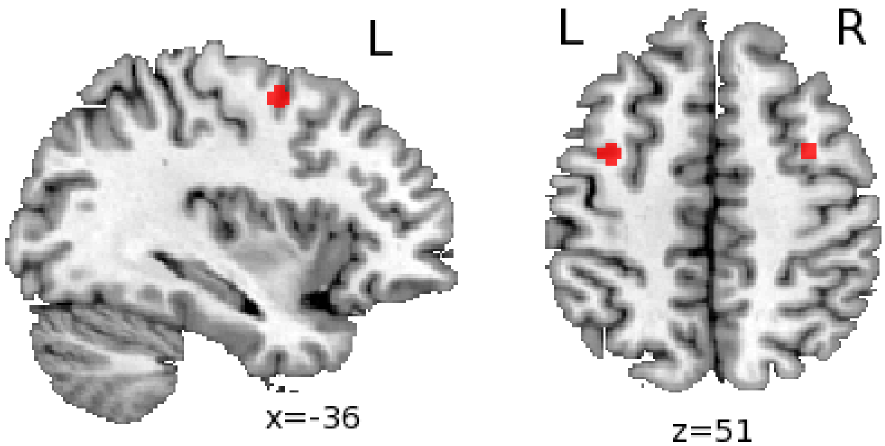
NonConcrete

Word	**CONC**	**IMG**	**NLET**	**T-L Freq**	**Subtlex**
the addition	339	347	8.000	2.389	2.597
the advice	291	352	6.000	2.545	3.389
the aim	324	383	3.000	2.041	2.880
the amount	335	316	6.000	2.821	3.101
the area	384	394	4.000	2.332	3.582
the aspect	217	233	6.000	1.964	2.294
the belief	270	328	6.000	2.326	2.589
the bid	364	394	3.000	1.940	2.808
the blame	293	356	5.000	2.580	3.477
the budget	366	394	6.000	2.185	2.710
the cause	287	282	5.000	2.973	4.199
the claim	331	321	5.000	2.561	3.112
the crisis	319	375	6.000	2.064	2.929
the culture	351	339	7.000	2.009	2.852
the cure	352	397	4.000	2.340	3.027
the custom	323	364	6.000	2.338	2.500
the deal	342	383	4.000	2.898	4.125
the despair	279	388	7.000	2.196	2.476
the dread	267	378	5.000	2.258	2.107
the duty	322	346	4.000	2.750	3.415

the ease	305	327	4.000	2.386	2.989
the effect	295	280	6.000	2.875	3.086
the envy	265	375	4.000	1.892	2.688
the factor	328	269	6.000	1.996	2.568
the fate	255	343	4.000	2.378	3.138
the fear	326	394	4.000	2.852	3.547
the folly	304	326	5.000	1.857	1.869
the gain	346	307	4.000	2.547	2.845
the glory	304	389	5.000	2.270	3.040
the grade	338	397	5.000	2.253	3.174
the guess	247	330	5.000	2.970	4.365
the guilt	299	381	5.000	1.863	2.881
the harm	244	362	4.000	2.408	3.210
the hint	312	343	4.000	2.241	2.671
the honesty	278	386	7.000	2.083	2.566
the ideal	253	331	5.000	2.598	2.573
the illusion	249	396	8.000	1.869	2.624
the import	320	361	6.000	1.934	2.045
the impulse	271	396	7.000	2.267	2.430
the issue	338	315	5.000	2.650	3.241
the justice	307	379	7.000	2.258	3.281
the lack	311	302	4.000	2.617	2.957
the length	365	395	6.000	2.516	2.554
the liberty	302	392	7.000	2.182	2.929
the lie	357	385	3.000	2.785	3.788
the luck	275	399	4.000	2.494	3.894
the manner	297	342	6.000	2.853	2.769
the memory	284	391	6.000	2.745	3.394
the mercy	239	373	5.000	2.170	3.111
the merit	308	380	5.000	1.929	2.238
the method	303	304	6.000	2.792	2.604
the minor	353	376	5.000	1.919	2.816
the mood	234	394	4.000	2.288	3.240
the moral	220	341	5.000	2.435	2.838
the motive	255	275	6.000	2.076	2.829
the occasion	346	305	8.000	2.627	2.926
the origin	319	306	6.000	1.792	2.356
the patience	266	363	8.000	2.143	2.894
the pause	306	347	5.000	2.690	2.439
the phase	360	319	5.000	1.959	2.799
the phrase	321	342	6.000	2.292	2.667
the pity	303	391	4.000	2.420	3.079
the portion	384	399	7.000	2.097	2.344
the proof	328	339	5.000	2.149	3.244
the purpose	280	280	7.000	2.774	3.253
the rate	308	311	4.000	2.589	3.104
the regret	260	359	6.000	2.356	3.141
the remark	368	321	6.000	2.738	2.350
the remedy	368	370	6.000	1.903	2.072

the result	318	324	6.000	2.953	3.003
the role	335	385	4.000	2.053	2.968
the safety	323	397	6.000	2.446	3.217
the save	314	365	4.000	2.941	3.918
the scheme	328	319	6.000	2.486	2.568
the scorn	290	364	5.000	1.973	1.771
the second	344	371	6.000	2.967	4.162
the series	373	398	6.000	2.467	3.012
the session	372	394	7.000	2.041	2.831
the skill	346	366	5.000	2.017	2.606
the soul	289	366	4.000	2.772	3.594
the system	356	340	6.000	2.741	3.669
the tale	352	363	4.000	2.336	2.787
the term	374	387	4.000	2.645	2.949
the theme	336	395	5.000	1.806	2.851
the theory	287	317	6.000	2.342	3.164
the topic	366	364	5.000	1.820	2.433
the trace	371	384	5.000	2.346	2.995
the treaty	361	321	6.000	1.857	2.378
the trend	328	373	5.000	1.875	2.025
the truth	261	374	5.000	2.844	3.991
the type	376	395	4.000	2.897	3.490
the unit	389	334	4.000	2.217	3.266
the value	260	289	5.000	2.584	3.040
the virtue	243	351	6.000	2.100	2.420
the welfare	309	362	7.000	2.041	2.604
the wisdom	275	381	6.000	2.143	2.752

AVERAGE	**CONC**	**IMG**	**NLET**	**T-L Freq**	**Subtlex**
CONCRETE	557.156	567.010	5.167	2.318	2.952
NONCONCRETE	312.875	354.552	5.344	2.354	2.938
T	45.143	36.848	0.972	0.746	0.193
p-value	0.000	0.000	0.333	0.457	0.847



Supplementary Fig. S1. Stimulation sites overlaid on a brain normalized to MNI space. Stimulation sites were based upon coordinates from a previous fMRI study with a similar design (Willems, Hagoort, & Casasanto, 2010).

References

Brysbaert, M., & New, B. (2009). Moving beyond Kucera and Francis: a critical evaluation of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behavior Research Methods, 41*(4), 977-990.

Coltheart, M. (1981). The MRC Psycholinguistic Database. *Quarterly Journal of Experimental Psychology, 33A*, 497-505.

Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: Neural evidence from right- and left-handers. *Psychological Science, 21*(1), 67-74.