

theories arguing that dispersed social systems, common in great ape but not monkey societies, caused selection pressures favouring advanced social cognitive abilities [10].

Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/7/R288/DC1>

Acknowledgments

We are indebted to the keepers at Zoo Leipzig for their support and to Bridget Waller and Katja Liebal for helpful comments. This research was supported by the Max Planck Society for the Advancement of Science and the European Commission (SEDSU Project #012-984 NEST- Pathfinder). The authors declare no competing financial interest. Correspondence and requests for materials should be addressed to D.B.M.H. (daniel.haun@port.ac.uk).

References

1. Nadel, J. (2002). Imitation and imitation recognition: functional use in preverbal infants and nonverbal children with autism. In *The Imitative Mind: Development, Evolution and Brain Bases*, A.N. Meltzoff and W. Prinz, eds. (Cambridge: Cambridge University Press), pp. 63–73.
2. Asendorpf, J.B., Warkentin, V., and Baudonniere, P.-M. (1996). Self-awareness and other-awareness 2: mirror self-recognition, social contingency awareness, and synchronic imitation. *Dev. Psych.* 32, 313–321.
3. Meltzoff, A.N. (1990). Foundations for developing a concept of self: the role of imitation in relating self to other and the value of social mirroring, social modelling, and the self practice in infancy. In *The Self in Transition: Infancy to Childhood*, D. Cicchetti and M. Beeghly, eds. (Chicago: University of Chicago Press), pp. 139–164.
4. Schütz-Bosbach, S., and Prinz, W. (2007). Perceptual resonance: action-induced modulation of perception. *Trends Cogn. Sci.* 11, 349–355.
5. Agnetta, B., and Rochat, P. (2004). Imitative games by 9-, 14-, and 18-month-old infants. *Infancy* 6, 1–36.
6. Paukner, A., Anderson, J.R., Borelli, E., Visalberghi, E., and Ferrari, P.F. (2005). Macaques (*Macaca nemestrina*) recognize when they are being imitated. *Biol. Lett.* 1, 219–222.
7. Nielsen, M., Collier-Baker, E., Davis, J.M., and Suddendorf, T. (2005). Imitation recognition in a captive chimpanzee (*Pan troglodytes*). *Anim. Cogn.* 8, 31–36.
8. Haun, D.B.M., Call, J., Janzen, G., and Levinson, S.C. (2006). Evolutionary psychology of spatial representations in the hominidae. *Curr. Biol.* 16, 1736–1740.
9. Haun, D.B.M., Rapold, C.J., Call, J., Janzen, G., and Levinson, S.C. (2006). Cognitive cladistics and cultural override in Hominid spatial cognition. *Proc. Natl. Acad. Sci. USA* 103, 17568–17573.
10. Barrett, L., Henzi, P., and Dunbar, R. (2003). Primate cognition: from 'what know?' to 'what if?' *Trends Cogn. Sci.* 7, 494–497.

¹Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. ²University of Portsmouth, Department of Psychology, King Henry Building, King Henry I Street, Portsmouth PO1 2DY, UK.
E-mail: Daniel.Haun@port.ac.uk

Use-induced motor plasticity affects the processing of abstract and concrete language

Arthur M. Glenberg¹, Marc Sato² and Luigi Cattaneo³

Traditional analyses of language [1] emphasize an arbitrary correspondence between linguistic symbols and their extensions in the world, but recent behavioral and neurophysiological [2,3] studies have demonstrated a processing link between a symbol and its extension: that is, comprehension of language about concrete events relies in part on a simulation process that calls on neural systems used in perceiving and acting on those extensions. It is an open question, however, whether this simulation process is necessary for abstract language understanding [4,5]. Here we report how, using a new technique based on use-induced neural plasticity [6], we have obtained evidence for a causal link between the motor system and the comprehension of both concrete and abstract language.

Participants were required to move, one at a time, 600 beans from a wide-mouthed container to a target — a narrow-mouthed container, an arm's length away. The movement direction was either toward or away from the body, as determined by the location of the target. After moving all the beans, participants read nonsense and sensible sentences describing transfer of concrete objects or abstract information toward or away from themselves (see Table S1 in the Supplemental Data for examples). On measuring the time required to judge the sentences as sensible, we observed an interaction between the direction of previous bean movement and the direction of described transfer (toward or away) for both the concrete and abstract sentences. That is, modifying the motor system affected processes used in the comprehension of both concrete and abstract language.

In the first experiment, after moving the beans (for approximately 20 minutes), participants read (for approximately 10 minutes) sensible

and nonsense sentences. The grammatical objects named concrete items or abstract information, and the sentences described transfer of the objects either toward the reader, away from the reader, or no transfer. There was a significant interaction such that participants were slower to make the sensible judgment, by pressing a key on a keyboard with the right index finger, when sentences described transfer in a direction that matched the direction of previous bean practice ($p = 0.02$; abstract alone, $p = 0.04$, see Figure 1 and details in Supplemental Data).

Repeated production or perception of a word results in a temporary loss of meaning termed semantic satiation [7]. If participants are covertly saying "toward" or "away" while performing the bean task, then later sentence comprehension might suffer because of the satiation phenomenon. We tested this alternative in experiment 2 by replacing the bean task with 600 trials of judging if a stimulus was a word ("toward" or "away") or an anagram of that word. Then, participants judged the same sentences as in experiment 1. The absence of any interactions ($ps > 0.35$) between stimulus word and sentence direction indicates that the interaction found in experiment 1 is not due to the sort of verbal repetition that produces semantic satiation.

The concrete sentences were changed in experiment 3 so that they did not describe any movement. Instead, they described events that were near or far from the grammatical subject, and manipulated the grammatical person of the sentence subject (see Table S1). We replicated the interaction for abstract sentences describing transfer (although at $p = 0.06$), but now in the absence of concrete sentences describing transfer that might have biased a motoric interpretation of the abstract sentences. Furthermore, failure to find the critical interaction for the concrete sentences demonstrates that, in the absence of language about transfer, differences in location ($p = 0.68$) or grammatical subject ($p = 0.11$ in the wrong direction) do not contribute to the effect.

How abstract are the motor system controllers that the bean task changes? In experiment 4, participants moved the beans with the right arm and hand, but half

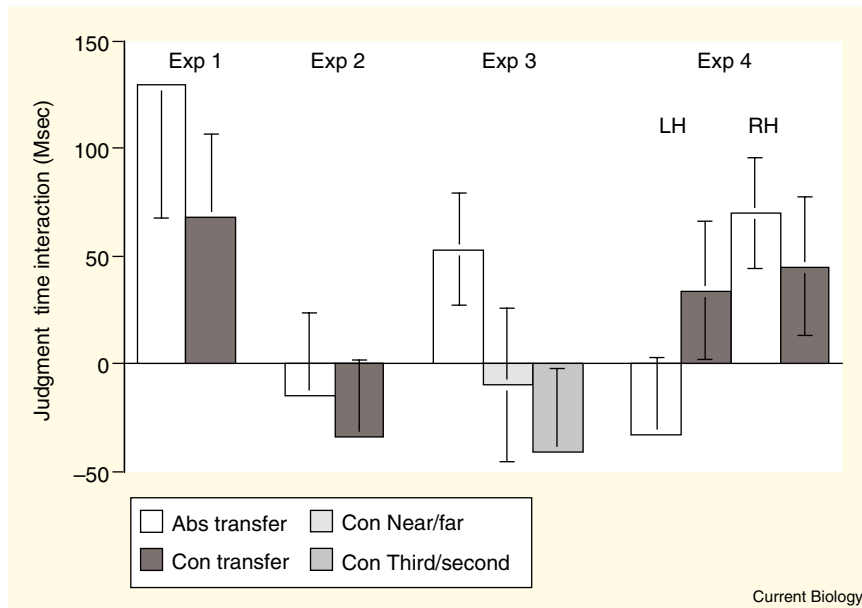


Figure 1. A link between the motor system and language comprehension.

The size of the interaction is computed so that positive going bars indicate that moving beans (or performing a lexical decision in experiment 2) slows judgments of sentences describing actions in the same direction [$(M_{11}-M_{12}) - (M_{21}-M_{22})$; where the first subscript indexes toward or away sentences and the second subscript indexes toward or away bean practice]. In experiment 3, the interaction for Near/Far is computed by treating near sentences as equivalent to toward sentences (because the transferred object in toward sentences ends up near the reader) and the interaction for grammatical person is computed by treating sentences with third person subjects as equivalent to toward sentences (because toward sentences always had third person subjects). The error bars are approximately one standard error computed as the square root of the quotient of the analysis variance interaction error term divided by the sample size. Abs, abstract; Con, concrete; LH, left hand index finger assigned to the “sensible” response; RH, right hand index finger assigned to the “sensible” response.

responded “sensible” with the right-hand index finger and half used the left-hand index finger. Considering the right-hand condition, the interaction was significant ($p = 0.02$; abstract alone, $p = 0.01$). However, the interactions were not significant when responding “sensible” with the left hand index finger ($ps > 0.28$).

Our interpretation of these results is that moving 600 beans with the right hand induces short-term plastic changes in the cortical representation of actions that are hypothesized to be primarily located in the left inferior frontal and parietal regions [8] and that affect language processing [3]. But why is linguistic processing slowed by use-induced plastic changes in the matching controller (for example, responding to away sentences is slowed by previous practice in the away direction)?

There are at least three (not necessarily mutually exclusive) interpretations for the observed slowing given the hypothesis that action planning and sentence

processing are carried out by the same system. First: bean movement in one direction induces peripheral fatigue in the effector. The action controllers respond to this fatigue by increasing their output, but with a loss of specificity to one action. Similar mechanisms are known to occur in response to muscular fatigue in the primary motor cortex [9]. Second: bean movement, although initially requiring voluntary initiation, may become a semiautomatic movement towards the end of the 600 trials, thus down-regulating the activity in the action-specific controllers, as has been previously shown during the overlearning and automatization of motor sequences [10]. And third, bean movement modifies the stimulus-response behavior of the action controllers so that they are increasingly tuned to the motor task of moving beans with a concomitant loss of responsiveness to the sentence processing task. Under all three interpretations, we assume that the comprehension of transfer of

abstract information engages action controllers because abstract transfer is grounded in concrete transfer early in learning [2,4].

In summary, these results provide the strongest evidence to date that comprehension of language describing both concrete and abstract events engages the motor system. In addition, they also demonstrate for the first time use-induced plasticity at the level of action, not just at the level of motor control [6].

Supplemental data

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Acknowledgments

This work was supported by NSF grant BCS-0315434 to Arthur Glenberg. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the funding agency.

References

1. Hauser, M.D., Chomsky, N., and Fitch, W.T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science* 298, 1569–1579.
2. Glenberg, A.M., Sato, M., Cattaneo, L., Riggio, L., Palumbo, D., Buccino, G. (2008). Processing abstract language modulates motor system activity. *Q. J. Exp. Psychol.*, in press.
3. Gallese, V. (2008). Mirror neurons and the social nature of language: The neural exploitation hypothesis. *Social Neurosci.*, in press.
4. Glenberg, A.M., and Kaschak, M.P. (2002). Grounding language in action. *Psychon. Bull. Rev.* 9, 558–565.
5. Aziz-Zadeh, L., Wilson, S.M., Rizzolatti, G., and Iacoboni, M. (2006). Embodied semantics and the premotor cortex: Congruent representations for visually presented actions and linguistic phrases describing actions. *Curr. Biol.* 16, 1818–1823.
6. Classen, J., Liepert, J., Wise, S.P., Hallett, M., and Cohen, L.G. (1998). Rapid plasticity of human cortical movement representation induced by practice. *J. Neurophysiol.* 79, 1117–1123.
7. Kounios, J., Kotz, S.A., and Holcomb, P.J. (2000). On the locus of the semantic satiation effect: Evidence from event-related brain potentials. *Mem. Cognit.* 28, 1366–1377.
8. Rizzolatti, G., and Luppino, G. (2001). The cortical motor system. *Neuron* 31, 889–901.
9. Gandevia, S.C. (2001). Spinal and supraspinal factors in human muscle fatigue. *Physiol. Rev.* 81, 1725–1789.
10. Wu, T., Kansaku, K., and Hallett, M. (2004). How self-initiated memorized movements become automatic: a functional MRI study. *J. Neurophysiol.* 91, 1690–1698.

¹Department of Psychology, Arizona State University, 950 S. McAllister, Tempe, Arizona 85287-1104, USA. ²GIPSA-LAB – UMR CNRS 5216, University of Grenoble, Domaine Universitaire, BP25,38031 Grenoble Cedex 9, France. ³Dipartimento di Neuroscienze, via Volturno 39, Università di Parma, 43100 Parma, Italy.
E-mail: glenberg@asu.edu