

Sports experience changes the neural processing of action language

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Experience alters behavior by producing enduring changes in the neural processes that support performance. For example, performing a specific action improves the execution of that action via changes in associated sensory and motor neural circuitry, and experience using language improves language comprehension by altering the anatomy and physiology of perisylvian neocortical brain regions. Here we provide evidence that specialized (sports) motor experience enhances action-related language understanding by recruitment of left dorsal lateral premotor cortex, a region normally devoted to higher-level action selection and implementation—even when there is no intention to perform a real action. Experience playing and watching sports has enduring effects on language understanding by changing the neural networks that subserve comprehension to incorporate areas active in performing sports skills. Without such experience, sport novices recruit lower-level sensory-motor regions, thought to support the instantiation of movement, during language processing, and activity in primary motor areas does not help comprehension. Thus, the language system is sufficiently plastic and dynamic to encompass expertise-related neural recruitment outside core language networks.

expertise | premotor | action planning | motor stimulation | comprehension

The mechanisms for language processing in adulthood are thought to be extremely stable and impervious to change (1). Yet, it may be that plastic change within the language system can arise from non-language-related activities. Background knowledge of a topic certainly aids comprehension and retention of language related to that topic (2–4) and such knowledge can even eliminate comprehension differences between those lower and higher in verbal ability (5). But what if one is not just knowledgeable in a particular area, but also has direct experience with the behaviors described in the language one uses? Could such experience actually modulate the neural substrates called on to support effective comprehension? When individuals hear language about action, they activate neural networks involved in producing these actions (6). Given that athletes and novices rely on different cognitive and neural operations during overt action production (7–12), the resources called on to support language comprehension might differ as a function of an individual's experience with the communicated actions. In the current work we ask whether athletic experience carries implications beyond the playing field to a very different activity: language comprehension, and more specifically, to the understanding of language about actions one has experience with. Furthermore, if a relationship does exist, is it based on conceptual knowledge of the motor skill or a more direct ability to use the neural networks subserving action to enhance language comprehension?

To answer this question, ice-hockey players (professional and intercollegiate players; $n = 12$), fans (extensive hockey viewing, but no playing experience; $n = 8$), and novices (no ice-hockey playing/viewing experience; $n = 9$) passively listened to sentences describing ice-hockey actions or everyday actions during functional magnetic resonance imaging (fMRI) and then performed a language task outside the scanner that gauged their

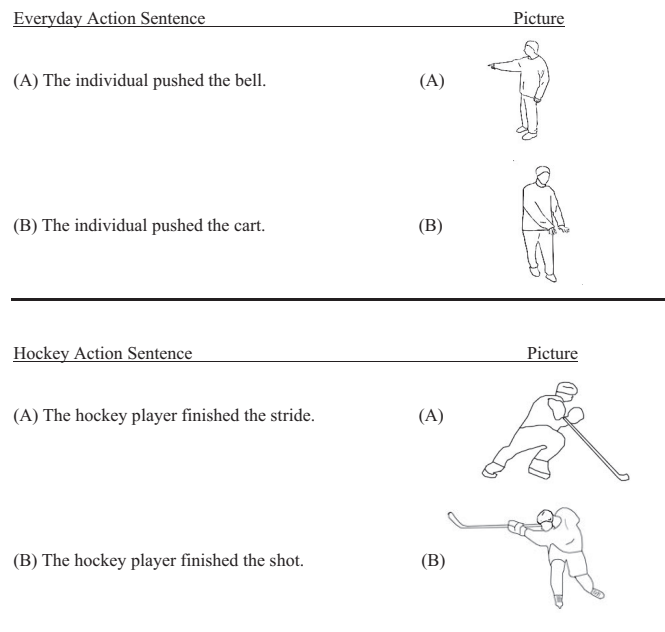


Fig. 1. Examples of the postscan comprehension task stimuli. Picture A serves as a match for Sentence A and a mismatch for Sentence B. Picture B serves as a match for Sentence B and a mismatch for Sentence A.

understanding of the heard scenarios (13–15). In this postscan comprehension task, subjects listened to sentences describing ice-hockey actions (e.g., “The hockey player finished the shot”) and everyday actions (e.g., “The individual pushed the door bell”). Following each sentence, participants were presented with a picture of an individual. Participants were told to judge as quickly as possible whether the pictured individual was mentioned in the sentence and to indicate this decision by pressing a “yes” or “no” button.

The pictures (Fig. 1) depicted either (i) an individual mentioned in the preceding sentence performing an action that matched the action implied in the sentence, (ii) an individual mentioned in the preceding sentence performing an action that was different from (or mismatched) the action implied in the sentence, or (iii) an individual not specifically mentioned in the sentence and performing an action that was not implied by

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Table 1. Significant regions for the whole-brain correlation maps for hockey action sentences at $P < 0.005$ (cluster-level corrected at $\alpha < 0.05$)

ROI (Brodmann's area)	Center of gravity			ROI size, mm ³	Correlation coefficient
	x	y	z		
<i>Left dorsal premotor cortex (BA6)</i>	-45	9	41	405	<i>0.608</i>
<i>Right dorsal primary sensory-motor cortex (BA4/1/2)</i>	22	-21	53	488	<i>-0.677</i>
Right post. cingulate gyrus (isthmus: BA30)	11	-35	2	1,178	-0.728
Left post. angular gyrus (BA39)	-39	-47	23	426	-0.644
Left post. cingulate gyrus (BA31)	-14	-54	27	639	-0.551
Left cuneus (BA18)	-14	-91	18	753	-0.597

Correlation coefficients are standardized r values ($N = 29$) and represent the average coefficient across all voxels in the cluster. Italicized regions are those that showed a significant relation between hockey experience and neural activity. Activity in these regions also significantly mediated the relation between hockey experience and hockey language comprehension (see Fig. 2). post., posterior.

the sentence. For this last category, pictures of hockey players were paired with everyday sentences (e.g., a picture of a hockey player skating followed the sentence, “The individual frosted the cake.”) and pictures of everyday individuals were paired with hockey sentences (e.g., a picture of a man buttoning his shirt followed the sentence, “The hockey player saved the shot.”). This last category required a “no” response (serving as fillers to equate “yes” and “no” responses across sentences) and was not analyzed. Trials of interest were those that required “yes” responses [i.e., (i) and (ii) above]. If individuals comprehend the actions described in the sentences (13–16), responses should be facilitated for pictured individuals whose actions match those implied in the sentence relative to those that do not. We termed this index of comprehension the action-match effect.

Results

Does hockey experience enhance language comprehension? All subjects, regardless of ice-hockey experience, showed a significant action-match effect for everyday sentences, responding faster to pictures of individuals performing actions that matched those implied in the sentences vs. pictures that did not [733 vs. 802 ms; $t(28) = 3.33$; $P < 0.01$; interaction with group, $F = 1$]. In contrast, only ice-hockey players [605 vs. 669 ms; $t(11) = 3.22$; $P < 0.01$] and fans [761 vs. 884 ms; $t(7) = 4.91$; $P < 0.01$] showed the action-match effect for hockey sentences. Novices' response times did not differ as a function of pictures that matched the sentence-implied hockey actions vs. those that did not [655 vs. 656 ms; $t(8) = 0.03$; $P = 0.98$]. Experience watching and playing ice-hockey facilitates comprehension specifically for hockey sentences.

To determine the neural mechanisms underlying this experience-dependent facilitation, we performed regression analyses relating neural activity during hockey-language listening to hockey experience and hockey-sentence comprehension. Importantly, we did not expect to find a significant relation among neural activity during everyday language listening, everyday sentence comprehension, and hockey experience because everyday language comprehension did not vary with hockey group. This expectation is not surprising given that everyone should have experience viewing and performing everyday actions.

We began by regressing, at the whole-brain level, our index of hockey sentence comprehension (i.e., the action-match effect) on neural activity measured while all subjects, irrespective of hockey experience, heard hockey sentences. Starting at the whole-brain level allows us to identify all possible neural areas that might mediate (or account for) the relation between hockey experience and hockey sentence comprehension. Neural activity in several brain regions was significantly related to hockey sentence comprehension (Table 1).

We next examined whether the regions that related to comprehension also significantly related to hockey experience. Here, and in the analyses below, we treated hockey experience as a categorical variable, rank ordering subjects based on hockey exposure from (1) no playing or viewing experience (novices), to (2) no playing, but viewing experience (fans), to (3) playing and viewing experience (players). This rank ordering, which captures relative degree of exposure to ice-hockey, allows us to test whether the facilitative effect of hockey experience on comprehension is mediated by neural activity during hockey language processing.⁸

Two brain regions related to hockey-sentence comprehension also related to the rank-ordering of hockey experience. Activation in left dorsal premotor cortex [Talairach center-of-gravity = ($\pm 45, 9, 41$)] positively correlated with hockey experience. Given that premotor regions are typically activated bilaterally within a larger network for action understanding in both action observation and language comprehension (17–19), we also looked at the analogous region in the opposite hemisphere. An interaction with hemisphere [$\beta = 0.29$, $t = 2.15$, $P < 0.05$] showed that this relation was limited to the left hemisphere ($r = 0.46$, $P < 0.02$). In addition, activation in right dorsal primary sensory-motor cortex [Tal ($\pm 22, -21, 53$)] negatively correlated with hockey experience ($r = -0.45$, $P < 0.02$). Not only did a lack of a hemisphere interaction ($P = 0.64$) support the bilaterality of the relation between primary sensory-motor activation and experience ($r = -0.43$, $P < 0.02$), but similarly high correlations were seen between average activation in right sensory-motor cortex and comprehension ($r = -0.68$, $P < 0.001$) and left primary sensory-motor cortex and comprehension ($r = -0.51$, $P < 0.005$). Thus, in the analyses from this point forward, we consider the relation among bilateral primary sensory-motor cortex activity, experience, and comprehension.

If the above relationships between neural activity and comprehension are because of experience-dependent changes in the neural networks subserving language understanding, then they should be limited to the domain in which subjects were selected to vary by experience (i.e., hockey). To test this hypothesis, we also correlated, at the whole-brain level, everyday action comprehension with neural activation while subjects listened to everyday sentences. Although one region, the left Lingual Gyrus [Tal ($\pm -10, -86, -9$)], related to comprehension ($r = 0.61$, $P < 0.001$), it was unrelated to hockey experience ($r = 0.15$, $P = 0.43$).

⁸Although our coding scheme was setup *a priori* to examine the relation between degree of exposure to ice-hockey and hockey-language comprehension, we also examined alternative ways of coding hockey experience. Considering fans and experts to be of equal experience, considering fans and novices to be of equal experience, or coding playing and watching experience separately did not produce the same significant correlations seen in the next paragraph and Fig. 2 between experience, comprehension, and neural activity, nor did it result in a better-fitting mediation model.

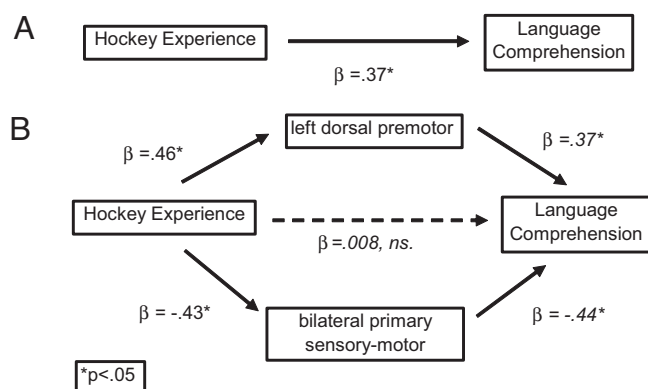


Fig. 2. Mediation analysis of the relation between hockey experience and hockey-action language comprehension. (A) A regression analysis established that hockey experience [as reflected in a rank ordering based on hockey exposure from (i) novices to (ii) fans to (iii) players] had a significant positive effect on hockey language comprehension ($\beta = 0.37$, $t = 2.06$, $P < 0.05$). (B) Hockey experience also had a significant positive effect on left dorsal premotor activity while passively listening to hockey-related sentences ($\beta = 0.46$, $t = 2.72$, $P < 0.02$) and bore a significant negative relation to bilateral primary sensory-motor activity while passively listening to hockey-related sentences ($\beta = -0.43$, $t = 2.49$, $P < 0.02$). Both left dorsal premotor activity ($\beta = 0.61$, $t = 3.98$, $P < 0.001$) and bilateral primary sensory-motor activity ($\beta = -0.64$, $t = 4.31$, $P < 0.001$) were significant predictors of language comprehension. When hockey experience, left dorsal premotor activity, and bilateral primary sensory-motor activity were simultaneously entered as predictors of hockey sentence comprehension, experience no longer significantly predicted comprehension ($\beta = 0.008$, ns), whereas both left dorsal premotor activity ($\beta = 0.37$, $t = 2.13$, $P < 0.05$) and bilateral primary sensory-motor activity ($\beta = -0.44$, $t = 2.55$, $P < 0.02$) remained significant in the equation. A Sobel test (45) of the reduction in the direct relation between experience and comprehension for both left premotor ($z = 2.24$, $P < 0.03$) and bilateral sensory-motor ($z = 2.80$, $P < 0.01$) was significant. This series of analyses provides support for our conclusion that hockey experience facilitates hockey language comprehension through relatively increased activity in left dorsal premotor cortex and relatively decreased activity in bilateral sensory-motor cortex.

Turning back to our original question regarding the impact of hockey experience on language comprehension, we asked whether the pattern of neural activity seen while listening to hockey language mediated (or accounted for) the impact of experience on hockey-language comprehension. As reflected above, the more hockey experience individuals had (ranging from novices to fans to players), the more effective they were in comprehending hockey sentences. This relation became nonsignificant when both left dorsal premotor and bilateral sensory-motor activity was also used to predict hockey comprehension. Only a strong positive relation between left dorsal premotor activity and hockey comprehension and a strong negative relation between bilateral primary sensory-motor activity and hockey comprehension remained (Fig. 2). The relation between experience and comprehension was fully mediated by left dorsal premotor and bilateral primary sensory-motor activity. Figs. 3 and 4 show the brain-behavior correlations, activation differences by hockey experience group, and the neural regions themselves.

Effective auditory comprehension of action-based language is accounted for by experience-dependent activation of the left dorsal premotor cortex, a region thought to support the selection of well learned action plans and procedures, often in response to learned symbolic associations (20–26). Evidence from lesion studies in monkeys (27) and humans (28, 29) shows that ablations of the dorsal premotor cortex prevents individuals from associating well learned motor response sequences (e.g., twisting a handle) with exogenous symbolic cues (e.g., a yellow placard or specific tone). Because subjects can independently perform the required movement se-

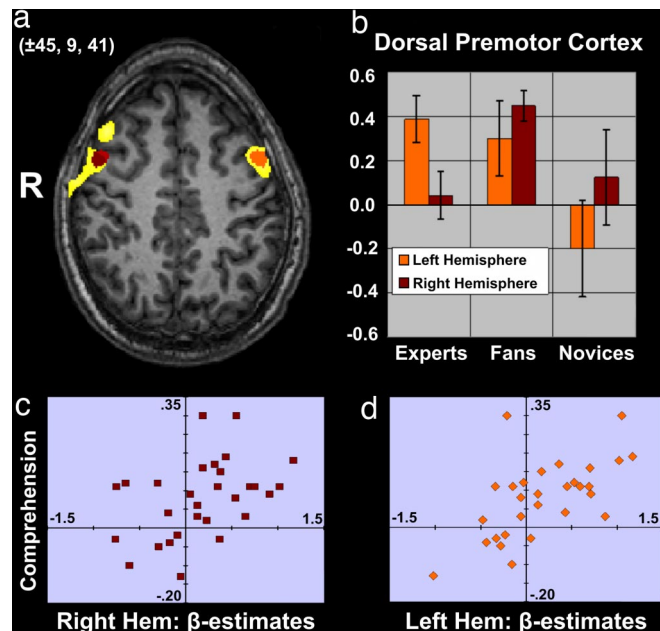


Fig. 3. Visualization of dorsal premotor cortex: positive correlation between neural activity when listening to hockey action sentences and postscan hockey language comprehension. (a) The left hemispheric region shown in orange was significant ($P < 0.005$, corrected) at the whole-brain level. To visualize this region as part of a larger premotor network, it is overlain onto voxels showing a positive correlation at the reduced threshold of $P < 0.05$, uncorrected (depicted in yellow). To test for laterality, this region was reflected over the y axis (shown in the right hemisphere in dark red). (b) Activity in the left and right ROIs broken down by hockey experience group. The y axis represents neural activity in the form of β -estimates for the hockey action sentences. Error bars represent SEM. (c and d) Visualization of the linear relationship (across all 29 subjects) between neural activity (represented as β -estimates) (see Methods) and hockey language comprehension for each hemisphere (left hemisphere: $r = 0.61$, $P < 0.001$; right hemisphere: $r = 0.41$, $P = 0.05$).

quence and recognize the symbolic stimuli, the dorsal premotor cortex is believed to support the selection of well learned plans for action. The left hemisphere has been shown to drive this selection, regardless of the effector involved (24, 30–32). Substantial prior experience viewing and performing ice-hockey actions enhances hockey-language comprehension, likely by enabling individuals to associate linguistically described action scenarios with motor plans for execution. This ability, in turn, gives individuals the type of robust and multimodal representation that is the hallmark of optimal comprehension.

Interestingly, facilitated comprehension of hockey action sentences was not limited to those with significant hockey motor experience (i.e., hockey players); Ice-hockey fans also showed the action-match effect for hockey scenarios. This comprehension effect in fans was accompanied by activation in the left dorsal premotor cortex while listening to the hockey action scenarios that was significantly above baseline [$t(7) = 3.21$, $P < 0.02$]. Players showed a similar pattern [$t(11) = 3.50$, $P < 0.005$]. Novices did not ($P = 0.25$). Moreover, increased dorsal-premotor activation during hockey-sentence comprehension was seen bilaterally for the fans but not the players (Fig. 3). This observation is true whether one looks at the region of interest (ROI) directly contralateral to the left dorsal premotor region or the peak activation in the right prefrontal cortex more generally. The bilateral premotor activation may be indicative of more effortful action selection in fans vs. players, a view consistent with overall longer response times for the fans [mean (M) = 822 ms; SE = 73] vs. players (M) = 637 ms; SE = 39) for hockey sentence comprehension [$t(18) = 2.44$, $P < 0.03$]. Nonetheless,

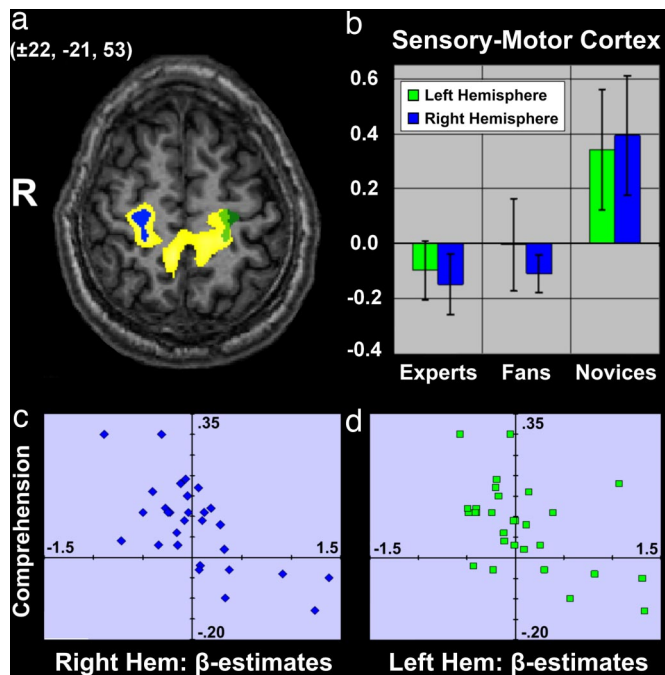


Fig. 4. Visualization of primary sensory-motor cortex: negative correlation between neural activity when listening to hockey action sentences and postscan hockey language comprehension. (a) The right hemispheric region shown in blue was significant ($P < 0.005$, corrected) at the whole-brain level. To visualize this region as part of a larger primary sensory-motor network, it is overlain onto voxels showing a negative correlation at the reduced threshold of $P < 0.05$, uncorrected (depicted in yellow). To test for laterality, this region was reflected over the y axis (shown in the left hemisphere in green). (b) Activity in the left and right ROIs broken down by group. The y axis represents neural activity in the form of β -estimates for the hockey action condition. Error bars represent SEM. (c and d) Visualization of the linear relationship (across all 29 subjects) between neural activity (represented as β -estimates) (see *Methods*) and hockey language comprehension for each hemisphere (left hemisphere: $r = -0.51$, $P < 0.005$; right hemisphere: $r = -0.68$, $P < 0.001$).

only activation in the left dorsal premotor cortex, and not bilateral premotor activation, mediated the impact of hockey experience on language comprehension. This finding is consistent with other findings that the left premotor cortex plays a dominant role in higher-level action selection, regardless of the side of the body involved (24, 30–32).

As mentioned above, the relation between hockey experience and hockey sentence comprehension was also fully mediated by bilateral dorsal primary sensory-motor activity while listening to hockey action sentences (Figs. 2 and 4). Primary sensory-motor regions are heavily involved in instantiating the specific step-by-step movements needed to carry out a novel task (17, 30, 32). Less hockey experience was associated with increased activity in bilateral primary sensory-motor regions during hockey language listening and decreased comprehension.

Previous work has shown that the neural substrates governing both observation of another's actions and imagining one's own actions differ as a function of whether these actions are part of one's preexisting motor skill repertoire (33, 34). Experienced actors call on brain regions implicated in higher-level action planning and selection more so than do those without experience (33, 34). In the current work, we show that those without the ability to associate plans for action with linguistic cues [most likely because they don't have such actions in their skill repertoires (novices)] instead show increased activity (vs. more experienced counterparts) in neural areas known to be involved in the

instantiation of simple movements. Such activation actually hurts comprehension, likely because it does not embody the higher-level action plans that effective comprehension relies on.

Discussion

The impact of athletic experience on comprehension is explained by greater involvement of brain regions that participate in higher-level action selection for those with hockey playing and watching experience and greater involvement of brain regions that participate in step-by-step action instantiation for those without such experience. These areas fall outside the neural networks usually implicated in language comprehension (35).

By demonstrating that specific patterns of neural activity in the motor system that occur when one listens to hockey language mediate the relation between hockey experience and comprehension (Fig. 2), we reveal how sports experience impacts language understanding. Specifically, our mediation analysis depicts a model of a causal chain of events (36) whereby experience alters the extent to which premotor and primary sensory-motor cortex are called on during language listening, which, in turn, produces differences in comprehension. As such, we show that experience-dependent activation of motor areas when listening to action-based language is not an epiphenomenal byproduct of comprehension, but is an integral component of effective understanding. These brain and behavioral changes reflect a deeper level of language understanding that is not only achieved by experience on the playing field or ice-rink, but also enhanced by experience in the viewing stands.

Methods

Subjects were right-handed males, aged 18–35 years ($SD = 4.76$), with an average of 14.38 ($SD = 1.38$) years of education. Twelve ice-hockey experts played professional or Division I intercollegiate hockey (15.7 ± 1.9 years playing experience). Eight fans had 13.3 ± 7.8 years watching experience and no hockey playing experience of any kind (including related sports such as roller hockey). Nine novices had no playing or watching experience. Neither age ($r = -0.11$, $P = 0.55$) nor years of education ($r = -0.256$, $P = 0.23$) significantly related to the rank ordering of hockey experience.

MRI data were acquired from a GE Signa LX 3T scanner and analyzed with BrainVoyager QX 1.9.9 (Brain Innovation). A forward-spiral T2*-weighted sequence (37) was used to acquire functional images covering the whole brain (30 axial slices) with a repetition time of 2,000 ms and an echo time of 30 ms. High-resolution anatomical images were acquired (120 slices) in the axial plane ($1.5 \times 1.41 \times 1.41$ mm) with a standard GE MPRage sequence. Functional images were manually aligned to the high-resolution T1 structural images and transformed into Talairach space (38). A two-gamma hemodynamic response function was used to model the expected blood-oxygen-level-dependent (BOLD) signal (39).

During fMRI scan acquisition, subjects passively listened to 44 hockey action sentences and 44 everyday action sentences equated for duration, syntax, and word frequency. Sentences were presented in a fixed-random order by using a jittered interstimulus interval (range: 0–16.11 s; $M: 2.21$ sec) within a rapid event-related design. The 88 action sentences were intermixed with 88 filler sentences not specifically action-related. Subjects listened to 176 sentences in total.

In the postscan comprehension task (administered immediately after exiting the scanner), subjects were auditorily presented with the same 88 action sentences they had heard in the scanner. An additional 88 sentences (half describing hockey actions and half describing everyday actions) were also included as filler sentences. For following presentation of a given sentence, subjects saw a computer-presented picture of a target individual. The pictures were line drawings produced from digital images. Subjects judged as quickly and accurately as possible whether the target individual was mentioned in the preceding sentence (by pressing one of two buttons labeled "yes" or "no"). For half of the trials, subjects saw a picture of an individual that was mentioned in the sentence. These "yes" response trials were those of interest. Half of the sentences in these trials were paired with pictures of individuals performing actions that matched that implied in the sentence (Match) and half were not (Mismatch). These pairings were counterbalanced across subjects. For the remaining half of the trials, subjects saw a picture of an individual not mentioned in the sentence. These "no" response filler trials were equally divided into hockey and everyday sentences. The pictures paired with the everyday filler sentences were hockey players, and the pictures paired with the hockey filler sentences consisted of everyday indi-

viduals. These filler trials were not analyzed. Across all trials, accuracy was high ($M = 89\%$, $SE = 3\%$) and did not differ as a function of hockey experience, sentence type, or picture.

The BOLD signal during fMRI was examined by using a multiple regression analysis of each functional time series (40) that took into account sentence type in a random-effects general linear model. The resulting hockey-action and everyday-action condition parameter estimates (β -estimates) in each voxel were submitted to separate whole-brain correlation analyses. In this analysis, the action-match effect [(Mismatch Reaction Time (RT) – Match RT)/Average RT] was regressed on the contrasts of hockey action sentences vs. baseline and everyday action sentences vs. baseline, respectively. This analysis was blind to hockey-experience-group membership. The statistical maps generated from these analyses were thresholded at $r(28) = 0.52$, $P < 0.005$, and subsequently corrected for multiple comparisons by using Monte Carlo simulation to yield a whole-brain significance of $\alpha = 0.05$ (41).

1. Lenneberg EH (1967) *Biological Foundations of Language* (Wiley).
2. Bransford J, Johnson M (1972) Contextual prerequisites for understanding: Some investigations of comprehension and recall. *J Verbal Learn Verbal Behav* 11:717–726.
3. Van Dijk T, Kintsch W (1983) *Strategies in discourse comprehension*. (Academic, New York).
4. Zwaan R, Radvansky G (1998) Situation models in language comprehension and memory. *Psychol Bull* 123:162–185.
5. Schneider W, Korkel J, Weinert F (1989) Domain-specific knowledge and memory performance: A comparison of high- and low-aptitude children. *J Ed Psychol* 81:306–312.
6. Tettamanti M, et al. (2005) Listening to action-related sentences activations frontoparietal motor circuits. *J Cogn Neurosci* 17:273–281.
7. Hatfield B, Landers D, Ray W (1984) Cognitive-processes during self-paced motor-performance: An electroencephalographic profile of skilled marksmen. *J Sport Psychol* 6:42–59.
8. Anderson JR (1993) *Rules of Mind* (Erlbaum, Hillsdale, NJ).
9. Beilock S, Carr T (2001) On the fragility of skilled performance: What governs choking under pressure? *J Exp Psychol Gen* 130:701–725.
10. Fitts PM, Posner MI (1967) *Human Performance* (Brooks/Cole, Belmont, CA).
11. Keele S (1986) in *Handbook of Perception and Human Performance*, eds Boff K, Kaufman L, Thomas J (Wiley, New York).
12. Proctor R, Dutta A (1995) *Skill Acquisition and Human Performance* (Sage Publications, Thousand Oaks, CA).
13. Stanfield R, Zwaan R (2001) The effect of implied orientation derived from verbal context on picture recognition. *Psychol Sci* 12:153–156.
14. Zwaan R, Stanfield R, Yaxley R (2002) Language comprehenders mentally represent the shapes of objects. *Psychol Sci* 13:168–171.
15. Holt L, Beilock S (2006) Expertise and its embodiment: Examining the impact of sensorimotor skill expertise on the representation of action-related text. *Psychon Bull Rev* 13:694–701.
16. Glenberg A, Kaschak M (2002) Grounding language in action. *Psychon Bull Rev* 9:558–565.
17. Rizzolatti G, Luppino G (2001) The cortical motor system. *Neuron* 31:889–901.
18. Buccino G, et al. (2001) Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *Eur J Neurosci* 13:400–404.
19. Hauk O, Johnsrude I, Pulvermüller F (2004) Somatotopic representation of action words in the human motor and premotor cortex. *Neuron* 41:301–307.
20. Grafton S, Fagg A, Arbib M (1998) Dorsal premotor cortex and conditional movement selection: A PET functional mapping study. *J Neurophysiol* 79:1092–1097.
21. O'Shea J, Johansen-Berg H, Trief D, Gobel S, Rushworth M (2007) Functionally specific reorganization in human premotor cortex. *Neuron* 54:479–490.
22. O'Shea J, Sebastian C, Boorman E, Johansen-Berg H, Rushworth M (2007) Functional specificity of human premotor-motor cortical interactions during action selection. *Eur J Neurosci* 26:2085–2095.
23. Rushworth M, Johansen-Berg H, Gobel S, Devlin J (2003) The left parietal and premotor cortices: Motor attention and selection. *Neuroimage* 20:589–100.
24. Schluter N, Krams M, Rushworth M, Passingham, R (2001) Cerebral dominance for action in the human brain: The selection of actions. *Neuropsychologia* 39:105–113.
25. Toni I, et al. (2002) Multiple movement representations in the human brain: An event-related fMRI study. *J Cogn Neurosci* 14:769–784.
26. Wise S, Murray E (2000) Arbitrary associations between antecedents and actions. *Trends Neurosci* 23:271–276.
27. Passingham R (1993) *The Frontal Lobes and Voluntary Action* (Oxford Univ Press, Oxford).
28. Davare M, Andres M, Cosnard G, Thonnard J, Olivier E (2006) Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *J Neurosci* 26:2260–2268.
29. Halsband U, Freund H (1990) Premotor cortex and conditional motor learning in man. *Brain* 113:207–222.
30. Grafton S, de C Hamilton A (2007) Evidence for a distributed hierarchy of action representation in the brain. *Hum Mov Sci* 26:590–616.
31. Haaland K, Elsinger C, Mayer A, Durgerian S, Rao S (2004) Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *J Cogn Neurosci* 16:621–636.
32. Schluter N, Rushworth M, Passingham R, Mills K (1998) Temporary interference in human lateral premotor cortex suggests dominance for the selection of movements. A study using transcranial magnetic stimulation. *Brain* 121:785–799.
33. Calvo-Merino B, Glaser D, Grezes J, Passingham R, Haggard P (2005) Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex* 15:1243–1249.
34. Cross ES, Hamilton AFC, Grafton ST (2006) Building a motor simulation de novo: Observation of dance by dancers. *Neuroimage* 31:1257–1267.
35. Poldrack R, Gabrieli J (2001) Characterizing the neural mechanisms of skill learning and repetition priming: Evidence from mirror reading. *Brain* 124:67–82.
36. Baron R, Kenny D (1986) The moderator-mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. *J Personality Soc Psychol* 51:1173–1182.
37. Noll D, Cohen J, Meyer C, Schneider W (1995) Spiral K-space MRI of Cortical Activation. *J Magn Reson Imaging* 5:49–56.
38. Talairach J, Tournoux P (1988) *Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: An Approach to Cerebral Imaging* (Thieme Medical Publishers, New York).
39. Friston K, et al. (1998) Event-related fMRI: Characterizing differential responses. *Neuroimage* 7:30–40.
40. Friston K, et al. (1994) Statistical parametric maps in functional imaging: A general linear approach. *Hum Brain Mapp* 2:189–210.
41. Forman S, et al. (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magn Reson Med* 33:636–647.
42. Coghill R, Gilron I, Iadarola M (2001) Hemispheric lateralization of somatosensory processing. *J Neurophysiol* 85:2602–2612.
43. Fox M, Corbetta M, Snyder A, Vincent J, Raichle M (2006) Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proc Natl Acad Sci USA* 103:10046–10051.
44. Kronbichler M, et al. (2004) The visual word form area and the frequency with which words are encountered: Evidence from a parametric fMRI study. *Neuroimage* 21:946–953.
45. Preacher K, Hayes A (2004) SPSS and SAS procedures for estimating indirect effects in simple mediation models. *Behav Res Meth, Instr Comput* 36:717–731.

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